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NOTES ON THE BIOGEOGRAPHY AND DORSAL COLORATION OF CICINDELA AMARGOSAE DAHL (COLEOPTERA: CARABIDAE)

Michael G. Kippenhan

ABSTRACT.—The widely distributed and fragmented populations of the tiger beetle Cicindela amargosae are documented for dorsal coloration, elytral maculation, habitat, and adult escape behavior. Currently, there are 2 recognized subspecies, C. a. amargosae and C. a. nyensis. The analysis of populations indicated that the variation in dorsal coloration did not coincide with the accepted subspecific criteria for this species, thus illustrating the difficulty in applying a subspecific category unequivocally to tiger beetles.

Key words: Cicindela amargosae, tiger beetle, subspecies, phenotypic variation, habitat.

Cicindela (Cicindelidia) amargosae Dahl is a polytypic species associated with grass margins of moist, often alkali-encrusted areas of drainages in southern Oregon, western Nevada, and eastern California (Fig. 1, Table 1). There are 2 recognized subspecific forms: Cicindela a. amargosae and C. a. nyensis Rumpp. Dahl (1939) described C. willistoni amargosae from “four miles north of Furnace Creek, Death Valley, Inyo County California.” This subspecies was separated from other geographical forms of the C. willistoni group by the combination of bright blue-green dorsal coloration, maculation pattern reduced to an apical lunule, and elytral punctation (Dahl 1939). Interestingly, Dahl (1939) believed this species to be a subspecies of C. willistoni even though C. willistoni pseudosenilis W. Horn was sympatric at the type locality. In a study of the Death Valley, California, tiger beetles, Rumpp (1956) elevated C. amargosae to specific rank based on the observations that it did not interbreed with C. w. pseudosenilis at the type locality and there was a lack of hybrids. Utilizing color and body length as diagnostic criteria, Rumpp (1956) described C. amargosae nyensis from “1.6 miles south of Springdale, Nye County, Nevada.” In addition to the allopatry from the nominate form, this subspecies was characterized by its matte-black dorsal coloration, “softer” elytra relative to the nominate form, and smaller overall body length. Various authors have considered C. amargosae to be a subspecific form of C. senilis G. Horn (Boyd et al. 1982, Werner 1994); however, Leffler (1979) presented distinguishing morphological and geographical attributes for the 2 species. Apart from studies by Dahl (1939) and Rumpp (1956), C. amargosae has received little attention in entomological literature except for Leffler (1979), who included this species as part of the Pacific Northwest tiger beetle fauna, and Freitag (1999), who listed all populations for this species outside Death Valley as C. a. nyensis.

In a geographic outline of the populations of C. amargosae, Rumpp (1956) found C. a. amargosae, along with C. w. pseudosenilis and C. californica pseudoerronea Rumpp, isolated along the natural springs associated with the alkali flats north of Furnace Creek, Death Valley, California. Cicindela a. amargosae was not found downstream of Furnace Creek at Saratoga Springs, even though C. w. pseudosenilis, C. c. pseudoerronea, and a 3rd species, C. n. nevadica LeConte, were present (Rumpp 1956). Interestingly, Rumpp’s tiger beetle collection at the California Academy of Sciences includes a series of C. a. amargosae collected at Saratoga Springs in 1963. Rumpp (1956) found C. a. nyensis associated with the intermittent channels of the Amargosa River near Springdale, Nye County, Nevada. Although the Death Valley and Springdale populations are in close proximity to one another (<80 km), small mountain ranges apparently are geographical barriers between the 2 type localities. Rumpp (1956) believed that populations connected to the Springdale and Furnace Creek populations
by the Amargosa River would have individuals expressing a variety of dorsal coloration indicative of hybridization. Accordingly, the populations downstream of Springdale at Ash Meadows, Nye County, Nevada, were categorized as "hybrid," inasmuch as individuals matched the description of both subspecific forms (Rumpp 1956; Table 2). In addition, Rumpp (1956) considered as "hybrids" populations from northwestern Nevada and adjacent California that exhibited dorsal coloration described as "black, green and bronze." Rumpp (1956) apparently was unaware of \textit{C. amargosae} populations outside California and Nevada; however, Leffler (1979) examined populations from Lake and Harney Counties, Oregon, all of which were placed as \textit{C. a. nyensis}.

During a study of the current distribution of \textit{C. amargosae} in 2002 and 2004, I made numerous observations that contradicted Rumpp's (1956) assertion that dorsal color variation was due to hybridization. Because most cicindelid taxonomy relies solely on morphological characters to determine subspecific status, the consideration of ecophenotypic characters and their role in cicindelid color expressions (Pearson and Vogler 2001, Schultz 2001) is often left unexplored. The objective of this study is to review the current distribution and habitat of \textit{C. amargosae} populations throughout its range while evaluating the correlation between distribution and dorsal coloration and maculation.

**Results and Discussion**

**Geography and Allopatry**

Vestiges of the ancient lakes that once occupied the Great Basin offer an understanding of the present-day distribution of \textit{C. amargosae} (Fig. 1). Leffler (1979) believed that \textit{C. amargosae} inhabited the shores of pluvial Lake Lahontan and associated lake basins. The reduction of these pluvial lakes in post-Pleistocene times to smaller remnant lakes (Reheis 1999) can be considered a valid explanation for the widespread and fragmented distribution of current populations in the northern half of the species range. Historically, it is likely the localized distribution of the Death Valley, California, populations had a much more widespread range along the shores of pluvial Lake Manly, which at one time was close to 161 km long (Sharp and Glazner 1997). Populations close to Tecopa, Inyo County, California, are associated with remnants of ancient Lake Tecopa, which occupied the area south of Death Valley until 500,000 years ago (Sharp and Glazner 1997).
The Death Valley and Tecopa populations, along with populations not directly associated with pluvial Lake Lahontan, such as Springdale and Ash Meadows, Nye County, Nevada, may have arrived via watercourses originating from the shores of pluvial lakes and are currently associated with the Amargosa River. The Fish Lake, Esmeralda County, Nevada, population is associated with remnants of pluvial Lake Rennie.

In June 2004 I searched for suitable habitats along Highway 140 between Lakeview, Lake County, Oregon, and Denio, Humbolt County, Nevada, for additional populations of Cicindela amargosae. Even though this area has small remnants of pluvial lakes and alkali areas, such as Bog Hot Valley, I discovered no populations of Cicindela amargosae. Due to (1) the large areas of inhospitable habitat between the fragmented suitable habitat and populations of Cicindela amargosae, and (2) the general limited dispersal abilities of Cicindela sp. (Pearson and Vogler 2001), it appears unlikely that gene flow exists between populations north of the Inyo County, California, and Nye County, Nevada, populations.

Dorsal Coloration and Elytral Maculation

Dorsal coloration and the extent of elytral maculation are common morphological characters used in identifying and separating adult tiger beetles and have traditionally been used to define subspecies (Pearson and Vogler 2001). Such is the case with Cicindela amargosae, where Rumpp (1956) characterized C. a. amargosae as “green” and C. a. nyensis as “black” without providing evidence regarding evolutionary implications of these 2 color forms. In an ecological role, color, elytral maculation, and ventral setae function as the primary mechanisms by which adult tiger beetles regulate body temperature (Schultz and Hadley 1987, Pearson and Vogler 2001). While C. a. amargosae and C. a. nyensis exhibit a very small degree of variation in elytral maculation and no difference in ventral setae, it is the dorsal (Table 2) and ventral (Table 3) coloration that demonstrates a marked degree of separation. While studies of the thermoregulatory performance of Cicindela amargosae’s color morphs have yet to be undertaken, the southwestern United States tiger beetle Cicindela hornii Schaupp can be utilized as a model, as populations of this species have individuals expressing similar morphs of green, blue, or black dorsal coloration. Interestingly, Schultz and Hadley (1987) found that the 3 color morphs of C. hornii illustrated no significant difference in regard to heat gain from shortwave radiation. Therefore, assuming that the green and black dorsal coloration of Cicindela amargosae have similar thermoregulatory performance as the color morphs of Cicindela hornii, evolutionary forces outside thermoregulation have resulted in the expressed variation of dorsal coloration in Cicindela amargosae.

When populations of Cicindela amargosae are examined, it becomes clear that most populations have individuals expressing numerous dorsal color morphs (Table 2). Rumpp (1956) believed that populations expressing coloration of both subspecies were “hybrid,” including individuals with dark green dorsal coloration found at Honey Lake, Lassen County, California, and

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**Table 1. Known populations of Cicindela amargosae (arranged north to south).**

<table>
<thead>
<tr>
<th>Location Source</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. OR: Harney Co., Alvord Hot Springs MGKC, CSUC^a</td>
<td>1. OR: Harney Co., Alvord Hot Springs MGKC, CSUC^a</td>
</tr>
<tr>
<td>2. OR: Lake Co., Crumb Lake Leffler 1979^b</td>
<td>2. OR: Lake Co., Crumb Lake Leffler 1979^b</td>
</tr>
<tr>
<td>3. CA: Modoc Co., Surprise Lake CASC^c</td>
<td>3. CA: Modoc Co., Surprise Lake CASC^c</td>
</tr>
<tr>
<td>5. CA: Lassen Co., Honey Lake LaRivers 1946</td>
<td>5. CA: Lassen Co., Honey Lake LaRivers 1946</td>
</tr>
<tr>
<td>7. NV: Esmeralda Co., Fish Lake CASC</td>
<td>7. NV: Esmeralda Co., Fish Lake CASC</td>
</tr>
</tbody>
</table>

^aColorado State University Collection, Fort Collins, CO
^bLiterature sources only
^cCalifornia Academy of Sciences, Golden Gate Park, San Francisco, CA
^dMichael G. Kippenhan Collection, Portland, OR
Gerlach, Wasco County, Nevada. Apparently, any connection in geologic time between the drainage of Honey Lake and Gerlach with Furnace Creek appears unlikely (Reheis 1999). In addition, the dark green dorsal coloration is associated with bronze ventral coloration, which is not found in any of Rumpp’s (1956) other so-called “hybrid” populations, and therefore the plausibility of hybridization as a source of color expression in these populations is in question.

The character state of elytral rigidity was utilized by Rumpp (1956) when differentiating *C. a. amargosae* and *C. a. nyensis*. An initial analysis of living adult specimens indicates a correlation between elytral color and elytra rigidity; however, while this characteristic’s potential as a quantifiable factor in subspecific determination is apparent, a method of measurement has yet to be developed.

An additional consideration not discussed by Rumpp (1956) is the dorsal coloration of sympatric tiger beetle species. Schultz (1986) documented convergent dorsal coloration for numerous populations of *C. oregona* LeConte and *C. tranquedarica* Herbst in the southwestern U.S. In each instance the dorsal color of each species corresponded with its associated substrate color; as a result, numerous subspecific names have been attributed to these populations. An examination of sympatric species present at the above sites indicates similar color forms (Table 4). For example, at Furnace Creek, the 3 species that inhabit the open alkali flats, *C. a. amargosae*, *C. c. pseudoronea*, and *C. w. pseudosenilis*, all exhibit iridescent dorsal coloration varying from green to dark blue and may represent a case of convergent evolution.

### Habitat and Adult Escape Behavior

The habitat of *C. a. amargosae* at Furnace Creek, the type locality, consists of narrow rivulets where trickling water passes through alkali-encrusted soil. This area is conspicuous due to the lack of vegetation and to the alkali encrustations that make the soil covering completely white (Fig. 2), creating blinding reflections during periods of sunlight. At this location *C. a. amargosae* adults are encountered along the exposed waterways where their green dorsal coloration makes them conspicuous on the alkali surface. When disturbed, adults took off in strong flights between 2 m and 6 m in a relatively straight pattern. Individuals would most often fly toward open, moist soil and were active upon landing.

The type locality of *C. a. nyensis* at Springdale, Nevada, is part of the broad flood plain of the Amargosa River and is covered with alkali-resistant plants, leaving only small areas (<12 cm²) of bare ground. A large portion of the area is covered by standing water during the seasonal period of adult activity (March to May). The open areas are characterized by dark, muddy soil with little or no evidence of alkali development. Adults of *C. a. nyensis* occur at the base of vegetation patches or on open areas, often in standing water. When disturbed, individuals took off in a short (<2 m) flight that was erratic in direction. These flights are characterized by sharper, vertical ascents terminating with the individual dropping back into the grass, most often with no post-landing movement. This behavior probably arose from the necessity to clear grass when ascending and landing in areas that are partially concealed by

### Table 2. Dorsal coloration and number of specimens of *Cicindela amargosae* examined and relative percent of dorsal coloration.

<table>
<thead>
<tr>
<th>Location</th>
<th>Collection</th>
<th>Total #</th>
<th>Blue</th>
<th>Green-blue</th>
<th>Green</th>
<th>Dark green</th>
<th>Black</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alvord Hot Springs</td>
<td>CSUC, MGKC</td>
<td>164</td>
<td>2 (1%)</td>
<td>162 (99%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surprise Lake</td>
<td>CASC</td>
<td>4</td>
<td>4 (100%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Honey Lake</td>
<td>CASC, MGKC</td>
<td>43</td>
<td>3 (7%)</td>
<td>40 (93%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gerlach</td>
<td>CASC, MGKC</td>
<td>30</td>
<td>25 (83%)</td>
<td>5 (17%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fish Lake</td>
<td>CASC</td>
<td>26</td>
<td>26 (100%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Springdale</td>
<td>CASC, MGKC</td>
<td>41</td>
<td>1 (2%)</td>
<td>40 (98%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ash Meadows</td>
<td>CASC, MGKC</td>
<td>73</td>
<td>7 (10%)</td>
<td>35 (48%)</td>
<td>5 (6%)</td>
<td></td>
<td>26 (36%)</td>
</tr>
<tr>
<td>Furnace Creek</td>
<td>CASC, MGKC</td>
<td>188</td>
<td>128 (68%)</td>
<td>59 (31.5%)</td>
<td>1 (0.5%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Saratoga Springs</td>
<td>CASC</td>
<td>14</td>
<td>2 (14%)</td>
<td>5 (36%)</td>
<td>1 (7%)</td>
<td></td>
<td>6 (43%)</td>
</tr>
<tr>
<td>Shoshone</td>
<td>CASC</td>
<td>3</td>
<td></td>
<td>3 (100%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tecopa Hot Springs</td>
<td>CASC</td>
<td>59</td>
<td>7 (12%)</td>
<td>13 (22%)</td>
<td>7 (12%)</td>
<td></td>
<td>32 (54%)</td>
</tr>
</tbody>
</table>

*Note: CSUC = California State University, MGKC = Museum of Geology, Keyes, CA.*
### Table 3. Ventral coloration and specimens of *Cicindela amargosae* examined.

<table>
<thead>
<tr>
<th>Location</th>
<th>Genae</th>
<th>Proepisternum</th>
<th>Metaepisternum</th>
<th>Abdomen</th>
<th>Femur</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alvord Hot Springs</td>
<td>dark blue-green to purple</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
</tr>
<tr>
<td>Gerlach</td>
<td>green with copper reflections</td>
<td>dark green to purple with strong copper reflections</td>
<td>dark green to purple with strong copper reflections</td>
<td>green to blue to blue-purple</td>
<td>dark green with copper reflections</td>
</tr>
<tr>
<td>Springdale</td>
<td>dark blue-green to purple</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
<td>black with blue-green to purple reflections</td>
</tr>
<tr>
<td>Furnace Creek</td>
<td>blue-green to blue to purple</td>
<td>purple to blue-green with strong green reflections</td>
<td>purple to blue-green with strong green reflections</td>
<td>purple with dark blue-green reflections</td>
<td>black with strong dark reflections</td>
</tr>
</tbody>
</table>

### Table 4. Dorsal coloration of associated species of *Cicindela* found at Furnace Creek, Inyo. Co., California; Gerlach, Wasco Co., Nevada; and Alvord Hot Springs, Harney Co., Oregon.

<table>
<thead>
<tr>
<th>Location</th>
<th>Species</th>
<th>Dorsal coloration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furnace Creek</td>
<td><em>Cicindela californica pseudoerronea</em></td>
<td>green-blue to dark blue green to dark green in purple</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela willistoni pseudoerronea</em></td>
<td>green to dark green</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela a. amargosae</em></td>
<td>green to purple</td>
</tr>
<tr>
<td>Gerlach</td>
<td><em>Cicindela willistoni echo</em></td>
<td>bronze-brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela h. haemorrhagica</em></td>
<td>brown to black-brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela a. amargosae</em></td>
<td>dark green to black</td>
</tr>
<tr>
<td>Alvord Hot Springs</td>
<td><em>Cicindela tenucincta</em></td>
<td>brown-green to brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela h. haemorrhagica</em></td>
<td>brown to black-brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela willistoni echo</em></td>
<td>bronze-brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela terricola imperfecta</em></td>
<td>brown-green to brown</td>
</tr>
<tr>
<td></td>
<td><em>Cicindela amargosae nyensis</em></td>
<td>black</td>
</tr>
</tbody>
</table>
grass, thus offering a relatively high level of immediate cover. This location is interesting in that as the season progresses (June) and adult activity declines, the dry soil is covered by a thick layer of alkali crust.

The habitat and habit of populations of *C. a. nyensis* outside the type locality were determined to have similar characteristics. Approximately 80 km downstream from Springdale, the habitat of the Ash Meadow population is almost identical to Springdale and is also associated with the Amargosa River. The habitat of Alvord Hot Springs is characterized by drainages from hot springs, which form large pools of standing water on the playa (Fig. 3). During June 2002 and 2004, I often observed adults of *C. a. nyensis* at Alvord Hot Springs standing in shallow water in the cover of vegetation. When disturbed, most individuals preferred to stay within close proximity of the wet, grassy areas with short, erratic flights. Adults that flew into the open playa were active upon landing and soon returned to the vicinity of the water. Honey Lake appeared similar to Alvord Hot Springs; however, since only 1 specimen was encountered, observations are inconclusive. Due to a lack of water runoff on the playa, no suitable habitat or specimens were located at the Modoc County location in June 2004. However, the description of this habitat, as well
as adult behavior (Smith and Bronson 2003), appears similar to the Alvord Hot Springs site.

The Gerlach population occurs in a habitat that can best be described as intermediate to Furnace Creek and Ash Meadows. This location is characterized by a large, open expanse of alkali-encrusted soil bordered by very dense vegetation and small areas of standing water. Here, adults of *C. amargosae* were encountered at the edges of vegetation and flew into the open expanses of alkali. This area did not have the total lack of vegetation as did Furnace Creek, but the open areas were much more exposed than either Springdale or Alvord Hot Springs. Similar to Gerlach, the Tecopa locality is also characterized by a large, open alkali area bordered by dense vegetation, and this location also supports individuals exhibiting color of both subspecies (Table 2). Neither the Fish Lake nor Saratoga Springs locations were examined during the course of this study.

### Total Body Length

Lengths of adults were also utilized by Rumpp (1956) to differentiate *C. a. amargosae* (average length male = 11.4 mm, *n* = 23; female = 12.2 mm, *n* = 46) and *C. a. nyensis* (average length male = 10.4 mm, *n* = 23; female = 10.9 mm, *n* = 27). Average length of adults at the Gerlach was 11.3 mm (*n* = 11) in males and 12.1 mm (*n* = 6) in females.

### Conclusions

Based on the analysis of the current populations of *C. amargosae*, I conclude that dorsal color does not necessarily correlate with geographical distribution of subspecific forms as defined by Rumpp (1956), and, in fact, most populations have individuals expressing a variety of colors (Table 2). The correlation between color and overall body length is consistent throughout the range of *C. amargosae*, with green dorsal coloration coinciding with larger...
average length, whereas black dorsal coloration occurs in individuals of smaller average body length. Even though the Gerlach population is unique for the high percentage of individuals with dark green dorsal and copper ventral coloration (Tables 2, 3), this population is best assigned to the nominate subspecies based on its elytral rigidity, elytral maculation, and overall body length.

Whatever the biological function of the specific colors, there is no doubt that selection is producing convergence in color patterns and color pattern variation among *C. amargosa* populations. It is conceivable that isolated populations of *C. amargosa* could lose morphs through drift such that the monomorphic populations of *C. amargosa* are a result of stochastic rather than deterministic processes. The hybrid populations of Rumpf (1956) are those that retain the original genotypic variation for color pattern and presumably remain under some sort of stabilizing selection (T. Schultz personal communication). Therefore, the interpopulation variation of dorsal coloration is more likely a result of an evolutionary response to ecological factors rather than hybridization. Instances such as those described here for *C. amargosa* illustrate the complexity of coloration as expressed in adult *Cicindela*.

**Acknowledgments**

Susan Agre-Kippenhan, Boris Kondratieff, Jeff Owens, Jason Schmidt, and Calvin Waterman helped collect specimens during the course of this study. Dave Brzoska (Naples, FL) provided collecting information. David Kavanaugh and Roberta Brett (CASC, San Francisco, CA) provided facilities and access to the N.L. Rumpp collection. C. Barry Knisley (Randolph Macon College, Ashland, VA), Richard Freitag (Lakehead University, Thunder Bay, ON, Canada), Dave L. Pearson (Arizona State University, Tempe), and Thomas Schultz (Denison University, Granville, OH) reviewed the manuscript and offered many practical and insightful comments. This study would not have been possible without the direction, support, and patience of Boris C. Kondratieff (Colorado State University, Fort Collins). Collecting in Death Valley National Monument was conducted under permit number DEVA-2002-SCI-0012, overseen by Richard Anderson.

**Literature Cited**


Received 8 March 2004

Accepted 9 September 2004
COMPETITIVE INTERACTIONS BETWEEN ENDANGERED KIT FOXES AND NONNATIVE RED FOXES

Howard O. Clark, Jr.1,2,3, Gregory D. Warrick4, Brian L. Cypher1, Patrick A. Kelly1, Daniel F. Williams1, and David E. Grubbs2

ABSTRACT.—We investigated interference and exploitative competition between endangered San Joaquin kit foxes (Vulpes macrotis mutica) and nonnative red foxes (V. vulpes). Seven kit foxes and 16 red foxes were radio-collared and tracked via radiotelemetry near Lost Hills, California. One kit fox was killed by a red fox. Home ranges of the 2 species did not overlap extensively. Although both species used similar habitats, they used different parcels of land. Kit foxes and red foxes primarily consumed rodents on the study site, and dietary overlap was considerable. Red foxes also may have been using dens formerly used by kit foxes. Thus, red foxes were engaging in both interference and exploitative competition with kit foxes, and red foxes constitute a potentially significant threat to kit foxes. Coyotes (Canis latrans) co-occur with kit foxes and may limit red fox abundance and distribution. Therefore, although they occasionally kill kit foxes, the presence of coyotes may benefit kit foxes by excluding red foxes.

Key words: California, competition, endangered species, kit fox, red fox, Vulpes macrotis mutica, Vulpes vulpes.

The San Joaquin kit fox is a federally endangered and state threatened species occurring in the San Joaquin Valley, California (United States Fish and Wildlife Service 1998). The historic range of the San Joaquin kit fox has been significantly reduced by habitat loss due to agricultural, industrial, and urban development. Remaining kit fox populations are threatened by continuing habitat conversion, as well as rodenticide use and interspecific competition (United States Fish and Wildlife Service 1998). Nonnative red foxes are increasing in abundance in the San Joaquin Valley (Jurek 1992, Lewis et al. 1999) and potentially could compete with kit foxes. Competitive interactions between kit foxes and red foxes have not been investigated.

Red foxes were introduced into the Sacramento Valley of California from the midwestern United States in the 1870s (Grinnell et al. 1937, Lewis et al. 1999) and since have spread as far south as San Luis Obispo, Orange, and Los Angeles Counties, California (Jurek 1992). Red foxes also have appeared throughout the San Joaquin Valley, including habitats occupied by kit foxes. Adverse impacts to kit foxes from red foxes have been documented. Ralls and White (1995) reported 2 San Joaquin kit fox mortalities due to red foxes. Also, red foxes have been observed using dens previously occupied by kit foxes (B. Cypher personal observation). Other potential impacts include competition for food and disease transmission (Cypher et al. 2001). Red foxes also have been found to adversely affect other fox species such as arctic foxes (Alopex lagopus; Frafjord et al. 1989, Hersteinsson and Macdonald 1992) and swift foxes (V. velox; A. Moehrenschlager personal communication). Thus, it is important to quantify competitive interactions between kit foxes and red foxes to determine whether red foxes are a potential threat to remaining kit fox populations.

We examined competitive interactions between San Joaquin kit foxes and nonnative red foxes near Lost Hills, California, during 1998–1999. Our objectives were (1) to examine sources of mortality and space use patterns of both species to determine whether interference competition was occurring, and (2) to examine habitat use and food habits of both species to determine whether exploitative competition was occurring.

1California State University–Stanislaus, Endangered Species Recovery Program, 1900 North Gateway Boulevard, Suite 101, Fresno, CA 93727.
2Department of Biology, California State University–Fresno, 2555 East San Ramon Avenue, Fresno, CA 93740.
3Corresponding author: H.T. Harvey & Associates, 423 West Fallbrook, Suite 202, Fresno, CA 93711.
4Center for Natural Lands Management, Box 20696, Bakersfield, CA 93390.
METHODS

Study Area

We conducted our study along an approximately 32-km segment of the California Aqueduct (aqueduct) near the community of Lost Hills, Kern County, California (Fig. 1). Kit foxes and red foxes co-occur in this area. The study area is predominantly flat with elevations ranging from approximately 80 m in the east to 150 m along the Lost Hills anticline. The Lost Hills, forming the western edge of the study area, are gentle, rolling hills that run in a northwest to southeast direction paralleling the aqueduct.

Climate is characterized by hot, dry summers and wet, cool winters with thick fog (National Climatic Data Center 2000). Weather data recorded 40 km east of Lost Hills in Wasco, California, indicate that average daily maximum temperatures range from 13.4°C in December to 37.5°C in July, and average daily minimums range from 2.1°C in December to 18.7°C in July. Precipitation, which averages 18.6 cm annually, was 41.6 cm in 1998 and 14.7 cm in 1999.

A strip of habitat approximately 60 m wide occurs along both sides of the aqueduct. This habitat is typical of Valley Grassland vegetation (Heady 1977), with red brome (Bromus madritensis) and filaree (Erodium spp.) dominating the herbaceous vegetation. Common shrubs include desert saltbush (Atriplex polycarpa) and spiny saltbush (A. spinifera). Honey mesquite (Prosopis glandulosa) occurs within the southern portion of the study area, and a few feral almond and pistachio trees are found in areas where the aqueduct borders orchards. Farmland covers most of the study area outside the aqueduct corridor. Major crops include cotton, barley, almonds, and pistachios. Less abundant crops are alfalfa, onions, lettuce, watermelon, olives, tomatoes, and vineyards. Annual crops are typically planted in late winter and harvested in the fall. After crops are harvested, the ground is disked and left bare until the following spring. Pistachio and almond groves are drip-irrigated and harvested in October of each year.

The west side of the study area is bounded by the Lost Hills oil field (approximately 1.5 km west of the aqueduct), which is primarily owned and operated by private oil companies. Although some portions of the oil field are heavily developed, significant expanses of natural vegetation typical of the Valley Grassland are present.

Field Methods

Kit foxes were captured during the non-breeding season (April–September) using Tomahawk™ wire-mesh traps (38 × 38 × 107 cm; Tomahawk, MI) baited with canned mackerel, wieners, bacon, or chicken. We captured red foxes during the dispersal season by plunging them from drainage culverts into handling bags. The plunger consisted of lengths of plastic pipe attached together with a foam ball taped to an end (O’Farrell 1987). Foxes were ear-tagged, measured, weighed, and fitted with radio-collars (Advanced Telemetry Systems, Isanti, MN). Collars contained mortality sensors that activated after 8 hours of nonmovement. Each radio-collar weighed approximately 50 g, or <3% of the animal body mass (Cypher 1997). We released the foxes at their individual capture sites and then radio-tracked them from January 1998 to December 1999 (Clark 2001).

Radio-collared foxes found dead were necropsied to determine cause of death. If the fox had contusions caused by tooth punctures, we considered predators the cause of death (Roy and Dorrance 1976). When possible, we measured distances between canine puncture wounds to determine which species caused the death (Disney and Spiegel 1992). If the cause of death could not be determined because the carcass was badly decomposed or scavenged, it was classified as unknown.

To determine space use patterns, foxes were radio-tracked weekly using 2 truck-mounted null tracking systems with paired 2-element antennae (White 1985). Stations were located along access roads of the aqueduct and separated by approximately 800 m. Researchers at 2 adjacent stations simultaneously took bearings on foxes. Four azimuths (referencing true north) were obtained: the azimuth to the fox from the south antenna, the azimuth to the fox from the north antenna, the azimuth from the south antenna to the north antenna, and vice versa. Survey grade GPS units (Pathfinder Pro XR/XRS, Trimble Navigation Limited, Sunnyvale, CA) were used to determine the locations of the antenna stations. We initiated telemetry sessions approximately 1 hour before sunset and continued for approximately 4.5 hours. The first 3–5 hours after sunset is typically
when kit fox activity is highest (Zoellick 1990). We collected locations on all collared foxes in the vicinity, and successive locations on individual foxes were separated by ≥10 min. When bearings intersected <20 degrees, we discarded locations. Locations of foxes were calculated using methodology described in White and Garrott (1990), and we entered these locations into a GIS layer for analyses using ARC/INFO (Environmental Systems Research Institute, Redlands, CA).

Accuracy of the telemetry system was determined by having 2 observers gather bearings on radio-collars (n = 30) placed at locations known only by a 3rd person. Locations derived from telemetry were then compared to the actual locations of the radio-collars (recorded using a survey grade GPS unit) to determine the average telemetric error (Springer 1979), which was 38 ± 7 m (range = 4–186 m). Eighty percent of triangulated locations had an error of <45 m. Tracking vehicles averaged 552 ± 35 m (range = 74–1318 m) from the reference transmitters.

To evaluate spatial overlap of foxes, we used the points collected throughout the year to delineate home ranges and core areas for each fox, but only for those with >30 locations (Chamberlain and Leopold 2000). Home ranges were delineated using the minimum convex polygon (MCP) method, which provides a conservative estimate of space use. Core areas were delineated using the adaptive kernel method (Worton 1989). Areas within the home range that fell within the 25% probability contour were considered core areas, defined as the portion of an animal’s home range that exceeded an equal-use pattern (Samuel et al. 1985). Core areas can be used to denote central areas of consistent or intense use (Kaufmann 1962). An ArcView program extension was used to delineate home ranges and core areas (Hooge and Eichenlaub 1997). Spatial overlap between kit foxes and red foxes was calculated for each

![Fig. 1. Location of study site near Lost Hills, California.](image-url)
animal by determining the percentage of each range that was overlapped by an individual of the other species.

To determine habitat use by the 2 fox species, we entered into an ARC/INFO layer the habitat information gathered using GPS units, United States Geological Survey maps, and ground mapping. Fox locations were plotted in ArcView, and each location was assigned a habitat type. Only those kit foxes and red foxes with overlapping home ranges were included in the habitat selection analysis. In 1998 home range overlap between species occurred only in the southern portion of the study area, and in 1999 only in the northern portion of the study area. One adult male kit fox in 1998 with an analyzed overlapping home range with a red fox had an analyzed overlapping home range in 1999; all other foxes were different individuals. To ensure data independence, we selected a single random location per fox per telemetry session (Swihart and Slade 1985). Available habitat was defined as being within 1.6 km of the aqueduct and 1.6 km from the most southerly and most northerly fox locations. Utilization-availability analysis was conducted using the method described in Neu et al. (1974) and Byers et al. (1984). To test whether foxes used each habitat category in proportion to its occurrence within the available area, we used the chi-square method described in Neu et al. (1974).

Habitat types included orchard, row crops, aqueduct right-of-way (ROW), vineyard, grassland, residential, and other. Orchards included almonds, olives, and pistachios. Annual row crops included cotton, barley, and tomatoes. Residential referred to any farmhouse, equipment staging area, or farm equipment storage yard. The category “other” included small parcels of tilled and miscellaneous land. Habitat types differed between 1998 and 1999 due to fox home range overlap occurring in different portions of the study area.

To assess overlap in food use, we analyzed scats collected from trapped foxes and known fox dens. A scat is defined as all fecal material deposited in 1 event. Scats were oven-dried for 24 hours at 60°C to facilitate handling and to destroy cysts of zoonotic parasites. Prey remains were identified using hairs (Mayer 1952, Stains 1958) and by comparing teeth, bones, scales, skin, exoskeletons, and seeds with reference specimens (Roest 1991). Food items were grouped to simplify analyses. Horn’s index (Horn 1966), \( R_0 \), was calculated to determine the amount of overlap between diets. A Shannon index of dietary diversity, \( H' \), was calculated for each species. A 2 × 10 contingency table chi-square test was conducted on the dietary data, and a 2 × 2 contingency table chi-square test was conducted on each item to determine if proportional use by the 2 fox species was similar (Zar 1999).

**RESULTS**

**Causes of Mortality**

During 1998–1999 we captured and radio-collared 4 adult (2 female, 2 male) and 3 juvenile male kit foxes, and 16 red fox juveniles (10 females, 6 males). It is likely that representatives from all kit fox and red fox family units were radio-collared during this 2-year period. Four radio-collared kit foxes (2 adults, 2 juveniles) were killed, 3 (1 adult, 2 juveniles) by coyotes and 1 adult by a red fox. Eleven radio-collared red foxes were found dead, 9 killed by coyotes. Cause of death could not be determined conclusively for 1 red fox (although probably a predator kill). The signal from the collar of another was emanating from the aqueduct and this fox was presumed to be dead.

**Spatial Overlap**

In 1998 we delineated space use for 4 kit foxes and 4 red foxes. The home ranges of 3 kit foxes were not overlapped by any radio-collared red foxes. The home range of the remaining kit fox was overlapped by 4 juvenile red foxes. Average home range overlap was 31% (range 14%–48%) for the kit fox and 55% (range 40%–81%) for the red foxes. The core area for this kit fox was partially overlapped by the home range of 1 red fox, but core areas of the 2 species did not overlap. The adult male kit fox with a home range overlapped by 4 juvenile red foxes moved 10 km north in December 1998 to pair bond with an adult female kit fox (see Clark 2003). He remained in the area throughout 1999.

In 1999 space use was delineated for 10 red foxes and 4 kit foxes (2 adults and 2 juveniles). The kit foxes were members of the same family group. Home ranges of 9 of the red foxes did not overlap home ranges of any radio-collared kit foxes. The home range of the remaining red fox overlapped home ranges of the 4 kit foxes.
foxes. Average overlap was 24% (range 14%–36%) for the kit foxes and 11% (range 5%–14%) for the red fox. Core areas for all 4 kit foxes were overlapped by the home range of the red fox, but the core area of the red fox was overlapped by the home range of only 1 kit fox. Core areas of the 2 species did not overlap.

On 3 occasions kit foxes and red foxes were located in the same general vicinity, providing an opportunity to observe interactions. It is unknown whether foxes not radio-collared or other animals in the area (e.g., coyotes) influenced these movements. On 26 August 1998, an adult kit fox and 4 juvenile red foxes were located within 0.5 km of each other. During a 1-hour period the kit fox maneuvered south through the 4 red foxes and continued south away from them. One red fox also moved south, but for a shorter distance than that traveled by the kit fox.

On 18 November 1998 we recorded an encounter between 2 kit foxes and 1 red fox. An adult male and an adult female kit fox were located within 250 m of a juvenile red fox during a 20-minute period. The female kit fox moved toward the initial location of the red fox, while the red fox and the male kit fox moved away from each other.

On 30 September 1999 we observed a juvenile red fox as it moved in a direction away from an approaching adult kit fox. It then moved back toward the kit fox and finally away again. The shortest distance between the 2 foxes was approximately 300 m within a 1-minute window. On 22 November 1999 these 2 foxes again were located in close proximity, and both foxes moved away from each other. The shortest distance between the 2 foxes was approximately 100 m.

Habitat Use

Habitat use by kit foxes was disproportionate to availability in both 1998 ($\chi^2 = 20.0$, df = 3, $P < 0.01$) and 1999 ($\chi^2 = 86.4$, df = 5, $P < 0.01$). Likewise, habitat use by red foxes was disproportionate to availability in both 1998 ($\chi^2 = 240.6$, df = 3, $P < 0.01$) and 1999 ($\chi^2 = 88.4$, df = 4, $P < 0.01$). In 1998 use of orchards by kit foxes was higher than expected while use of row crops and other habitats was lower than expected (Fig. 2). For red foxes in 1998, use of the aqueduct ROW and orchards by kit foxes was higher than expected while use of row crops and other habitats was lower than expected (Fig. 3). For red foxes in 1999, use of the aqueduct ROW was higher than expected while use of row crops was lower than expected (Fig. 3). During the study red foxes sometimes used residential areas, grasslands, and vineyards, whereas kit foxes never were located in these habitats.

Diet

In 1999 we collected 207 kit fox scats, with most (204) being found at known dens during April (32.4%), June (64.3%), and July (1.9%). Rodents were the most frequently occurring item in kit fox scats (88.4%), followed by insects (18.4%), other arthropods (11.6%), leporids (8.7%), human-derived items (6.3%), and birds (1.9%). Species of rodents occurring in kit fox scats include house mice (Mus musculus, 34.3%), deer mice (Peromyscus maniculatus, 17.9%), pocket gophers (Thomomys bottae, 9.7%), California voles (Microtus californicus, 3.9%), harvest mice (Reithrodontomys megalotis, 3.4%), and San Joaquin pocket mice (Perognathus innomatus, 1.5%). In addition, 27.0% of the scats contained murid rodents that could not be identified to species, and 4.8% of the scats contained rodents that could not be identified to species. Insect species include field crickets (family Gryllidae, 9.7%), grasshoppers (family Acrididae, 4.4%), ants (family Formicidae, 4.4%), and beetles (order Coleoptera, 2.9%). Other arthropod remains were not identifiable. Bird remains in scats typically consisted of a few feathers and were not identified to species. Human-derived items included plastic (1.9%), string (1.9%), paper (1.5%), and rubber (1.0%).

In 1999 we gathered 140 scats from known red fox dens in February (10%), June (67%), and September (23%). Murids were the most frequently occurring item in red fox scats (91.4%), followed by insects (16.4%), leporids (11.4%), birds (7.1%), and human-derived items (4.9%). Species of rodents that occurred in red fox scats include California voles (31.4%), house mice (28.6%), deer mice (4.3%), pocket gophers (2.9%), and harvest mice (0.7%). In addition, 27.1% of the scats contained murid rodents that could not be identified to species, and 6.4% of the scats contained rodents that could not be identified to species. Insect species included ants (7.9%), field crickets (7.1%), and beetles
Bird remains in scats typically consisted of a few feathers and were not identified to species. Human-derived items included paper (2.8%), plastic (0.7%), string (0.7%), and rubber (0.7%). Most of the scats contained some vegetation, such as grass and seeds of brome. Four scats (2.8%) contained almonds, and 1 scat contained a barley seed head.

Proportional item use by kit foxes differed significantly from that of red foxes ($\chi^2 = 78.0$, df = 9, $P < 0.01$; Fig. 4). Proportional use of voles ($\chi^2 = 47.7$, df = 1, $P < 0.01$) and birds ($\chi^2 = 4.6$, df = 1, $P = 0.03$) was greater among red foxes than kit foxes. Conversely, proportional use of deer mice ($\chi^2 = 12.9$, df = 1, $P < 0.01$), gophers ($\chi^2 = 5.0$, df = 1, $P = 0.03$), and other items ($\chi^2 = 3.9$, df = 1, $P = 0.05$) was greater among kit foxes than red foxes, and use of orthopterans ($\chi^2 = 3.3$, df = 1, $P = 0.07$) and arthropods ($\chi^2 = 2.9$, df = 1, $P = 0.09$) was marginally greater. Proportional use of house mice ($\chi^2 = 1.0$, df = 1, $P = 0.31$), unknown murids ($\chi^2 = 2.0$, df = 1, $P = 0.92$), and leporids ($\chi^2 = 0.4$, df = 1, $P = 0.51$) did not differ significantly between kit foxes and red foxes. Diets are identical if their $R_0$ value = 1.0; a value of zero means the diets have no dietary items in common. The calculated $R_0$ value between kit fox and red fox diets was 0.87, indicating the diet overlap between the fox species was high. The Shannon diversity indices for kit fox and red fox diets were 0.91 and 0.90, respectively.

**DISCUSSION**

**Interference Competition**

Interference competition can consist of direct mortality, spatial exclusion, or avoidance behavior. During this investigation, 1 kit fox was killed by a red fox, as has been observed elsewhere (Ralls and White 1995). Red foxes are larger than kit foxes (3–7 kg vs. 2–3 kg), and therefore kit foxes are at greater risk of injury or death in agonistic interactions. Red foxes also have been reported to kill other fox species such as arctic foxes (Frafjord et al. 1989, Bailey 1992) and swift foxes (A. Moehrensclager personal communication).

Space use patterns of kit foxes and red foxes monitored simultaneously suggested possible avoidance behavior, although there was no way...
to verify causation. Kit foxes were observed to move away from red foxes on 2 occasions. Both instances involved adult kit foxes avoiding red foxes. Red foxes also were observed to move away from kit foxes on 2 occasions. However, both instances involved juvenile red foxes. Although larger than adult kit foxes, juvenile red foxes may be more cautious than adult red foxes in interspecific encounters.

Habitat use by kit foxes and red foxes generally was similar. Both species selectively used some habitats (e.g., aqueduct ROW, orchards) and avoided others (e.g., annual row crops). These similar habitat use patterns likely increase the potential for interspecific encounters.

Exploitative Competition

Exploitative competition occurs between 2 sympatric species when both use the same resources. Such overlapping use patterns can result in resource availability being limited for 1 or both species. For kit foxes and red foxes, food and dens could be limiting factors. Overlapping habitat use patterns observed on our study site increased the potential for exploitative competition. However, competitive pressure probably was reduced because the 2 species frequently used different parcels of land. Red foxes also used some habitats that kit foxes did not use, which also may have reduced competition.

The aqueduct ROW may have been selectively used by both fox species due to a relatively high abundance of food. Small mammal diversity and abundance were higher along the aqueduct ROW relative to row crops and orchards (Clark 2001). Also, jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus audubonii*) were observed more frequently in the aqueduct ROW compared with other habitats (H. Clark personal observation). Conversely, food items did not appear to be abundant in orchards (Clark 2001). Thus, the reason for the disproportionately high use of orchards by both fox species is unclear.

Both fox species may have avoided row crops due to relatively low food availability and frequent disturbance. Abundance of small mammals and other foods (e.g., leporids) was relatively low in row crops (Clark 2001). Also, row crops were subjected to weekly inundation during irrigation. This impedes foraging and precludes the establishment of earthen dens. Other frequent disturbances in row crops included cultivation, fertilization, and pesticide application.

Both fox species consumed a diversity of food items. During prey surveys conducted in 1998 and 1999, murid rodents were the most frequently captured small mammals on the study site (Clark 2001), and these rodents were important food items in the diets of both
fox species. Kit foxes also commonly consumed other rodents including deer mice and gophers. Both fox species commonly consumed invertebrates, although use by kit foxes generally was higher than that of red foxes. This may be an artifact of gathering scat samples at pupping dens, where most of the scats probably were from pups. Pups are not very experienced at capturing prey and consume a high proportion of invertebrates, which are more easily captured than vertebrate prey (Cutter 1958). Red foxes exhibited high use of California voles, which are a commonly used food item in many other parts of their range (Samuel and Nelson 1982). Voles were not captured during small mammal surveys (Clark 2001), and the habitat(s) in which red foxes were finding voles is not known.

The high overlap in kit fox and red fox diets indicates potential competition for food resources. However, frequencies of occurrence of food items differed between species, indicating that both species used similar items but did not consume them in the same proportions. These differences in diet would contribute to resource partitioning, which would help ameliorate competition.

Competition for dens was difficult to assess. Kit foxes are obligatory den users and are found in a den almost every day (Grinnell et al. 1937, Morrell 1972). Dens are used for bearing and rearing young, diurnal resting cover, escaping predators, and avoiding temperature extremes. Thus, dens are a critical aspect of kit fox ecology. Conversely, red foxes primarily use dens just during pup rearing. White et al. (2000) reported that red foxes usurped several dens that were used by kit foxes during previous years at a study site. Red foxes have been observed using kit fox dens in the city of Bakersfield (B. Cypher unpublished data). Dens being used by red foxes are unavailable to kit foxes. Similarly, red foxes are expanding into arctic fox range in Norway and usurping arctic fox dens (Frafjord 2003).

Role of Coyotes in Kit Fox–Red Fox Interactions

Coyotes engage in both interference and exploitative competition with kit foxes. In many locations coyotes are the primary cause of kit fox mortality (Ralls and White 1995, Spiegel 1996, Cypher et al. 2000), as was the case on our study site. Coyotes also use some of the same foods as kit foxes (Cypher and Spencer 1998). However, kit foxes have coevolved with coyotes and have adaptive strategies for coexisting with coyotes including year-round den use, efficient exploitation of certain food resources not extensively used by coyotes (e.g., heteromyid rodents; White et al. 1995, Cypher and Spencer 1998), and possibly some level of

![Fig. 4. Food item use by kit foxes and red foxes at Lost Hills, California, 1999. Bars are the proportion of scats with each food item.](image-url)
habitat partitioning (White et al. 1995, Warrick and Cypher 1998). In general, coyotes do not competitively exclude kit foxes, and both species co-occur in most areas.

Coyotes also engage in both interference and exploitative competition with red foxes. Coyotes are a significant source of mortality for red foxes (Sargeant and Allen 1989). On our study site coyotes were the predominant cause of mortality for red foxes, killing over half the red foxes we monitored. The historic ranges of red foxes and coyotes may have been relatively disjunct (Kamler and Ballard 2002), and therefore red foxes may not have evolved strategies for coexisting with coyotes. Thus, coyotes may significantly influence red fox abundance and distribution (Dekker 1983, Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987).

Because of the negative effects of coyote-fox interactions to red foxes, kit foxes actually might benefit from the presence of coyotes (Cypher et al. 2001). Coyotes may limit red fox abundance and even prevent them from colonizing certain areas within the kit fox range. Red foxes are rarely observed in areas where coyotes are abundant (Balls and White 1995, Spiegel 1996, Cypher et al. 2000). White et al. (2000) cautioned against the removal of coyotes in kit fox habitat where red foxes also are present. In essence, coyotes may constitute a biological control strategy for red foxes. Indeed, coyotes have been proposed as a control agent for red foxes in coastal areas of California where foxes are preying on endangered California Least Terns (Sterna antillarum brevirostris longirostris levipes; Jurek 2000). Coyotes also have been recommended for controlling red foxes in the Prairie Pothole Region of North America to reduce red fox predation on duck nests (Sargeant and Arnold 1984).

Conclusions

Red foxes engage in interference competition with kit foxes through direct mortality and possibly through spatial exclusion. Predator escape mechanisms of kit foxes, such as den use, may not be as effective against red foxes, as the relatively similar size of the 2 species permits red foxes to enter kit fox dens. Kit fox mortality attributable to red foxes may be additive, as the presence of red foxes does not reduce the abundance of coyotes, which are the primary source of kit fox mortality. Red foxes also may engage in exploitative competition with kit foxes through use of kit fox dens and overlapping habitat use and food habit patterns. Furthermore, the 2 species are congeneric, increasing the potential for disease transmission. Thus, nonnative red foxes in the San Joaquin Valley constitute a potentially significant threat to kit foxes (Cypher et al. 2001).

The threat of red foxes to kit foxes may be somewhat ameliorated by several factors. Red foxes are less adapted to arid lands than kit foxes and may have limited ability to colonize kit fox habitat in which free water is scarce or not present. Also, the presence of coyotes may limit red fox abundance in optimal kit fox habitat. Conservation of large blocks of quality arid habitat with healthy coyote populations, as called for in recovery strategies for San Joaquin kit foxes (U.S. Fish and Wildlife Service 1998), should help limit impacts of red foxes on kit foxes.

Acknowledgments

This study was funded by the U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, California Department of Fish and Game, and the Fresno State University Office of the Dean. Field assistance was provided by E. Sheehan, G. Gray, A. Harpster, S. Clifton, L. Hamilton, T. Sandoval, R. Zwerdling-Morales, R. Bate, M. McFall, P. Morrison, M. Selmon, J. Smith, C. Van Horn Job, and J. McMullin. GIS support was provided by S. Phillips and P. Brandy, and administrative support was provided by C. Lopez and C.G. Lopez. K. Balle and S. Spiegel loaned equipment, and M. Constantnescu, R. Anthes, and G. Schales piloted aircraft during aerial surveys. Various landowners provided access to their lands. The California Department of Water Resources permitted admittance to the California Aqueduct. W. Standley provided invaluable assistance with the kit fox literature references. Four referees made helpful and constructive comments on the manuscript. This work was a partial fulfillment of a master’s thesis for H. Clark at Fresno State University.

Literature Cited


National Climatic Data Center. 2000. Local climatological data, Wasco, California, USA. National Climatological Data Center, Asheville, NC.


Received 30 January 2004
Accepted 6 August 2004
While identifying contract macroinvertebrate samples from Idaho waters for the Idaho Department of Environmental Quality Beneficial Use Reconnaissance Program (Beneficial Use Reconnaissance Project Technical Advisory Committee 1999), taxonomists at EcoAnalysts, Inc. (Moscow, ID), encountered *Orconectes virilis* (Hagen 1870), a species of crayfish not previously known from Idaho. *Orconectes virilis* is known from lakes and streams east of the Continental Divide in eastern Canada from Saskatchewan to Ontario, and in the United States from Montana to Arkansas, east to New York and Maine (Hobbs 1972, 1974, 1989); it has been introduced into California, Utah, Arizona, New Mexico, Maryland, parts of New England and Tennessee, western Colorado, and parts of Canada (Riegel 1959, Hobbs 1974, Bouchard 1977, Unger 1978). Invasive populations of *O. virilis* may be a threat to freshwater biodiversity (Bouchard 1977, Chambers et al. 1990, Hanson et al. 1990, Savino and Miller 1991, Miller et al. 1992, Warren 1997, Lodge et al. 2000). Clark and Wroten (1978) reported a depauperate Idaho crayfish fauna, with only 3 native species in the genus *Pacifasticus*, and 1 introduced species, *Procambarus clarkii* (Girard 1852). Miller (1960) did not find *O. virilis* in Oregon.

**MATERIALS AND METHODS**

Field methods used to collect benthic macroinvertebrate samples are described in detail in Beneficial Use Reconnaissance Project Technical Advisory Committee (1999). In Idaho the macroinvertebrates in wadeable streams were collected in 3 riffle samples per stream reach using a Hess sampler with a 500-micron mesh net (Hess 1941) with the “Canton modification” (Canton and Chadwick 1984). A kick-net was used to collect additional specimens at the China Creek locality (Fig. 1). Samples were preserved in 70% ETOH and stored separately in the field. In the laboratory the 3 samples were composited, counted, and 500 randomly selected individual invertebrates were identified.

The species was initially identified using Smith (2001) and Thorpe and Covich (2001). Specimens were sent to Christopher A. Taylor, Illinois Natural History Survey, for verification. Voucher specimens of *Orconectes virilis* are deposited in the Orma J. Smith Museum of Natural History, Albertson College of Idaho (ALBRCIDA), Caldwell, the EcoAnalysts, Inc.
Fig. 1. Known distribution (collection localities) of *Orconectes virilis* (Hagen) in Idaho, USA.

TABLE 1. Water quality and habitat variables for *Orconectes virilis* (Hagen) in Idaho. N/A = data not taken.

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<th>Variable</th>
<th>China Creek</th>
<th>Jim Ford Creek</th>
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<td>Date</td>
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<td>14 July 2000</td>
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<td>Temperature (°C)</td>
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<tr>
<td>Dissolved oxygen (mg · L⁻¹)</td>
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<td>pH (SU)</td>
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<td>N/P ratio</td>
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Table 2. Invertebrate associates of *Orconectes virilis* (Hagen) in Idaho.

<table>
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<th>Associated taxa</th>
<th>China Creek 5 August 1999</th>
<th>Jim Ford Creek (both locations) 14 July 2000</th>
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</table>

(Materials Examined)

**IDAHO: Clearwater County:** Jim Ford Creek: 2 specimens (EI), 0.5 m upstream from Hwy 11 bridge, 46°22.545′N, 115°56.953′W, 918 m elev., 20 October 2000, J. Davis. Jim Ford Creek: 1 specimen (ALBRCIDA), 10 m above hydroelectric diversion, 46°23.004′N, 115°56.953′W, 913 m elev., 20 October 2000, J. Davis.

**IDAHO: Twin Falls County:** China Creek: 1 specimen (EI) 42°03′31″N, 114°46′11″W, 1530 m elev., 29 June 2000, W.H. Clark (collection event #10,233).

**RESULTS AND DISCUSSION**

These collection records for *Orconectes virilis* represent the 1st report of the genus and species for the State of Idaho as well as for the Pacific Northwest, USA. The proximity of the China Creek locality (Fig. 1) to Nevada suggests that the species may also be found there. The genus *Orconectes* is naturally distributed in North America east of the Continental Divide. In the northwestern United States and adjacent Canada, only 2 species of *Orconectes* occur: *O. virilis*, which is widespread in Montana, Wyoming, Alberta, and Saskatchewan,
with introduced populations in Utah and northern California; and *O. immunis* (Hagen 1870), which occurs in Montana and Wyoming (Hobbs 1974, 1989). To further the general knowledge of crayfish in the state of Idaho and adjacent areas, we present a checklist of the recent species reported from Idaho.

### Checklist of Recent Crayfishes Known to Occur in Idaho

**ASTACIDAE**

- *Pacifastacus (Hobbsastacus) connectus* (Faxon 1914). Native to ID and OR.
- *Pacifastacus (Hobbsastacus) gambelii* (Girard 1852). Native to WA, OR, ID, MT, northern CA, NV, and UT.
- *Pacifastacus (Pacifasticus) binecetus group*
- *Crypochironomus sp.*
- *Dierotendipes sp.*
- *Eukiefferiella sp.*
- *Eukiefferiella decoucia group*
- *Micropsectra sp.*
- *Nanocladius sp.*
- *Orthocladius annectens*
- *Parametriocnemus sp.*
- *Paratanytarsus sp.*
- *Paratendipes sp.*
- *Pentaneura sp.*
- *Phaenopsectra sp.*
- *Polyplephelin sp.*
- *Sictochironomus sp.*
- *Tanypodinae* X
- *Thienemanniella sp.*
- *Thienemanniina group*
- *Tøttenia bavarica group*

**MOLLUSCA**

- *Bivalvia*
- *Sphaerididae* X
- *Gastropoda*
- *Ferrisia sp.* X
- *Physa sp.* X

**TOTAL TAXA** 30 36
Physical habitat and water-quality variables for sampling locations are presented in Table 1. These data help describe the physical habitat structure and summer water-quality conditions in which *O. virilis* has been found in Idaho. Table 1 shows that both waters are small-order, low-gradient streams impacted from grazing and other agricultural practices. In the summer, at least, they appear to be characterized by warm temperatures and corresponding low dissolved oxygen concentrations. The stream sites were characterized by low water velocity and appeared to be impacted by fine sediment (Table 1).

The invertebrates associated with *O. virilis* at these 2 sites are listed in Table 2. The groups and taxa listed are considered to be more pollution tolerant as would be expected to be found in more degraded systems (Hilsenhoff 1987, Barbour et al. 1999, Relyea et al. 2000).

Because nonindigenous crayfishes including *O. virilis* have been shown to impact freshwater biodiversity including the macroinvertebrate fauna (Bouchard 1977, Chambers et al. 1990, Hanson et al. 1990, Miller et al. 1992, Warren 1997, Lodge et al. 2000), we present the macroinvertebrate community associated with *O. virilis* in Idaho (Table 2). These 2 locations have similar invertebrate assemblages (Table 2), with the following major differences. The China Creek site had a taxa richness of 36 and included 4 major groups not found at the Jim Ford Creek sites, and that was Trichoptera, Jim Ford Creek had a taxa richness of 36 and included 4 major groups not found in the China Creek samples: Megaloptera, Nematoda, Gastropoda, and Ostracoda.

We suggest that this species be monitored in the Pacific Northwest to determine its impacts on the native invertebrate fauna in the region. It is worthy of note that no native crayfish were found at the 2 collection sites in which *O. virilis* occurred (Table 2).

**Acknowledgments**

The authors thank Christopher Taylor (Illinois Natural History Survey) for verifying the initial identification of *Orconectes virilis*. John Pfeiffer (EcoAnalysts, Inc.) originally identified the specimens and brought them to the attention of the second author (GTL). Sean Woodhead and Darren Brant (Idaho DEQ) assisted with logistical support. Christopher Rogers (EcoAnalysts, Inc.) kindly reviewed a draft of this paper and offered helpful comments. Sean Coyle (Idaho DEQ) made Figure 1.

**Literature Cited**


Received 29 December 2003
Accepted 12 October 2004
Brechmorhoga mendax (Hagen 1861) and B. pertinax (Hagen 1861) are the only 2 libellulid clubskimmer dragonfly species reported in the United States (Needham et al. 2000, Donnelly 2004). Brechmorhoga mendax is found across the southern plains and southwestern United States, from South Dakota to Arkansas, west to northern California, and south into Mexico (Beckemeyer 1996, Needham et al. 2000, Manolis 2003, Donnelly 2004). It has been reported throughout Arizona, except in Yuma County in the southwestern corner of the state and in the northeast in Navajo and Apache Counties. It has been reported from the Virgin River drainage in southwestern Utah and southeastern Nevada, and in central Grand Canyon (Donnelly 2004). In contrast, B. pertinax is very rare or accidental in the United States: the only previous record to our knowledge is a single specimen taken by M. Westfall at John Hands Campground in the Chiricahua Mountains, Cochise County, Arizona, on 25–26 June 1958. Brechmorhoga pertinax’s range extends south through Mexico, Guatemala, Nicaragua, and Costa Rica (Gutiérrez 1995, Needham et al. 2000). Here we report a more limited distribution of B. mendax in Arizona and several highly isolated populations of B. pertinax along small, perennial, spring-fed streams emanating from the south side of Grand Canyon in northern Arizona.

METHODS

We collected numerous adult Odonata during biological inventories of >300 aquatic habitats across the 3500 m elevation gradient in Coconino, Mohave, and Yavapai Counties, and in and around Grand Canyon in northern Arizona over the past decade (Fig. 1). These inventories focused on water sources, particularly springs, the several dozen perennial streams that are tributaries of the Colorado River, as well as natural and anthropogenic ponds, lakes, and reservoirs (Stevens et al. 1997, Grand Canyon Wildlands Council 2002, 2004, RAB and LES unpublished data). By convention, distances along the Colorado River in Grand Canyon are measured in miles from Lees Ferry in Coconino County at the upstream end of Grand Canyon.

Specimen identities were verified by RAB, with the northern phenotype of B. pertinax distinguished from B. mendax on the basis of

Key words: biogeography, Brechmorhoga, Colorado River, Grand Canyon, isolated populations, Neotropical, Odonata, springs.
several features: (1) a darker, more slender form; (2) dark interpleural and metapleural stripes that are fused along the entire margins; (3) divergent white spots on abdominal segment 7; (4) male hamules that are straighter (not as curved as a question mark); (5) lack of metepisternal pale stripes; and (6) a dark metallic blue labrum and epicranium, with brown at the rear of the head (Needham et al. 2000).

The abdomen:hindwing length ratio of *B. mendax* has been described as being >1 and that of *B. pertinax* <1. However, in some of our *B. pertinax* specimens, the abdomen is longer than the hindwing, and this characteristic appears to be unreliable.

**RESULTS AND DISCUSSION**

Our inventories yielded 20 adult *Brechmorhoga* specimens from the Grand Canyon region and numerous visual observations across a wide array of habitats in northern Arizona. Specimens are housed in the invertebrate collection of the Museum of Northern Arizona, Flagstaff.

*Brechmorhoga mendax* is reported to be widely distributed on and around the southern Colorado Plateau and the lower Colorado River. Our data reveal that *B. mendax* exists from 110 m to 1460 m elevation in this region and flies from at least 22 April to at least 20 October (Table 1, Fig. 1). This species exists along the Colorado River and its tributaries from Parker, Arizona, north to southern Nevada and northwestern Arizona. It occurs at Warm Springs and along the upper Muddy River (Clark County, NV; U.S. Geological Survey 2003), as well as the lower Virgin River (Utah; Donnelly 2004), both of which are tributaries to the Colorado River. It occurs in Arizona in Mohave County at Tassi Spring in Grand Wash (RM 285) in Lake Mead National Recreation Area. Its range in Grand Canyon extends upstream in Mohave and Coconino Counties, into lower Diamond 2005]
Creek (RM 225) and Spring Canyon (RM 204; and probably the larval specimens identified to genus by Oberlin et al. 1999), and into central Grand Canyon at least to RM 132, but it has not been detected in upper Grand Canyon. We and our colleagues also detected Brechmorhoga mendax in Coconino County along lower Sycamore Creek in Sycamore Canyon Wilderness Area (12 km N of Clarkdale; LES, 9 Sept.) and along Oak Creek up to an elevation of 1450 m (C. Olsen, 14 July; L. Haury, 2 August); Greenlee County along the Blue River (D. Danforth, 20 July); Gila County on the East Verde River northeast of Payson (P. Savacevi, 29 June); and Yavapai County in the Verde River drainage along the southern margin of the Colorado Plateau, from Camp Verde at the Interstate 17 bridge (29 Aug), at elevations of 1000–1050 m (LES). Reports of this species in northeastern Arizona have yet to be substantiated: the only localities in Arizona’s northeastern counties are in drainages that flow southward in the White Mountains in the Salt-Gila River basin.

Brechmorhoga mendax is riparian in its adult stages, rarely straying from the moderately swift-flowing water of small to large streams throughout its range. It patrols relatively large (>50 m long) territories along these often heavily vegetated streams, and it occurs in low densities along the highly regulated Colorado River in Grand Canyon (e.g., RM 132, 600 m elevation; LES, 17 August 2004).

Brechmorhoga pertinax occurs in Central America, and northward to east central Sonora and along the east side of the Sierra Madre Occidental in Mexico. In Grand Canyon this species has been detected at 5 perennial, spring-fed tributaries on the south side of the Colorado River, from RM 81 to RM 95 (all localities in Coconino County) at elevations of 172

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*designates an observation or collection; “0” designates no Brechmorhoga detection; asterisk indicates specimen observed by LES.
850–1150 m (Table 1, Fig. 1). It flies from at least 19 July until at least 21 October, a flight range far longer than the 25 June–3 July previously reported by Needham et al. (2000). Our farthest upstream record in the Colorado River drainage was from East Grapevine Spring on the Tonto Trail (N36.04279°, W112.01381°) at 1120 m elevation. No Brechmorhoga were detected at apparently suitable habitat 5 km east in the Cottonwood Creek drainage, despite intensive collecting efforts there from 2000 to 2003. Brechmorhoga pertinax occurred west of Grapevine Creek in 4 other perennial spring-fed creeks with runout streams >100 m, including Pipe Creek (N36.07316°, W112.10249°), Indian Gardens (N36.08005°, W112.12668°), Monument Creek (N36.06290°, W112.17489°), and Hermit Creek (N36.08207°, W112.21489°). The springs supporting these streams are threatened by regional groundwater extraction on the Coconino Platform, south of Grand Canyon.

The relatively fast-flowing runs and small pools in streams at which B. pertinax was detected are geomorphically and geochemically consistent with descriptions of its larval habitat in Central America (Gutiérrez 1995). The small streams supporting B. pertinax in Grand Canyon were rather similar in flow and water chemistry: flows were typically small, averaging 0.04–19.3 L s\(^{-1}\); mean water temperature ranged from 14.7°C to 18.0°C, except for East Grapevine Spring, which averaged 11.1°C and is more variable; pH varied from 7.5 to 8.4; mean specific conductance ranged from 393 to 1037 µS cm\(^{-1}\); and mean field CaCO\(_3\) varied from 187.5 to 301.7 mg L\(^{-1}\) (J. Rihs, NPS hydrologist, Grand Canyon, written communication). In contrast, the streams supporting B. mendax varied rather widely in flow (up to 4359 L s\(^{-1}\)) and geochemistry (specific conductance may exceed 1120 µS cm\(^{-1}\)).

Although both the larval and adult habitats seem appropriate and sampling has been intensive, Brechmorhoga were not detected at East Boucher Spring or “Erhart Spring” in Boucher Canyon (RM 96), immediately west of Hermit Creek. Also, Brechmorhoga have yet to be detected along north side tributaries of the Colorado River in central and eastern Grand Canyon, including Nankoweap (RM 53), Bright Angel (RM 88), Crystal (RM 98), Shinumo (RM 109), Tapeats (RM 134), Deer (RM 136), or Kanab (RM 143) Creeks, except a visual observation by LES at Stone Creek (RM 132) in August 2004. Water chemistry, climate and flow changes, fidelity of Brechmorhoga to the stream habitats of their larval stages, adult territorial and reproductive behavior (Alcock 1989, Cordoba 1994), sampling effort, and the vagaries of colonization for this rather low-vagility, relatively stenotolerant species may account for its apparently restricted distribution in Grand Canyon.

Biogeographically, Grand Canyon’s aquatic and wetland invertebrate fauna reflects a minor Neotropical influence. With this report, Brechmorhoga pertinax joins the ranks of Ochterus rotundus (Hemiptera: Ochteridae; Polhemus and Polhemus 1976) and Polyplecton (Tripodura) obelos Sublette and Sasa (Diptera: Chironomidae; Sublette et al. 1998) as Neotropical aquatic invertebrates with disjunct ranges extending from Guatemala or southern Mexico into isolated microhabitats in Grand Canyon. The extent and duration of isolation of Grand Canyon B. pertinax from Mexican populations remains to be determined through genetics analyses. However, the persistence of B. pertinax and other rare aquatic and wetland plant and invertebrate populations may be jeopardized by the depletion of deep aquifers and the dewatering of Grand Canyon springs (Grand Canyon Wildlands Council 2002, 2004).

Grand Canyon has been recognized as an important corridor of desert habitat through an otherwise inhospitable, high-elevation landscape, but its biogeographic function as a refuge for isolated or endemic taxa is only recently becoming apparent. The Colorado River and its tributaries serve as a partial range corridor through the high-elevation Colorado Plateau for numerous desert riparian species. The range of B. mendax extends partway upstream through Grand Canyon, a range similar to that of several common desert plant species including Yucca whipplei, Foquieria splendens, Ferocactus cylindraceus, and Larrea tridentata (Phillips et al. 1987). In contrast, B. pertinax populations in the United States appear to be restricted to a few remote spring-fed stream refugia with relatively uniform water quality at slightly higher elevations in central Grand Canyon.

Other Grand Canyon taxa displaying a similar refugial response to this landscape include the following; the previously mentioned, highly
restricted *Octerus rotundus* (Polhemus and Polhemus 1976); endemic McDougall’s flaveria (*Flaveria mc doug allii*), which occupies a few remote springs in middle Grand Canyon (Phillips et al. 1987); endemic *Cicindela hemorrhapica arizonae* Wickham (Coleoptera: Cicindelidae), the range of which almost exactly overlaps that of *B. pertinax* (Stevens and Huber 2004); and endemic Grand Canyon rattlesnakes (*Crotalus viridis abyssus*; Reed and Douglas 2002). The rarity of refugial and endemic taxa has been attributed to Pleistocene-Holocene climate changes and the limited time this region has existed as desert habitat (Stevens and Huber 2004), but this hypothesis may need revision as additional refugial taxa are identified in Grand Canyon. Overall, the discovery of isolated *B. pertinax* populations in Grand Canyon is consistent with an emerging understanding of invertebrate biogeography and conservation issues in this large, deep canyon ecoregion.

ACKNOWLEDGMENTS

This project was partially funded by Grand Canyon Wildlands Council, Inc. and National Park Service Contract WPF-230, through the Arizona Water Protection Fund. We particularly thank John Rihs, NPS hydrologist, for project support. We extend our gratitude to Margaret Erhart, Terry Griswold, Ann Hadley, Loren Haury, Krissy Killoy, Eric North, and Bianca Perla for enthusiastic field assistance during inventories. We thank Sandy Upson and Douglas Danforth for taxonomic advice. Chris Brod (Spatial Science Solutions, LLC) provided invaluable assistance with georeferencing and map preparation. We thank Boris Kondratieff and 2 anonymous reviewers for helpful editorial comments.

LITERATURE CITED


**HAGEN, H.A.** 1861. Synopsis of the Neuroptera of North America, with a list of the South American species. Smithsonian Miscellaneous Collections 4:1–347.


**Received 8 June 2004**

**Accepted 3 November 2004**
Studies that examine cottonwood (Populus spp.) response to increasing soil moisture are important for several reasons. First, cottonwoods are dominant trees of many western intermountain river ecosystems of the United States. Populus angustifolia (narrow leaf cottonwood), P. fremontii (Fremont cottonwood), and their natural hybrids are often described as facultative phreatophytes (Snyder and Williams 2000, Horton et al. 2001a, 2001b, 2003; but see Busch et al. 1992). They are generally restricted to riparian areas where they are the dominant plant species and play a major role in ecosystem processes (Driebe and Whitham 2000, Schweitzer et al. 2004, Fischer et al. 2004). Second, it is important to know how riparian species may respond to altered hydrological patterns induced by global change. For example, many modeling efforts predict increased pulse-event summer rainfall in the southwestern United States (National Assessment Synthesis Team 2002), but knowledge of intermountain and southwestern riparian species responses to these rainfall events is incomplete. Finally, many studies on cottonwood responses to water additions have been conducted in plantations. Results from these studies have been interpreted in the context of implications for silviculture (Marron et al. 2002) rather than in terms of the functioning of native forests (Horton et al. 2001a, 2001b). Understanding how cottonwoods respond to changing water availability is important to conservation and restoration for this threatened habitat (cottonwood riparian forests).

Cottonwoods may alternate water source use between groundwater and surface soil moisture (Smith et al. 1991, 1998, Rood et al. 2003) or act as obligate phreatophytes (Busch et al. 1992) by depending entirely on groundwater. For instance, in the spring, cottonwoods may derive water mostly from near-surface sources and in the summer mostly from deeper groundwater sources (Zhang et al. 1999). Cottonwood response to surface moisture may also be dependent on life history and adaptation to local weather patterns. For example, isotope studies in regions where summer precipitation and soil surface moisture are historically unreliable have found evidence that cottonwoods do not use vadose zone water (i.e., Busch et al. 1992, Horton et al. 2003). Thus, it is unclear whether cottonwoods are able to use water sources when water becomes suddenly available where it was previously scarce.
Cottonwood trees also have highly adaptable root systems and have been documented to show rapid growth in response to changes in water and nutrient availability (Pregitzer and Friend 1996). These rapid responses suggest that these trees may be capable of responding physiologically to short-term surface water additions through the rapid root growth and uptake of surface moisture. If this were the case, we would expect that short-term water additions and intense pulse summer rainfall events (Loik et al. 2004) would quickly stimulate surface fine root regrowth and tree transpiration and would improve tree water status. A short-term response (within 3 weeks) to surface water is important to consider because it is unlikely that a longer response time could have ecologically important consequences for vegetative response to pulse precipitation events (see Loik et al. 2004). Another key study of a facultative phreatophyte found that water uptake from the surface soil occurred only after 4 weeks of a watering treatment (Devitt et al. 1997).

We hypothesized that increasing water availability in the upper reaches of the soil profile during a drought would increase whole-tree water use and plant water status. To address this hypothesis, we posed 3 questions: (1) Do whole-tree water use and canopy conductance respond to water additions in native cottonwood genotypes? (2) Does cottonwood whole-tree physiology vary differently with changes in surface soil moisture versus measured leaf predawn water potentials? (3) What roles do tree architecture and drought-induced leaf loss play in possible mitigation of the negative consequences of low surface soil moisture?

**MATERIALS AND METHODS**

**Study Site**

Our study site is a restored riparian area at the Ogden Nature Center (41°11′N, 111°56′W; elevation 1370 m) in Ogden, Utah. The site receives approximately 440 mm of precipitation annually, with an average of 20.1 mm in August. Along the Weber River drainage, surface soil moisture generally declines from late spring into summer and fall (http://waterdata.usgs.gov/ut/nwis/rt [accessed 21 July 2004]). Soil moisture is at its lowest when temperatures are at their highest. Mean annual air temperature is 10.4°C, and mean daily air temperature is 32.1°C for August (climatic data summaries for Ogden Sugar House Weather Station; http://www.wrcc.dri.edu/summary/climsmlc.html [accessed 21 July 2004]). In August 2002 drought for the area was rated as severe to extreme by the National Drought Mitigation Center (http://www.drought.unl.edu [accessed 21 July 2004]). Between 1 August and 5 September 2002 (the period of this study), 1.0 mm of precipitation (19.1 mm below average for August; see above) fell, and average daytime and daily air temperatures were 24.9°C, and 23.6°C, respectively. However, in previous recent years more significant precipitation had been documented during this period. For example, in 2001 we recorded 7.36 mm of precipitation between 1 August and 5 September (focused [83%] in 2 individual pulse events).

In 1991 cuttings from *P. fremontii*, *P. angustifolia*, and their hybrids were taken from individuals growing along the nearby Weber River. These cuttings were then planted at 4-m spacing at the Ogden Nature Center in a drainage thought to have been historically occupied by cottonwood riparian forests. Cuttings were from trees of known genotype based on previous RFLP work (see Martinsen et al. 2001 for details). Minirhizotron measurements down to a depth of 45 cm in this “restored” forest versus 7 other natural stands along the Weber River do not indicate a difference in fine root growth morphology (data not shown).

**Experimental Watering Treatment**

Measurements of sap flux density of the study trees began on 1 August (day of year [DOY] 214), and experimental watering treatments began on 12 August (DOY 226). Experimental watering treatments were begun after we collected sap flux density data for 12 days, allowing for a baseline sap flux density rate to be established for each study tree. Our study trees consisted of 6 *P. angustifolia*, 4 backcross hybrids, and 2 F1 hybrid genotypes. For each genotype we had 2 tree replicates: one would receive the watering treatment, and the other would serve as the control. Those receiving the treatment were administered extra water via drip irrigation and bucket watering applied to the ground evenly beneath individual tree canopies (see Fig. 1). Treatment trees were clumped together or spatially isolated in an effort to avoid extra water diffusing through
the soil to the root zone of the control trees. Watered trees were at least 50 m from unwatered trees and were separated by a 30-cm-deep trench or a road. Watering treatment continued until the end of the study on 5 September (DOY 248). By this time each treatment tree had received 935 L of water more than each control tree; averaged over the entire period that the irrigation treatment was applied, this amount is equivalent to an increase in water addition of 42.5 L tree⁻¹ d⁻¹. If completely transpired, this would equal about 2 mm d⁻¹ for a tree with a crown area of 20 m² (median for our watered treatment). This transpirational rate could easily occur at our site given that potential evapotranspiration averaged 5.2 mm d⁻¹ ± 0.14 (s) over the study period.

Gravimetric soil water content (105°C, 48 hours) was measured 4 times throughout the course of the study. Measurements were taken once at the beginning of the study, once just before treatment began, once midway through treatment, and once again at the end of the study. Soil samples (0–15 cm depth) were taken within the same area of each tree, 0.5 m north
from the bole using a 1-cm-diameter soil corer. The depth of 15 cm was justified because (1) these are rocky riparian soils in which repeatable deeper measurements are difficult, and (2) root distribution in trenches and minirhizotron measurements suggest that about half of surface roots are in the first 15 cm (data not shown).

Whole-tree Physiology

We measured sap flux and transpiration for each study tree (g H$_2$O m$^{-2}$ sapwood s$^{-1}$) using the Granier sap flux method at the base of the live crown in each study tree from DOY 214 to 248 during 2002 (Granier 1987, Granier and Loustau 1994, Granier et al. 1996, Clearwater et al. 1999). The Granier method uses a heated probe inserted 10 cm above a nonheated probe in the sapwood. Each probe is 2 cm long with a copper constantan wire thermocouple inserted inside at the midpoint. We calculated sap flux density based on the temperature difference between the heated and nonheated probe by Granier’s empirical equation (Granier 1987, Clearwater et al. 1999). Sensors were placed at up to 4 depths (0–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm), depending on the diameter of the tree. In all cases we attempted to measure the entire length of the hydroactive xylem from the bark to the heartwood. Sensors were placed at 1 randomly chosen aspect on each tree to randomize over aspect effects. Data were collected every 30 seconds and averages stored every 15 minutes using a Campbell Scientific CR10X data logger and a Campbell Scientific AM416 multiplexer (Logan, UT). Whole-tree sap flux was calculated by apportioning sap flux density rates from each probe to its corresponding sapwood area and summing data from all sapwood areas. Transpiration was expressed as total daily whole-tree leaf specific transpiration rate (L H$_2$O m$^{-2}$ LA d$^{-1}$), which was calculated by dividing whole-tree sap flux by whole-tree leaf area (LA; see below).

On all trees used for sap flux measurements, we measured predawn and midday plant water potentials with a pressure chamber (PMS Instruments, Corvallis, OR; Ritchie and Hinckley 1975) 5 times during the last 10 days of the study. Predawn values provide an estimate of the soil water potential in the rooting zone of the tree, while midday water potentials provide an estimate of tree water stress (Ritchie and Hinckley 1975, Koide et al. 1990). Measurements were taken on mid-canopy branch tips between 0400 and 0600 hours for predawn water potential estimates ($\Psi$$_{pre}$) and between 1400 and 1600 hours from sun-exposed parts of the tree for midday water potential ($\Psi$$_{mid}$) values. Branches from each tree were measured until 2 measurements within 0.1 MPa were obtained, and these were averaged to obtain a mean value for the tree.

Canopy conductance and whole-tree hydraulic conductance were determined for each study tree. Mean leaf-specific canopy conductance ($G_c$) was calculated over 15-minute periods for each tree with the following model used by Fischer et al. (2002), which substitutes vapor pressure deficit for the difference in water potential between leaf and air (Montieth and Unsworth 1990):

$$G_c = \frac{E_l}{(VPD/A_p)},$$

where $G_c$ is canopy conductance, $E_l$ is leaf specific transpiration rate (L H$_2$O m$^{-2}$ LA s$^{-1}$), VPD is vapor pressure deficit (kPa), and $A_p$ is average atmospheric pressure for the location of the study (~86.1 kPa for our site).

Whole-tree hydraulic conductance was calculated in a manner similar to that of Ryan et al. (2000) and Fischer et al. (2002):

$$K_h = \frac{E_l}{(\Psi_{pre} - \Psi_{mid})},$$

where $K_h$ is whole-tree hydraulic conductance (g H$_2$O m$^{-2}$ s$^{-1}$ MPa$^{-1}$). Calculation of $K_h$ was limited to those dates when water potential was measured.

We determined projected leaf area and sapwood area of each study tree. Leaf area was estimated for all trees using an allometric equation based on branch diameter. We developed the equation by removing 3 branches of 3 size classes from each tree at the end of our study. All leaves were removed, dried (72 hours at 70°C), and weighed. A subsample of 10 leaves from each branch was used to determine specific leaf area (m$^2$ kg$^{-1}$) using an Agvis Imaging System (Decagon Devices, Pullman, WA). To estimate projected leaf area, we multiplied dried leaf weights from each branch by specific leaf area. These data were combined with data from a previous study from other trees at the site (Fischer et al. 2004) to construct a more robust equation for estimation of projected leaf area (cm$^2$) based on the diameters (cm) of removed branches ($R^2 = 0.86, P <$
COTTONWOOD WATER RESPONSE DURING DROUGHT

0.01, leaf area = –32730.66 + 17007.86 * (branch diameter) + 4634.64 * (branch diameter – 3.03)2. This equation was applied to the diameter at the base of the live crown (DBLC) to yield an estimate of projected leaf area for each tree. To evaluate the accuracy of this approach, we compared this branch-based estimate with whole-canopy leaf area estimates measured on other nearby trees; these 2 approaches gave similar values (data not shown). Sapwood area (SA) was estimated using tree-cores for each tree, taken at the same height and aspect as the sap flux sensors (base of the live crown), and visually distinguishing between light-colored sapwood and dark-colored heartwood.

We determined whole-tree leaf loss over the course of the study for each study tree. On DOY 229, before significant drought-induced leaf loss, a litter bucket was placed under the canopy of each tree. At the end of the study, we collected litter in each bucket, dried (72 hours at 70°C) it, and then weighed it. Using the mass of each sample and the specific leaf area values, we calculated leaf area loss. Crown area of each tree was estimated using perpendicular measurements of crown diameter and using the average of the values to calculate crown area. This value was divided by bucket area, and the result was multiplied by leaf area from each bucket to estimate total crown leaf loss during the course of the study.

Air temperature and relative humidity were measured in an open field near the study site using a Campbell Scientific CS500 air temperature and humidity measurement probe (Logan, UT, USA). We collected weather data every 30 seconds and averaged it hourly with a Campbell Scientific CR10X data logger (Logan, UT). We calculated vapor pressure deficit (VPD) from ambient temperature and relative humidity measurements, assuming relative humidity inside the leaves was 100% (Montieth and Unsworth 1990).

All statistical analyses were done with the SAS JMP-IN statistical package (Version 4.0.4, SAS Institute, Cary, NC), with an α of 0.05. Relationships among tree characteristics and physiological and environmental parameters were analyzed using least-squares linear regression. Paired t tests of overall means were used to evaluate irrigation treatment effects on physiological variables; repeated measures analyses of variance (RM ANOVAs) on daily and weekly averages were also used to evaluate irrigation effects.

RESULTS

Mean daily transpiration (\( E_d \)) was similar between watered trees and unwatered trees prior to experimental water additions (\( P = 0.95, \text{Fig. 1A} \)), as was mean daily canopy conductance (\( G_c; P = 0.93; \text{data not shown} \)). Gravimetric soil water content also was similar between watered and unwatered trees prior to the watering treatment (\( P = 0.06; \text{Fig. 1B} \)).

Water addition significantly increased the gravimetric soil water content (\( P = 0.03 \)). During the study period gravimetric soil water content under watered trees increased significantly from 5.9% (+0.41 \( s_{\bar{y}} \)) to 22.7% (+0.98 \( s_{\bar{y}} \); \( P = 0.03 \)) during the same period, gravimetric soil water content among unwatered trees decreased significantly from 7.0% (+0.67 \( s_{\bar{y}} \)) to 6.2% (+0.41 \( s_{\bar{y}} \); \( P = 0.02; \text{Fig. 1B} \)). Although supplemental watering was effective in increasing surface soil moisture, \( E_d (P = 0.47; \text{Fig. 1A}) \), \( G_c (P = 0.84; \text{Fig. 2B} \), and whole tree hydraulic conductance (\( K_h; P = 0.63 \)) were not significantly different between watered and unwatered trees. Both \( \Psi^\text{pre} \) and \( \Psi^\text{mid} \) also were similar between watered and unwatered trees (\( \Psi^\text{pre}; P = 0.83, \Psi^\text{mid}; P = 0.62 \)), with \( \Psi^\text{pre} \) averaging about -0.54 MPa and \( \Psi^\text{mid} \) approximately -1.58 MPa during the measurement period (Fig. 1C).

We found a significant inverse linear relationship between \( \Psi^\text{pre} \) and \( G_c (P = 0.02, r^2 = 0.44; \text{Fig. 2A} \). However, there was no relationship between soil gravimetric water content and \( G_c (P = 0.47; \text{Fig. 2B} \). Similarly, we found a significant inverse relationship between \( \Psi^\text{pre} \) and \( E_d (P = 0.04, r^2 = 0.35; \text{Fig. 2C} \), but there was no significant relationship between gravimetric soil water content and \( E_d (P = 0.34; \text{Fig. 2D} \). Relationships between VPD and \( E_d \) were significant (\( P < 0.05, \text{Fig. 3A} \)) for both watered trees (\( r^2 = 0.33 \)) and unwatered trees (\( r^2 = 0.21 \)), as were relationships between VPD and \( G_c (P < 0.01, r^2 = 0.42 \) [watered] and 0.44 [unwatered]; \text{Fig. 3B} \). Slopes of response curves for \( G_c \) versus VPD relationships had overlapping 95% confidence intervals between watered and unwatered trees and thus were not considered different.

Both \( E_d \) and \( G_c \) were not significantly correlated with either DBLC (\( P = 0.17 \) and 0.20,
respectively) or LA:SA ratios ($P = 0.12$ and $0.18$, respectively; Fig. 4A). Whole-tree hydraulic conductance ($K_h$) was unrelated to DBLC ($P = 0.14$); however, a significant ($P = 0.02, r^2 = 0.43$) inverse power ($y = m * x^{-b}$) relationship was found between $K_h$ and the LA:SA ratio (Fig. 4B). $E_l$ was also related to $K_h$, but this is likely driven by the calculation of $K_h$ (eq. 2).

Supplemental watering had no detectable effect on leaf abscission during drought; percent leaf area lost was similar between watered and unwatered trees ($P = 0.29$; data not shown). Furthermore, we found no significant relationships between percent leaf area lost and $K_h$, $G_c$, or $E_l$ ($P = 0.90, 0.39,$ and $0.53$, respectively). However, leaf area loss was negatively correlated with $\Psi_{pre}$ ($r^2 = 0.37, P = 0.04$), suggesting that low water availability may have led to leaf loss. Study trees lost between $0\%$ and $29\%$ of their leaf area during the course of the study (mean leaf loss = $9\%$, median leaf loss = $4\%$), and leaf area varied from $75.2 \text{ m}^2$ to $505.2 \text{ m}^2$ among study trees (Table 1).

**DISCUSSION**

Previous research has suggested that at certain times of the year cottonwood trees access water from the unsaturated (vadose) zone (i.e., part of the soil profile above the groundwater table and the capillary fringe zone), acting as facultative phreatophytes (Smith et al. 1991, Snyder and Williams 2000). Other research suggests that the principal source of water for tree uptake may shift through a growing season (Zhang et al. 1999), and cottonwood trees are known to have plastic and adaptable root systems (Pregitzer and Friend 1996). However, significant evidence exists to support an alternative hypothesis that cottonwoods exhibit response to surface water commensurate with the climatic history of their region. For example, Busch et al. (1992) did not find evidence of soil moisture uptake at a study site that has historically unreliable summer precipitation patterns, and this suggested phreatophytic behavior. Conversely, Snyder and Williams (2000) found evidence of soil moisture uptake at a study site where summer monsoonal pulse rainfall events are common. Our study site has a historically predictable summer drought, and our results are consistent with this regional climate hypothesis.

Despite (1) successful increases in soil moisture within the upper $15 \text{ cm}$ of soil (Fig. 1), (2) observations that most study trees showed some
signs of water stress (e.g., yellowing of leaf tips and loss of leaves), and (3) environmental conditions conducive to water availability limiting growth (e.g., lack of recent precipitation, high VPD, summer drought), our results indicate that watered trees did not increase their rates of leaf-specific transpiration, canopy conductance, or whole-tree hydraulic conductance relative to trees that did not receive supplemental water (Fig. 2). Averaged over the entire experimental period, watered trees received 42.5 L more water per day than unwatered control trees (Fig. 1). Sap flux measurements scaled to the whole-tree level indicate that both watered and unwatered trees transpired an average of 24.7 L water d⁻¹. Hence, water additions should have been more than enough to stimulate transpiration rates that were low compared with other studies (Zhang et al. 1999, Schaeffer et al. 2000, Nagler et al. 2003). Similarly, canopy conductance was relatively low in all trees over our study period (e.g., Zhang et al. 1999, Horton 2005)
et al. 2001a; but see Fischer et al. 2004), but hydraulic conductance was not exceptionally low compared with other angiosperms (Becker et al. 1999). Dickmann et al. (1994) also found no difference in net photosynthesis rates between irrigated and nonirrigated cottonwood saplings, and our results are consistent with responses of *Populus* clones to a 40% reduction in soil moisture in a study by Braatne et al. (1992). We conclude that during the height of summer drought, any uptake of increased soil moisture was insufficient to influence important physiological variables such as hydraulic conductance, canopy conductance, or transpiration. This may be consistent with factors other than water limiting both photosynthesis and, by default, water use as has been found in at least 1 other species in our region (Snyder et al. 2004).

We speculate there are several other possible explanations for the lack of response to water additions in our study trees. First, greater loss of leaf area in unwatered trees relative to watered trees may have partially compensated for lower water availability to the trees, reducing any differences in leaf-specific transpiration rates. However, we found no difference in leaf area loss between watered and unwatered trees, suggesting that this potential mechanism cannot account for the lack of physiological response of the cottonwood trees to water additions.

Second, xylem dysfunction in the roots of study trees might have impaired uptake of water supplied to the trees by irrigation treatments. Cottonwoods are mostly drought intolerant, limited to riparian corridors, and dependent on groundwater, and they typically have

### Table 1. Selected characteristics of trees monitored in this study. Clone codes serve as markers for individual genotypes but otherwise have no relation to cross type. Cross types are A (*Populus angustifolia*), B (backcross hybrids), and F₁ (F₁ hybrids).

<table>
<thead>
<tr>
<th>Clone</th>
<th>Status</th>
<th>Diameter at base of live crown (cm)</th>
<th>Cross type</th>
<th>Leaf area (m²)</th>
<th>Sapwood area (cm²)</th>
<th>Leaf area: sapwood area (m² cm⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>wc-5</td>
<td>Unwatered</td>
<td>13.9</td>
<td>A</td>
<td>75.2</td>
<td>149.1</td>
<td>0.50</td>
</tr>
<tr>
<td>wc-5</td>
<td>Watered</td>
<td>17.6</td>
<td>A</td>
<td>125.1</td>
<td>167.5</td>
<td>0.75</td>
</tr>
<tr>
<td>1008</td>
<td>Unwatered</td>
<td>21.3</td>
<td>A</td>
<td>187.7</td>
<td>203</td>
<td>0.92</td>
</tr>
<tr>
<td>1008</td>
<td>Watered</td>
<td>16.4</td>
<td>A</td>
<td>107.5</td>
<td>105.6</td>
<td>1.02</td>
</tr>
<tr>
<td>t-15</td>
<td>Unwatered</td>
<td>19.3</td>
<td>A</td>
<td>152.3</td>
<td>161.8</td>
<td>0.91</td>
</tr>
<tr>
<td>t-15</td>
<td>Watered</td>
<td>20.5</td>
<td>A</td>
<td>173.1</td>
<td>173</td>
<td>1.00</td>
</tr>
<tr>
<td>996</td>
<td>Unwatered</td>
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<td>B</td>
<td>210.7</td>
<td>225.9</td>
<td>0.93</td>
</tr>
<tr>
<td>996</td>
<td>Watered</td>
<td>17.7</td>
<td>B</td>
<td>126.6</td>
<td>105.8</td>
<td>1.20</td>
</tr>
<tr>
<td>11</td>
<td>Unwatered</td>
<td>18.3</td>
<td>B</td>
<td>136</td>
<td>90.9</td>
<td>1.36</td>
</tr>
<tr>
<td>11</td>
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<td>B</td>
<td>218.7</td>
<td>221.7</td>
<td>0.99</td>
</tr>
<tr>
<td>1994</td>
<td>Unwatered</td>
<td>34.2</td>
<td>F₁</td>
<td>505.2</td>
<td>704.9</td>
<td>0.72</td>
</tr>
<tr>
<td>1994</td>
<td>Watered</td>
<td>30.7</td>
<td>F₁</td>
<td>403.8</td>
<td>775.2</td>
<td>0.52</td>
</tr>
</tbody>
</table>

Fig. 4. Architectural controls of whole-tree physiology; A, leaf-specific transpiration (Eₐ) versus leaf area to sapwood area ratio (LA:SA); B, whole-tree hydraulic conductance (Kₕ) versus LA:SA.
high vulnerability to cavitation (Blake et al. 1996). On day 245 of the study, $\Psi_{\text{mid}}$ of study trees averaged $-2.0$ MPa (Fig. 1); this value corresponds to approximately a 70% loss of hydraulic conductivity in stems due to xylem embolism according to one $P$ angustifolia vulnerability curve (Tyree et al. 1994), and potentially 100% loss in some tissues according to Blake et al. (1996). Because we did not assess the origin of the water transpired by trees in our current study, we cannot conclude unequivocally that they did not take up surface soil moisture. However, since $\Psi_{\text{mid}}$ values indicate high levels of stem xylem embolism (but see Blake et al. 1996) and since roots are more susceptible to xylem embolism than stems (Sperry and Saliendra 1994, Hacke and Sauter 1996, Sperry and Ikeda 1997), it is probable that xylem dysfunction occurred during our study period. If significant xylem dysfunction did occur in surface roots, and if embolism repair in cavitated roots was too slow to reestablish function, then this might account for the lack of physiological response in cottonwoods to the irrigation treatment in our study.

Finally, it is possible that our irrigation treatments, which lasted 3 weeks, may not have been long enough to elicit a physiological response. For instance, Devitt et al. (1997) found a physiological response to surface irrigation in trees from arid environments after 4 weeks. However, given that sporadic pulse precipitation events are common and short-lived in the region (Loik et al. 2004), it is unlikely that a 4-week response time to increased surface moisture is ecologically meaningful unless early precipitation events are harbingers of prolonged wet periods. Thus, a lack of response within the time frame used in our study may be ecologically equivalent to a lack of response.

This lack of responsiveness in cottonwoods to surface water additions may reflect an evolutionary constraint on soil water uptake due to a long regional history of low summer precipitation in northern Utah. For example, lack of significant response to soil moisture may be a successful carbon allocation strategy of cottonwoods. The timing of our irrigation treatments corresponded with a period of seasonally dry soils, when infrequent rains only temporarily elevate soil moisture. A long-term evolutionary response, maximizing carbon allocation and limiting unnecessary growth (i.e., easily cavitated root tissues; Sperry and Saliendra 1994, Hacke and Sauter 1996, Sperry and Ikeda, 1997), may avoid xylem embolism repair in such tissues during seasonal drought periods. This level of genetic specificity would not be surprising given the extensive documented genetic variation in cottonwood water-stress tolerance, root growth, and water use (Tschanpilinski and Blake 1989a, 1989b, Blake et al. 1996, Pregitzer and Friend 1996, Fischer et al. 2004). When surface soil moisture levels are more consistently high, whole-tree response to soil moisture increases may be more common.

We found a significant relationship between average daily $E_l$ and $\Psi_{\text{pre}}$, and average daily $G_c$ and $\Psi_{\text{pre}}$. However, in both cases the relationship was opposite of our hypothesized relationship; both $E_l$ and $G_c$ decreased rather than increased with increasing $\Psi_{\text{pre}}$ values (Fig. 2). This pattern may be partially due to the high transpiration rates of some cottonwood trees and their poor stomatal regulation (Stettler et al. 1996, Fischer et al. 2004); the relatively high transpiration rates may have led to progressively poor whole-plant water status (as measured by lower $\Psi_{\text{pre}}$ values), reflecting that some cottonwood trees seem to operate with a small margin of safety from cavitation events (Blake et al. 1996). Furthermore, these statistically significant negative correlations may be somewhat spurious given that they were fairly weak ($r^2 = 0.35$ and 0.44, respectively) and occurred over a fairly narrow range of $\Psi_{\text{pre}}$ values ($-0.45$ to $-0.65$ MPa).

Our results suggest that, while some species may show strong physiologic responses to pulse increases in soil moisture (Donovan and Ehleringer 1994, Cui and Caldwell 1997; also see Ogle and Reynolds 2004, Schwining and Sala 2004), some cottonwood trees may exhibit little immediate physiological response to increases in soil moisture from precipitation events. This lack of response may be related to a water-use strategy associated with regional climate patterns, cavitation recovery, or other physical determinants of water use such as depth to groundwater. Cottonwood riparian forests represent some of the most biologically productive ecosystems in the West, and our data suggest that it is important to consider potential nonresponsiveness to changes in soil water availability when evaluating the impact of climate change on these important and productive ecosystems.
ACKNOWLEDGMENTS

We thank the Ogden Nature Center for supporting our common garden facilities and the Mill Creek Youth Center juvenile detention facility for helping logistically. We thank National Science Foundation grant DEB-0078280 and a Research Experience for Undergraduates award under NSF grant DEB-0078280 for financial support. We also thank Nathan Lojewski, Kevin Simonin, Gina Wimp, Jen Schweitzer, Tom Kolb, A.J. Thompson, and the Hart and Whitham laboratories for field assistance, consultation, and providing comments on earlier versions of the manuscript. Finally, we thank R.W. Baumann and 2 anonymous reviewers for thoughtful reviews of this manuscript.

LITERATURE CITED


Received 12 January 2004
Accepted 14 September 2004
LAND SNAIL DIVERSITY IN WIND CAVE NATIONAL PARK, SOUTH DAKOTA

Tamara K. Anderson

ABSTRACT.—Eighty-two soil samples and additional hand-collection in Wind Cave National Park yielded over 2000 terrestrial gastropod specimens. The specimens represent 26 different species, including a South Dakota species of concern, *Vertigo arthuri*. New South Dakota state records for *Gastrocopta pellucida* and *Vertigo tridentata* were recorded. Samples from grassland habitats were less likely to contain snails and had lower species richness than samples from either forest or shrubland habitats. Canyons, creek beds, bases of limestone cliffs, and shrublands are important habitats for snails in the park.

Key words: land snails, South Dakota, national parks, gastropod, diversity.

Pilsbry (1948:978) commented that “the molluscan fauna of the upper Missouri valley still remains almost unknown.” More than 50 years later, only a limited number of general works have been issued on terrestrial mollusks in the Great Plains (see Leonard 1959, and portions of Burch 1962, Hubricht 1985). In 1985, Hubricht still included South Dakota as one of the states most in need of snail surveys. Indeed, for the northern Great Plains, more questions remain than have been answered on molluscan diversity, distribution, taxonomy, and natural variation. The lack of information makes management and conservation efforts difficult. Although conservation priorities for land snails can be set using museum records alone (Heller and Safriel 1995), if few museum records exist for a region (such as the Black Hills), the priorities will be less reliable. The National Park Service’s Resource Challenge Initiative emphasizes the need to inventory natural resources in the national parks to better manage these resources (NPS 2000).

The purpose of this study was to survey land snail species at Wind Cave National Park (hereafter referred to as WCNP). A survey of snails in WCNP has not been conducted previously, although surveys have been conducted elsewhere in South Dakota (Henderson 1927, Jones 1932, Over 1942, Roscoe 1954, 1955), including other parts of the Black Hills (Frest and Johannes 2002, Jass et al. 2002). I sampled land snails in many WCNP vegetation communities. Strong relationships between snails and vegetation communities have long been recognized (i.e., Shimek 1930, Burch 1956). Vegetation provides food and shelter for snails, and the structure and density of the vegetation determine thermal and moisture conditions for soil-dwelling species. This study provides information on land snail richness, distribution, and local habitat relationships in WCNP that may help improve land snail habitat conservation.

STUDY AREA

The Black Hills is a unique area biologically and geologically (Froiland 1999). It is 900 m to 1200 m higher than the surrounding Great Plains, and the area was not glaciated during the Pleistocene. The Black Hills also serves as a biological nexus where eastern, western, northern, and southern ranges of many organisms meet. A description of the wide variety of vegetation communities in the Black Hills can be found in Larson and Johnson (1999). Wind Cave National Park (WCNP) is located at the southern end of the Black Hills in southwestern South Dakota (Fig. 1). Famous for its underground wonders as home to the 6th largest cave in the world, WCNP also includes 11,454 ha of aboveground habitats, ranging from mixed grasslands to ponderosa pine (*Pinus ponderosa*) stands, to canyons in limestone and sandstone.
Materials and Methods

Fieldwork was conducted in May and June 2002. Points for soil sampling were located in 27 different vegetation types (Table 1; as defined by park vegetation surveys and satellite mapping research of Cogan et al. 1999) to maximize the potential diversity of snails found. Three locations distributed around the park in each habitat type were sampled where possible. Specific locations of samples within these vegetation types were selected on the ground to maximize richness per sample. Maximizing richness by selecting likely microhabitats has been used successfully in other studies (Emberton et al. 1996, Nekola 1999). In this study I took samples from moist areas with good litter cover or small, rocky debris, if such areas were available within the vegetation type. When vegetation types did not contain such microhabitats, I selected the sample location that was most representative of that vegetation type.

GPS locations (UTM coordinates, WGS 1984 Datum) of the sampling sites were recorded using Garmin (GPS 12XL) and Trimble (Geo-Explorer 3, version 1.04) units. GPS locations

Fig. 1. Species richness varied across WCNP. Several locations (especially canyons/creekbeds) had high richness levels.
were used to create maps with ArcView software (version 8.2; ESRI 2001). At each sampling location, 3.8 L of soil and litter was collected from within a 0.25-m² quadrat. Soils were sifted through a sieve series (Newark and Hubbard brands), from 4 mm (#5 mesh size) to 0.25 mm (#60). Soil from each sieve layer was visually searched and any snails or shells were removed. Individual shells were examined under a microscope, counted, and identified to species where possible. In several samples, shells were broken or immature and could not be positively identified.

Additional locations along watersheds were searched visually for snails. At 6 of these locations, I also took canyon/creekbed soil samples for analysis. Two soil samples were also taken in a prairie dog (Cynomys ludovicianus) town after a prairie dog researcher reported finding shells in soil prairie dogs kicked out of their burrows.

The many different individual vegetation classes with few samples did not allow a robust analysis of vegetation versus snail presence. Therefore vegetation classes were grouped into general habitat categories: grassland, shrubland, and forest. These general habitat categories were used to determine if a relationship existed between snail species richness or abundance among habitats.

**RESULTS**

I collected 82 soil samples, of which 59 contained snails and/or shells. An additional 6 areas were spot-searched for snails, and snails were found at 2 of these areas (Dry Creek and Cold Brook Canyon). Over 2000 whole and broken shells were examined, with 1738 identified to species. Live specimens were found at only 6 locations. Twenty-six different species were identified (Table 2). Specimens have been deposited at the Field Museum of Natural History in Chicago.

**Species Descriptions**

Identification of most species was fairly straightforward using Pilsbry (1946, 1948) and Burch (1962). Because live specimens were
not available for most species (see below for discussion of the lack of living specimens), shell characters alone were used for identification. Scientific names from this study follow Turgeon et al. (1998). A few points to note on the identifications are explored here.

**CATINELLA.**—Specimens in the genus Catinella were not assigned to species level. Succineids (including Catinella, Oxyloma, and Succinea) have few shell characteristics that can be used for identification purposes. The specimens in this study were assigned to the genus Catinella based on work by Burch (1962:67) that describes Catinella with a "shell relatively small, generally 11 mm or less in length, dull; spire long, almost as long as the shell aperture." Frest and Johannes (2002:70) state that "shell characters of Catinella gelida are sufficiently distinctive as to make it unlikely to be confused with other described North American succineids." In contrast, others have cautioned against the use of shell characters alone in assigning succineids to species (Burch 1962, Hoagland and Davis 1987). Since no living specimens of Catinella were found, the WCNP samples could not confidently be assigned to a particular species.

**COLUMELLA.**—Specimens tended to be cylindrical as is the Columella columella alticola pictured in Jass et al. (2002), and they are therefore identified as such. The only Columella species Frest and Johannes (2002) identified was C. simplex, which narrows at the top of the shell. It remains unclear whether the 2 species reside in different portions of the Black Hills, or if the WCNP specimens show different variation in shape than the Frest and Johannes (2002) specimens.

**GASTROCOPTA.**—Several Gastrocopta species were identified. All except Gastrocopta pellucida had been reported previously from South Dakota. Gastrocopta pellucida is distinguished from other Gastrocopta by its narrow diameter, tooth structure, and thin lip (Pilsbry 1948, 1951).

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<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>Number of sites</th>
<th>Average per site</th>
<th>Habitat types (F,S,C)</th>
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<tr>
<td>Catinella sp.</td>
<td>13</td>
<td>3</td>
<td>F,S,C</td>
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<tr>
<td>Cionella lubrica (glossy pillar)</td>
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<td>4</td>
<td>F</td>
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<td>Columella columella alticola (mellow column)</td>
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<td>3</td>
<td>F</td>
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<tr>
<td>Deroceras laeve (meadow slug)</td>
<td>2</td>
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<td>Discus catskillensis (angular disc)</td>
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<td>3</td>
<td>F</td>
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<td>Discus echinatus (forest disc)</td>
<td>5</td>
<td>8</td>
<td>F,C</td>
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<td>Gastrocopta annifer (armed snaggletooth)</td>
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<td>6</td>
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<td>Papoidea albilabris (white-lip dagger)</td>
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<td>Striatulanulla (fine-ribbed striate)</td>
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<td>Vallonia gracilicosta (multirib vallonia)</td>
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<td>Vallonia pulchella (lovely vallonia)</td>
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<td>Vertigo tridentata (honey vertigo)</td>
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<td>Vitrina alaskana</td>
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<tr>
<td>Zonitoides arboreus (quick gloss)</td>
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*No common name is listed in Turgeon et al. (1998).

*Turgeon et al. (1998) list Vitrina pellucida as the “western glass-snail.” However, Pilsbry (1946) considered South Dakota specimens to be V. alaskana, and that convention is followed here.*
The previously reported range included Florida west to California with reports as far north as Colorado and isolated locations in New Jersey and Maryland (Pilsbry 1948, Burch 1962, Hubricht 1985).

**PUPILLA.**—Two of the *Pupilla* species identified in this study, *P. hebes* and *P. muscorum*, were also found by Jass et al. (2002). The 3rd, *P. blandi*, was the only *Pupilla* found by Frest and Johannes (2002). Further analysis is needed to determine whether these species are restricted to different portions of the Black Hills.

**VALLONIA.**—The main shell characteristics used to define differences in *Vallonia* species include shell diameter, umbilicus diameter, and number of ribs on the shell (see Burch 1962). However, the specimens from this survey did not neatly fit in the defined categories, generally having rib numbers within the range for multiple species. Frest and Johannes (2002) include 3 ribbed *Vallonia* species—*V. gracilicosta*, *V. cyclophorella*, and *V. perspectiva*—in their report from the Black Hills. However, a recent revision of the genus *Vallonia*, which includes specimens from all over the world, found considerable variability within Rocky Mountain populations of *V. gracilicosta* (Gerber 1996). For the purposes of this study, larger specimens (>2 mm) were considered *V. gracilicosta*, while smaller specimens (<2 mm).

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### Table 3. Comparison of WCNP gastropod species found in studies from the Black Hills and western South Dakota.

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<td><em>Arion fasciatus</em></td>
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<td><em>Carychium exiguum</em></td>
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<td><em>Deroceras laeve</em></td>
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<td><em>Discus catskillensis</em></td>
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<td><em>Pupilla blandi</em></td>
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<td><em>Pupilla hebes</em></td>
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190 WES TERN NORTH AMERICAN NATURALIST [Volume 65
were considered *V. parvula*. These assignments follow Burch (1962), but a more conservative assignment would be to consider all *Vallonia* specimens as *V. gracilicosta*.

*Vallonia* *pulchella* has no ribs and so should be easy to distinguish from other *Vallonia*. However, in the current study, ribs on a few older *Vallonia* specimens were wearing off, which could result in worn shells being incorrectly identified. In this study specimens with no sign of ribs were considered to be *V. pulchella*.

**VERTIGO.**—Two *Vertigo* species were found: *V. arthuri* and *V. tridentata*. These species are differentiated by the number and position of the teeth (Pilsbry 1948). *Vertigo arthuri* is a species whose distribution is not fully understood. Originally it was recognized only from North Dakota (Pilsbry 1948). It had been previously identified in the Black Hills by Freist and Johannes (2002) and has been recently reported by Nekola (2002) from upper Midwest locations.

*Vertigo tridentata*, with only 3 teeth, was not previously reported from South Dakota. The previously recognized range for *V. tridentata* stretched from Maine south to Tennessee in the east and Minnesota south to Texas in the west (Pilsbry 1948, Burch 1962, Hubricht 1985).

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**TABLE 3. Continued.**

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\(^{\text{a}}\)These studies report species from areas of eastern South Dakota as well.

\(^{\text{b}}\)The identity of Over’s (1942) *Pulita hammonis* is unclear. *Pulita* was a former name for Oxychilus, but the only *hammonis* in the Zonitinae recorded in Pilsbry is a species of *Neocassida*. Over (1942) may have been referring to *Neocassida electrina* or *N. binneyana*.

\(^{\text{c}}\)Frest and Johannes refer to their specimens as *Choclicopa lubricella*. *Choclicopa* is considered a synonym of *Cionella* (Pilsbry 1948, Turgeon et al. 1998). Turgeon et al. (1998) state that *C. lubrica* is the only species found in North America. Hubricht (1985) recognizes both species, but offers no distinction between them. For the purposes of this table, they are considered the same entity.

\(^{\text{d}}\)Only *Vitrina pellucida* is recognized by Turgeon et al. (1998). Other sources mention only *V. alaskana* in the western U.S. (Hubricht 1985). Pilsbry (1946:502) states that *V. alaskana* is distinct from the European *V. pellucida*. 

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2005] _LAND SNAILS OF WIND CAVE NATIONAL PARK_ 191
Richness and Habitat Characteristics

Individual soil samples contained from 0 to 210 shells. WCNP contains 35% of the land snail diversity known for western South Dakota (Table 3). On average, samples with snails contained 29 individuals of 3 different species. Sixty-three samples from WCNP contained 3 or fewer species. Common species dominated the samples, with just 5 species (Vallonia gracilicosta, Gastrocopta holzingeri, Nesovitrea binneyana, Vallonia parvula, and Euconulus fulvus) accounting for 75% of the individuals identified.

Snail shells were found in at least 1 sample from all surveyed vegetation types except purple three-awn/fetid marigold herbaceous community and redbeds (silt/sandstone) with sparse vegetation. Chi-square analyses showed that general habitat categories (forest, grassland, shrubland) were significantly different in the number of sites where snails were present. Samples from grassland habitats were more likely to contain no snails.

Species richness also varied across the landscape (Fig. 1), but the highest levels appear centered along creek beds in canyons. Species richness was also lower in grassland habitats than in either forests or shrubland habitats.

A few species were associated with a particular habitat category or categories. Table 2 shows associations between snail species and their preferred habitats. Cionella lubrica and Columella columella alticola were found only in forested habitat. Deroceras laeve was found only in canyons or along creek beds. Nesovitrea binneyana was more abundant in forests than in either grasslands or shrublands, although it was present in all habitats. Gastrocopta armifera was equally abundant in shrublands and forests. Other species tested showed no difference in abundance among habitat types.

Discussion

Comparison of Species List with Other Studies

The species found in this study are similar to those found in other studies in the region (i.e., Over 1942, Roscoe 1954, 1955, Frest and Johannes 2002, Jass et al. 2002; Table 3). Two species reported here, Gastrocopta pellucida and Vertigo tridentata, were not reported in earlier studies. Both were rare in WCNP, with only a single location each.

Notably absent from WCNP are specimens of Oreohelix. Although fairly common on shaded talus slopes in more northern areas of the Black Hills, Oreohelix becomes less frequent in the central and southern areas of the Black Hills (Frest and Johannes 2002). Jass et al. (2002) also did not find any evidence of Oreohelix in their study, which included the extreme southern Black Hills. The southern extent of the Black Hills differs in soil type, geology, moisture, and number of deciduous trees (Froiland 1999). Any or all of these factors may contribute to slight differences in snail communities.

The South Dakota Department of Game, Fish and Parks includes 5 gastropods among their rare species: Vertigo arthuri, Vertigo paradoxus, Discus shimekii, Catinella gelida, and Oreohelix strigosa cooperi (SDDGFP 2001). Vertigo arthuri was found in WCNP. The Catinella specimens found here may be C. gelida but cannot be confidently assigned to species without analysis of internal anatomy. The other 3 species were not found in WCNP, although they have been reported elsewhere in the Black Hills (Frest and Johannes 2002).

Species Richness

A previous Black Hills study reported 0 to 17 species per site with an average of 4.3 when only sites with snails present were included (Frest and Johannes 2002). A few species (Discus whitneyi, Zonitoides arboreus, Euconulus fulvus, Nesovitrea binneyana, and Vitrina pellucida) also dominated Frest and Johannes’s (2002) study. Their reported dominance is based on occurrence, not abundance, since they did not count all individuals. Nevertheless, the frequency of D. whitneyi, Z. arboreus, and V. pellucida is interesting since these species were relatively rare at WCNP. This may be attributable to site selection because Frest and James (2002) focused on moister habitats and talus slopes, which are rare in WCNP, rather than more evenly sampling across all vegetation types.

Species richness in the Black Hills is not unlike results from Beetle’s (1997) study in Yellowstone aspen stands, which reported 3 to 5 snails per stand. These stands were studied after a wildfire burned the area. Richness increased to 11 species in a “damp site . . . [with]
favorable litter, soil, and moisture” (Beetle 1997:8).

Studies from other regions have reported even higher levels of species richness. In Wisconsin, 1-m² quadrats averaged 6.6 species (Nekola and Smith 1999). A study including sites across the Great Lakes region found 11% of samples contained 24 or more species (Nekola 1999). These observed richness numbers are far below the 61 species ⋅ km⁻² reported from a tropical rainforest in Malaysian Borneo (Schilthuizen and Rutjes 2001). Emberton (1995) reported that the highest diversity of terrestrial gastropods in the United States was 44 species in <4 ha found by Leslie Hubricht in the mountains of Kentucky. Coniferous forests and grasslands are expected to have lower diversities of land snails than other habitat types (Solem 1984).

Observed numbers per sample (Table 2) are also lower than in other studies. Van Es and Boag (1981) found an average of 11.6 Vitrina alaskana, 48.9 Discus whitneyi, and 27.3 Euconulus fulvus per sample. It is not clear whether their litter samples from 0.5-m² areas in size represent the same volume of soil as in the WCNP study. Because their study also occurred in a forest in Alberta with abundant deciduous trees (Populus spp.), it is expected that more snails would be present.

Few Living Specimens

The low number of living specimens collected in WCNP cannot be easily explained. Frest and Johannes (2002) do not indicate what percentage of their findings were alive but suggest that living snails were commonly observed. Emberton et al. (1996) found soil samples had fewer live samples than other sampling methods, but they reported living representatives of 28% of snail species in soil samples.

One potential explanation for the low number of live specimens is a possible die-off of snails. One of the main factors in snail death is dessication (Solem 1984). Snail populations may fluctuate with environmental stress, and since WCNP has been under drought conditions for the past few years, it is likely many snails have died. Another explanation is that shells collected are only remains from a time period when the habitat was more suitable for snails. Pearce (2002, personal communication) found that shells in eastern forests exist in the soil about 30 years before completely decaying. Shells in the drier climates of the Great Plains likely persist slightly longer, but even so, shells recovered in this study must represent snails that were alive within the recent past. A 3rd explanation is that during these unfavorable drought conditions, snails in WCNP have sought refuge in areas not sampled. Unfortunately, these hypotheses cannot be tested with the available data.

Size of Specimens

Several species of WCNP land snails were smaller in size than reported in previous descriptions. Cionella lubrica was 2.8 mm tall and had only 4 whorls although they are listed in Pilsbry (1948) as being 5–6.5 mm and having 5.5 to 6 whors. Vitrina alaskana specimens ranged from 2.3 mm to 3.8 mm in diameter, although Pilsbry (1946) described them as 5 mm or larger. WCNP snails were only slightly smaller than those in Alberta aspen/poplar forests (Van Es and Boag 1981). For example, their Vitrina alaskana specimens averaged 4.35 mm (n = 152). Pilsbry (1948:932) discussed a small form of Papilla blandi east of the Rocky Mountains, adding that “it is probably a ‘hunger form’ occupying arid situations.” Since this phenomenon was observed in several species, WCNP may not be optimal for maximizing growth.

Habitat Type

Seven generalist species (Euconulus fulvus, Gastrocopta holzingeri, Hawaiia minuscula, Pupilla muscorum, Pupoides albilabris, Vallonia gracilicosta, and Vallonia parvula) were found in all habitats (Table 2), while other species were more specialized. For example, Deroceras laeve was found only in canyon/creek bed areas. Cionella lubrica and Columella columella were only in forest habitat. Nesovitrea binneyana was more abundant in forested habitat. Gastrocopta pellucida was found only at 1 site in shrubland. Nesovitrea electrina, Striatura milium, and Pupilla hebes were also only at 1 location. Discus catskillensis may prefer forested habitat, although it was also found in a wetland sample. Some shrubland areas were also important snail habitats at WCNP. Six of the 12 samples from mountain mahogany (Cercocarpus montanus), chokecherry (Prunus virginiana), and creeping juniper (Juniperus horizontalis) sites had species richnesses of 5 or higher.
No species were found only in grasslands, in contrast to the ordination analyses of Nekola (2003) that showed many snail species, including several found at WCNP (Cochlicopa lubrica, Discus whitneyi, Nesovitrea electrina, Gastrocopta armifera, Gastrocopta procera, Pupilla muscorum, Pupoides albilabris, Vallonia parvula, and Vallonia pulchella) appeared to be grassland specialists. Nekola incorporated more samples across a much larger spatial scale which gives his results more credence. However, because the grasslands of the Great Lakes region of Nekola’s study are moister than the arid region of western South Dakota, those grasslands may be able to support more species. Nekola apparently did not sample shrubland, which may have influenced the preferences shown at WCNP.

Earlier studies questioned whether snails occupy coniferous forests in western North America. Karlin’s (1961) surveys across Montana, Colorado, and New Mexico reported that 99% of snails occurred within forests where deciduous trees were a significant component. Kralka (1986) also found most snail species preferred areas dominated by deciduous vegetation in Alberta, Canada. He did note that Vertigo gouldi preferred coniferous habitats. WCNP data and those of Frest and Johannes (2002) contradict those findings, since most WCNP forest sites are dominated by ponderosa pine. Locaciulli and Boag (1987) also found the highest densities of snails in coniferous forests in Alberta. Although the most diverse (12 species) location in WCNP was a stand of bur oak, Quercus macrocarpa, a cliff site dominated by ponderosa pine had 7 species. Carbonate cliffs and canyons often provide important habitats for snails (Beetle 1989, Nekola and Smith 1999). Two samples along Dry Creek contained over 300 individuals and 11 species total. In WCNP these areas tend to have calcareous soils (Ensz 1990, Ford 2002).

**Conclusions**

WCNP supports a relatively high diversity of land snails, with 35% of the regional species represented. Recent droughts have probably affected snail populations in the park, based on the large number of empty shells found in this study. Riparian areas (especially Dry Creek and Cold Creek), shrubland, and limestone cliffs are especially important for WCNP snail diversity and should be managed with care.

**Acknowledgments**

This project was funded by NPS Contract P1505020021. Collection permits were obtained from NPS (WICA-2002-SCI-0028) and South Dakota (License 33). Special thanks go to Barb Muenchau of WCNP. Ed Delaney formerly of WCNP and Jochen Gerber of the Field Museum of Natural History.

**Literature Cited**


ESRI. 2001. ArcView 8.2. ESRI, Redlands, CA


Hubricht, L. 1985. The distributions of the native land mollusks of the eastern United States. Fieldiana
Zoology No. 24, Field Museum of Natural History, Chicago, IL.


SDDGFP. 2001. Rare, threatened, and endangered animal species tracked by the South Dakota Natural Heritage Program. South Dakota Department of Game, Fish and Parks. www.state.sd.us/gfp/Diversity/RareAnimal.htm.


Received 23 April 2003
Accepted 4 October 2004
Nest predation on eggs and nestlings profoundly affects reproductive success of birds and is considered the primary cause of nest failure in most land birds (Ricklefs 1969, Rotenberry and Wiens 1989, Major et al. 1994, Martin 1995). Birds have evolved numerous defenses to reduce predation risk, and studies have shown increased rates of nest predation to be associated with habitat fragmentation, nest location within a patch, and nest type (Donovan et al. 1995, Robinson et al. 1995, Dion et al. 2000, Flaspohler et al. 2001, Manolis et al. 2002). In the desert Southwest nest construction of most passerine nests can be divided into 3 categories: open-cup ground nests such as Horned Larks (Eremophila alpestris) and Eastern Meadowlarks (Sturnella magna), open-cup shrub nests within 3 m of the ground such as Black-throated Sparrows (Amphispiza bilineata), and Cactus Wrens (Campylorhynchus brunneicapillus), were placed in 10 grasslands of tobosa (Pleuraphis mutica) and black grama (Bouteloua eripoda) with low and heavy levels of mesquite encroachment. Nest predation varied among nest types, grassland types, and shrub encroachment, with highest levels of predation occurring on open-cup shrub nests in tobosa grasslands with heavy shrub encroachment. We detected a significant interaction between nest type and shrub encroachment, but not between grassland type and nest type or grassland type and shrub encroachment. Combined predation rates from the 3 nest types were positively associated with shrub density. The encroachment of shrubs into desert grasslands may act as a corridor for a diversity of species historically not associated with desert grasslands to occupy or move through a patch, increasing vulnerability to nest predation.

In the Chihuahuan Desert grasslands, the transformation of desert grasslands to a shrub-dominated system in the Chihuahuan Desert has been an ongoing process over the past 150 years. This desertification of the landscape has been primarily attributed to the introduction of domestic livestock to the region in the late 1800s combined with periodic drought (Buffington and Herbel 1965, Fredrickson et al. 1998, Kerley and Whitford 2000). Former open grasslands dominated by black grama (Bouteloua eripoda) and tobosa (Pleuraphis mutica), the 2 grassland types diagnostic of Chihuahuan Desert grasslands, are being replaced by shrubs, primarily honey mesquite (Prosopis glandulosa) and creosote bush (Larrea tridentata). For example, on the USDA Jornada Long Term Experimental Range (LTER) in southern New Mexico, plots with >90% grass cover in the 1950s had <25% grass cover by 1963 (Buffington and Herbel 1965).

The system-level response to these landscape-scale changes has not been thoroughly investigated. Whitford (1997) found that species richness, diversity, and abundance of birds and small mammals were higher in desertified sites. He attributed this to grassland species persisting while shrub-adapted species colonized these sites. Pidgeon et al. (2001) found avian diversity was highest in mesquite-dominated plots compared to black grama grasslands and...
2 other shrub community types. While similarities were apparent among communities, they found that 30% of the avifauna was unique to each of the 4 vegetation communities. They suggest shrub encroachment has resulted in a major turnover in the avifauna of the region. In addition to these observed shifts in avian and mammalian species composition, Kerley and Whitford (2000) report that rodents have replaced ants as the primary granivore in the Chihuahuan Desert.

Shifts in ecosystem structure and function will have long-term consequences on survival and reproduction of associated fauna. We were particularly interested in the effects of this shift on nest predation in birds. Many species of small mammals and birds are nest predators, and the higher diversity and abundance of these taxa in desertified sites in the southwestern United States may contribute to a shift in the role of predation on avian nests in this system. We hypothesized nest predation in tobosa and black grama grassland patches would not differ between patch type but would differ between high and low levels of shrub encroachment, with higher rates of predation in shrub-encroached sites. We hypothesized that predation rates and types of predators would differ among the 3 nest types due to variability in detection. We predicted predation rates would be highest for open-cup ground nests and lowest for spherical shrub nests due to differences in accessibility and concealment from predators. Spherical shrub nests have greater concealment of nest contents than open-cup nest types, and others have suggested open-cup ground nests experience higher rates of predation in grassland systems (Martin 1993a). We predicted small mammals would be the primary predator on ground nests, whereas avian predators would be the primary predator for both types of shrub nests.

**STUDY AREA**

Research was conducted during summer 2003 on the USDA Jornada LTER, located 30 miles north of Las Cruces, New Mexico. This area is primarily a mosaic of black grama, tobosa, and dropseed (Sporobolus spp.) grasslands in various stages of desertification, including heavy mesquite encroachment and coppice dune formation. Other dominant vegetation includes three-awns (Aristida spp.), burrograss (Scleropogon brevifolius), fluffgrass (Dasyochloa pulchela), snakeweed (Gutierrezia spp.), creosote bush (Larrea tridentata), tarbush (Flourensia cernua), soaptree and torrey yucca (Yucca elata and Y. torreyi), and cane cholla (Opuntia imbricata). Annual precipitation averages 23 cm but can be variable, and most rainfall comes in the form of monsoonal summer rains between July and September (Brown 1982).

**METHODS**

We selected 10 grassland patches from the Jornada LTER’s GIS database of cover types based on 3 criteria: dominant grassland type (black grama or tobosa), size of the grassland patch, and level of shrub encroachment. We attempted to select an even number of open and shrub-encroached tobosa and black grama grasslands and to avoid complications due to grassland patch size. With one exception (19 ha) all grassland patches were >40 ha (19–522 ha), and all transects were located centrally within each patch to avoid edge effects. The center of each grassland patch was selected from the GIS database, its coordinates determined, and a 1050-m transect was established using the center of the plot as the transect center.

Artificial nests were placed in patches beginning 28 June and monitored every 4 days over a 12-day period, mimicking the incubation period of most passerines (Davison and Bollinger 2000, Dion et al. 2000). Data collection was completed by 13 July. In the desert Southwest peak nesting is timed with the monsoonal rains (Mendez 2000, Agudelo and Desmond unpublished data), which typically arrive in mid-July. Three types of artificial nests were used in this study: open-cup ground nests, open-cup shrub nests, and spherical (enclosed) shrub nests. We constructed open-cup ground nests by creating a small scrape within a grass clump and lining the scrape with live and dead grass to mimic the natural nest of an Eastern Meadowlark. Open-cup shrub nests and spherical shrub nests were commercial finch and canary nests constructed of wicker and hemp, respectively. Open-cup shrub nests were lined with dead grass to mimic the natural nest of a Black-throated Sparrow, and spherical shrub nests were lined with dead grass and covered with natural vegetation, small sticks, and forbs to mimic the natural nest of a Cactus Wren. These
nests were placed in shrubs 1–2 m from the ground. Commercial canary nests, constructed of hemp, were stained to achieve a more natural color and along with finch nests were left outside for a week prior to use in this study to take on a natural odor. Attempts were made to mimic the design and placement of natural nests such that artificial nests would not be more conspicuous to a visual predator (Martin 1987, 1995).

Twenty-one nests, spaced 50 m apart, were placed within each grassland patch at alternating distances of 18 m from the transect line or to the nearest appropriate shrub or grass patch. We alternated nest types and recorded their coordinates with a GPS unit. Two eggs were placed within each nest, a Japanese Quail (Coturnix coturnix) egg and an artificial egg. Artificial eggs were constructed from a non-hardening modeling clay, permoplast, and were modeled to mimic quail eggs. Nests were considered predated if the quail egg was missing or damaged or the nest destroyed (Dion et al. 2000). Clay eggs were used to determine predator type and not rates of predation (Davison and Bollinger 2000, Part and Wretenberg 2002).

To determine predator type when a quail egg was damaged or destroyed, we analyzed the clay eggs. Marks left on clay eggs were compared to the dentition of native species, and these nest predators were divided into broad categories, including small mammals, larger mammals, avian, and snakes. Avian predators are typically thought to leave a single narrow hole in the egg or an obvious beak mark. A destroyed nest site or teeth and claw marks in the clay eggs are generally considered mammalian predation. Snakes leave the nest site undisturbed or may create a hole in the nest bottom, removing the quail egg but leaving no marks on clay eggs (Davison and Bollinger 2000, Dion et al. 2000, Pietz and Granfors 2000). We handled all nests, nest material, and eggs using latex gloves, and our boots were washed upon arrival at each study site.

We counted all shrubs along a 1000 × 3-m transect in the center of each plot. These shrub counts were used as a relative index of shrub encroachment within each patch and were used to classify sites as relatively open or shrub encroached.

We tested whether predation rates differed as a function of grassland type (black grama vs. tobosa), shrub encroachment (high vs. low), and nest type (open-cup ground, open-cup shrub, or spherical shrub) using a 3-way analysis of variance. Rates of predation among nests placed in cholla, mesquite, and yucca shrubs were examined using a 1-way analysis of variance for spherical and open-cup shrub nests combined. Simple linear regression was used to examine the association between predation rate and shrub density.

**Results**

Of 210 nests placed in Chihuahuan Desert grasslands, 89 (39%) were lost to predation. Rates of predation varied among nest types \( (F_{2,18} = 4.77, P = 0.022) \), with significantly higher predation on open-cup shrub nests; 60% of open-cup shrub nests, 41% of spherical shrub nests, and 16% of open-cup ground nests were lost to predators throughout the study (Table 1). Predation also varied between grassland types \( (F_{1,18} = 7.94, P = 0.011; \) Table 1) with significantly higher rates of predation on tobosa grasslands. Grassland patches were divided into 4 open and 6 shrub-encroached sites based on shrub counts within 3000-m² transects; sites with low shrub encroachment had 26–94 shrubs per transect (\( \leq 313 \) shrubs \( \cdot \) ha\(^{-1}\)) compared to 156–282 shrubs per transect (520–940 shrubs \( \cdot \) ha\(^{-1}\)) at high encroached sites. A detectable difference was found in nest predation between grassland patches with high and low shrub encroachment \( (F_{1,18} = 8.63, P = 0.009; \) Table 1), with significantly higher predation on the high shrub-encroached sites. A significant interaction was detected between nest type and shrub encroachment \( (F_{2,18} = 3.65, P = 0.047) \). No interactions were detected between nest type and grassland type, shrub encroachment and grassland type, or among all 3 variables \( (P > 0.05) \). Rates of predation did not differ among nests located in cholla, mesquite, and yucca shrubs \( (P > 0.05; \) Table 2). Overall, predation was found to increase linearly with the number of shrubs \( (R^{2} = 0.47, df = 9, P = 0.028) \).

Determination of nest predators using permoplast eggs was difficult to confirm, and no strong quantitative determination could be made. Avian predators appeared to be the most common predator, followed by mammals and possibly snakes. However, 28% of the permoplast eggs analyzed could not be grouped into a predator category.
DISCUSSION

Predation rates did vary between the 2 grassland types, with higher predation in tobosa-dominated grasslands. This is contrary to our prediction and was likely related to several factors that could not be controlled in our site selection. Although no differences were detected in rates of predation among shrub types, rates of predation were lower for yuccas compared with mesquite and cholla, and this shrub type occurred almost exclusively in black grama grasslands. The predominance of cholla and mesquite in tobosa grasslands and mesquite and yucca in black grama grasslands may have contributed to a cumulative difference in predation rates among grassland types. Although we attempted to control for grassland size, 2 of our tobosa grassland patches were <50 ha (19 and 42), and all shrub nests within each of these 2 patches were destroyed by predators, suggesting patch size may influence predation rates within desert grasslands. However, the limited number of plots and the distribution of shrub types among plots prevented a thorough investigation of the interaction of shrub and grassland type and the effect of patch size.

Contrary to our prediction, nests in shrubs were more vulnerable to predation than open-cup ground nests. This was particularly true for open-cup shrub nests, which appeared more vulnerable to visual predators. Visual cues for locating nests seemed important; most predators leaving marks on permoplast eggs left marks consistent with avian predators. However, recent studies using video cameras have concluded that identification of specific predators based on sign left at the nest can be misleading (Pietz and Granfors 2000, Thompson and Burhans 2003). Specifically, snakes will sometimes leave a hole in the bottom of the nest, and contrary to common belief, large mammals will often leave the nest site undisturbed (Pietz and Granfors 2000, Thompson and Burhans 2003). Open-cup ground nests appeared to be better concealed and more difficult for predators to locate regardless of the level of shrub encroachment. This agrees with Vander Haegen et al. (2000), who found a positive relationship between patch size and predation rates for shrub-nesting species such as Sage Thrashers and Brewer’s Sparrows but no relationship for the ground-nesting Vesper Sparrow. However, Davison and Bollinger (2000) found no difference in predation rates between ground and elevated nests in Conservation Reserve Program grasslands in Illinois.

Several studies (Major and Kendal 1996, Part and Wretenberg 2002) using artificial nests to measure vulnerability of nest predation have cautioned that rates of predation differ between

<table>
<thead>
<tr>
<th>Nest type</th>
<th>Grassland type</th>
<th>Shrub encroachment</th>
<th>Predation rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>O.C. ground (7)</td>
<td>Black grama</td>
<td>Low</td>
<td>0.14</td>
</tr>
<tr>
<td>O.C. ground (21)</td>
<td>Black grama</td>
<td>High</td>
<td>0.09</td>
</tr>
<tr>
<td>O.C. ground (21)</td>
<td>Tobosa</td>
<td>Low</td>
<td>0.24</td>
</tr>
<tr>
<td>O.C. ground (21)</td>
<td>Tobosa</td>
<td>High</td>
<td>0.14</td>
</tr>
<tr>
<td>O.C. shrub (7)</td>
<td>Black grama</td>
<td>Low</td>
<td>0.14</td>
</tr>
<tr>
<td>O.C. shrub (21)</td>
<td>Black grama</td>
<td>High</td>
<td>0.48</td>
</tr>
<tr>
<td>O.C. shrub (21)</td>
<td>Tobosa</td>
<td>Low</td>
<td>0.48</td>
</tr>
<tr>
<td>O.C. shrub (21)</td>
<td>Tobosa</td>
<td>High</td>
<td>1.00</td>
</tr>
<tr>
<td>Spherical shrub (7)</td>
<td>Black grama</td>
<td>Low</td>
<td>0.00</td>
</tr>
<tr>
<td>Spherical shrub (21)</td>
<td>Black grama</td>
<td>High</td>
<td>0.29</td>
</tr>
<tr>
<td>Spherical shrub (21)</td>
<td>Tobosa</td>
<td>Low</td>
<td>0.14</td>
</tr>
<tr>
<td>Spherical shrub (21)</td>
<td>Tobosa</td>
<td>High</td>
<td>0.86</td>
</tr>
</tbody>
</table>

### Table 2

Rates of nest predation of artificial nests in southern New Mexico in relation to shrub type. Fourteen nests are not included in this table because they were placed in other shrub types including creosote bush, tarbush, ephedra, and acacia spp.

<table>
<thead>
<tr>
<th>Nest substrate</th>
<th>N</th>
<th>Predation rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesquite</td>
<td>61</td>
<td>0.58</td>
</tr>
<tr>
<td>Cholla</td>
<td>39</td>
<td>0.50</td>
</tr>
<tr>
<td>Yucca</td>
<td>26</td>
<td>0.37</td>
</tr>
<tr>
<td>Ground</td>
<td>70</td>
<td>0.14</td>
</tr>
</tbody>
</table>
real and artificial nests because they are perceived differently by predators. Activity of adult birds at the nest site may attract predators (Roper and Goldstein 1997), or differential search modes among predator types such as olfactory versus visual cues may result in differential rates of predation (Major and Kendal 1995, Martin 1993b). Relative rates of predation on artificial nests can, however, be compared among patch types and nest types and are useful for identifying vulnerability to predation and potential predators (Sieving et al. 1998, Dion et al. 2000). Davison and Bollinger (2000) found similar rates of predation between real and artificial nests in grasslands in Illinois when artificial nests more closely mimicked natural nests. In this study it appears that the combination of shrub encroachment and search behavior likely interacted to increase rates of nest predation. However, the significant interaction detected between shrub encroachment and nest type and the positive association of predation with shrub density indicate that shrub encroachment may be a major factor affecting predation on nests in this habitat.

More traditional studies of fragmentation, with clearly defined edges, have demonstrated that forest or grassland fragmentation contributes to increased rates of predation and brood parasitism (Flaspholer et al. 2001, Manolis et al. 2002). In this study the encroachment of shrubs into grassland patches is a form of fragmentation, but the ecotone between the 2 habitat types is less clearly defined. The increased presence of shrubs throughout grassland patches in the desert Southwest may act as a corridor for a diversity of species historically not associated with desert grasslands to occupy or move through the patch. Other studies have reported higher abundance and diversity of small mammals and birds in desertified sites (Whitford 1997, Pidgeon et al. 2001). Many birds and small mammals are recognized egg predators and likely contributed to higher rates of predation in mesquite-encroached grasslands.

Several factors may account for the higher rates of nest predation observed in desertified sites. As part of the desertification process, there has been a decline in the cover of perennial grasslands and a change in the spatial distribution of vegetative cover from a homogeneous distribution to a spatially clumped or heterogeneous distribution (Buffington and Herbel 1965, Neilson 1986, Schlesinger et al. 1990). Desertified sites may be easier for predators to search because of the clumped distribution of resource patches. The higher avian and mammalian diversity observed in desertified sites (Whitford 1997, Kerley and Whitford 2000, Pidgeon et al. 2001) may support a higher abundance of predators as well as a spatially clumped distribution of potential prey sources. Predators may concentrate in desertified areas because they are easier to search and have a higher density of prey including nesting birds. To confirm these results, we recommend that this experiment be repeated on natural nests within open and shrub-encroached Chihuahuan Desert grasslands.

**ACKNOWLEDGMENTS**

We are particularly grateful to the staff at the Jornada LTER, including B. Nolan, E. Fredrickson, E. Garcia, and G. Yao for access and assistance in location of study plots. D. Ginter and C. Turner assisted with data collection. This study was supported by funds from the International Arid Lands Consortium, New Mexico State University, and the National Science Foundation–funded ADVANCE Institutional Transformation Program at New Mexico State University, Fund #NSF 0123690. This is a contribution to the New Mexico State University, College of Agriculture and Home Economics, Agricultural Experiment Station.

**LITERATURE CITED**


Received 30 January 2004
Accepted 14 June 2004
Descriptive studies have been conducted on squamate reproduction in many different environments of Mexico, such as temperate high elevation (Guillette 1982, Ramírez-Bautista et al. 1998, 2002), tropical rain forest (Benabib 1994), and tropical dry forest (Ramírez-Bautista and Vitt 1997, 1998, Lemos-Espinal et al. 1999), but very few studies have been conducted in tropical arid habitats (Ramírez-Bautista 2003). These studies have provided data to allow contextualization of the reproductive patterns in each environment. For example, reproduction of many lizard species from seasonal tropical and temperate environments is cyclical (Guillette 1982, Ramírez-Bautista and Vitt 1997), with courtship, mating, and copulation occurring at the onset of the rainy season (Ramírez-Bautista and Vitt 1997). Egg production and incubation usually occur at the onset of the rainy season, with hatchlings emerging at the end of the rainy season (Ramírez-Bautista and Vitt 1998). Seasonal reproductive activity has been associated with rainfall, temperature, and photoperiod (Marion 1982, Ramírez-Bautista et al. 1998).

Variation in reproductive characteristics within and among populations also is associated with seasonal and annual environmental fluctuations (Ballinger 1977, Benabib 1994). Environmental factors such as food availability, precipitation, and temperature can affect growth rates, survivorship, clutch size, clutch frequency, and age and size at maturity (Ballinger 1977, Dunham 1982, Benabib 1994). During the past 2 decades, studies have shown that a portion of life history variation among species is historical (Dunham and Miles 1985, Vitt 1992). That is, related species tend to be more similar in life history characteristics than unrelated ones (Miles and Dunham 1992, Valdéz-González and Ramírez-Bautista 2002). For example, SVL at sexual maturity, clutch and egg size, and clutch frequency in the genus Sceloporus are more similar within species than between species.

ABSTRACT.—We studied the reproductive characteristics of 2 syntopic lizard species, Sceloporus gadoviae and Sceloporus jalapae (Phrynosomatidae). Specimens of S. gadoviae (N = 105) and S. jalapae (N = 41) were collected in a tropical arid forest from Tehuacán Valley, Puebla, México. Males of S. gadoviae reached sexual maturity at the same snout-vent length (SVL; 45.0 mm) as S. jalapae, and a similar pattern occurred in females of both species (SVL; 41.0 and 42.0 mm, respectively). Males of S. gadoviae exhibited reproductive activity throughout the year, with a longer activity during the dry (November to May) and part of the wet season (June to September). In contrast, reproductive activity in S. jalapae males occurred during the wet season (July to September). Females of S. gadoviae showed continuous reproduction, whereas females of S. jalapae exhibited seasonal reproduction. Mean SVL of sexually mature females was higher for S. gadoviae (x̄ ± sx= 50.4 ± 0.52) than for S. jalapae (46.0 ± 0.54, P < 0.0001). Mean clutch size for S. gadoviae was lower (3.9 ± 0.14 eggs) than for S. jalapae (5.6 ± 0.43). There was no significant correlation between snout-vent length of females and clutch size of S. gadoviae (r² = 0.22, P > 0.05) or S. jalapae (r² = 0.48, P > 0.05). Our study suggests that although both species inhabit the same environment, they have different reproductive characteristics.

Key words: Sceloporus gadoviae, Sceloporus jalapae, Mexico, reproductive cycle, clutch size, Reptilia, Sauria, Phrynosomatidae.

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groups (scalaris, spinosus, torquatus) than between them (Valdés-González and Ramírez-Bautista 2002). However, many of the data used in these conclusions were based on lizard species of small and medium size from the wet tropics and temperate regions (Guillette 1982, Benabib 1994, Ramírez-Bautista et al. 2002).

At present, few studies exist on reproductive patterns from tropical arid lizards (Ramírez-Bautista 2003). Thus, one might suspect that the often extreme seasonality of temperate regions could result in reproductive cycles and patterns different from those that might be observed in tropical arid environments (Tinkle et al. 1970).

Although the life histories of several species of Sceloporus have been intensively studied (Benabib 1994, Valdés-González and Ramírez-Bautista 2002), little has been published on reproductive characteristics of the Mexican endemic species Sceloporus gadoviae and S. jalapae from Tehuacán Valley, Puebla, México (Ramírez-Bautista 2003). Sceloporus gadoviae belongs to the gadoviae group, and S. jalapae to the jalapae group (Wiens and Reeder 1997).

In this study we focused on male and female reproductive characteristics of the small-sized lizard species S. gadoviae and S. jalapae. We addressed the following questions: (1) Do males and females become sexually mature at the same size? (2) Do males and females differ in morphological traits? (3) What is the annual reproductive cycle for these species? (4) How large are their clutches? (5) Is clutch size related to female size? (6) Are reproductive characteristics of both species similar to other populations and other spiny lizards of similar body size? This study adds to a growing body of data for groups of species that have been relatively underrepresented in large comparative studies.

**MATERIALS AND METHODS**

This study was conducted at Tehuacán Valley, Puebla, near Zapotitlán Salinas, México (18°07’18”N, 97°39’06”W) at an elevation of 1420 m. The climate is dry and temperate, with most precipitation occurring during the summer months (June–September); the dry season is from November to May. Mean annual temperature is 21°C (range 17°–24°C), and precipitation is 450 mm (García 1981). Dominant vegetation consists of thorn forest, xerophytic brushland, deciduous tropical forest, and columnar cacti (Dávila et al. 1993).

We collected data for S. gadoviae (72 females and 33 males) and S. jalapae (24 females and 17 males) from January to December, except March and April (for S. gadoviae) and January, April, June, October, and December (for S. jalapae) during the period 1999–2002. Because samples were often small for individual months and varied considerably among years, we pooled the data to describe general annual reproductive characteristics. We measured snout-vent length (SVL) of the lizards to the nearest 1.0 mm, after which they were sacrificed and fixed with 10% formalin and subjected to gonadal examination.

During the gonadal examination of females, we counted the number of vitellogenic follicles or oviductal eggs and recorded the length and width of left and right vitellogenic follicles or freshly ovulated eggs to the nearest 0.1 mm. Length and width of the gonads were used to obtain follicular and egg volume (V) using the formula for volume of an ellipsoid (Selby 1965):

\[ V = \frac{4}{3} \pi a^2 b, \]

where \( a \) is half the shortest diameter and \( b \) is half the longest diameter. The smallest female (considering SVL) with either the largest vitellogenic follicles or oviductal eggs was used to estimate minimum size at maturity. Clutch size was determined by counting eggs in the oviduct or vitellogenic follicles of adult females during the reproductive season (Ramírez-Bautista et al. 2000, 2002). We calculated a Pearson’s product-moment correlation coefficient to test for a relationship between clutch size and SVL of females.

Males were recorded as sexually mature if they contained enlarged testes and convoluted epidymides typically associated with sperm production (Goldberg and Lowe 1966). Data on lizard SVL and organ volume were transformed to log (base 10) for linearized regressions. Because organ volume usually varies with SVL, we first calculated regressions of log10-transformed organ volume data against log10 of female SVL. For regressions that were significant (indicating a body size effect), we calculated residuals from the relationship of organ volume to SVL (all variables log10-transformed) to produce SVL-adjusted variables.
We used these residuals to describe the organ volume and reproductive cycles (for S. gadoviae). This technique maintains variation because of extrinsic factors while minimizing the confounding effect of individual variation in SVL (Valdés-González and Ramírez-Bautista 2002). We performed 1-way ANOVA on the organ volumes (with month as the factor) to determine whether significant monthly variation existed, including only those months for which $N \geq 3$ (Ramírez-Bautista et al. 2000).

Variables used to test sexual size differences were snout-vent length (SVL, mm), head length (HL, mm), forearm length (FL, mm), and tibia length (TL, mm) of females and males. Residuals of SVL regressions were calculated for these morphological variables. We then used these residuals to examine sexual size differences between mature males and females, and performed a Mann-Whitney $U$-test on HL, FL, and TL. We used a cutoff of $P < 0.05$ to assess statistical significance. Results are expressed as untransformed mean ± s.e. Statistical analyses were performed with StatView IV (Abacus Concepts 1992). Specimens are deposited at the Colección Nacional de Anfibios y Reptiles (CNAR), Universidad Nacional Autónoma de México in México City.

**RESULTS**

**Body Size and Sexual Maturity**

In S. gadoviae sexually mature males ranged in size from 45.0 to 73.0 mm SVL, and females ranged from 41.0 to 67.0 mm SVL, whereas the range in S. jalapae was 45.0–62.0 mm SVL and 42.0–50.0 mm SVL, respectively (Table 1). Males of both S. gadoviae ($Z = -4.75$, $P < 0.0001$) and S. jalapae (Mann-Whitney $U$ test, $Z = -2.70$, $P = 0.001$) were larger in SVL than females (Table 2). Mean SVL of females was higher in S. gadoviae than in S. jalapae females ($Z = -4.89$, $P < 0.0001$), and the males exhibited a similar pattern ($Z = -3.84$, $P < 0.0001$). Males of S. gadoviae also had larger HL ($Z = -5.25$, $P < 0.0001$), FL ($Z = -4.85$, $P < 0.0001$), and TL ($Z = -4.19$, $P < 0.0001$) than females (Table 2), and the same pattern was observed in S. jalapae for HL ($Z = -4.38$, $P < 0.0001$), FL ($Z = -4.16$, $P < 0.0001$), and TL ($Z = -4.49$, $P < 0.0001$).

**Male Reproductive Cycle**

There were significant positive relationships between male log$_{10}$ SVL and log$_{10}$ testes volume ($r^2 = 0.65$, $F_{1,31} = 55.7$, $P < 0.0001$, $N = 33$), log$_{10}$ fat body mass ($r^2 = 0.13$, $F_{1,31} = 4.32$, $P < 0.05$), and log$_{10}$ liver mass ($r^2 = 0.29$, $P < 0.001$) in S. gadoviae. In contrast, in S. jalapae there were no relationships between male log$_{10}$ SVL and log$_{10}$ testes volume ($F_{1,15} = 0.125$, $P > 0.05$) or log$_{10}$ fat body mass ($F_{1,12} = 0.462$, $P > 0.05$), but there was a significant positive relationship between male log$_{10}$ SVL and log$_{10}$ liver mass ($F_{1,11} = 36.53$, $P < 0.0001$). ANOVAs on the residuals of these regressions revealed significant variation among months in testes volume ($F_{9,23} = 2.35$, $P < 0.05$), but not in fat body mass ($F_{9,23} = 0.759$, $P > 0.05$) or liver mass ($F_{9,18} = 0.655$, $P > 0.05$) for S. gadoviae (Fig. 1). For S. jalapae, variation was not significant among months for testes volume ($F_{3,13} = 2.55$, $P > 0.05$), fat body mass ($F_{1,13} = 1.55$, $P > 0.05$), or liver mass ($F_{3,9} = 1.78$, $P > 0.05$). In S. gadoviae, testicular volume increased from January through July and again in October, November, and December (Fig. 1). In contrast, testicular volume in S. jalapae increased in July ($\bar{x} = 14.0 \pm 4.4$ mm$^3$), August ($\bar{x} = 20.6 \pm 4.3$ mm$^3$), and September ($\bar{x} = 34.2 \pm 11.5$ mm$^3$).

**Female Reproductive Cycle**

There was a significant linear relationship between female log$_{10}$ SVL and log$_{10}$ gonadal volume ($r^2 = 0.21$, $F_{1,69} = 16.0$, $P < 0.0005$), log$_{10}$ fat body mass ($r^2 = 0.11$, $F_{1,69} = 5.69$, $P < 0.005$), and log$_{10}$ liver mass ($r^2 = 0.23$, $F_{1,67} = 3.75$, $P < 0.05$) in S. gadoviae, but not in S. jalapae ($r^2 = 0.07$, $r^2 = 0.13$, $r^2 = 0.06$, all $P > 0.05$, respectively). ANOVAs on residuals of these regressions revealed significant variation among months on gonadal volume ($F_{10,60} = 4.32$, $P < 0.0001$), fat body mass ($F_{10,60} = 8.81$, $P < 0.0001$), and liver mass ($F_{10,58} = 2.55$, $P < 0.05$) in S. gadoviae (Fig. 2). In contrast, in S. jalapae only gonad volume varied significantly among months ($F_{6,15} = 3.25$, $P < 0.05$).

*Sceloporus gadoviae* females have continuous reproduction. The average female gonadal volume began to increase in October and continued until July of the following year; volume then decreased from July to October (Fig. 2). In contrast, reproductive activity in *S. jalapae*
seems to be seasonal; gonadal volume increased in May ($\bar{x} = 24.2 \pm 2.3 \text{ mm}^3$), July ($\bar{x} = 92.5 \pm 53.5 \text{ mm}^3$), August ($\bar{x} = 157.0 \pm 15.8 \text{ mm}^3$), and September ($\bar{x} = 109.6 \pm 52.1 \text{ mm}^3$) in females with vitellogenic follicles or oviductal eggs. Females of *S. gadoviae* were found with oviductal eggs from January to December, but with a maximum egg production from May to September. In contrast, females of *S. jalapae* were found with vitellogenic follicles and oviductal eggs from March to September.

### Clutch Size

Mean clutch size of vitellogenic follicles of *S. gadoviae* was not different from that of oviductal eggs ($Z = -1.42, P > 0.05$; Table 1). Considering both egg classes, mean clutch size was $3.9 \pm 0.11$ eggs (range 2–5, $N = 35$; Table 1). In contrast, in *S. jalapae* females the mean clutch size of vitellogenic follicles was different from that of oviductal eggs ($Z = -2.69, P = 0.005$; Table 1). Clutch size was higher in *S. jalapae* than in *S. gadoviae* ($Z = -3.35, P < 0.005$). Clutch size was not related to female SVL in *S. gadoviae* ($r^2 = 0.22, F_{1,33} = 1.67, P > 0.05$) nor in *S. jalapae* ($r^2 = 0.48, F_{1,4} = 0.90, P > 0.05$). However, total egg mass in females was significantly correlated with female SVL in *S. gadoviae* ($r^2 = 0.69, F_{1,19} = 17.1, P < 0.001$) and *S. jalapae* ($r^2 = 0.72, F_{1,9} = 8.81, P < 0.01$). Three of 21 *S. gadoviae* females (14.3%) had both vitellogenic follicles and oviductal eggs at the same time, suggesting that females of this species might lay 2 or more clutches during the reproductive season, but this was not the case with females of *S. jalapae*. Egg production for *S. gadoviae* occurred throughout the year, but the peak was from May to September, while the peak for *S. jalapae* was from July to September.

The volume of vitellogenic follicles of *S. gadoviae* was different from that of oviductal eggs ($Z = -5.18, P < 0.0001$); a similar pattern was observed for *S. jalapae* ($Z = -2.78, P < 0.005$; Table 1).

### Discussion

Sceloporus gadoviae and *S. jalapae* males reached sexual maturity at the same size, and both species showed sexual dimorphism, whereby males were larger than females. This is common among other species of the genus Sceloporus (Fitch 1978, Benabib 1994, Ramírez-Bautista and Gutiérrez-Mayén 2003). Males of
both species were larger in other morphological structures (HL, FL, TL). Sexual dimorphism in *S. gadoviae* and *S. jalapae*, as in other species of the genus, may be a response of sexual selection, with larger males having an advantage over smaller ones in obtaining mates (Fitch 1981, Stamps 1983, Shine 1989). Sexual selection can help maintain large body size in male lizards if larger males mate more frequently than smaller ones. During the reproductive season (July–August), larger males of both species were observed on cactus (*S. jalapae*) and on rocks (*S. gadoviae*), exhibiting their bright ventral region to smaller males and driving the smaller individuals from their areas as occurs in other lizard species (Trivers 1976, Ruby 1981).

The reproductive cycles of *S. gadoviae* and *S. jalapae* differ in timing and duration. The male reproductive period of *S. gadoviae* was during the dry (November to May) and wet (June to September) seasons. In contrast, males
of *S. jalapae* showed a seasonal reproductive period during the wet season (July to September). These data suggest that both species have different reproductive requirements, even though they inhabit the same area. *Sceloporus jalapae* seems to be responding to the environmental factors of the wet season as shown by other species inhabiting tropical dry forest (Ramírez-Bautista and Vitt 1997, 1998). Male and female reproductive cycles in *S. jalapae* appear to be synchronized because females showed vitellogenic follicles and oviductal eggs from May to September; this pattern is similar to other oviparous lizard species inhabiting arid environments (Jones and Ballinger 1987, Smith et al. 1995).

Reproductive cycles for both sexes of *S. gadoviae* are synchronized from January to December. In *S. gadoviae* the longer reproductive season, larger clutch size, larger oviductal egg volume, and smaller mean SVL of sexually mature adult females than other populations of the same species could be influenced by contrasting conditions of precipitation (450 vs. 730 mm), altitude (1420 vs. 600 m), and temperature (21°C vs. 27.8°C) in the Tehuacán Valley and Cañón del Zopilote (Lemos-Espinal et al. 1999). Another difference associated with the longer reproductive season is that individual females may lay 2 or more clutches rather than a single clutch as occurs in other small-bodied species (Ramírez-Bautista et al. 1995).

Differences in the reproductive characteristics between *S. gadoviae* and *S. jalapae*, such as reproductive period, snout-vent length of adults, mean number of vitellogenic follicles, clutch size, and oviductal egg volume, suggest that each species is responding to a different way to environmental cues. Differences in reproductive characteristics between both species could reflect their phylogenetic distance (different groups) and the microhabitat used by each species (Miles and Dunham 1992). Resources such as food abundance are strongly correlated with precipitation in several environments, and variation in resource abundance in turn is related to variations in reproductive characteristics in many lizard species (Ballinger 1977, Benabib 1994, Ramírez-Bautista and Vitt 1997, 1998). This could be the case for the populations of *S. gadoviae* because both females and males are larger at sexual maturity (mean SVL) than *S. jalapae* of either sex. The variation in body size of females of both species could result from a demographic response that may influence clutch size and egg size or volume as in other species (Dunham 1982, Benabib 1994, Ramírez-Bautista and Vitt 1997, 1998) and congeners (Ramírez-Bautista et al. 2002, Valdés-González and Ramírez-Bautista 2002).

The smaller clutch size and the larger egg volume for *S. gadoviae* compared with *S. jalapae* might be considered a reproductive strategy because production of several clutches of small size might subject offspring to excessive predation. The larger egg volume in *S. gadoviae* results in hatchlings with a larger SVL (25.0 mm) than the smaller egg volume clutches of *S. jalapae* (SVL = 23.0 mm). These data show that *S. gadoviae* females have smaller clutch sizes, laying 2 or more clutches during the reproductive season, but the hatchlings are larger in SVL than hatchlings of *S. jalapae* females from a single egg clutch. This pattern is similar to other small-bodied species with multiple egg clutches (Benabib 1994, Ramírez-Bautista and Vitt 1998).

Although both species belong to the Phrynosomatidae family, if the difference in clutch size between the 2 species does not reflect their phylogeny, it might be a response to different environmental pressure. Most small-bodied species of this family have multiple egg clutches of small size. However, exceptions exist such as in *S. siniferus* (5.0 eggs; Fitch 1978), *S. pyrocephalus* (5.8 eggs; Ramírez-Bautista and Oliver-Beccerril 2004), and *S. jalapae* (5.6 eggs; this study) with a single egg clutch. Although clutch sizes differ between both species, *S. jalapae* is closer to species of smaller clutch size than to other large-bodied species (Valdés-González and Ramírez-Bautista 2002). The variation among populations of the same or different species of this family (Phrynosomatidae) could reflect either adaptive differences that evolved as a result of different environments or proximate effects of different environments (Dunham and Miles 1985, Vitt 1990, 1992).

Females of *S. gadoviae* are able to lay 2 or more clutches during the reproductive season. Like most small-bodied species, some *S. gadoviae* females (14.3%) are capable of laying 2 or more clutches during reproduction, since vitellogenic follicles and oviductal eggs were present at the same time. This pattern is similar to other oviparous species of small body size found in tropical dry forest, tropical wet

Much remains to be learned about the reproductive cycles of the lizards Sceloporus gadoviae and S. jalapae, especially those inhabiting tropical arid environments. It is clear that S. gadoviae has multiple clutches during the reproductive season, but data do not exist about clutch frequency for the small-bodied lizard S. jalapae. Our data in this present study suggest that further research in other regions of the geographic range of both species is necessary to provide additional information about variations in their reproductive characteristics.

ACKNOWLEDGMENTS

We thank V. Mata-Silva and L. Oliver for their assistance in the field, A. Valiente for permitting us to use his home while we gathered data in the field, R. León-Rico for logistic help, D. Gernandt for reading the initial version of this manuscript, and the anonymous reviewers for critical comments and suggestions on the manuscript. This study was supported by PAPCA 1, PROMEP and UAHG0-PTC-165 projects.

LITERATURE CITED


Received 17 May 2004
Accepted 3 November 2004
It is widely accepted that members of the flea genus *Foxella* Wagner, 1929 are true parasites of pocket gophers. Miller and Ward (1960) found all 4 species of Colorado pocket gophers (*Pappogeomys castanops* Baird, 1852; *Geomys bursarius* Shaw, 1800; *Thomomys bottae* Eydoux and Gervais, 1836; and *T. talpoides* Richardson, 1828) infested with *Foxella ignota* Baker, 1895. They performed their survey during August 1957 in the southeastern part of Colorado, where the northern pocket gopher (*T. talpoides*) was the most abundant host. In an earlier study the same species of flea was recovered from northern pocket gophers in Park County (Eads 1949). These and other reports of *F. ignota* from the Rocky Mountains area have not often indicated a subspecies designation because of considerable morphological variation (Hubbard 1947).

Several flea genera have been reported from *T. talpoides* throughout its range. These include *Foxella* Wagner, 1929; *Dactylopsylla* Jordan, 1929; and *Spicata* I. Fox, 1940 (Lewis 2003). These genera can also occur on the other 3 pocket gopher species in Colorado (*G. bursarius, T. bottae, and E. castanops*). The *F. ignota* complex ranges from Indiana (Lake and Newton Counties), where they are found on *G. bursarius*; westward through Montana, Wyoming, and Colorado to Oregon and into California, where they are found on *T. bottae*; and north into Canada from Manitoba to British Columbia and south into Arizona, New Mexico, Texas, and Mexico (R.E. Lewis personal communication). According to Lewis, fleas within the complex increase in size from east to west and from north to south. Holland (1985) lists 12 other species from *T. talpoides*, but these are typically found on ecological associates such as woodrats, ground squirrels, mice, and voles.

Northern pocket gophers have an extensive range in North America similar to, but somewhat smaller than, that of the genus *Foxella*. The range of northern pocket gophers extends westward from the Dakotas and Nebraska to include Colorado, Wyoming, Montana, Idaho, and northward into the southern portion of the Canadian provinces from Manitoba to British Columbia. In the western United States, this rodent occurs east of the Cascades in Washington and Oregon but has a more limited distribution in northern California, Utah, Nevada, New Mexico, and Arizona (Baker et al. 2003).

Longanecker and Burroughs (1952) studied the relationship between temperature, humidity, and flea abundance in burrows of the California...
ground squirrel, *Spermophilus beecheyi* Richardson, 1829. They also found that numbers of *Hoplopsyllus anomalus* Baker, 1904 varied during the year, with a marked increase in abundance during the warmer months. Reichardt and Galloway (1994) studied the incidence and prevalence of *Oropsylla brunerii* Baker, 1895 on *S. franklinii* Sabine, 1822 in Manitoba, with emphasis on the reproductive status of the female fleas and their nondependence on the host’s hormones for timing of reproduction. They found that the proportion of female fleas on *S. franklinii* exceeded male fleas during some months. Lang (1996) investigated the effect of biotic and abiotic factors on abundance of *Oropsylla montana* Baker, 1895 and *H. anomalus* on *S. beecheyi*, and of *Orchopeas sexdentatus* Baker, 1904 on woodrats in southern California. He found an increased abundance of *O. montana* and *O. sexdentatus* correlated with decreased ambient temperature in autumn and early winter. *Hoplopsyllus anomalus* abundance, however, increased with the warmer temperatures of summer. None of the 3 species of fleas appeared hormonally synchronized with the breeding cycle of their hosts. Similar studies have not been reported regarding flea abundance on *T. talpoides*. We hypothesized that the number of fleas infesting this host might vary over the course of a calendar year because of the activity and abundance of hosts, as well as seasonal changes in temperature and humidity. In this study we examined flea abundance on hosts but did not investigate abiotic factors.

**Materials and Methods**

We collected 247 *T. talpoides* (99 males, 148 females) in the Kiowa Creek valley, Elbert County, Colorado. Pocket gophers were collected in both irrigated and nonirrigated alfalfa fields. Animals were trapped for 13 months using Death-Klutch-1 (DK-1) traps (October 2002–October 2003). Animals were placed in Ziploc® plastic bags and were stored frozen. When later thawed, they were brushed for fleas over a white enamel pan. Those collected were placed in 70% ethanol for short-term storage and later cleared in 10% KOH, neutralized, dehydrated in ethanol and then in xylene, and finally mounted on slides using Canada balsam. Fleas were examined microscopically for identity and sex. Flea abundance was compared using descriptive statistical methods for differences based on time of year as well as host sex.

**Results**

A total of 532 fleas were collected from 247 *T. talpoides*. Of these fleas, 526 were identified as *F. i. ignota* (269 males, 257 females), 2 males and 1 female as *S. rara* I. Fox, 1940, 1 female as *H. dippiei* ssp., 1 male as *O. idahoensis* Baker, 1904, and 1 female as *Oropsylla (Opisocrostis)* sp.

Numbers of fleas per host ranged from 0 to 26, and median numbers are shown in Table 1. Throughout the study the median flea infestation rate remained between 0 and 2 except in May when it rose to 5. Mean intensity (total number of fleas divided by the number of hosts with fleas) and relative density (total number of fleas divided by the number of hosts examined) of fleas per host are also shown in Table 1. While median number of fleas per host peaked in May, mean intensity of fleas peaked in April and declined slightly in May. Relative density, however, mirrored the peak of the median in May. All 3 values dropped slightly in June and then rose slightly in July. Male pocket gophers constituted 40% of those collected; 71.7% of them had fleas, while 56.8% of the females were infested. In all, 62.8% of the animals had ≥1 fleas. The ratio of male to female fleas on hosts varied by month and by sex of the host animal. Except during December, February, and July, a higher percentage of male pocket gophers had fleas than did females (Table 2). The ratio of male to female fleas for the duration of the study was 1.05, but the ratio showed considerable variation by month and by sex of the host.

**Discussion**

**Flea Species**

The most abundant flea collected was *F. i. ignota* (526/532). This subspecies is the only member of the genus found in central Colorado east of the Rocky Mountains, and it is the dominant flea on all 4 species of pocket gophers in Colorado. Miller and Ward (1960) did not designate which subspecies of *F. ignota* or of *T. talpoides* they collected. We assume that it
was *F. i. ignota* from *T. talpoides* populations if they trapped on the eastern side of the Front Range.

Some members of the genus *Spicata* have been described as possible nest fleas (Hubbard 1947). *Spicata rara* was first collected from *T. talpoides* in Jackson County, Colorado, by I. Fox (1940) and subsequently reported from *Thomomys* sp. in Iron County, Utah (Stark 1959). Additional, but limited, collections have been made in Montezuma County, Colorado, and in Big Horn County, Wyoming (Lewis 2003). Thus far, all collection sites are separated by 150–300 miles. Lewis suggested that *S. rara* might be a “winter species,” with higher population numbers present in pocket gopher burrows during the winter months. The 3 specimens we collected were taken in January, February, and May, thus supporting this assertion. Very few *S. rara* have been collected from any single locale, but with this new Elbert County record, we believe that *S. rara* is widely dispersed in low numbers throughout Colorado and adjacent montane regions.

*Hystrichopsylla dippiei* ssp. was first reported from mustelids, but it has also been taken from a wide array of sciurids, cricetids, and geomyrid rodents including *T. talpoides* (Hubbard 1947, Holland 1985). Lewis and Lewis (1994) stated that members of this genus show little host specificity, occurring on many different species of small mammals. According to Hubbard (1947) and Holland (1957), these large fleas are usually collected as single individuals or in groups of 2 and 3. Unlike *S. rara*, however, *H. dippiei* ssp. can occur on ecological associates that use pocket gopher burrows.

*Oropsylla idahoensis* has a wide distribution in western North America, including collections from Colorado ground squirrels (Hubbard 1947). According to Lewis (2002), *O. idahoensis* has an equally broad host range, having been reported from 54 species, 5 of which are birds. A few thirteen-lined ground squirrels, *S. tridecemlineatus*, were found in pocket gopher burrows during our study, suggesting that this host was the source of the single *O. idahoensis* collected.

The single flea identified as *Oropsylla* (*Opiscrostis*) sp. was a female. It may belong to the species *O. idahoensis* or other closely related species, but males are required for a specific identification.

### Flea Abundance

The number of fleas present on *T. talpoides* not only varied seasonally but also varied by sex of the host. Seasonal abundance was similar to that which Longanecker and Burroughs (1952) described for *H. anomalus* from *S. beecheyi* in California. As the temperature increased from April through July, so too did the total number of fleas collected from *T. talpoides*. Although we did not measure temperature and humidity levels within pocket gopher burrows, we assumed that temperatures rose and humidity increased in warmer months in the burrows.

Reichardt and Galloway (1994) live-trapped *S. franklinii* biweekly and found that female fleas outnumbered male fleas during most of

<table>
<thead>
<tr>
<th>Month</th>
<th>Median numbers of fleas</th>
<th>Range of flea numbers</th>
<th>Mean intensity</th>
<th>Relative density</th>
</tr>
</thead>
<tbody>
<tr>
<td>October</td>
<td>1</td>
<td>0–5</td>
<td>1.75</td>
<td>1.08</td>
</tr>
<tr>
<td>November</td>
<td>1</td>
<td>0–6</td>
<td>3.2</td>
<td>1.52</td>
</tr>
<tr>
<td>December</td>
<td>0.5</td>
<td>0–2</td>
<td>1.4</td>
<td>0.7</td>
</tr>
<tr>
<td>January</td>
<td>1</td>
<td>0–4</td>
<td>1.69</td>
<td>1.1</td>
</tr>
<tr>
<td>February</td>
<td>1</td>
<td>0–8</td>
<td>2.73</td>
<td>2.05</td>
</tr>
<tr>
<td>March</td>
<td>1</td>
<td>0–5</td>
<td>1.86</td>
<td>1.18</td>
</tr>
<tr>
<td>April</td>
<td>0.5</td>
<td>0–23</td>
<td>7.25</td>
<td>3.63</td>
</tr>
<tr>
<td>May</td>
<td>5</td>
<td>0–16</td>
<td>6</td>
<td>5.57</td>
</tr>
<tr>
<td>June</td>
<td>1</td>
<td>0–17</td>
<td>3.25</td>
<td>2.83</td>
</tr>
<tr>
<td>July</td>
<td>2</td>
<td>0–15</td>
<td>5.15</td>
<td>3.05</td>
</tr>
<tr>
<td>August</td>
<td>0</td>
<td>0–9</td>
<td>2.54</td>
<td>1.14</td>
</tr>
<tr>
<td>September</td>
<td>1</td>
<td>0–11</td>
<td>3.43</td>
<td>2.09</td>
</tr>
<tr>
<td>October</td>
<td>1</td>
<td>0–26</td>
<td>4</td>
<td>3.33</td>
</tr>
</tbody>
</table>
their study, except during early May and late June or early July. They suggested that the temporarily altered sex ratio represented newly emerged male fleas. We found that male *F. ignota* outnumbered female *F. ignota* about half the time on hosts of both sexes (Table 2) and that there was a large peak in the male-to-female ratio from March through May, with smaller peaks in December and October. This may represent a postemergent increase of male fleas.

Mead-Briggs et al. (1975) reported the migration of the rabbit flea, *Spilopsyllus cuniculi* (Dale), from bucks to does of *Oryctolagus cuniculus* (L.) in response to reproductive cues. Does yielded greater numbers of fleas than males during mid- to late pregnancy. Our study indicated no evidence of a similar hormonally induced migration of *F. i. ignota* onto female pocket gophers. The percent of male pocket gophers with fleas from March through June was greater than that for females even though these months encompass the host’s breeding season (Hansen 1960). The ratio of fleas on female pocket gophers did not increase during this time, as would be expected if hormonal changes during pregnancy of these animals led to synchronization of flea breeding. Male *T. talpoides* exhibited a higher percentage of flea infestation than females for all but 3 months (Table 2). This may be a collection artifact, but it is similar to the findings of Longanecker and Burroughs (1952), Lang (1996), and Larson et al. (1996), because the numbers of fleas peaked during a period of 3–4 months, possibly related to changes in ambient temperature and relative humidity within the burrows.

During the summer months, when many young-of-the-year are present, factors such as increased temperature, elevated humidity in the burrows, and greater numbers of gophers might account for the higher numbers of fleas (Table 1).

Further studies of *F. i. ignota* in Colorado could explore the timing of flea reproduction, numbers of individuals produced in one pocket gopher burrow, and the sex ratio of the newly emerged cohort. A yearlong study to monitor temperature and relative humidity in the burrows would be interesting but labor intensive. Such data might explain seasonal fluctuations in flea abundance and elucidate their population dynamics on northern pocket gophers.

ACKNOWLEDGMENTS

We thank Charles Carnahan of the Carnahan Ranches, Darren Oljkers of the Oljkers Ranch, and the Peaceful Valley Scout Ranch for permission to collect northern pocket gophers on their lands. We gratefully acknowledge R.E. Lewis for verification of flea identification, D.L. Hall for assistance with statistical analysis, O.R. Larson for critiquing the manuscript, the 2003 Animal Ecology class from University of Colorado, Colorado Springs, and K. Whelan for assistance in collecting animals.

### Table 2. Flea infestation on male and female *Thomomys talpoides* in 2002–2003 Elbert Co., Colorado, by month. The standard deviation is ±0.197 for males and ±0.167 for females, and the number of hosts is in parentheses after each percent.

<table>
<thead>
<tr>
<th>Month</th>
<th>Number of <em>T. talpoides</em></th>
<th>Percent of <em>T. talpoides</em> with fleas</th>
<th>Ratio of <em>δ</em> : <em>♀</em> fleas on <em>δ</em> hosts</th>
<th>Percent of <em>♀</em> fleas on <em>♀</em> hosts</th>
<th>Ratio of <em>δ</em> : <em>♀</em> fleas on <em>♀</em> hosts</th>
</tr>
</thead>
<tbody>
<tr>
<td>October</td>
<td>26</td>
<td>73 (11)</td>
<td>1.38</td>
<td>53 (15)</td>
<td>2</td>
</tr>
<tr>
<td>November</td>
<td>21</td>
<td>57 (7)</td>
<td>2</td>
<td>50 (14)</td>
<td>0.53</td>
</tr>
<tr>
<td>December</td>
<td>10</td>
<td>33 (3)</td>
<td>0</td>
<td>57 (7)</td>
<td>1</td>
</tr>
<tr>
<td>January</td>
<td>20</td>
<td>78 (9)</td>
<td>0.5</td>
<td>55 (11)</td>
<td>2.5</td>
</tr>
<tr>
<td>February</td>
<td>20</td>
<td>71 (7)</td>
<td>3.5</td>
<td>77 (13)</td>
<td>0.77</td>
</tr>
<tr>
<td>March</td>
<td>11</td>
<td>100 (4)</td>
<td>4</td>
<td>43 (7)</td>
<td>0.67</td>
</tr>
<tr>
<td>April</td>
<td>16</td>
<td>60 (10)</td>
<td>1.72</td>
<td>33 (6)</td>
<td>1.25</td>
</tr>
<tr>
<td>May</td>
<td>14</td>
<td>100 (4)</td>
<td>1.18</td>
<td>90 (10)</td>
<td>1.08</td>
</tr>
<tr>
<td>June</td>
<td>23</td>
<td>83 (6)</td>
<td>0.67</td>
<td>76 (17)</td>
<td>0.84</td>
</tr>
<tr>
<td>July</td>
<td>22</td>
<td>50 (6)</td>
<td>0.58</td>
<td>63 (16)</td>
<td>1.18</td>
</tr>
<tr>
<td>August</td>
<td>29</td>
<td>57 (12)</td>
<td>0.8</td>
<td>33 (17)</td>
<td>0.5</td>
</tr>
<tr>
<td>September</td>
<td>23</td>
<td>70 (10)</td>
<td>1.56</td>
<td>54 (13)</td>
<td>1.27</td>
</tr>
<tr>
<td>October</td>
<td>12</td>
<td>90 (10)</td>
<td>0.46</td>
<td>50 (2)</td>
<td>1</td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td></td>
<td>71 (99)</td>
<td>1.41</td>
<td>56 (148)</td>
<td>1.13</td>
</tr>
</tbody>
</table>
LITERATURE CITED


LANG, J.D. 1996. Factors affecting the seasonal abundance of ground squirrel and woodrat fleas (Siphonaptera) in San Diego County, California. Journal of Medical Entomology 33:790–804.


Received 28 June 2004
Accepted 12 October 2004
The spotted bat, *Euderma maculatum*, is widespread throughout arid portions of western North America, but it is patchily distributed and only locally common within its range (Fenton et al. 1987, Navo et al. 1992, Pierson and Rainey 1998, Geluso 2000). Unique habitat requirements, namely the presence of large cliffs and water, appear to limit its distribution (Luce 2005). But even within areas of apparently suitable habitat, spotted bats are often absent or infrequently encountered (Geluso 2000). Estimated flying heights of spotted bats ranged from 3 m to 50 m aboveground. The species was difficult to capture and was captured only after considerable experimentation with methods and materials. Three spotted bats were captured toward the end of the project in 2003 and accounted for only 0.5% of all bats captured during the study. Although we attached radio transmitters to 2 spotted bats, we found no roost locations. We believe additional spotted bat surveys in Oregon are warranted, especially in higher-elevation habitats, but recommend that to increase their effectiveness, surveys accommodate the unique foraging behavior of the species.

Key words: spotted bat, *Euderma maculatum*, distribution, foraging behavior, capture results, Oregon.

The spotted bat, *Euderma maculatum*, is widespread throughout arid portions of western North America, but it is patchily distributed and only locally common within its range (Fenton et al. 1987, Navo et al. 1992, Pierson and Rainey 1998, Geluso 2000). Unique habitat requirements, namely the presence of large cliffs and water, appear to limit its distribution (Luce 2005). But even within areas of apparently suitable habitat, spotted bats are often absent or infrequently encountered (Geluso 2000). This apparent rarity has prompted most regional and state authorities to list the species either as threatened or of concern (Luce 2005). In Oregon the species has remained largely unknown and the state wildlife agency has not yet assigned it a conservation status (Verts and Carraway 1998, Csuti et al. 2001, Oregon Natural Heritage Program 2001).

Maps of the predicted distribution of the spotted bat have consistently shown central Oregon to be on the periphery of its range (Watkins 1977, Hall 1981, Verts and Carraway 1998, Csuti et al. 2001). However, recent surveys for spotted bats in surrounding states have led to the identification of new localities in habitats similar to those that exist in central Oregon (Sarell and McGuiness 1993, Doering and Keller 1998, Pierson and Rainey 1998, Geluso 2000, Gitzen et al. 2001). Approximately two-thirds of the state of Oregon lies east of the Cascade mountain range and contains numerous steeply walled canyons and meadow complexes characteristic of the Intermountain West. These landscapes are typical of spotted bat habitat (e.g., Pierson and Rainey 1998), and the lack of documented spotted bat activity in the region is incongruous with the availability of apparently suitable habitat. Only 2 voucher specimens exist for Oregon, and the only other state records come from 3 isolated reports based on audible detections made during the 1990s along the Snake River on the Oregon border (McMahon et al. 1981, Barss and Forbes 1984, Ormsbee and Risdal 2004).

The most westerly of the historic Oregon records came from a dead specimen found in 1984 in a cliff along the John Day River, but no effort had been made to determine if the species regularly occurred there (Barss and
Forbes 1984). In July 2002, as part of an ongoing National Park Service (NPS) mammal inventory, we began a search for spotted bats in the John Day River valley. The survey effort continued through October 2003 and was expanded to include areas along the Deschutes and Crooked Rivers west of the John Day Basin and a dry canyon east of the town of Bend, southwest of the Crooked River. The objectives of this study were (1) to determine if spotted bats were present in the historic locality reported by Barss and Forbes (1984), (2) to identify new localities along the John Day River and adjacent drainages, and (3) to capture the species in order to obtain photographic vouchers and information on sex, age, and reproductive condition.

**STUDY AREA**

We searched for spotted bats in 14 search areas located along a 290-km section of the John Day River and 3 major tributaries; at selected locations on the Deschutes and Crooked Rivers, a large parallel drainage located to the west of the John Day basin; and at Dry River canyon, 27 km east of the town of Bend, in north central Oregon (see Fig. 1). Our search areas were located near large cliffs and rimrock features in Deschutes, Gilliam, Grant, Jefferson, Wasco, and Wheeler Counties. Along the John Day River, most search areas were concentrated around the 3 widely separated units of the John Day Fossil Beds National Monument (areas 2–9, Table 1). One search area was located at the mouth of a large upland cave 4.5 km off the John Day River (area 7, Table 1). The Dry River search area (area 14, Table 1) was approximately 20 km from the Crooked River, which is a much greater distance from a perennial creek or river than the other 13 search areas. Search area elevations range from 180 m to 1278 m. Elevations of nearby buttes and plateaus range from 1200 m to 1600 m. The climate of the study region is semiarid, dominated by hot, dry summers and cool, dry winters. Mean annual precipitation from weather stations near search areas for the period 1973–2003 ranged from 20 cm to 27 cm (Oregon Climate Service 2003). Juniper-sagebrush steppe vegetation consists of open woodlands of western juniper (Juniperus occidentalis), sagebrush (Artemisia tridentata), and a variety of annual and perennial grasses. Irrigated agricultural fields or previously cultivated old fields are present along the riverine floodplain terraces and on top of rimrock plateaus near all search areas except the Dry River area (area 14, Table 1).

**METHODS**

This study was conducted simultaneously with ongoing mammal inventory work and a telemetry project involving other species of bats in the John Day Fossil Beds National Monument. We conducted surveys in 2002 from 15 July to 10 September. In 2003 we were conducted from 1 May to 18 October. During the course of the study, we visited 24 survey sites, grouped into 14 search areas. Survey site selection was based on suitability for mist-netting and proximity to large cliff complexes. Single visits were made to 11 survey sites, and 13 sites had 2 or more visits made during the study. Survey activities conducted during site visits included mist-netting, recording of echolocation calls, and audiovisual observations of passing spotted bats. Durations of site visits were variable and were dictated by weather and logistical considerations. The average visit was 3.5 hours, with visits ranging from 20 minutes to 9 hours. On some nights we visited more than 1 site. Incidental observations of spotted bats were made while conducting other project activities throughout the study.

Spotted bats produce distinctive echolocation calls audible to the unaided human ear, and the detection of these calls was the primary method of observation (Woodsworth et al. 1981, Leonard and Fenton 1984). Large hand-held spotlights were used in conjunction with audible detections to illuminate spotted bats and to aid in estimating flying height, direction of travel, and other observations of foraging behavior. Each observation was categorized as a “pass,” since most observations consisted of bats flying past an observer. Most passes were discrete, unidirectional events, although some events included long periods (e.g., 1–20 minutes) during which individual bats remained within hearing or spotlight distance of an observer. The presence of multiple
individuals was determined by illuminating >1 bat simultaneously, by observing a passing bat at the same time a captured bat was still in hand, and by hearing calls in clearly distinguishable directions. Foraging height estimates were aided by comparing flying height of illuminated bats to the tops of nearby visible structures such as telephone poles and tree-tops.

An Anabat bat echolocation recording and analysis system (Titley Electronics, Ballina, NSW, Australia; Corben Scientific, Rohnert Park, CA, USA) was used to record spotted bat calls and supplement audiovisual observations. This tool was useful primarily as a means of aiding in species identification and providing a vouchering system. Recordings were also made of calls produced by hand-released spotted bats captured late in the project.

Mist-nets were employed throughout the project both to complete the goals of the NPS inventory and to try to specifically capture spotted bats for this project. Spotted bats are difficult to capture in many areas (Navo et al. 2005).
1992, Gitzen et al. 2001), and extensive effort was made to catch the species in our study area. Mist-nets of various lengths (2.6–18 m) were placed across pools and channels of open water along the John Day River and tributaries, across open fields, across a cave opening, and on top of a cliff. Using aluminum electrical conduit, we elevated nets as high as 4.5 m aboveground to try to intercept high-flying bats.

Radio-transmitters were attached to 2 captured spotted bats. Transmitters weighing 0.51 g (LB-2 model, Holohil, Inc. Guelph, Canada) were attached with Skin-Bond surgical adhesive (Smith and Nephew, Ltd., Largo, FL, USA) to the intra-scapular region of the bats. Transmitters weighed less than 5% of the mass of instrumented bats. Bats were tracked using receivers with omni-directional magnetic vehicle roof antennas and 5-element hand-held directional antennas (Wildlife Materials, Inc, Carbondale, IL). The University of Idaho Animal Care and Use Committee approved all capture and handling procedures used during the study.

**Results**

In total, we spent 343 hours of mist-netting, recording, and audiovisual observations during 80 nights. Spotted bats were encountered at 14 of 24 survey sites (58%) in 11 of 14 search areas (78%) on 38 of 80 survey nights (48%). Incidental observations of spotted bats were made on 12 additional nights. A total of 138 spotted bat passes were observed throughout the study. At Pine Creek and Clarno (areas 2, 3), where survey effort was most intense, spotted bats were active during all months of the study, from May through October. Several incidental observations of spotted bats were made along Pine Creek during April 2003. We also found spotted bats repeatedly at Smith Rocks State Park (area 13) in June, August, and September 2003. At all other search areas, spotted bats were encountered only during August–October. The species was found in all 6 Oregon counties where search areas were located. Multiple individuals were found at 5 sites in 4 search areas (areas 2, 4, 13, 14), and repeat observations of multiple individuals were made at 3 of those locations (areas 2, 13). We never confirmed more than 3 individuals at a time.

Two male spotted bats were captured on different nights at 1 location on the John Day River (area 2), and a 3rd individual was captured in a different location along the John Day River (area 7) but escaped from the net before it could be processed. Both male bats were instrumented with radio transmitters during late August and early September 2003, but roosts were not located despite extensive searching. After searching for 4 days and nights, we...
briefly encountered 1 bat foraging approximately 8 km upriver from the capture site, but we could not relocate it again. The 2nd bat was tracked upriver for several hours after being released but was not relocated on subsequent days and nights.

Spotted bats were active at all hours of the night during the study. The earliest observed flights of the species were recorded at Smith Rocks (area 13) on the Crooked River. There, spotted bats were observed flying within 38 minutes after civil sunset in dusky, low-light conditions. At the Dry River canyon (area 14), spotted bats were first heard 43 minutes after sunset. Along the John Day River, the earliest observation was made in the Clarno area (area 2) 63 minutes after sunset, although spotted bats normally did not arrive there until much later in the evening. As a point of reference, emergence times of western small-footed myotis (*Myotis ciliolabrum*) and pallid bats (*Antrozous pallidus*) tracked to day roosts in the John Day Valley during the same study period averaged 24 minutes and 47 minutes after sunset, respectively. Dawn observations of spotted bats were also made on several occasions, including one made 78 minutes before civil sunrise.

We noted considerable variability in the presence and timing of spotted bats at survey sites. While spotted bats were repeatedly encountered at many sites, the species was never encountered at some locations with seemingly ideal habitat (e.g., large cliffs along rivers; areas 5, 8, 9). One incidental observation made at Cathedral Rock (area 6) was the only detection made at that site, despite 3 other nights of formal surveys conducted there. At 7 sites where spotted bats were encountered at least once, the species was detected in only 25 of 53 visits lasting 1 hour or more. During visits to Smith Rocks (area 13) when observers were in place before sunset, spotted bats were first detected 38 and 39 minutes after sunset. The predictability in the timing of the initial arrival of spotted bats there was not consistent with observations made in other areas. During 2 consecutive visits to 1 site in Pine Creek (area 3), 1st arrival in the 2nd visit occurred 30 minutes after 1st arrival on the previous night, and both 1st arrivals occurred more than 3 hours after sunset. Along Bridge Creek (area 4), we observed 2 spotted bats flying together 4 hours after sunset; no other passes were recorded at that site during 5 additional nights of mist-netting.

Spotted bats were repeatedly encountered foraging high over irrigated fields and old fields, low upland slopes of juniper and sagebrush, and along the rims of cliffs. Estimates of flying height made for 61 passes ranged from 3 m to 50 m, and average flying height was 20 m. No spotted bats were observed coming down to drink, although bats were occasionally observed flying high over water. Likewise, on no occasion did we observe spotted bats flying low enough for standard use of mist-nets to be effective. Only after considerable effort and experimentation with elevated nets were we able to capture the species. The most successful net configuration consisted of four 12-m nets erected on 4.5-m poles placed along the rim of a cliff overlooking the John Day River (area 2). This net arrangement was placed where spotted bats had been previously observed cresting low over the top of the cliff. A 3rd spotted bat was captured in a mist-net placed across the mouth of a large upland cave (area 7). Although this net was not elevated, the cave itself is located in the middle of a steep, cliff-like slope. Spotted bats accounted for only 3 of 548 bat captures (0.5%) made during 300 hours of netting on 65 nights. However, this rate is much higher when effort includes only the number of hours that elevated nets were employed. Elevated nets were employed for 87 hours on 15 nights, and spotted bats accounted for 2 of 16 bats caught. A total of 14 species of bats were captured during the entire study period, but only 6 species were caught in elevated nets.

**Discussion**

Prior to this study, only 1 spotted bat had been captured in Oregon (McMahon et al. 1981). That record and those from Barss and Forbes (1984) and the 3 records from the Snake River (Ormsbee and Risdal 2004) suggested a pattern of random and rare occurrences in the state. A search for spotted bats in eastern Oregon in 1983 failed to document the species, further supporting this perception (Fenton et al. 1987). While the spotted bat has an undetermined conservation status with the Oregon Department of Fish and Wildlife, the Oregon Natural Heritage Program placed the spotted
bat on a list of species at risk of extirpation and peripheral species (Oregon Natural Heritage Program 2001). Our results suggest that spotted bats may be much more common and widespread in Oregon than historic evidence suggests. Spotted bats appear to be well established in the lower Deschutes and John Day basins. The presence of spotted bats at the Dry River canyon southeast of Bend provides evidence that the species may occur widely in drier uplands far from large water bodies as well.

In a recent review of the literature, Luce (2005) also suggested that spotted bats might be more common than historic records indicate. Our study and others (Pierson and Rainey 1998, Geluso 2000) that have specifically searched for spotted bats in suitable habitat have added many new localities in recent years. This may be due to an increasing reliance on audible detections rather than capture results. While some investigators have suggested that spotted bat capture results adequately represent abundance, our results suggest otherwise (Fenton et al. 1983, Berna 1990). Without concerted effort using alternative methods, spotted bats would not have been captured at all in our study area, perhaps leading to the spurious conclusion that the species was absent from the region. Navo et al. (1992) and Gitzen et al. (2001) also reported that the species was difficult to capture. Pierson and Rainey (1998) reported captures from only 4 of 28 new spotted bat localities in California. Geluso (2000) reported multiple captures of spotted bats from some locations in Nevada but reported that the species had not been successfully captured in several other locations where it had been detected acoustically.

Clearly, the high-flying behavior of foraging spotted bats encountered in our study played a significant role in capture difficulty. Navo et al. (1992) regularly observed the species flying 10 m or more aboveground and did not observe the species flying low enough to be caught in mist-nets. Others have reported this behavior as well, and we know of at least 1 other investigator resorting to unusual mist-net tactics similar to ours to catch spotted bats (Jason Williams, Nevada Division of Wildlife, personal communication). In areas where the species has been more easily captured in mist-nets, topography and limited open water may force spotted bats to fly at lower heights or in more discrete flight paths, making them more susceptible to capture (Poche 1981, Geluso 2000).

While we propose that spotted bats may be relatively common in central Oregon, we found night-to-night activity somewhat variable. The species was encountered in 78% of search areas, but on only 48% of survey nights. Spotted bats arrived early and regularly at the Smith Rocks area but were much less predictable along the John Day River. Spotted bats were once considered a late-emerging species, but several studies have demonstrated the species to emerge relatively early (Easterla 1965, Wai-ping and Fenton 1989, Navo et al 1992). Our results are consistent with this, and we believe that perceptions of spotted bat emergence times are influenced by the distance of an observation point to roosts. We interpret our results to suggest that spotted bats were roosting close to our observation points at Smith Rocks State Park and Dry River canyon and much farther away from observations made along the John Day River. In the sites where spotted bats were encountered early, the intervals between passes became longer as the night progressed. These late-night activity patterns resembled those in sites with consistently late first-arrival encounters. It may be that the predictability in spotted bat activity patterns declines as bats fly farther from roosts.

An additional consideration to the issue of variability in the timing and presence of spotted bats at search areas is that of transient bats. It seems likely that at least some of the bats encountered in May, June, and July were roosting locally as “resident” bats. However, the disappearance of the 2 male spotted bats fitted with radio transmitters late in August and September provides some evidence of transience, and this behavior may account for some of the variability observed during the study. It may also account for the single encounters at search areas where multiple surveys were made (areas 4, 6, 7). All encounters at these sites occurred in August and September. Several investigators have hypothesized that spotted bats undertake localized migrations to higher elevations in midsummer and return to lower elevations in late August and September (Poche 1981, Berna 1990, and Geluso 2000). Likewise, Rabe et al. (1998) demonstrated that spotted bats are capable of undertaking long daily movements over 30 km. Very little
additional information is available on this topic, but it may be that spotted bats travel considerable distances in central Oregon between roosting and foraging areas and between summer roosts and winter hibernacula.

Woodsworth et al. (1981) reported remarkable regularity in the arrival, direction, and duration of foraging spotted bats on consecutive nights in southern British Columbia. Several other surveys have successfully relied on short (e.g., ≤20 minutes) observation periods (Fenton et al. 1987, Navo et al. 1992, Pierson and Rainey 1998). Based on our experience in central Oregon, however, surveys may be more effective if longer observation periods are used. While some survey objectives may best be served by many short observations, these also may lead to the conclusion that spotted bats are absent from areas where they actually occur.

Despite our assertion that spotted bats are more common than previously believed in Oregon, the species is certainly much less concentrated and locally abundant than, for example, species of *Myotis* where dozens of individuals can be captured during a single night. We were unable to confirm concentrations of more than 3 individual spotted bats during our study, although this was a conservative estimate. It is entirely plausible that, even as new surveys dramatically increase the number of known spotted bat localities throughout its range, the species will continue to be perceived as rare and require conservation attention. Much needs to be learned about the species before this can be ascertained. We strongly recommend that additional surveys be conducted in Oregon in the many areas of potential habitat that have not yet been searched. Higher-elevation forest habitats in eastern Oregon where open meadows and cliffs are present seem to us to be particularly important areas to investigate. There may also be areas of suitable habitat in the southwestern portion of the state where semiarid conditions extend west of the Cascade Mountains. The discovery of spotted bats in Siskiyou County, California, less than 50 miles from the Oregon border, certainly suggests that this may be worthwhile (Pierson and Rainey 1998). Only after more of the distribution and habitat association gaps have been filled can a meaningful spotted bat conservation status be determined for Oregon.

**ACKNOWLEDGMENTS**

This project was conducted through funding from the National Park Service Natural Resource Challenge Fund (subagreement 20, cooperative agreement CA9000-95-018), a grant from the Pacific Northwest Cooperative Ecological Studies Unit (cooperative agreement CA9088-A-0008), and additional materials and support from Ken Hyde of the John Day Fossil Beds National Monument. We thank Pat Ormsbee for making the Oregon Bat Database available to us. We also thank Bob Luce for providing us with a copy of the forthcoming USFS Region 2 spotted bat conservation assessment. We thank Matt Smith for his assistance in the field. We are especially grateful to the Confederated Tribes of Warm Springs for providing access to Pine Creek Ranch and to Kelly McGeer for providing access to private land along the John Day River. We are indebted to the Oregon Museum of Science Industry for providing room and board at the Hancock Field Station. David Waldien provided helpful comments on an earlier draft of this manuscript. We thank Burr Betts and an anonymous reviewer for their thoughtful review of this manuscript.

**LITERATURE CITED**


GELUSO, K. 2005. Spotted Bat in Central Oregon 221


Received 29 January 2004
Accepted 3 August 2004
The Mountain Plover (Charadrius montanus) is endemic to the grasslands of North America, particularly the western Great Plains and Colorado Plateau. It nests in shortgrass prairie habitats historically used by large herbivores, specifically bison (Bison bison), pronghorn (Antilocapra americana), and prairie dogs (Cynomys spp.), and in more xeric, desert shrub zones to the west (Knopf 1996). However, this tendency for Mountain Plovers to select native habitats with substantial bare ground, coupled with its former cohabitation with large herds of bison, pronghorn, elk, and prairie dogs, has led some to argue that it is a disturbed-prairie or semidesert species rather than a shortgrass associate (Knopf and Miller 1994). Laun (1957) found the bird on the arid mixed-grass plains surrounding Laramie, where sheep and cattle grazing has occurred for over 100 years. In the southern portion of their range, Mountain Plovers also nest on recently plowed fields, often with comparable success to rangeland nesters (Dreitz et al. in press). Likewise, wintering birds in California make extensive use of cultivated farmlands, land that was once native prairie supporting tule elk (Cervus elaphus), pronghorn, and kangaroo rats (Dipodomys spp.; Knopf and Rupert 1995).

Knopf and Miller (1994) reported 32% bare ground at nest sites in Colorado and suggest that 30% bare ground is a minimum habitat requirement for nesting Mountain Plovers. Ellison et al. (2001) found reduced grass cover at nest sites in Utah, while Parrish et al. (1993) reported 72% bare ground at nest sites and 79% bare ground in Wyoming. Beauvais and Smith (2003) were able to correctly classify 87% of points in an independent data set using a model that predicted Mountain Plover presence as a function of cover and slope in western Wyoming. These studies indicate that bare ground or, conversely, lack of vegetative cover, may be one of the most influential predictors of Mountain Plover nesting habitat, particularly on the shrub-steppe.

Our study objectives were to (1) describe nesting phenology of breeding birds across the state, (2) report on hatching success of Mountain Plover nests in Wyoming relative to other regions, (3) describe major vegetative associations at nest sites, and (4) report on presence of grazing at nest sites.

**STUDY AREAS**

Nest searching was conducted throughout the state at locations where historic records of

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1Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Dept. 3166, 1000 E. University Ave., Laramie, WY 82071-3166.
2U.S. Geological Survey, Fort Collins Science Center, 2150-C Centre Avenue, Fort Collins, CO 80526-8118.
Mountain Plover sightings occurred. We focused search efforts at sites with high densities of records in Wyoming Game and Fish Department files. High-density sites include grassland landscapes in the Powder River, Shirley, and Laramie Basins, and desert-shrub zones in the Big Horn, Great Divide, and Washakie Basins. The Powder River basin study sites are located on Thunder Basin National Grassland. The Laramie and Shirley Basin sites include portions of the Laramie Plains extending north and west from Laramie to Medicine Bow and Foote Creek Rim, and the central portion of Shirley Basin, roughly delineated by the 2 intersections of Wyoming Highways 77 and 487 in northeastern Carbon County. These basins are characterized by interspersed short- and mixed-grass prairie. Shortgrass species that occur include blue grama (Bouteloua gracilis) and buffalo grass (Buchloe dactyloides). Commonly occurring mixed-grass species include needle-and-thread grass (Stipa comata), western wheatgrass (Agropyron smithii), Sandberg bluegrass (Poa sandbergii), threadleaf sedge (Carex filifolia), Indian ricegrass (Oryzopsis hymenoides), and pricklypear cactus (Opuntia polyacantha). Shrub species including big sagebrush (Artemisia tridentata), budsage (A. spinescens), and fourwing saltbush (Atriplex canescens) are also present. Black-tailed prairie dog (Cynomys ludovicianus) colonies are common, and grazing by domestic cattle and pronghorn antelope is pervasive. Wind power development occurs in portions of the Laramie Basin.

Primary desert-shrub sites include the Mexican Flats, located west of the town of Dad between Wamsutter and Baggs in the Washakie Basin, a portion of the Great Divide Basin of the Red Desert located south of Cyclone Rim in northern Sweetwater County, and parts of the Big Horn Basin near Cody and Powell (Park County) and Greybull (Big Horn County), particularly Polecat and Chapman Benches. These shrubland areas are typified by saline soils and are dominated by greasewood (Sarcobatus vermiculatus), shadscale (Atriplex confertifolia), fourwing saltbush, and Gardner saltbush (A. gardneri), with winterfat (Ceratoides lanata), cushion plants, and pricklypear cactus interspersed. A mosaic is often formed with stands of big sagebrush, saltbush, and greasewood. Mixed-grass species are also present. Oil and gas development is common, particularly in the Mexican Flats study area. The landscape is grazed by domestic sheep and cattle, pronghorn antelope, and wild horses. White-tailed prairie dog (Cynomys leucurus) colonies are common throughout.

Nest searching also occurred in numerous low-density areas including lands managed by the Kremmer Field Office of the Bureau of Land Management (Lincoln County), the desert landscape west of Flaming Gorge Reservoir (Sweetwater County), and Hannah Basin in central Wyoming (Carbon County). Few breeding birds and no nests were located in low-density areas. For this reason, low-density sites are not described in detail.

**METHODS**

**Nest Searches**

Nest searches in 2002 were conducted in areas with historic Mountain Plover sightings, and in 2003 in areas previously established as concentration areas for breeding plovers (Plumb 2004; breeding concentration areas were sites that averaged >30 Mountain Plover detections in 2002). Survey protocol was modeled after Mountain Plover guidelines (U.S. Fish and Wildlife Service 2002). Driving transects were conducted along an established paved or dirt road. Stops were made at 0.25-mile intervals for visual scans. Scans were conducted outside the vehicle and lasted long enough for a 360° panorama. Nest searching occurred on sites where plovers showed signs of breeding activity upon detection (e.g., head bobbing, seated position, courtship displays, or unwillingness to leave immediate area; U.S. Fish and Wildlife Service 2002).

**Data Collection at Nest**

At least 2 eggs from each clutch were floated in water to estimate clutch age and to approximate hatch date (Alberico 1995, Mabee 1997). We revisited nests soon after projected hatch date to verify hatch. The relationship of projected hatch date to nest elevation and latitude was evaluated using linear regression.

Hatch success of at least 1 egg was inferred by the presence of small eggshell fragments in the nest scrape (Mabee 1997). Adult Mountain Plovers remove large shell parts from the nest as eggs hatch, but chicks breaking through the eggshell leave small pipped fragments. We collected addled or abandoned eggs at this time for embryo aging.
In 2002 vegetation was sampled at four 1.0-m² plots at each nest site. The 1st plot was centered on the nest, and consecutive plots were spaced at distances of 25, 50, and 100 m from the nest along a straight-line transect in a randomly selected cardinal direction determined by 2 coin tosses. We generated 4 random plots in the vicinity of each nest by traveling along the nearest road for an arbitrarily chosen distance of 1.6 km, randomly selecting a cardinal direction by coin tosses, and sampling 1.0-m² plots at 0-, 25-, 50-, and 100-m increments along a straight-line transect. Plots were delineated with a meter stick, and coverage by vegetation classes, including bare ground and grass, was estimated for all 1.0-m² plots. Nest plots were compared to respective random plots using Student’s t test (α = 0.05) for all nests.

Evidences of disturbance regimes, including grazing by wild or domestic ungulates, prairie dog activity, or industrial development visible within 400 m of nest sites, were described. We also considered general topography at the nest site (i.e., plateaus versus open plains or basins).

In 2002 we marked nests by placing a rock on the road shoulder immediately perpendicular to the nest. Distance from the road to the nest was paced and GPS coordinates were taken (Garmin 12). This method did not allow for relocation of nests. In 2003 we marked nests with 2 small stones labeled with Xs and placed them precisely 1 m to the north and south of the scrape. GPS locations and detailed descriptions of the immediate nest environment were taken.

RESULTS

Clutch Size and Breeding Phenology

Between 28 May and 10 July 2002, we located 31 Mountain Plover nests. An additional 24 nests were found between 22 May and 26 June 2003 (Fig. 1). Of 55 clutches, 51 (93%) had 3 eggs and 4 (7%) had 2 eggs. Projected hatch date ranged from 6 June to 24 July 2002 and from 7 June to 7 July 2003. Average projected hatch date was 26 June 2002 and 21 June 2003. Egg hatch date was influenced by neither nest elevation (r² = 0.02, P = 0.36, n = 55) nor latitude (r² = 0.05, P = 0.18, n = 41).

Hatch Success and Condition of Unhatched Eggs

Eggs successfully hatched in 14 of 22 (64%) revisited nests in 2003 as indicated by the
presence of shell fragments in the nest cup. Of the remaining 8 clutches, 5 were devoid of eggshell fragments although predation could be confirmed in only 1 case. The remaining 3 clutches had been abandoned, and all eggs were collected. Also, 4 eggs were collected from otherwise successful clutches. Nests were not revisited in 2002. In total, 13 eggs were collected from 6 nests and their contents examined. Shell thickness was not quantified, but 9 eggs had shells that appeared thinner than others and were noticeably fragile. Eight of the 13 were either infertile or had minimally developed embryos (<3 days). The remaining 5 were moderately developed (≈8–17 days).

Nest Habitat Attributes

Bare ground was the largest component of 1.0-m² nest plots in both grassland and desert areas (Table 1). Nest plots at 0 m had less grass coverage (Table 1) and reduced grass height (Table 2) than corresponding random plots in all cases. There was no difference in grass coverage, bare ground coverage, or grass height between nest plots and corresponding random plots at distances ≥25 m.

All grassland nest sites and most desert nest sites showed evidence of grazing in 2002 and 2003, predominantly by domestic cattle and sheep. Pronghorn and wild horses were also present at some sites. Prairie dogs were

**Table 1.** Comparison of mean grass and mean bare ground coverage (% ± s_e) of 1.0-m² grassland and desert nest plots and 1.0-m² random plots at 4 distances from nest or random start point. Plots sampled in 2002.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Grassland Sites (n = 18)</th>
<th>Desert Sites (n = 13)</th>
<th>t (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nest plot</td>
<td>Random plot</td>
<td>Nest plot</td>
</tr>
<tr>
<td>0 m</td>
<td>13.9 ± 3.3</td>
<td>20.3 ± 3.0</td>
<td>8.5 ± 1.4</td>
</tr>
<tr>
<td>25 m</td>
<td>20.0 ± 2.4</td>
<td>19.7 ± 1.8</td>
<td>13.5 ± 3.3</td>
</tr>
<tr>
<td>50 m</td>
<td>19.0 ± 3.0</td>
<td>17.8 ± 1.7</td>
<td>15.8 ± 4.5</td>
</tr>
<tr>
<td>100 m</td>
<td>19.4 ± 3.8</td>
<td>19.7 ± 4.6</td>
<td>16.5 ± 4.4</td>
</tr>
</tbody>
</table>

*Degrees of freedom range from 48 to 59.

bReported t tests are for grassland and desert samples combined.

**Table 2.** Comparison of mean grass height (± s_e) in centimeters of 1.0-m² grassland and desert nest plots and 1.0-m² random plots at 4 distances from nest or random start point. Plots sampled in 2002.

<table>
<thead>
<tr>
<th>Distance</th>
<th>Grassland Sites (n = 18)</th>
<th>Desert Sites (n = 13)</th>
<th>t (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nest plot</td>
<td>Random plot</td>
<td>Nest plot</td>
</tr>
<tr>
<td>0 m</td>
<td>47.2 ± 4.5</td>
<td>35.3 ± 4.4</td>
<td>61.2 ± 5.6</td>
</tr>
<tr>
<td>25 m</td>
<td>42.2 ± 4.6</td>
<td>44.2 ± 3.3</td>
<td>60.0 ± 6.6</td>
</tr>
<tr>
<td>50 m</td>
<td>56.9 ± 4.3</td>
<td>46.4 ± 3.8</td>
<td>63.9 ± 7.0</td>
</tr>
<tr>
<td>100 m</td>
<td>48.9 ± 4.6</td>
<td>41.9 ± 5.4</td>
<td>56.9 ± 5.9</td>
</tr>
</tbody>
</table>

*Degrees of freedom range from 40 to 55.

bReported t tests are for grassland and desert samples combined.
present on 17 of 32 grassland nest sites (53%; black-tailed) and 3 of 23 desert sites (13%; white-tailed). Thirty-four of 55 nests (62%) were located on plateaus elevated at least 100 m above surrounding terrain. The remaining 21 nests occurred in broad basins or on high plains.

**DISCUSSION**

**Hatch Success and Condition of Unhatched Eggs**

Our hatch rate across Wyoming was similar to Graul’s (1975) findings on the Pawnee National Grassland, Weld County, Colorado, where at least 1 egg hatched in 65% of 80 nests, and was higher than those reported by Knopf and Rupert (1996; 26%–50%), also on the Pawnee National Grassland. Dinsmore et al. (2003) reported that at least 1 egg hatched in 55% of 600 monitored nests on the Charles M. Russell National Wildlife Refuge, Philips County, Montana. Mountain Plover nest failure is often attributed to predation or flooding (Miller and Knopf 1993, Knopf and Rupert 1996, Dinsmore et al. 2003), and these variable nest success rates might be expected as predator populations, habitat quality, and climatic conditions fluctuate.

**Nest Habitat Attributes**

Results from this study are in accordance with previous reports that Mountain Plover nesting habitat is typified by 27%–72% bare ground (Olson and Edge 1985, Parrish et al. 1993, Knopf and Miller 1994) and minimal grass coverage. Plovers have also been shown to use cultivated fields for nesting and brood-rearing (Knopf and Rupert 1999, Dreitz et al. in press). On average, our nest plots were 53% bare ground. This value is higher than results from Colorado and Montana (32%) and is likely due to the large number of Wyoming nest sites in xeric landscapes where bare ground accounts for >50% of coverage at random sites and >60% of coverage at nest sites.

Ungulate grazers were present at all grassland and most desert sites. Thus, open-range livestock grazing is compatible with Mountain Plover reproduction (Kantrud and Kologiski 1982, Knopf 1996). When correctly managed, open-range grazing emulates presettlement conditions much more effectively than do urban development and cultivation, both of which are more pervasive in surrounding states. Thus, Wyoming is of unique value to shortgrass and desert ground-nesters like the Mountain Plover because it boasts vast expanses of rangeland where habitat is kept open through grazing.

Although some studies have shown strong selection for black-tailed prairie dog colonies by Mountain Plovers breeding at mixed-grass prairie sites (Knowles et al. 1982, Olson and Edge 1985, Dinsmore et al. 2003), prairie dogs were absent at many of our Mountain Plover nest sites in Wyoming. Black-tailed prairie dogs were present at 53% of grassland sites and white-tailed prairie dogs at 13% of desert sites. Similarly, Parrish et al. (1993) reported that Mountain Plovers in the Powder River basin did not have a strong affinity for black-tailed prairie dog towns on Thunder Basin National Grassland, with only 1 of 15 nests occurring on a town. Pervasive livestock grazing may be adequate at Wyoming sites to attract breeding plovers in the absence of prairie dog colonies. Alternatively, soil quality, precipitation levels, and vegetative cover may be adequately low to curb the need for additional landscape disturbance.

It is notable that 62% of nests found were located on plateaus elevated at least 100 m above surrounding terrain, particularly since most surveys were not conducted on plateaus. Mountain Plovers also select plateaus for nesting in Phillips County, Montana (Knopf personal communication 2003). Elevated plateaus may host a greater bare ground component than the surrounding landscape due to increased wind scour and precipitation runoff. The Mountain Plover’s tendency to nest on arid, elevated plateaus further substantiates claims that the bird is also a disturbed-desert species rather than a strict associate of the shortgrass prairie.

**LITERATURE CITED**


Fecal sac dispersal by parent White-breasted Nuthatches (Sitta carolinensis) has not been reported in the literature, although Tree Swallows (Tachycineta bicolor), White-crowned Sparrows (Zonotrichia leucophrys), and Eastern Bluebirds (Sialia sialis) have been frequently reported.

Upon removal, fecal sacs can be consumed, dropped, placed on substrate, or a combination of these possibilities. While many passerines do not remove nestling feces, parent White-breasted Nuthatches remove and disperse fecal sacs away from the nest. Petit and Petit (1988) concluded that the significance of fecal sac removal deserves attention in the future, and Lang et al. (2002) observed that this parental behavior remains a neglected topic.

The purpose of this study was to contribute to our knowledge of fecal sac dispersal by parent White-breasted Nuthatches during the nestling stage.

**STUDY AREA AND METHODS**

This field study of fecal sac dispersal by parent White-breasted Nuthatches was made 19 km south of Reno, Nevada, at 1828 m elevation, on the eastern slopes of the Sierra Nevada. Big sagebrush (Artemisia tridentata), mountain mahogany (Cercocarpus ledifolius), and other aridland vegetation give way to mature ponderosa pine (Pinus ponderosa) and Jeffrey pine (Pinus jeffreyi) of higher elevation.


**WHITE-BREASTED NUTHATCH (SITTA CAROLINENSIS)**

**FECAL SAC DISPERSAL IN NORTHWESTERN NEVADA**

Norman H. Weitzel

**ABSTRACT.**—Field research on the dispersal of fecal sacs by parent White-breasted Nuthatches (Sitta carolinensis) was conducted on the eastern slopes of the Sierra Nevada in northwestern Nevada. Fecal sacs were dropped 6–60 m from the nest, with 56% of the total droppings (n = 66) being dropped 48–60 m away. Ninety-five percent of sac dispersal was in the southwest quadrant, the food-foraging site. Also, 75% of non-sac flights during the nestling phase were in the direction of the foraging area, a dead, mature Jeffrey pine (Pinus jeffreyi). Fecal sac dispersal by parent White-breasted Nuthatches may reduce or eliminate detection of nestlings by avian predators.

**Key words:** fecal sac dispersal, White-breasted Nuthatch, Sitta carolinensis, Nevada.

Fecal sac dispersal by parent White-breasted Nuthatches (Sitta carolinensis) has not been reported in the literature, although Tree Swallows (Tachycineta bicolor), White-crowned Sparrows (Zonotrichia leucophrys), and Eastern Bluebirds (Sialia sialis) have been frequently reported.

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The White-breasted Nuthatches are year-round residents nesting in May.

Although observations and fecal sac counts were made in 2001 and 2002, only in 2003 did I record accurate and reliable data to support this study. My observations during the nestling phase (3–19 May) were made daily between 0700 and 1600 with 10 × 50 binoculars and a 40-power spotting scope from the dining and great rooms of my home 34 m east of the nest. Also, observations were made from a blind 6 m southeast of the nest and another blind 26 m south of the nest. I was able to accurately count and mark fecal sac droppings as or where they were dropped by making an extensive survey of bare ground, driveway and parking area, and mowed grasses in the remaining area (Fig. 1).

The nest cavity was 2.7 m above the ground in a dead, partially delimbed Jeffrey pine snag 3.7 m in height. From the nest as point of origin, I established northwest, northeast, southwest, and southeast quadrants (Fig. 1). I recorded the distance and direction of sac dispersal and tabulated flights with and without fecal sacs.

**RESULTS AND DISCUSSION**

**Distance of Dispersal**

Parent White-breasted Nuthatches dispersed fecal sacs 6–60 m from the nest, with 56% of total droppings (n = 66) being dropped 48–60 m away. Seventeen percent were dropped at the end distance of 60 m (Fig. 2). This dropping
distance was opposite of what I reported (Weitzel 2003) in Western Bluebirds (*Sialia mexicana*), where 56% of the sacs were dropped within 20 m of the nest. I attributed this greater dispersal distance by White-breasted Nuthatches to nestling protection behavior by the parents because of common and ever-present predators: Black-billed Magpies (*Pica pica*), Scrub Jays (*Aphelocoma coerulescens*), Steller Jays (*Cyanocitta stelleri*), and European Starlings (*Sturnus vulgaris*). In my Western Bluebird field study, predators were absent. Tree Swallow parents dispersed fecal sacs 20–50 m away (Weatherhead 1984), approximately 40 m in Prothonotary Warblers (*Protonotaria citrea*; Petit and Petit 1987), and 91 m ± 11 m in Eastern Bluebirds (Lang et al. 2002).

**Direction of Dispersal**

Ninety-five percent of total fecal sac dispersals were in the southwest quadrant, 4% in the southeast quadrant, 1% in the northwest quadrant, and 0% in the northeast quadrant (Fig. 3). In the southwest quadrant, a standing, 3-year-dead, mature Jeffrey pine was the predominant foraging site. It had an abundance of various stages of bark beetles, termites, ants, bugs, and other insects, as well as arachnids and other arthropods. Parent White-breasted Nuthatches collected food items at the dead tree and delivered them to the nestlings. Most flights with and without fecal sacs were in the direction of the dead pine tree in the southwest quadrant (Fig. 3). I found that 95% of fecal-sac flights and 75% of non-sac flights were in the direction of the foraging tree. All but 6 fecal sacs dropped in the southwest quadrant were within a narrow, 12-m, nest-to-foraging-pine corridor even though 65 other pines grew there (Fig. 1). Most flights from the nest were to the foraging area during the nestling phase in Western Bluebirds (Weitzel 2003).
When a Tree Swallow made a sac-carrying flight, it apparently flew to a foraging area after dropping the fecal sac (Weatherhead 1984). Petit et al. (1989) suggested that when dispersing fecal sacs, birds do not have to deviate from preferred foraging pathways. I did not observe any attempt by parent White-breasted Nuthatches to disperse sacs at random 360° around the nest.

As the nestlings aged from day 1 to day 16, fecal sac droppings increased in number and distance from the nest (Fig. 4). These data suggest that as the nestlings aged, parental investment increased and the brood became more valuable. Weitzel (2003) found this parental behavior true in Western Bluebirds.

Many passerines dispose of fecal sacs in various patterns from the nest so as to reduce or eliminate detection of nestlings by predators. The pattern depends on the species and ecological factors such as the presence or absence

Fig. 2. Distance of fecal sac droppings (n = 66) from the nest by White-breasted Nuthatches.

Fig. 3. Comparison of flights with and without fecal sacs by White-breasted Nuthatches.
of predators and a dependable food source. Greater attention in field research is given to food items brought to the nest than to fecal sacs brought out. Complete understanding of fecal sac dispersal requires future field studies.

LITERATURE CITED


Received 30 December 2003
Accepted 2 June 2004

Fig. 4. Distance of fecal sac droppings from hatching to fledging in White-breasted Nuthatches. (n) = number of sac droppings.
Competitive relationships between invasive plants and grasses partially regulate plant community response to invasive plant management. For example, the change in grass biomass production that results from invasive plant control and the change in invasive plant biomass that results from grass seeding partially depend on competition intensity. Therefore, incomplete understanding of competitive relationships will result in imprecise predictions of management-induced shifts in invasive plant and grass abundances.

Developing a more complete understanding of competitive relationships between invasive plants and grasses requires knowing if these relationships vary temporally and/or spatially. If competitive relationships between invasive plants and grasses do vary temporally and spatially, a substantial portion of this variation is likely related to temporal and spatial variation in plant productivity, which can be attributed to variation in environmental conditions such as nutrient and water availability (Grime 2001).

While it has been shown that some aspects of plant competition do vary with environmental conditions (Moloney 1990, Briones et al. 1998, Keddy et al. 2000), the relationship between competition intensity and plant productivity has been a point of contention between ecologists (Grime 1973, Newman 1973, Reader et al. 1994). Grime (2001) believes the preponderance of evidence indicates a positive relationship between competition intensity and plant productivity. However, at least one elaborate study suggests that wide productivity gradients are necessary to detect changes in competition intensity, and therefore variation in plant productivity might not strongly influence competition intensity within the productivity range that a single invasive plant species occupies (Reader et al. 1994).

Water availability often governs plant productivity in the semiarid regions where many invasive plants occur, and water availability varies with precipitation and soil water-holding characteristics (e.g., very coarse soils maintain less plant-available water; Bailey 1979). The ability of soil to hold water is regulated by soil type, landscape position, and soil management practices, among other factors.
If plant productivity (i.e., water availability) influences competition intensity between grasses and invasive plants in semiarid regions, per-unit-biomass competitive relationships will vary temporally and spatially with plant-available soil water. Per-unit-biomass competitive relationships can also vary by species, and a single invasive plant species can grow in association with different grasses within each of several habitat types it infests. For example, spotted knapweed (Centaurea maculata) grows in association with western wheatgrass (Agropyron smithii), Kentucky bluegrass (Poa pratensis), needle-and-thread (Stipa comata), blue grama (Bouteloua gracilis), crested wheatgrass (Agropyron cristatum), rough fescue (Festuca scabrella), blue-bunch wheatgrass (Pseudoroegneria spicata), prairie junegrass (Koeleria cristata), Idaho fescue (Festuca idahoensis), and other grasses (Fay et al. 1991, Sheley et al. 2000). Studying competitive relationships between spotted knapweed and each of these grasses would require resource-intensive experiments. The number of by-species competitive relationships that need to be estimated will further increase if per-unit-biomass competitive effects vary considerably by species because some regions harbor many invasive plant species. Using a small number of grasses to study the magnitude of variation in by-species competitive effects will elucidate the quantity of species-specific inquiries needed to understand competition between an invasive plant species and all grasses with which the invasive plant commonly coexists.

Our objective was to determine the influence of soil water on competition among leafy spurge, Kentucky bluegrass, and western wheatgrass in a greenhouse. Leafy spurge is a cool-season, nonnative, perennial invasive plant that infests close to 1.2 million ha in 29 states in the USA (Lajeunesse et al. 1999). Kentucky bluegrass is a cool-season, nonnative, perennial grass that occurs throughout much of the United States. Western wheatgrass is a native, cool-season, rhizomatous, perennial grass that occurs in many rangeland ecosystems of the western United States and Canada (Taylor and Lacey 1994). These grasses often grow in association with leafy spurge.

It was hypothesized that per-unit-plant-abundance competitive relationships would not vary (1) by grass species and (2) with the number of water applications (i.e., plant productivity). Because the factors that limit plant growth are different at varying levels of water availability, we hypothesized that (3) the magnitude of variation in competitive relationships would change with water availability. If observed, this change would reflect different magnitudes of variation in the underlying factors that limit plant growth (e.g., soil nutrient availability) at different levels of soil water.

Materials and Methods

Procedures

Plastic pots (7.6-L) were filled with a pasteurized soil mixture containing equal parts of a silt loam soil (classification unknown), washed concrete sand, and Canadian sphagnum peat moss. The wetting agent AquaGro® 2000 G was added at 0.5 kg m\(^{-3}\), and the mixture was steam pasteurized at 80°C.

Percent germination of leafy spurge, Kentucky bluegrass, and western wheatgrass was estimated by sowing 30 seeds of each species in 1-L pots in a greenhouse (1 pot per species). Seeds were covered with approximately 2 mm of soil, and the soil was misted with water every other day for 20 days. We then calculated the following ratio for each type of seed: seedlings emerged:seeds planted. These ratios were used to adjust seeding rates and achieve target plant densities.

Target densities were 0, 670, 1340, and 2010 plants m\(^{-2}\) for each species. Three addition series matrices consisting of all possible seed density combinations were established (4 Kentucky bluegrass densities × 4 western wheatgrass densities × 4 leafy spurge densities = 64 pots per density matrix × 3 density matrices = 192 pots per experiment) in the 7.6-L pots (Spitters 1983). These density matrices also contained between 2 and 8 isolated plants of each species (depending on survival).

Density matrices were arranged in a completely randomized design in a greenhouse. Pots were periodically rearranged to average the influence of environmental gradients across all plants. Greenhouse photoperiod was extended to 14 hours with 1000-W metal halide bulbs, and temperature was maintained at approximately 22°C during the light period and 18°C during the dark period. Seeds were uniformly scattered over the soil surface and covered with about 2 mm of soil. To encourage
germination, we misted the soil surface with water every other day for 27 days. After the misting period (28 days after planting), all pots were watered to capacity. Pots in 2 density matrices were watered to capacity 61 days after planting, and 1 of these matrices was watered to capacity a 3rd time 94 days after planting. Hereafter, pots watered once, twice, or 3 times will be said to have received dry, intermediate, or wet treatments, respectively. After receiving final water applications, plants in the pots were harvested by clipping at the soil surface upon showing signs of severe water stress, or 127 days after planting, whichever occurred first. All plants were then dried to a constant weight at 50°C. The experiment was conducted during the winter of 1999 (run 1) and was repeated during the winter of 2000 (run 2).

Soil Water Sampling

To determine gravimetric water content, pots were weighed the day before each watering, and pots that were watered were reweighed the day after watering. Pots were weighed after harvest, and soil was removed and thoroughly mixed. We took a uniform sample from each pot, each of which was weighed, dried to a constant weight at 50°C, and reweighed to determine soil dry weight (soil dry weight = post-harvest soil weight × sample dry weight / sample wet weight – pot weight). Two soil samples were submitted to the Montana State University Soil Testing Laboratory where pressure plate analysis was used to determine gravimetric water content at matric pressures of 0.01, 0.03, 0.1, 0.5, and 1.5 MPa.

Plant Sampling

Number of plants per pot of each species was counted at harvest. Aboveground biomass of each species was determined after plants were dried to a constant weight at 50°C.

Soil Data Analysis

The van Genuchten (1980) water retention relationship was fit to pressure plate analysis data by minimizing the sum of squared errors ($r^2 = 0.98$) to estimate the relationship between matric pressure and gravimetric water content. An index of overall matric pressure was calculated by computing the average of matric pressure measurements. Measurements from each measurement period were included until a pot received its final water application and pot matric pressure reached 1.5 MPa (permanent wilting point). If pots did not reach 1.5 MPa by the end of the experiment, then all matric pressure measurements were included in the average.

Plant Data Analysis

Plant data were fit to the following inverse yield models by minimizing the sum of squared errors (Spitters 1983).

$$\frac{1}{pw_{ls}} = B + B_{ls,den} \cdot den_{ls} + B_{kb,biot} \cdot bio_{kb} + B_{ww,biot} \cdot bio_{ww}$$ (1)

$$\frac{1}{pw_{kb}} = B + B_{kb,den} \cdot den_{kb} + B_{ls,biot} \cdot bio_{ls} + B_{ww,biot} \cdot bio_{ww}$$ (2)

$$\frac{1}{pw_{ww}} = B + B_{ww,den} \cdot den_{ww} + B_{ls,biot} \cdot bio_{ls} + B_{kb,biot} \cdot bio_{kb}$$ (3)

Inverse plant weight was used to linearize relationships. The subscripts ls, kb, and ww denote leafy spurge, Kentucky bluegrass, and western wheatgrass, respectively. The response variable $1/pw$ is the inverse of average individual plant weight per pot. Regression coefficients without subscripts (Bs) are intercept terms and Bs subscripted with den and bio are competition coefficients that describe the influence of plant density and biomass, respectively. Density was used to describe intraspecific competition instead of biomass because of the complex relationship between $pw$ and bio. Models were independently fit to data from the dry, intermediate, and wet treatments to yield a total of 9 models (9 models = 3 water treatments × 3 species).

Regression coefficients of 1, 2, and 3 were compared to test the null hypothesis that per-unit-plant-abundance competitive effects do not vary with the number of water applications and also to test the null hypothesis that per-unit-plant-abundance competitive effects do not vary by species. Density coefficients were compared within a species across water treatments, and biomass coefficients were compared across species when comparing within a water treatment and within a species when comparing across water treatments. Standard deviations of regression coefficients were evaluated to test the null hypothesis that the magnitude of variation in competitive relationships would change with water availability.
The following model:
\[
\text{amp}_{sp} = B + B_{ls\text{-}bio} \times \text{bio}_{ls} + B_{kb\text{-}bio} \times \text{bio}_{kb} + B_{ww\text{-}bio} \times \text{bio}_{ww}
\] (4)
in which amp is an index of average matric pressure, was used to assess whether or not the 3 species used the same amount of water in producing a unit of biomass. This model was fit to data from each water treatment to yield a total of 3 models.

A bootstrap algorithm was used to compare regression coefficients (Efron and Tibshirani 1993, Hjorth 1994). Cases from data sets were randomly selected with replacement and inserted into a bootstrap sample until the number of cases was equal to the number of cases in the original data set, and the model of interest was then fit to the bootstrap sample to generate least-squares estimates of X and Y. For this example, the variables X and Y are regression coefficients that are being compared, and the least-squares estimate of X is greater than that of Y. These steps were repeated 1000 times to generate vectors (x and y) of bootstrap regression coefficient estimates with 1000 elements. The number of cases in which \(x_i > y_j\) was evaluated for \(i = 1, 2,...,1000\) and \(j = 1, 2,...,1000\). This resulted in \(x \times y = 1,000,000\) comparisons. The quantity \((1 - (\text{number of cases where } x_i > y_j) / 1,000,000) \times 2\) is a 2-tailed hypothesis test of \(H_0: (X = Y)\). When regression coefficients were compared to 0, a similar approach was used with each observation in the vector of bootstrap regression coefficient estimates compared to 0. P-values were calculated independently for each comparison and were not adjusted to provide “tablewise” or “experimentwise” error protection.

**Results**

Regression coefficients in tables will be referenced without the letter B, the comma (,) will be replaced by a hyphen (-), and the coefficients will not be subscripted. For example, \(B_{ls\text{-}bio} = ls\text{-bio} \) and \(B_{ls\text{-}den} = ls\text{-den} \). Because the dependent variable is inverse plant weight, the magnitude of competition coefficients and competition intensity is positively related.

In interpreting results it is important to remember that matric pressure is negatively related to soil water content. Therefore, as water availability decreases, matric pressure increases.

**Influence of Competition on Leafy Spurge Individual Plant Weight**

Leafy spurge density became less negatively related to leafy spurge individual plant weight as the number of water applications increased in run 1 (Table 1), while the intensity of this intraspecific competition was unrelated to water treatment in run 2. Kentucky bluegrass and western wheatgrass biomass negatively affected leafy spurge plant weight in the dry and intermediate treatments but did not negatively affect plant weight in the wet treatment in run 1. The competitive effect of grasses on leafy spurge did not vary significantly with water treatments in run 2, and per-unit-biomass effects of Kentucky bluegrass and western wheatgrass on leafy spurge were similar to one another in both runs.

**Influence of Competition on Kentucky Bluegrass Individual Plant Weight**

Kentucky bluegrass density had a similar negative effect on Kentucky bluegrass individual plant weight in the dry and intermediate treatments but had little or no effect in the wet treatment in run 1 (Table 2). Kentucky bluegrass density had a negative effect on Kentucky bluegrass plant weight in run 2, but the relationship was independent of water treatment. The effect of western wheatgrass and leafy spurge biomass on Kentucky bluegrass plant weight diminished as the number of water applications increased in both runs. Western wheatgrass was more competitive with Kentucky bluegrass than was leafy spurge in both runs.

**Influence of Competition on Western Wheatgrass Individual Plant Weight**

Western wheatgrass density had a greater negative effect on western wheatgrass individual plant weight in the dry and intermediate treatments than in the wet treatment in both runs (Table 3). Similarly, Kentucky bluegrass and leafy spurge became less competitive with western wheatgrass as the number of water applications increased in both runs. Kentucky bluegrass was less competitive with western wheatgrass than was leafy spurge in the dry and intermediate treatments in both runs, and
Table 1. Competition coefficient estimates, $r^2$, standard deviations ($s$) of coefficient estimates, and comparisons of coefficients at the 5% level of confidence. The coefficients are from a multiple linear regression model fit to data from a greenhouse study with inverse of leafy spurge individual plant weight as the dependent variable and leafy spurge plant density and western wheatgrass and Kentucky bluegrass plant biomass as the independent variables.

<table>
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<th>Water treatment</th>
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<th>Comparisons of regression coefficients</th>
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Table 2. Competition coefficient estimates, $r^2$, standard deviations ($s$) of coefficient estimates, and comparisons of coefficients at the 5% level of confidence. The coefficients are from a multiple linear regression model fit to data from a greenhouse study with inverse of Kentucky bluegrass individual plant weight as the dependent variable and Kentucky bluegrass plant density and western wheatgrass and leafy spurge biomass as the independent variables.

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<td>=ww_intermediate =ww_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td></td>
<td>Wet</td>
<td></td>
<td>ls-bio: 2.91, 1.59</td>
<td></td>
<td>=ww_intermediate =ww_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td>2</td>
<td>Dry</td>
<td>0.60</td>
<td>kb-den: 0.18, 0.15</td>
<td></td>
<td>=kb_intermediate =kb_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td></td>
<td>ww-bio: 17.07, 2.56</td>
<td></td>
<td>=kb_intermediate =kb_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td></td>
<td>Dry</td>
<td></td>
<td>ls-bio: 46.99, 9.17</td>
<td></td>
<td>=ls_intermediate =ls_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td>0.71</td>
<td>kb-den: 0.20, 0.05</td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>Intermediate</td>
<td></td>
<td>ls-bio: 11.45, 2.59</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Wet</td>
<td>0.41</td>
<td>kb-den: 0.10, 0.05</td>
<td></td>
<td>=ls_intermediate =ls_wet =ww_intermediate =ww_wet</td>
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<tr>
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<td>Wet</td>
<td></td>
<td>ww-bio: 1.86, 0.33</td>
<td></td>
<td>=ww_intermediate =ww_wet =ww_intermediate =ww_wet</td>
</tr>
<tr>
<td></td>
<td>Wet</td>
<td></td>
<td>ls-bio: 3.36, 1.89</td>
<td></td>
<td>=ww_intermediate =ww_wet =ww_intermediate =ww_wet</td>
</tr>
</tbody>
</table>
Influence of Water Availability on Variation in Competition Intensity

With few exceptions, estimates of the standard deviation of competition coefficients decreased or stayed the same as the number of water applications increased. This indicates that there was less variation in competitive effects when water was applied more frequently. On the other hand, there was no clear relationship between \( r^2 \) of models and the number of water applications. Whereas the competitive interactions were less variable when water was applied more frequently, factors not included in models 1, 2, and 3 (e.g., plant diseases and genetics and nutrient availability) caused greater random error when water was applied more frequently.

Influence of Plant Biomass on Average Matric Pressure

Leafy spurge and grasses had a similar effect on average matric pressure in the dry treatment in run 1 (Table 4). In the dry treatment in run 2, leafy spurge used more water in producing a unit of biomass than did the grasses, and western wheatgrass used more water in producing a unit of biomass than did Kentucky bluegrass. In the intermediate and wet treatments in run 1, leafy spurge used less water in producing a unit of biomass than did grasses, while the opposite was true for these 2 treatments in run 2.

**DISCUSSION**

There are 2 prevalent competing theories regarding the influence of plant productivity on competition. One theory contends that competition becomes more intense as plant productivity increases because plant biomass increases, which results in increased competition for light and space (Grime 1973, 2001, Keddy 1989). The other theory predicts that competition is similar in habitats with high and low productivity because belowground competition for nutrients is more intense in habitats with low standing crop (Newman 1973, Wilson and Tilman 1991). In this view, the intensity of above- and belowground competition is negatively related, so that net competition intensity remains similar along productivity gradients. Several field studies have relied on the response of a target plant to removal of
surrounding vegetation as a measure of competition intensity along productivity gradients, and differences in competition intensity have (Del Moral 1983, Reader and Best 1989) and have not (Wilson and Tilman 1991, 1993) been detected.

In this greenhouse study competition intensity stayed similar or decreased as the number of water applications (i.e., plant productivity) increased (Tables 1–3), and therefore the null hypothesis that competition would be unaffected by the frequency of water application is rejected. Competition staying similar is consistent with one of the prevalent theories that relates competition intensity to plant productivity (Newman 1973, Wilson and Tilman 1991), but an inverse relationship between competition intensity and frequency of water application is inconsistent with both theories. This finding is also inconsistent with studies in which interspecific competition among 3 desert plants and intraspecific competition of a desert annual intensified when water was added in the field (Kadmon 1995, Briones et al. 1998). All plants were still quite small (<25 cm in height) by the end of these greenhouse experiments, signifying that competition for light may not have offset competition for water in treatments that resulted in high water availability (i.e., treatments with low seeding densities and 3 water applications).

Competition intensity decreased when water supply was increased in a field experiment that studied competition between tree seedlings and herbaceous species (Davis et al. 1998), which is similar to the findings of these greenhouse experiments. One explanation for the inverse relationship between competition intensity and water availability found in both experiments is supplied by a theory predicting that competition intensity will decrease when high supplies of new resources become available (Huston and DeAngelis 1994). If competition does become less intense as the number of precipitation events increases in the field, competition between grasses and leafy spurge is less intense in years and locations with both frequent and substantial precipitation events.

These greenhouse experiments contribute to our ultimate goal of developing models that predict invasive plant and grass biomass response to management strategies in the field. The fact that competition coefficient standard deviations tended to decrease as the number of water applications increased suggests that models will predict plant biomass more accurately in wet years (Tables 1–3; Welden and Slauson 1986), which suggests that models will account for variation in plant biomass equally well in years with few and many precipitation events. It appears that the influence of competition became less variable when water was applied more frequently, but other factors that cause variation in plant weight (disease, genetics, nutrients) had a more pronounced effect when water was applied more frequently. The null hypothesis that variation in competition intensity is related to the number of water applications is not rejected.

The competitive influence of Kentucky bluegrass biomass on leafy spurge plant weight was similar to that of western wheatgrass biomass regardless of water treatment (Table 1). The null hypothesis that per-unit abundance competitive effects of the grasses are similar is not rejected. Biesboer et al. (1994) reported that 5 grasses did not affect leafy spurge shoot

### Table 4. Model $r^2$ and coefficient estimates for multiple linear regression model with average matric pressure as the dependent variable and plant biomasses as independent variables in a greenhouse study.

| Water treatment | $r^2$ | kb-bio | ww-bio | ls-bio |
|-----------------|------|--------|--------|--------!|
| Run 1
| Dry             | 0.37 | -0.05a | 0.01a  | -0.02a |
| Intermediate    | 0.40 | 0.09a  | 0.04a  | -0.03b |
| Wet             | 0.37 | 0.09a  | 0.09a  | -0.01b |
| Run 2
| Dry             | 0.41 | 0.05a  | 0.16b  | 0.44c  |
| Intermediate    | 0.24 | 0.05a  | 0.06a  | 0.18b  |
| Wet             | 0.44 | 0.08a  | 0.14a  | 0.55b  |

*Coefficients within a row that are followed by the same letter are not significantly different at the 5% level of confidence.*
weight in a greenhouse, but these grasses did decrease root weight with the magnitude of the effect depending on the grass species. Different grass species also affect leafy spurge aboveground biomass production differently in the field (Ferrell et al. 1992, Biesboer et al. 1994, Lym and Tober 1997). However, unlike the analysis reported in this manuscript, the effect of a grass species was confounded by the amount of biomass the species produced in these studies, and all of the grasses may have competed similarly if competitive effects were expressed on a per-unit-biomass basis. Several studies support the theory that per-unit-biomass competitive effects of many plant species are similar (Goldberg 1987, Mitchell et al. 1999, Aguiar et al. 2001, Peltzer and Kochy 2001). If our results hold true in the field, Kentucky bluegrass, western wheatgrass, and probably other grasses may be considered collectively in estimating the influence of grass production on leafy spurge production.

Results from this greenhouse study might improve our ability to predict the influence of environmental conditions on relationships between invasive plants and grasses if conclusions can be extrapolated to natural conditions. However, conclusions should be viewed very cautiously because there are substantial differences between greenhouse and field conditions. An even-aged, somewhat even-sized cohort of juvenile plants was used in this study, while most biomass is attributed to mature plants in the field. This resulted in a contrived partitioning of soil resources because leafy spurge was not capable of accumulating resources from substantially deeper depths than grasses, as is the case in the field (Bakke 1936). Grasses and leafy spurge attained similar heights in this study, while leafy spurge is usually taller than grasses in the field. Pots with high densities of leafy spurge may have misrepresented high-density patches of leafy spurge, because leafy spurge may be a better competitor for light under field conditions. Also, evidence suggests that shading can decrease plant water stress in dry soils, which indicates that competition for water may diminish with plant height (Salisbury and Chandler 1993). Results from this study provide some insight into the influence of water availability on competition between grasses and leafy spurge, but it will be necessary to compare results to field experiment results to substantiate the findings. If field and greenhouse results are similar, results from future greenhouse studies might be viewed with more confidence.

**Literature Cited**


Received 16 September 2003
Accepted 7 October 2004
Orobanche fasciculata Nutt. (clustered broomrape or clustered cancerroot) belongs to the Orobanchaceae or broomrape family, members of which are parasitic on the roots of flowering plants (Reuter 1986, Welsh et al. 1993, Wolfe and dePamphilis 1997). The genus Orobanche contains over 100 species (Parker and Riches 1993), all of which are annual or monocarpic (Kuijt 1969), obligate, herbaceous parasites (Parker and Riches 1993). Orobanche fasciculata parasitizes a variety of host species, especially species of Artemisia (Welsh et al. 1993). It is purplish to yellowish in color and grows in a split stem to between 5 cm and 10 cm above the soil surface (Welsh et al. 1993).

Seeds of Orobanche spp. germinate after being stimulated chemically from 1 to 2 weeks by exudates from the host’s root (Sauerborn 1991, Parker and Riches 1993). Upon germination Orobanche seed develops a radicle that grows in the direction of the chemical stimuli of the host’s root. This distance is generally not more than a few centimeters from the Orobanche seed. Once the radicle reaches the host root, a haustorium (that part of the parasite that grows inside the host) is produced, which attaches the Orobanche seedling to the host. The haustorium is also the site where the bud and shoot of the parasite emerge and elongate (Parker and Riches 1993). A parasite can have primary and secondary haustoria, the former located where the shoot of the parasite emerges and the latter where the roots from the parasite attach to the roots of the host. Parasites that develop more advanced haustoria have little or no root system. Such is the case with O. fasciculata (Kuijt 1969). The main purpose of the haustorium is uptake of water, organic compounds, and mineral nutrients from the host plant.

Orobanche species are found in over 58 countries, with some species having large populations in areas of intensive agriculture (Jordan and Nile River valleys) and other species being endemic to small, localized areas (Sauerborn 1991). Generally, they grow in infertile soils, such as the alkaline soils of the Middle East. Few Orobanche species grow in acidic soils, as the lower pH causes the seeds to germinate at distances so far from the host that contact between parasite seedling and host root is not accomplished, thus resulting in the seedling’s eventual death (Parker and Riches 1993). Most Orobanche species are found in the Mediterranean region with its characteristic climate, but are also found in humid, subtropical, arid, semiarid, and temperate climates. They are associated with both irrigated and nonirrigated lands (Sauerborn 1991). Orobanche fasciculata is endemic to North America, ranging...
in distribution from the Yukon Territory, south to Mexico, east to Michigan, and west to California. Within this range, *O. fasciculata* is associated with sand dune ecosystems, arid shrublands and grasslands, pinyon/juniper woodlands, aspen, and fir communities up to 3260 m in elevation (Reuter 1986, Welsh et al. 1993). However, *O. fasciculata* is an uncommon species. As such, several states have listed it as rare (Indiana and the province of Ontario), threatened (Wisconsin and Michigan), and even endangered (Illinois; Sheviak 1978, Bacone and Hedge 1980, Argus and White 1982, Brynildson and Alverson 1982, Beaman et al. 1985). No listing of *O. fasciculata* as threatened or endangered is known in Utah.

Other than taxonomic studies, little research has been done on *O. fasciculata*. Reuter (1986) studied the habitat and reproductive ecology of *O. fasciculata* in a sand dune ecosystem in Wisconsin. She concluded that *O. fasciculata* has the ability to reproduce parthenogenetically, that it produces many seeds which disperse across long distances and yet as a species would be considered uncommon, a fact thought to be associated with parasite seed dispersal and host growth dynamics.

*Artemisia pygmaea* Gray, or pygmy sagebrush, is found in Arizona, Nevada, and Utah growing in shallow, infertile calcareous soils (Ward 1953). It has been collected in 13 counties from Utah’s desert and mountainous regions where it grows on clay loam soils associated with Green River shale, igneous and calcareous gravels, and dolomitic outcrops or gravels (Welsh et al. 1993). A dwarf shrub (0.5–2 dm tall), *A. pygmaea* grows in patches and is not useful as browse (McArthur et al. 1979). Welsh et al. (1993) indicate *A. pygmaea* is often associated with rare plant species, such as *O. fasciculata*.

The purpose of this study is to analyze the host-parasite relationships between *A. pygmaea* Gray and *O. fasciculata* Nutt. regarding nutrient uptake and transfer between host and parasite on populations found in the Uinta Basin of Utah, USA.

**STUDY SITE**

The study site is located 20.5 km (33 miles) south of Ouray, Utah, on the Ute Indian Reservation in Duchesne County. The site is on a gentle 2%–3%, west-facing slope on the plateau of Hill Creek. The study site covers 0.8–1.2 ha and is located on highly clay loam Green River shale soils underlain by fractured sandstone layers called Hill Creek Rock, which has been mined and used as ornamental building material. *Artemisia pygmaea* is the dominant shrub on the site, although its population densities are low. Low-growing shrubs and grasses including *Eriogonum corymbosum*, *Elymus spicatus*, *Atriplex confertifolia*, *Stipa hymenoides*, and *Artemisia tridentata* dominate areas adjacent to the study area (Brotherson 1967).

Soils are shallow, sandy clay loams, residual in nature, sandstone based, and rocky. Calcareous and basic, they contain elevated levels of soluble salts in the upper 46 cm of the soil profile. Clay increases with depth to 15 cm and then decreases. Cation exchange capacity ranges from 20 to 25 meq per 100 grams of soil and increases with depth. Calcium, potassium, and sodium concentrations decrease with depth while magnesium increases (Brotherson 1967). Macronutrient concentrations are low (<215 ppm), with nitrogen, phosphorus, potassium, and sodium being the lowest. Micronutrients were more abundant than macronutrients.

The area receives between 30 and 40 cm of rain annually, 10–20 cm falling as snow from October to April and 10–20 cm from summer thunderstorms between May and September. During the winter months temperature lows average between −18° and −16°C, while mean highs range from −2° to 0°C. In the summer lower temperatures average 9° to 13°C and the highs range from 27° to 31°C (Greer et al. 1981).

The study site has had a grazing history of primarily wild horses, mule deer, and rabbits. Occasional sheep and cattle grazing has also occurred.

**METHODS**

**Field Methods**

Data were taken in August 1986 and 1987. Data taken during 1986 reflect nutrient flows from the soil to *A. pygmaea* roots to *O. fasciculata*. The 1987 samples include data taken to reflect nutrient flows from soil to roots to stems and leaves of the host plants along with the soil-root-parasite relationship. We collected a total of 20 soil samples, 10 per year. Fifty-eight plant samples were also collected during the
2-year study, 20 in 1986 and 38 in 1987. Those taken in 1986 include 10 of *A. pygmaea* roots and 10 of *O. fasciculata*; the 1987 samples mirrored the 1986 samples with the addition of 9 stem and 9 leaf samples of *A. pygmaea*. Plant and soil samples were collected as a set, with the plants sampled being randomly selected from across the study site with the use of a random numbers table. Once the plants to be sampled were selected, a soil sample was collected within the root zone and packaged for transport to the laboratory for later analysis to determine available nutrients for the plant.

Plant samples were divided into roots, stems, leaves, and associated parasites and were individually packaged in air-breathing bags for transport to the laboratory where they were dried at room temperature (23°C) in a Napco model 630 drying oven.

**Lab and Statistical Methods**

All soil and plant samples collected from the field were analyzed by the Brigham Young University Soil and Plant Analysis Laboratory for nutrient content of both macro- and micro-nutrients in 1990. Macronutrients analyzed were nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), sodium (Na), and magnesium (Mg). Micronutrients were zinc (Zn), iron (Fe), manganese (Mn), and copper (Cu). Exchangeable calcium, magnesium, potassium, and sodium in the soil were extracted using a buffered neutral 1.0 normal ammonium acetate solution (Jackson 1958, Hesse 1971, Jones 1973). DTPA (diethylene-triaminepentaacetic acid) was used to extract iron, zinc, manganese, and copper from the soil (Lindsay and Norvell 1969). Soil phosphorus and nitrogen were determined using sodium bicarbonate and macro-Kjeldahl procedures, respectively (Olsen et al. 1954, Jackson 1958).

Individual plant samples were ground and passed through a 20-mm-mesh screen using a Thomas-Wiley mill. Ion concentrations of nitrogen, phosphorus, potassium, calcium, magnesium, sodium, iron, zinc, manganese, and copper in the plant tissue were identified using procedures described by Graham et al. (1970).

Mean concentrations, standard deviations, minimums, and maximums were calculated for each element analyzed in both the soil and plant material. Tukey’s Honestly Significant Difference (HSD) tests were conducted on the means of each element to identify any that varied significantly in concentration between the soil, *A. pygmaea* plant parts, and *O. fasciculata*. The results were then analyzed to determine the amount of each element that *O. fasciculata* was taking from the roots of *A. pygmaea* and the concentrations of each nutrient along the gradient (i.e., from roots to stems to leaves) of *A. pygmaea*. Plant nomenclature follows Welch et al. 1993.

**RESULTS AND DISCUSSION**

Mean ion concentrations (ppm) for each nutrient studied in the soil, in the roots, stems, and leaves of *A. pygmaea*, and in *O. fasciculata* are found in Table 1. This table shows patterns of nutrient enrichment with respect to ion movement from soil to *A. pygmaea* roots then to stems and leaves, and from soil to *A. pygmaea* roots to parasite. The soil nutrient concentration levels (macro- and micronutrients) were low, reflecting the poor quality of the soil. Nitrogen, phosphorus, potassium, and zinc showed an increase in concentration along the flow gradient in *A. pygmaea*. Magnesium, iron, and manganese increased through the stems and then decreased in the leaves to concentrations less than the roots. Such selective exclusion of magnesium and iron may be related to high potassium levels in the leaf in that elevated levels of potassium have been shown to induce deficiencies in these ions. The low levels of manganese may be due to *A. pygmaea*’s selective exclusion of manganese along with a decreased capacity to translocate manganese from stems to leaves (Treshow 1970).

Calcium and sodium increased from the soil to the roots and then decreased or remained static, respectively, as they flowed from the stems to the leaves. Individual element uptake can often be inhibited by the presence of other elements (Bargagli 1998). The significant decrease of calcium may be due to high potassium levels in the leaf in that elevated levels of potassium have been shown to induce deficiencies in these ions. The low levels of manganese may be due to *A. pygmaea*’s selective exclusion of manganese along with a decreased capacity to translocate manganese from stems to leaves (Treshow 1970). Copper increased in concentration in
the roots, decreased in the stems, and then showed a slight increase again in the leaves.

Table 1 illustrates the relationship between nutrient concentrations in the soil and corresponding nutrient concentrations in the roots of *A. pygmaea* and in the parasite *O. fasciculata*. As shown, nutrient levels in the plant mirror nutrient levels in the soil. In other words, if nutrient concentrations are high in the soil, they will be correspondingly high in the plant tissues. This phenomenon, termed luxury consumption, asserts that a plant will absorb and accumulate more nutrients than it needs simply because the nutrients are more abundant in the soil (Treshow 1970, Brotherston 1992). Further, the uptake of the micronutrients zinc, iron, manganese, and copper is enhanced when these ions exist in the divalent form, a form that allows them to adhere more strongly to roots.

Table 2 also shows that although nutrients are higher in *O. fasciculata* than in the soil, this parasite does exclude some nutrients over others. For example, *O. fasciculata* takes up calcium on a 1:1 ratio with the soil (Table 2). This is probably due to interactions between high levels of sodium and potassium, which have been shown to inhibit calcium absorption in other plants (Boynton and Burrell 1944).

Compared with *A. pygmaea* roots, *O. fasciculata* absorbed significantly higher concentrations ($\bar{x} = 2.83$ times) of phosphorus, potassium, and sodium. Otherwise, *O. fasciculata* contained the lowest concentrations ($\bar{x} = 0.59$ times) of magnesium and copper.

### Table 1. Means (ppm) and significant differences in nutrient concentrations for plant parts and the soil. All values are significantly different ($P \leq 0.05$) from each other unless otherwise noted.*

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Soil</th>
<th>Root</th>
<th>Stems</th>
<th>Leaves</th>
<th><em>O. fasciculata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>6</td>
<td>7200</td>
<td>8800</td>
<td>12200</td>
<td>4600</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>7</td>
<td>400</td>
<td>600</td>
<td>700</td>
<td>1000</td>
</tr>
<tr>
<td>Potassium</td>
<td>214</td>
<td>4400 c</td>
<td>8900 cf</td>
<td>12600 f</td>
<td>19600</td>
</tr>
<tr>
<td>Calcium</td>
<td>9116 a</td>
<td>28500 g</td>
<td>23100 fg</td>
<td>16700 fi</td>
<td>13300 ai</td>
</tr>
<tr>
<td>Sodium</td>
<td>30 bj</td>
<td>1000</td>
<td>300 f</td>
<td>300 hf</td>
<td>1600</td>
</tr>
<tr>
<td>Magnesium</td>
<td>900</td>
<td>7400 ec</td>
<td>8800 cf</td>
<td>6000 ef</td>
<td>3600 i</td>
</tr>
<tr>
<td>Zinc</td>
<td>0.41</td>
<td>24 c</td>
<td>37 cf</td>
<td>33 f</td>
<td>18</td>
</tr>
<tr>
<td>Iron</td>
<td>11</td>
<td>2242 c</td>
<td>2834 c</td>
<td>1260 i</td>
<td>1196 i</td>
</tr>
<tr>
<td>Manganese</td>
<td>11</td>
<td>66 e</td>
<td>101 i</td>
<td>63 ei</td>
<td>-43 i</td>
</tr>
<tr>
<td>Copper</td>
<td>3</td>
<td>22</td>
<td>15 fh</td>
<td>18 f</td>
<td>13 h</td>
</tr>
<tr>
<td>Macronutrients*</td>
<td>10300</td>
<td>41400 edg</td>
<td>41200 fgh</td>
<td>35700 ef</td>
<td>38100 dhi</td>
</tr>
<tr>
<td>Micronutrients</td>
<td>26</td>
<td>2355 g</td>
<td>2977 g</td>
<td>1374 fh</td>
<td>1269 i</td>
</tr>
</tbody>
</table>

*Values are not significantly different between the following:
  a = soil – Orobanche
  b = soil – roots
  c = roots – stems
  d = roots – Orobanche
  e = roots – leaves
  f = stems – leaves
  g = stems – roots
  h = stems – Orobanche
  i = leaves – Orobanche
  j = stems – soil

### Table 2. Ratios (ppm plant part/ppm soil) between each plant part of *A. pygmaea* compared with the soil for all nutrients. For example, a ratio of 1200 indicates that *A. pygmaea* roots have that much greater concentration of a nutrient than found in the soil.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Root</th>
<th><em>O. fasciculata</em></th>
<th>Stem</th>
<th>Leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>1200</td>
<td>767</td>
<td>1467</td>
<td>2033</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>57</td>
<td>143</td>
<td>86</td>
<td>100</td>
</tr>
<tr>
<td>Potassium</td>
<td>21</td>
<td>92</td>
<td>3</td>
<td>59</td>
</tr>
<tr>
<td>Calcium</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Sodium</td>
<td>33</td>
<td>53</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Magnesium</td>
<td>8</td>
<td>4</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Zinc</td>
<td>59</td>
<td>44</td>
<td>66</td>
<td>80</td>
</tr>
<tr>
<td>Iron</td>
<td>204</td>
<td>109</td>
<td>258</td>
<td>115</td>
</tr>
<tr>
<td>Manganese</td>
<td>6</td>
<td>4</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Copper</td>
<td>7</td>
<td>4</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>Macronutrients</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Micronutrients</td>
<td>91</td>
<td>49</td>
<td>115</td>
<td>5</td>
</tr>
</tbody>
</table>
times) of all other macro- and micronutrients (N, Ca, Mg, Zn, Fe, Mn, and Cu; Table 3). Concentrations of all nutrients were significantly different ($P < 0.05$) between roots of *A. pygmaea* and *O. fasciculata*. Differences between nutrient concentrations in *O. fasciculata* and other plant organs also existed. However, such differences appear to be of little value in explaining patterns of nutrient uptake in the parasite since it parasitizes roots only.

Table 3 presents the nutrient concentration gradients (i.e., parasites to root, stem to root, and leaf to stem ratios) of *A. pygmaea* and *O. fasciculata* according to the path of nutrient flow. All nutrient concentration gradients show a negative relationship ($<1.0$) between host roots and parasite except for phosphorus, potassium, and sodium (Table 3). Magnification of these nutrients by the parasite may be luxury consumption or it may be that they are important to *Orobanche*’s physiology. Phosphorus, for example, is a major component of adenosine triphosphate (ATP), which must be present in high amounts to provide energy for nutrient uptake. Potassium and sodium would likely be absorbed in high quantities because they act in osmotic regulation of cellular fluids and produce an osmotic potential in the body of the parasite that when in combination with the parasite’s production of mannitol will aid in the uptake of all other needed nutrients (Parker and Riches 1993). Without such enhancement of the parasite’s osmotic potential, the parasite would be unable to take up enough nutrients for its survival. In contrast to *A. pygmaea*, *O. fasciculata* is very selective in its nutrient uptake, as is illustrated by its excluding or reducing uptake of major quantities of most of the sampled nutrients in the study (Fig. 1).

**Table 3.** Ratios (ppm/ppm) of mineral nutrient concentrations in the soil and plant parts according to nutrient flow from the soil to roots to stems to leaves and to *Orobanche fasciculata*.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Roots/Soil</th>
<th>Stems/Roots</th>
<th>Leaves/Stems</th>
<th><em>Orobanche</em>/Roots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>1200</td>
<td>1.22</td>
<td>1.39</td>
<td>0.64</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>57</td>
<td>1.5</td>
<td>1.17</td>
<td>2.5</td>
</tr>
<tr>
<td>Potassium</td>
<td>21</td>
<td>2.02</td>
<td>1.42</td>
<td>4.45</td>
</tr>
<tr>
<td>Calcium</td>
<td>3</td>
<td>0.81</td>
<td>0.72</td>
<td>0.47</td>
</tr>
<tr>
<td>Sodium</td>
<td>33</td>
<td>0.3</td>
<td>1</td>
<td>1.6</td>
</tr>
<tr>
<td>Magnesium</td>
<td>8</td>
<td>1.2</td>
<td>0.68</td>
<td>0.49</td>
</tr>
<tr>
<td>Zinc</td>
<td>59</td>
<td>1.13</td>
<td>1.22</td>
<td>0.75</td>
</tr>
<tr>
<td>Iron</td>
<td>195</td>
<td>1.26</td>
<td>0.44</td>
<td>0.53</td>
</tr>
<tr>
<td>Manganese</td>
<td>6</td>
<td>1.53</td>
<td>0.62</td>
<td>0.65</td>
</tr>
<tr>
<td>Copper</td>
<td>8</td>
<td>0.68</td>
<td>1.2</td>
<td>0.59</td>
</tr>
<tr>
<td>Macronutrients</td>
<td>4</td>
<td>1</td>
<td>0.57</td>
<td>0.92</td>
</tr>
<tr>
<td>Micronutrients</td>
<td>91</td>
<td>1.26</td>
<td>0.05</td>
<td>0.54</td>
</tr>
</tbody>
</table>

![Fig. 1](image-url). Ratio of nutrients in *Orobanche fasciculata* compared with nutrient levels in *Artemisia pygmaea* roots.
For example, *Orobanche* species are limited in their use of inorganic nitrogen (NO₃⁻) because they do not synthesize nitrate reductase (Parker and Riches 1993). Instead, *O. fasciculata* and other *Orobanche* spp. utilize ammonium nitrogen, which can be metabolized with glutamine synthetase in the GS1 form. It is also presumed that these parasites can obtain their necessary amino acids directly from the host's xylem and phloem (Parker and Riches 1993). The nitrogen balance between *A. pygmaea* and *O. fasciculata* is delicate as increased nitrogen levels in the host plant would allow the host to reverse the osmotic potential in favor of itself, thus decreasing the vigor and even killing the parasite (Sauerborn 1991).

Host plants can be damaged or even killed when parasitized by *Orobanche* spp. When heavily parasitized, host plant growth declines or even stops and severe wilting occurs in some instances (Sauerborn 1991). Biomass production has been shown to be severely reduced or even eliminated in crop plants when heavily parasitized by *Orobanche* (Sauerborn 1991).

**LITERATURE CITED**


Food storage takes 2 general forms. Larder-hoarding is the accumulating of a relatively large quantity of food at one or a few locations as the result of numerous foraging excursions. The larder is almost always in some sort of cavity (e.g., underground chamber, hollow tree). An important trait of a larder is that its contents change over time; larder size is the sum of repeated provisioning visits minus consumption. Scatter-hoarding, on the other hand, is characterized by spacing food items in or on the surface of some substrate such as soil, bark, or foliage. Natural cavities are seldom involved. Because each cache is usually the result of one visit to the site, contents of caches generally do not change; they are simply present or absent. Hereafter, we will use “cache” to refer to scatter-hoarded food and “larder” to refer to larder-hoarded food.

The caches of many scatter-hoarding rodents and birds have been well characterized (e.g., Haftorn 1956, Macdonald 1976, Cowie et al. 1981, James and Verbeek 1983, Daly et al. 1992, Waite and Reeve 1993, Vander Wall 2003) because it is often easy to observe these animals make caches and examine cache contents. This has led to a wealth of studies that have examined cache spacing (Stapanian and Smith 1978, Clarkson et al. 1986), cache retrieval (Sherry et al. 1981, Brodin 1994), cache pilferage (Vander Wall and Jenkins 2003), and other aspects of cache dynamics. On the other hand, little is known about the contents and characteristics of larders (Horne et al. 1998). Because larders are often large and valuable to the hoarder, animals hide them better than caches. Animals can be seen delivering food to their burrow, but manipulation of food within larders is seldom observed (the larders of red squirrels, Tamiasciurus hudsonicus, and acorn woodpeckers, Melanerpes formicivorus, are notable exceptions). The burrow or nest of an animal often has to be excavated to examine the contents of a larder, although in some instances artificial dens or nests can be used to monitor larder contents (Horne et al. 1998). For most animals, destruction of larders during excavation makes it difficult to monitor how they change over time. Descriptions of larder contents (e.g., Broadbooks 1958, Smith 1968, Elliott 1978, Post et al. 1993, Dearing 1997) are often little more than snapshots of the larders at a

PILFERING OF STORED SEEDS AND THE RELATIVE COSTS OF SCATTER-HOARDING VERSUS LARDER-HOARDING IN YELLOW PINE CHIPMUNKS

Stephen B. Vander Wall1, Elaine C. H. Hager1, and Kellie M. Kuhn1

ABSTRACT.—Yellow pine chipmunks (Tamias amoenus) scatter-hoard food during summer and autumn but must form a larder as a winter food source before winter begins. Yellow pine chipmunks do not larder-hoard large quantities of food during the summer; apparently because a summer larder could not be defended from pilferers. We tested the assumption that the rate of pilferage from an unguarded larder would be significantly greater than the rate of pilferage from surface caches (which are also unguarded by yellow pine chipmunks) during the summer and autumn. Buried plastic buckets were used as artificial nests containing larders of 1000 sunflower seeds or 200 Jeffrey pine (Pinus jeffreyi) seeds. The pilferage of larder contents was monitored daily and compared to pilferage of surface caches. Animals (yellow pine chipmunks and deer mice, Peromyscus maniculatus) removed sunflower seeds from caches much faster than from larders, but caches of Jeffrey pine seeds disappeared much more slowly than pine seeds in larders. Further, animals removed pine seeds from larders more quickly than they did sunflower seeds from larders. The difference between seed species was probably because sunflower seeds have much stronger odors, which rodents readily detect, and because chipmunks prefer pine seeds over sunflower seeds. Yellow pine chipmunks must spend a considerable portion of their time foraging for seeds and may not be able to defend a large larder during summer.

Key words: food storage, granivory, Peromyscus maniculatus, pilferage, Tamias amoenus.
It is important to have a better understanding of larders and how animals use them. Seasonal changes in larder size and composition have implications for survival (Novakowski 1967, Seeley and Visscher 1985, Dearing 1997). Some animals that prepare both caches and larders switch from scatter-hoarding to larder-hoarding food seasonally (Clarke and Kramer 1994, K.M. Kuhn unpublished data). In some taxa (e.g., sciurid and heteromyid rodents), different species store food in different ways. For example, fox squirrels (Sciurus niger) scatter-hoard (Stapanian and Smith 1978), whereas red squirrels usually larder-hoard food (Smith 1968, Hurly and Robertson 1990). If we are to understand better the selective pressures that influence how animals store food and how the mode of food storage evolves, we need to understand how larders are constructed, used, and sometimes exploited by other animals.

Yellow pine chipmunks (Tamias amoenus) are common residents of semiarid pine forests in the western United States (Broadbooks 1958). They have relatively large home ranges (≈2 ha) that they share with dozens of conspecifics and other rodents (Broadbooks 1970, Kuhn unpublished data). They forage primarily for seeds. Observational studies (Kuhn unpublished data) and experiments using radioactive seeds (Vander Wall 1992, 1993) provide no evidence that yellow pine chipmunks larder-hoard food during summer and early autumn. Instead, they scatter-hoard seeds throughout their home range at depths of 5–40 mm. Burrow fidelity during summer and autumn is low. They construct winter nests in late autumn of plant fibers in a small chamber ≈20–40 cm deep with 1 or 2 narrow tunnels ≈30–50 cm long leading to the surface (Broadbooks 1958, Kuhn unpublished data). Burrow entrances are very inconspicuous, and the individuals that occupy the burrows are seldom seen near them. Instead, they spend most daylight hours foraging, grooming, and interacting with other chipmunks (Kuhn unpublished data). Several weeks before the onset of winter (late October to early November) yellow pine chipmunks construct a larder in their winter nest chamber. During this time yellow pine chipmunks transfer food from aboveground caches and store it in the floor and walls of their winter nests. Because they do not deposit body fat and do not forage during winter, failure to accumulate a sufficiently large winter larder would likely result in death before spring.

The objective of this study was to investigate ecological reasons why yellow pine chipmunks refrain from larder-hoarding during summer. Because these chipmunks store food throughout summer and autumn, and because they need to have a large larder by winter, it is not clear why they do not form a larder during summer and maintain it until winter when they need it. A large accumulation of seeds in a nest chamber would be attractive to other animals, and so it would have to be defended to prevent pilferage. But larder defense takes time and restricts the movements of the larder owner, which would reduce the amount of time for searching for unhoarded seeds. Scatter-hoarding ensures that food resources are available to the forager during periods of food scarcity. This strategy may be particularly important in habitats where food availability is unpredictable. Defending a larder in summer and autumn likely would reduce the amount of food that could be gathered and scatter-hoarded. The larder defensibility hypothesis is based on the assumption that the rate of pilferage from an unguarded larder would be significantly greater than the rate of pilferage from caches (which are also unguarded in yellow pine chipmunks) during the summer and autumn.

We tested this assumption by constructing artificial but realistic yellow pine chipmunk nests and monitoring pilfering from larders placed in those nests while simultaneously monitoring pilfering of scatter-hoarded seeds. The relatively simple and shallow nests of yellow pine chipmunks make them ideal for studying larder pilferage using artificial nests constructed with man-made materials. A series of experiments (Vander Wall 2000, Vander Wall et al. 2003) has demonstrated that chipmunks and other rodents will readily adopt plastic buckets as temporary nests. In addition to their construction, these artificial nests are unrealistic in one important way: there is no nest “owner.” However, this is not an issue in this experiment because we seek to test the consequences of having a summer larder that is not guarded because the owner spends most
of its time away searching for more food (as do yellow pine chipmunks during summer and autumn).

**METHODS**

We conducted this study in the Whittell Forest and Wildlife Area in Little Valley, Washoe County, about 30 km south of Reno, Nevada, USA (39°15′0″N, 119°52′35″W). Little Valley is in the Carson Range in extreme western Nevada at an elevation of ≈1975 m. Open Jeffrey pine (*Pinus jeffreyi*) forests with an understory of antelope bitterbrush (*Purshia tridentata*), greenleaf manzanita (*Arctostaphylos patula*), tobacco bush (*Ceanothus velutinus*), and Sierra chinquapin (*Castanopsis sempervirens*) dominate the lower slopes of the valley. Soil consists of decomposed granite. The region experiences summer droughts from June to October.

We constructed artificial nests using 7.6-L plastic buckets 24 cm high × 22 cm wide (Fig. 1). A partition divided the nest bucket into 2 nearly equal-sized chambers. We placed seeds (the larder) in the bottom compartment. A slightly inclined segment of PVC pipe ≈60 cm long connected the upper chamber to the ground surface. The whole “nest” was buried under 2–5 cm of soil (bottom of nest was 25–30 cm deep) next to a shrub such that the PVC pipe met the ground near the base of the shrub among plant litter. We attempted to make the nest entrance inconspicuous by covering the entrance pipe with plant litter.

To determine what size (species) rodents might pilfer artificial chipmunk larders, we used entrance pipes of 3 inside diameters: small (25 mm), medium (34 mm), and large (50 mm). In previous studies we found that an entrance pipe 34 mm wide was appropriate for yellow pine chipmunks. Henceforth, we refer to these as small-(S), medium-(M), and large-(L) diameter nests, indicating the size of the largest rodents that could potentially enter them. Small nests accommodate deer mice (*Peromyscus maniculatus*, 15–20 g) and juvenile yellow pine chipmunks. Medium nests permit entry of these rodents and adult yellow pine chipmunks (40–50 g). Large nests accommodate all these rodents plus long-eared chipmunks (*Tamias quadrimaculatus*, 70–90 g) and golden-mantled ground squirrels (*Spermophilus lateralis*, 150–250 g).

We selected 2 sites about 500 m apart and established 30 nest buckets at each site during mid-June 2002. At each site there were 10 nests of each of the 3 entrance sizes spaced ≈20 m apart and arranged in regular order along a transect (i.e., S, M, L, S, M, L, etc.). We conducted 2 series of trials with nest buckets at the same sites, the 1st with larders consisting of ≈1000 black-oil sunflower seeds (≈55 g) and the 2nd with larders consisting of 200 Jeffrey pine seeds (≈20 g). These larders are smaller than real winter larders, which often contain >200 g of seeds. Jeffrey pine seeds are native, highly preferred seeds frequently eaten by rodents at this site, and sunflower seeds are

![Fig. 1. Cross section of a nest bucket: o = outer lid buried about 2 cm under the ground surface (s); i = inner lid constructed of styrofoam insulation 17 mm thick to moderate nest temperature; p = plywood partition (6 mm thick with a 64-mm-diameter hole) dividing nest into upper (u) and lower (l) compartments; t = plastic tray containing the larder; e = entrance made of PVC pipe connecting upper nest chamber to ground surface. The nest entrance was placed under a shrub. Three diameters of entrance pipes were used to permit access by different sized rodents.](image-url)
nonnative seeds, which we included to determine whether seed species influenced the rate of pilferage. At each site there were typically 20–50 yellow pine chipmunks, 2–13 long-eared chipmunks, 5–10 deer mice, and 2–10 golden-mantled ground squirrels (Vander Wall 2003, Roth and Vander Wall in press), all of which occupy large, overlapping home ranges and exhibit little or no territoriality.

We initiated the sunflower seed trials on 1 August and the Jeffrey pine seed trials on 20 August 2002 by placing a larder in the lower nest chamber. We visited each nest daily to inspect larders, and, if we suspected that rodents had entered the nest (e.g., presence of seed shells, feces, foreign material in the nest chamber), we estimated how many seeds had been eaten, removed, or, in 2 nests, added. We estimated eaten sunflower seeds by measuring the volume of seed shells (we determined in the laboratory that 1 mL of seed shells equals ≈5 intact seeds). Eaten pine seeds were determined by counting shells. The number of intact seeds remaining was estimated by measuring seed volume and comparing it to the initial volume of the larder (180 mL for sunflower and 92 mL for Jeffrey pine). We identified rodent visitors by size of fecal pellets in nests, presence of nest material moved into nests (only by deer mice), and directly by seeing animals in or fleeing from nests. At the end of each visit, we returned all remaining intact seeds to the larder, reburied the nest bucket, and made sure the entrance was open (some rodents filled the PVC pipe with soil). At the end of the sunflower trials, we removed any remaining sunflower seeds and left the nests empty for 2 weeks until the pine seed trials began. Nest buckets remained fairly cool, registering 19°–23°C during midday, several degrees below ambient temperature.

To evaluate the impact of pilfering from larders relative to scatter caches, we established transects of artificial caches in the same area. Each cache contained 10 sunflower (initiated 1 August) or 2 Jeffrey pine seeds (initiated 20 August) buried 10 mm deep. We established 60 caches at each site (total 120 caches) spaced ≈5 m apart. The cache sites changed between the sunflower and pine seed trials. We did not touch seeds or the ground near the cache sites during preparation to prevent human odors from providing cues to foraging rodents (Duncan et al. 2002). We also did not use any man-made markers (e.g., pin flags or stakes) to relocate caches because rodents use them to find buried seeds (Vander Wall and Peterson 1996). Instead, we used natural objects (e.g., twigs, pine cones, pebbles) in unique patterns to mark stations (Vander Wall 1994). We monitored these caches daily immediately after examining the larders. We conducted larder and caching trials simultaneously during dry periods (no rain during preceding 14 days) to limit the olfactory signal emitted by seeds (Vander Wall et al. 2003). Digging by rodents at the cache site indicated that seeds had been removed.

Seeds pilfered from larders could be eaten, moved to a new larder, or scatter-hoarded on the ground surface. We hypothesized that during summer and early autumn most seeds removed from larders would be scatter-hoarded because that is what happens to experimental seeds placed at bait stations aboveground (e.g., Vander Wall 2003). To determine the fate of seeds pilfered from larders, we established 5 nest buckets at a location >300 m from the other sites and placed 200 radioactively labeled Jeffrey pine seeds in each nest. Each nest bucket was equipped with a large-diameter (50 mm) entrance to permit entry of all rodent species. We arranged these nests in a “+” pattern with 1 nest at the center and the other 4 nests 20 m apart in cardinal directions. The seeds in each bucket were dyed a different color so that the origin of any relocated seeds could be determined. We labeled seeds by soaking each lot in 3 mL distilled water and scandium-46 until the seeds were thoroughly wetted, and then they were allowed to dry for 2 days. A single seed could be detected from ≈30 cm using a Geiger counter. We placed the seeds in nest buckets on 4 September 2002. Nine days later we examined all larders to record how many seeds had been removed or eaten and began surveying the vicinity within ≈30 m of nests with Geiger counters looking for seed caches and seed shells. When we found a cache, we removed the seeds and recorded seed color, number of seeds in the cache, and cache depth. Finally, we mapped the location of caches relative to the central larder using cardinal direction as axes.

We assessed the effects of larder entrance diameter (small, medium, or large), storage type
(larder or scattered caches), and seed species (sunflower or Jeffrey pine) on the rate of seed removal using survival analysis and a Weibull distribution (Allison 1995). The response variables were the lower and upper limits on the time a larder or cache was known to have been present, expressed as days since the beginning of a trial. As some larders were removed piece-meal over 2 or more days, we arbitrarily deemed larders removed if 50% or more of the seeds had been taken. We made post-hoc comparisons among larder entrance sizes, storage types, and seed species by calculating chi-square statistics as described in Allison (1995). Bonferroni alpha levels were used to assess the significance of chi-square tests: $\alpha = 0.003 \ (0.05/15 \ tests)$.

**Results**

In sunflower seed trials, rodents took 89.7% of seeds from large-diameter nests, 82.3% from medium-diameter nests, and 72.5% from small-diameter nests within 6 days (Table 1). In addition, rodents ate 10.3% of seeds in large-diameter nests, 12.9% in medium-diameter nests, and 15.7% in small-diameter nests. Removal rates decreased with decreasing nest entrance diameter (Fig. 2A). Removal rates from large nests averaged 93.4% per day, medium nests averaged 57.3%, and small nests 30.1%. Rodents removed seeds from nests with large entrances 2.4 times faster than from nests with medium entrances ($\chi^2 = 25.23, P < 0.0001$), and they removed seeds from nests with medium entrances 2.0 times faster than those from small entrances ($\chi^2 = 15.03, P < 0.001$). Larders in nests with large entrances usually were emptied within 1 day after being discovered (12 of 20 cases), whereas nests with medium-sized entrances were emptied or nearly emptied within 1 day of being discovered on only 6 occasions. Nests with small entrances, on the other hand, disappeared more slowly, taking an average of >5 days to be depleted once discovered.

We found chipmunk feces in large- and medium-diameter nests on 10 occasions and observed juvenile yellow pine chipmunks emerging from nests with small-diameter entrances. We found deer mouse feces in small-diameter nests on 2 occasions, and deer mice brought nest material into small nests on 10 occasions. One of the small-diameter nest buckets was adopted by a deer mouse as its nest. Over a period of 6 days, the mouse repeatedly brought nest material into the bucket and added seeds to the larder, increasing its volume by ≈50%. New seeds brought into the nest included sunflower (from other nest buckets) as well as those of bitterbrush and manzanita. We found no evidence that golden-mantled ground squirrels had entered large-diameter nests.

Scatter-hoarded sunflower seeds (10 seeds per cache) disappeared very rapidly (Fig. 2A). Removal rates along 2 transects were the same: 98.3% per day. Seeds in scattered caches did not disappear significantly faster than seeds in large-diameter nests ($\chi^2 = 3.48, P = 0.062$), but sunflower seeds in caches disappeared 1.9 times faster than seeds in medium-diameter nests ($\chi^2 = 23.32, P < 0.0001$).

In the Jeffrey pine seed trials, rodents took 94.0% of seeds ($n = 200$) from large-diameter nests, 92.5% from medium-diameter nests, and 74.5% from small-diameter nests (Table 1) within 4 days. In addition, rodents ate 6.0%, 7.5%, and 25.5% of seeds in large-, medium-, and small-diameter nests, respectively. Removal rates from medium- and large-diameter nests were the same, averaging 96.2% per day ($\chi^2 = 0.32, P > 0.50$). Removal of seeds from nests

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Table 1. Fate of artificial sunflower seed larders (1000 seeds) after 6 days and Jeffrey pine seed larders (200 seeds) after 4 days. Data are means ± 1s. Eaten refers to seeds eaten in the nest chamber. There were 10 artificial nests for each nest entrance diameter and seed species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Nest entrance diameter</th>
<th>Eaten</th>
<th>Remaining</th>
<th>Taken</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunflower</td>
<td>large</td>
<td>103 ± 82</td>
<td>0 ± 0</td>
<td>897 ± 82</td>
</tr>
<tr>
<td></td>
<td>medium</td>
<td>129 ± 69</td>
<td>48 ± 214</td>
<td>823 ± 197</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>157 ± 133</td>
<td>118 ± 293</td>
<td>725 ± 264</td>
</tr>
<tr>
<td>Jeffrey pine</td>
<td>large</td>
<td>12 ± 8</td>
<td>0 ± 0</td>
<td>188 ± 8</td>
</tr>
<tr>
<td></td>
<td>medium</td>
<td>15 ± 8</td>
<td>0 ± 0</td>
<td>185 ± 8</td>
</tr>
<tr>
<td></td>
<td>small</td>
<td>51 ± 25</td>
<td>0 ± 0</td>
<td>149 ± 25</td>
</tr>
</tbody>
</table>
with small entrances (78.2% per day) was slower, only about 0.36 and 0.32 times as fast as seeds in medium- and large-diameter nests ($\chi^2 = 29.43$ and $\chi^2 = 32.90$, respectively, $P < 0.0001$ for both). Larders with large or medium entrances were always emptied within 1 day of being discovered, but only 8 small-diameter nests were emptied within 1 day of being discovered.

In the pine seed trials, deer mouse feces occurred in 1 large, 1 medium, and 6 small nests. One small-diameter nest bucket, the same one as in the sunflower trial, was adopted by a deer mouse, which moved in nest material and more seeds. By day 3 it had increased the volume of the larder by 91%. New seeds included sunflower (apparently from the previous trial), Jeffrey pine (from other nests or native seeds), and those of bitterbrush and manzanita. By day 4 the nest and larder had been destroyed by a black bear ($Ursus americanus$). We found chipmunk feces in 14 large-diameter nests, 19 medium-diameter nests, and 4 small-diameter nests. Golden-mantled ground squirrel feces were found in 4 large-diameter nests.

Scatter-hoarded Jeffrey pine seeds (2 seeds per cache) were removed very slowly. Mean rate of removal was 0.55% per day. Jeffrey pine seeds in large-diameter nests disappeared 86 times faster than seeds in scattered caches ($\chi^2 = 297.28$, $P < 0.0001$), seeds in medium-diameter nests disappeared 76 times faster than seeds in scattered caches ($\chi^2 = 305.16$, $P < 0.0001$), and seeds in small-diameter nests disappeared 27 times faster than seeds in scattered caches ($\chi^2 = 202.52$, $P < 0.0001$).

The rate of sunflower and Jeffrey pine seed removal from nests with large entrances was not significantly different, but pine seeds were removed 3.3 times faster from medium-diameter ($\chi^2 = 14.46$, $P < 0.0001$) and 2.3 times faster from small-diameter ($\chi^2 = 23.20$, $P < 0.0001$) nests than were sunflower seeds. However, sunflower seeds were removed 43 times faster from surface caches than pine seeds ($\chi^2 = 352.03$, $P < 0.0001$).

In the radioactive Jeffrey pine seed experiment, 4 of the nests were emptied within 3 days, and the 5th nest was not emptied until 9 days after initiation of the experiment. We found a total of 380 caches in the vicinity of the 5 experimental nests (Fig. 3). Caches from the first 4 nests appeared to be the work of yellow pine chipmunks (based on size, depth, and distance from the source), whereas caches from the 5th nest appeared to be made by deer mice. The chipmunk caches ($n = 258$) contained 429 seeds with $1.7 \pm 0.9$ seeds per cache (mean $\pm 1\sigma$). Mean distance between source nests and caches was $14.6 \pm 9.4$ m (range = 0.8–53.2 m). The deer mouse caches were smaller ($1.2 \pm 0.7$ seeds per cache), shallower, and closer to the nest bucket ($5.9 \pm 3.4$ m, range 0.5–17.1 m away). Overall, we accounted for 77% of the seeds originally placed in larders.

**DISCUSSION**

Several lines of evidence from the nest buckets indicated that chipmunks had pilfered seeds from most of the medium- and large-diameter larders. The yellow pine chipmunk is the most abundant species of rodent in the study area (Vander Wall 2002). Long-eared chipmunks are less common and cannot fit...
into the medium-sized nest entrances. We found chipmunk feces in numerous buckets, and we observed yellow pine chipmunks near or emerging from several nests. The much slower rate of removal from the small-diameter nests suggests that the smaller and less common deer mice were active in those nests. In the Jeffrey pine trial, we found some evidence that yellow pine chipmunks also were entering small nests. These individuals were probably males, which are ≈10%–15% smaller than females, or juveniles. Golden-mantled ground squirrels had visited several of the large nests in the Jeffrey pine trial, but most activity in the large nests appeared to be that of yellow pine chipmunks. This general pattern was confirmed in the radioactive seed experiment; caches from 4 larders matched those made by yellow pine chipmunks, and 1 set of caches was similar to those made by deer mice.

We obtained strikingly different results when larders and caches were composed of sunflower seeds than Jeffrey pine seeds (Fig. 2). Rodents removed sunflower seeds from larders fairly rapidly, especially those with large-or medium-diameter entrances, but scatter-hoarded sunflower seeds disappeared significantly faster than larder-hoarded sunflower seeds. These data suggest that it would be safer for a chipmunk to larder-hoard sunflower seeds in a burrow with a small- or medium-sized entrance than scatter-hoard them on the ground surface because the larder-hoarded seeds would be pilfered at a slower rate. In contrast, pilferage rates of scatter-hoarded Jeffrey pine seeds were extremely slow, while larder-hoarded seeds disappeared very rapidly.

Seeds in nests with small- and medium-diameter entrances disappeared faster in the Jeffrey pine trials than in the sunflower trials, probably because Jeffrey pine seeds are highly...
preferred by forest rodents. Yellow pine chipmunks readily accept sunflower seeds but sometimes ignore them when Jeffrey pine seeds are available. We suspect that the dramatic difference in rate of pilferage of surface caches of sunflower and Jeffrey pine seeds occurred because sunflower seeds emit relatively strong odors. Native seeds, represented here by Jeffrey pine, have probably experienced strong selection for minimizing emitted odors (we are exploring this possibility in a separate series of experiments, and preliminary results support this hypothesis). Detected seeds are more likely to be eaten whereas undetected seeds might eventually germinate. Thus, the strength of seed odors is likely to be inversely correlated with plant fitness. Sunflower seeds, on the other hand, have been subjected to strong artificial selection for size and oil content and any selection against odor has probably been relaxed. The difference in removal rates between sunflower and pine seeds indicates that the nonnative sunflower seeds are not good surrogates for native seeds in certain kinds of experiments, and preliminary results support this hypothesis. Detected seeds are more likely to be eaten whereas undetected seeds might eventually germinate. Thus, the strength of seed odors is likely to be inversely correlated with plant fitness. Sunflower seeds, on the other hand, have been subjected to strong artificial selection for size and oil content and any selection against odor has probably been relaxed. The difference in removal rates between sunflower and pine seeds indicates that the nonnative sunflower seeds are not good surrogates for native seeds in certain kinds of experiments, and that they could give misleading results in some studies of caching behavior because of the strong odors they emit. In this study we regard the test of relative pilferage rates in larders versus caches using sunflower seeds to be invalid because the pilferage rates of scattered caches differed so strikingly from those of caches of natural Jeffrey pine seed (Fig. 2). We recommend that sunflower seeds not be used in studies of cache pilferage; native seeds are more likely to yield meaningful results.

Scatter-hoarded Jeffrey pine seeds appear to be relatively safe from pilferers compared with unguarded larder-hoarded seeds. Scatter-hoarded Jeffrey pine seeds buried in dry soil appear to emit little or no detectable odors (Vander Wall 1995, 1998, 2000). If it should rain, however, seeds become more detectable by other rodents, but this does not appear to be too damaging to yellow pine chipmunks because the caches of all individuals are equally vulnerable (Vander Wall 2000, Vander Wall and Jenkins 2003). Larder-hoarded seeds, on the other hand, are vulnerable under all conditions. When eastern chipmunks (Tamias striatus), which maintain larders at all seasons whenever excess food is available, discover an unguarded nest of a conspecific, they make repeated pilfering trips with filled cheek pouches until the owner of the burrow returns (Elliott 1978, Clarke and Kramer 1994). Kangaroo rats behave similarly (Daly et al. 1992). In our experimental larders, a yellow pine chipmunk could remove all 200 Jeffrey pine seeds in 8–10 visits, which could take as little as an hour. Deer mice, which can carry only 2–4 Jeffrey pine seeds per load (Vander Wall and Longland 1999), work much more slowly but could deplete a larder containing 200 seeds in a single night.

The radioactive seed study demonstrated a simple point: most seeds pilfered from larders are scatter-hoarded. This seems to be true for both yellow pine chipmunks and deer mice. Because a foraging yellow pine chipmunk cannot guard its larder, and because larder-hoarded seeds are likely to be pilfered and scatter-hoarded anyway, it would be more efficient for the foraging chipmunk simply to scatter-hoard the seeds itself. This behavior would benefit a forager in 3 ways. First, it would save time traveling to and from the nest, time that could be invested in other activities such as additional foraging, grooming, or predator surveillance. If food is found at some distance from the nest, which is generally the case for yellow pine chipmunks, a scatter-hoarding forager is likely to be much more efficient than one that larder-hoards because of reduced travel time. Second, by caching seeds itself (rather than having them cached by a pilferer), the forager retains a recovery advantage relative to other animals with which it shares its home range. The individual that makes caches retains spatial memories of its cache sites (Jacobs and Liman 1991, Vander Wall 1991, Jacobs 1992). Pilferers lack these memories and must depend on olfaction, which works poorly when the soil is dry (Vander Wall 1995, 1998), and random digging to find buried seeds. As long as seeds do not emit strong odors (which is probably true of most native seeds in dry soil), the animal that caches a seed has a recovery advantage (Vander Wall and Jenkins 2003, Vander Wall et al. 2003). Third, by scatter-hoarding, the cacher shields itself from catastrophic losses. An inherent advantage of scatter-hoarding over larder-hoarding is that when losses occur from a larder, they can be catastrophic (Henry 1986), whereas losses from scattered caches, although damaging, are usually far less serious.

In this experiment we did not move nest buckets to new locations between trials. This
procedure allowed for the possibility that rodents could learn the locations of artificial nests and return to pilfer larders repeatedly in successive trials. We believe that this condition accurately reflected the natural situation. Rodents can be expected to learn the location and explore the characteristics of all burrows and refuges in their home range (Elliott 1978). Knowledge of these sites may become important when an animal is at risk of predation or requires a resting site. Yellow pine chipmunks appear to change sleeping sites frequently during summer (Kühn unpublished data), and summer sleeping burrows are probably visited frequently by other chipmunks during the day while the owner is away foraging. If we had moved our artificial nests to new sites between trials we might have underestimated the probability of larder pilferage in real summer nests.

On 2 occasions during this study, black bears destroyed nest buckets and consumed the larder. We suspect that bears first detected the odor of plastic and learned to associate the buckets with a food reward. Actual chipmunk nests are probably far more difficult for bears to detect, but this result does demonstrate an important principle: larders are vulnerable to a wider variety of pilferers than are caches and when pilferage of a larder does occur, it is usually catastrophic. From the chipmunk’s perspective, this sort of pilferage is far more destructive than pilferage from caches because the larder is consumed. When caches are pilfered by other rodents, most of the seeds are recached elsewhere, and, consequently, the seeds are still potentially available to the animal that originally stored them (Vander Wall and Jenkins 2003).

Food-storage behavior of yellow pine chipmunks and eastern chipmunks is very different. Eastern chipmunks larder-hoard extensively during all seasons and also scatter-hoard some food during the spring and summer (Elliott 1978, Clarke and Kramer 1994). Eastern chipmunks have a relatively small home range; when they scatter-hoard, they cache most food near the nest entrance and defend these caches from potential pilferers. Cache residence time (i.e., amount of time an average seed remains at a cache site) is relatively short (=1 hour; Clarke and Kramer 1994). Yellow pine chipmunks, on the other hand, forage over much larger areas (=2 ha), appear to scatter-hoard seeds throughout their home range, and do not attempt to defend their caches. Mean cache residence time is unknown but is on the order of weeks (Vander Wall 2002, Vander Wall and Joyner 1998). Yellow pine chipmunks must eventually accumulate a large mass of food to ensure survival over winter, but they delay formation of the winter larder until a few weeks before the onset of winter conditions, apparently because of the high rates of pilferage an undefended larder is likely to experience.

It is unclear whether the nest buckets might have influenced the rate of pilferage of artificial larders. The odor of the plastic buckets seems weak to humans but might be easily detected by rodents. We assume that most rodents initially detected artificial nests by searching visually for a burrow opening, which animals are likely to explore as potential refuges, future nest sites, or food sources. The odor of seeds and plastic may have been secondary cues, but this has not been established. Our daily digging and soil disturbance when we checked nest buckets might also have served as cues to foraging rodents. Studies of the dynamics of rodent larders (i.e., changes because of foraging or pilferage) are complicated by the destructive nature of sampling larders over time, and so some form of artificial burrow and larder may need to be part of any experimental design. Future studies should try to develop more realistic nest chambers that can be checked easily with minimal disturbance.

ACKNOWLEDGMENTS

We thank Adam York for his help in working out details of the experimental design in pilot studies. Ying Wang assisted us with fieldwork. We thank the Whittell Forest, University of Nevada, for permission to conduct the study in Little Valley. This research was supported by NSF grant DEB-9708155.

LITERATURE CITED


Received 11 May 2004
Accepted 15 November 2004
Shelley et al. (2005) observed that the discovery of a single individual of many millipede species from the region between the Mississippi River and the Central Plains, where distributions are usually poorly known, can alter knowledge so significantly that published documentation is in order. This was necessary with the polydesmids Scytonotus granulatus (Say) (Polydesmidae) and Pleuroloma flavipes Rafinesque (Xystodesmidae) (Shelley et al. 2004, 2005), and is now necessary for the blaniulid julidan Virgoiulus minutus (Bradt). Distribution statements for this species in most modern accounts are either general lists of states without specific localities or brief summary range descriptions. As part of the 1st author’s ongoing survey of myriapods in the “Ark-La-Tex” region, V. minutus was reported from 17 new counties in Arkansas by McAllister et al. (2003), and the millipede has recently been discovered in southeastern Oklahoma and 4 counties in eastern Texas; coupled with a preserved sample from Angelina County, Texas, these represent new state records. As the only detailed locality data for V. minutus are those of McAllister et al. (2003), it is desirable to publish these and other unreported sites to fully document its distribution; to this end the 2nd author borrowed material from the ensuing list of repositories, which contained the 1st samples from Mississippi.

Williams and Hefner (1928), Chamberlin and Hoffman (1958), Loomis (1968), and Shelley (1978a, 1978b) considered V. minutus (then referenced as Nopoiulus minutus) to be a European introduction, but we believe that V. minutus is an endemic Nearctic species and the only indigenous blaniulid in the New World, for the following reasons. To begin with, the millipede has never been encountered in Europe, as have all the known Palearctic introductions, nor, in fact, outside the coherent range depicted in Figure 1. Second, while V. minutus does occur in urban environments, particularly in the Southeast, it also is found well removed from human influence, in contrast to the introduced North American blaniulids that occur exclusively in association with man either in urban environments or in agricultural areas where they sometimes feed on crops, especially fruits like strawberries. Finally, the distribution pattern of V. minutus (Fig. 1) counters those of all widely introduced millipedes in North America, which occur across

ABSTRACT.—Virgoiulus minutus (Brandt 1841) (Julida: Blaniulidae), the only indigenous representative of the family in the New World, occurs, or can be expected, in parts or all of 24 states east of the Central Plains plus the District of Columbia; it is documented for the 1st time from Mississippi, Oklahoma, and Texas. The northern-, southern-, and westernmost localities are in Berrien County, Michigan; Putnam County, Florida; and Angelina/Rusk Counties, Texas, respectively. New England, Utah, Wyoming, Canada, and Mexico are deleted from the range, and specific localities are reported to augment previous generalized citations; those from Mexico represent misidentifications of Nopoiulus kochii (Gervais, 1847), an introduced European species that is recorded from Mexico City, Distrito Federal. Records of V. minutus from Pennsylvania, Virginia, South Carolina, Georgia, Alabama, West Virginia, Ohio, Illinois, Michigan, and Missouri are the 1st definite localities from these states; a sample from “Anechar,” believed to be a misspelling of “Arrochar,” a neighborhood in Staten Island, is considered the 1st definite record from New York. The published statement of occurrence in Delaware in general is the only known record of an indigenous diplod pod from this state.

Key words: Virgoiulus minutus, Nopoiulus minutus, Nopoiulus kochii, Blaniulidae, Mississippi, Texas, distribution.

1Biology Department, Texas A&M University–Texarkana, Texarkana, TX 75505.
2Research Lab, North Carolina State Museum of Natural Sciences, 4301 Reedy Creek Road, Raleigh, NC 27607.
3Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.
the continent to varying degrees and north into Canada, as opposed to a large, coherent area in a single general region. If *V. minutus* were introduced, we would expect it to occur across the continent—for example in New England, California, the Pacific Northwest, and Canada—and exclusively in association with man in cities and towns. Consequently, the distribution pattern in *V. minutus*, in both urban and rural habitats in one broad, definable area east of the Central Plains, is not that of an introduced millipede but rather, we think,
definitive evidence that it is indeed an indigenous species.

Enghoff and Shelley (1979) first raised the possibility that V. minutus might be native, and Enghoff (1984a;400) stated that “if not introduced, it is the only indigenous blaniulid in America.” In an account of the introduced blaniulid Nopoiulus kochii (Gervais, 1847), Shelley (1988) reported that V. minutus is endemic to the Nearctic, and Hoffman (1999) stated that Virgoiulus was presumed to be endemic to southeastern North America. Five other blaniulids are known from this continent, all native European species that have been introduced by man and now occur to varying extents across the U.S., Canada, and Mexico, primarily in urban habitats (Chamberlin and Hoffman 1958, Enghoff and Shelley 1979, Enghoff 1984a, 1984b, Shelley 1988, 1990, 2002, Hoffman 1999): Archiboreoiulus pallidulus (Brade-Birks, 1920), Blaniulus guttulatus (Fabricius, 1798), Proteroiulus fuscus (Am Stein, 1857), Choneiulus palmatus (Némec, 1895), and N. kochii. These blaniulids are all narrow, fragile, cylindrical (“juliform”) diplopods whose widths are roughly equivalent to the lead of a mechanical pencil, and V. minutus is distinguished, even in juvenile stages, by the arrangement of the ocelli in a single row and by the extremely short, microscopic, pleurotergal setae that are invisible under a stereomicroscope even at magnifications of around 100X. The setae are easily seen on other ocellate blaniulids, for example P. fuscus, whose ocelli are arranged in 2 unequal rows, and N. kochii. As noted by Enghoff and Shelley (1979), males are less numerous than females in most blaniulid species, but they are particularly rare in V. minutus, which is surely parthenogenetic. To our knowledge only 2 males have ever been reported, one of which was illustrated by Enghoff and Shelley (1979, figs. 5–10).

Occasionally, V. minutus is found in deciduous leaf litter, but the great majority of specimens are encountered in association with decaying logs and stumps, principally pines and primarily beneath loose bark. Its preference for subcortical pine habitats was first recognized by Say (1821:106), who stated that it was “found commonly under pine bark on the eastern shore of Virginia.” Chamberlin (1921) noted that it was often found under bark of decaying trees but did not mention pines specifically, and Shelley (1978a) reported that the millipede is particularly abundant in southeastern pine forests that have been ravaged by the southern pine beetle (Dendroctonus frontalis Zimmerman, 1868), in which dead pine logs are plentiful. This association with pines makes V. minutus one of the few North American millipedes that collectors can search for deliberately with a high probability of success, by visiting predominantly pine forests and peeling bark off decaying logs. The individuals from Oklahoma and Bowie and Cass Counties, Texas, were discovered in this manner; those from Oklahoma were under bark of a pine stump on the edge of a wooded area; those from Bowie County were under bark of decaying pine logs in a predominantly loblolly pine forest (Pinus taeda L.) with scattered southern red oaks (Quercus falcata Michaux) and other hardwoods; and the specimen from Cass County was in litter associated with these trees. However, the individuals from Newton and Rusk Counties, Texas, were encountered under bark of decaying oak logs.

Though plentiful, published records of V. minutus are somewhat difficult to trace because of its contorted nomenclatural history. The first account was by Say (1821), who described it as “Julus pusillus,” but this binomial is preoccupied by J. pusillus Leach, 1815; Brandt’s (1841) name, minutus, is thus the oldest available specific name. The main reason for the uncertainties, however, is confusion between V. minutus and N. kochii, which has an even more complicated nomenclatural history (see Enghoff and Shelley 1979, Enghoff 1984a). The name minutus was neglected by European diplopodologists until Chamberlin (1921, 1922) brought it into the synonymy of N. kochii, and Enghoff and Shelley (1979) showed that minutus and kochii are 2 different species. Enghoff (1984a) referred minutus to the new, monotypic genus, Virgoiulus, which occupies a basal position in the phylogeny of the blaniulid subfamily Nopoiulinae and is an endemic North American genus.

We present below distributional data for V. minutus beginning with deletions that were probably based on misidentifications of other blaniulids or narrow-bodied representatives of other julidan families like the Nemastomatidae. Subsequently, we compile published records beginning with generalized range statements and then provide detailed locality records. Missing data were not provided on vial labels,
and the number of specimens, all being females or juveniles, is provided after the institutional acronym except for samples with too many individuals to count, indicated by “several.” Based on occurrences in adjacent states, we predict that *V. minutus* will be discovered in southeastern Wisconsin (at least Kenosha County) and perhaps more broadly across the southern border of the state; occurrences in southeastern Iowa and throughout the eastern periphery of Oklahoma are also plausible. The overall distribution (Fig. 1) encompasses around 850 miles (1360 km) north–south and 1060 miles (1696 km) east–west, and can be characterized as follows: the United States east of the Central Plains from, north–south, central Missouri, northern Illinois and Ohio, and Long Island, New York, to the latitude of Gainesville, Alachua County, Florida (actually known from Putnam County, the adjacent county to the east), the Gulf Coast, and southern Louisiana; east–west, from the area of New York City, the Outer Banks of North Carolina, and northeastern Florida to central Missouri and the eastern peripheries of Texas and Oklahoma. There are no new or published records from New England and the District of Columbia, but *V. minutus* is expected there, so its area encompasses parts of 24 states plus DC and all of 14 states: Maryland, Delaware, Virginia, North and South Carolina, Georgia, Alabama, Mississippi, Tennessee, Kentucky, West Virginia, Indiana, Arkansas, and Louisiana. The northernmost record is from Berrien County, Michigan; the easternmost localities are in New York and Dare County, North Carolina; the southernmost is in Putnam County, Florida; and the westernmost are in Angelina and Rusk Counties, Texas. Acronyms of sample repositories are as follows: AMNH—American Museum of Natural History, New York; FMNH—Field Museum of Natural History, Chicago, Illinois; FSNS–Florida State Collection of Arthropods, Gainesville; INHS—Illinois Natural History Survey, Champaign; JAB–private collection of J.A. Beatty, Carbondale, Illinois; MCZ–Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MEM–Mississippi Entomological Museum, Mississippi State University, Starkville; MPM–Milwaukee Public Museum, Milwaukee, Wisconsin; NCSM–North Carolina State Museum of Natural Sciences, Raleigh; NMNH–National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UAAM–University of Arkansas Arthropod Museum, Fayetteville; UMO–Enns Entomological Museum, University of Missouri, Columbia; VMNH–Virginia Museum of Natural History, Martinsville; ZMUC–Natural History Museum of Denmark, Copenhagen.

**Deletions**

New England, Utah, and Wyoming; Canada; Mexico. Chamberlin (1921) cited *N. minutus* from New England, but there are no preserved specimens in any American repository. Chamberlin and Hoffman (1958) stated that the species occurs sporadically as far west as Utah, and Chamberlin (1943a, 1951) reported *N. minutus* from Casper, Natrona County, Wyoming, and Salt Lake City and Salem, Salt Lake and Utah Counties, Utah, all of which are well west of the coherent distribution shown in Figure 1. The Utah records probably refer to *Orinisobates utus* (Chamberlin, 1912) (Nematomatidae), which is common in canyons and along watercourses in Salt Lake and Utah Counties and northern Utah in general (Enghoff 1985, plus unreported specimens examined by the 2nd author). We have not seen any blaniulids from Casper, Wyoming, but surmise that this record refers to an introduced species like *N. kochii*, as it is well removed from the known range of *O. utus*, whose only Wyoming records are from the Teton Mountains adjacent to Idaho (Enghoff 1985).

Chamberlin and Hoffman (1958) included eastern Canada in the range of *N. minutus*, and Loomis (1968) gave the range as the “United States and Canada.” However, Shelley (1988, 2002) stated that it is not probable for any region of Canada, even the most proximate part of southern Ontario (Essex County), because at that time the species was not known from north of southern Ohio. We report sites from Lorain County, Ohio, near metropolitan Cleveland, and Berrien and Hillsdale Counties, Michigan, and Snider (1991) recorded questionable occurrences from Lenawee and Saginaw Counties, Michigan. These samples are not available and the latter is still doubtful, but Lenawee County is adjacent to Hillsdale and hence is plausible, so we denote it with a dot in Figure 1. Thus, while we still exclude Canada from the distribution, *V. minutus* is now known from only 75 miles (120 km) southwest
of Essex County, and discovery in southern Ontario is plausible.

Chamberlin (1943b) and Loomis (1968) reported *N. minutus* from Chapultepec Park in Mexico City and Salazar, Distrito Federal, Mexico. The 2nd author recently discovered the samples from Chapultepec Park at the NMNH, and the 3rd author identified them as *N. kochii*. This is the 2nd Mexican record of *N. kochii*, the 1st being that of Jawlowski (1930), who recorded the synonym *N. armatus* (Némec, 1895) (see Enghoff 1984b), from Patzcuaro, Michoacan, which was reiterated by Loomis (1968). Sample data follow: Distrito Federal, Mexico City, Chapultepec Forest Park, in leaf litter, δ, 2 °, 3 juvs., 7 October 1939, F. Bonet (NMNH).

**Published Records**

“**Middle States**” in general (Say 1821, Brandt 1841, Golovatch and Hoffman 2000).

**United States East of the Mississippi River** (Chamberlin 1921).

**Widespread over Eastern United States as far South as Delaware and Virginia and West to Tennessee** (Chamberlin and Hoffman 1958).


**Southeastern North America, West to Arkansas, North to Illinois and Pennsylvania** (Enghoff 1984a).

**Eastern United States, from Pennsylvania and Missouri South to Florida and Louisiana** (Hoffman 1999).

**New York**: New York in general (Chamberlin 1921, Bailey 1928).

**New Jersey**: New Jersey in general (Chamberlin 1921).


**Delaware**: Delaware in general (Chamberlin 1921, Chamberlin and Hoffman 1958). To the best of our knowledge, this is the only published record of an indigenous milliped from the state of Delaware.


**South Carolina**: South Carolina in general (Enghoff and Shelley 1979). Coastal zone in general (Shelley 1978b).

**Georgia**: Georgia in general (Enghoff and Shelley 1979).


**Alabama**: Alabama in general (Enghoff and Shelley 1979).


**Kentucky**: Kentucky in general (Enghoff and Shelley 1979). **Powell Co.**, below Raven Rock (stated by Enghoff [1979] as probably in Kentucky, which is correct).

**West Virginia**: West Virginia in general (Enghoff and Shelley 1979).

**Ohio**: Ohio in general (Chamberlin 1921, Williams and Hefner 1928, Enghoff and Shelley 1979).

**Indiana**: Indiana in general (Chamberlin 1921, Enghoff and Shelley 1979). **Clark Co.**, New Providence (Bollman 1888b). **Marion Co.**, Indianapolis (Bollman 1888b). **Monroe Co.**, Bloomington (Bollman 1887, 1888b). **Washington Co.**, Salem (Bollman 1888b).

DISTRIBUTION OF VirgoIulus minutus


MISSOURI: Missouri in general (Enghoff and Shelley 1979, Hoffman 1999).


LOUISIANA: Louisiana in general (Enghoff and Shelley 1979, Hoffman 1999). Caddo Par., (Causey 1963, as undetermined females of the Nemasomidae [=Nemasomatidae]).

NEW RECORDS


**KENTUCKY:**  **Edmonson Co.**, Mammoth Cave Nat. Pk., Mammoth Cave Hollow, 25 September 1960, D.E. Reichle (FSCA 31). **Fayette Co.**, Lexington, 4 February 1944, PO. Ritcher (INHS 1), and in cave, May 1947, M.W. Sanderson (INHS several). **Grayson Co.**, 7 miles (11.2 km) NW Leitchfield, Rough River Lake, 27 May 1984, D. & M. Hildebrandt (MPM 1).


**Michigan:**  **Berrien Co.**, Warren Dunes along Lake Michigan, 30 October 1959, W. Suter (FSCA several). **Hillsdale Co.**, Austin, C.H. Bollman (NMNH 2). First definite state records.


**Arkansas:**  **Baxter Co.**, September 1977 (UAAM 2). **Bradley Co.**, 14 December 1964 (FSCA 1). **Miller Co.**, 1.6 miles (2.6 km) S Genoa off AR Hwy. 196, 10 March 2002, C.S. Harris (NCSM 1). **Pulaski Co.**, Little Rock, 16 March 1962, N.B. Causey (FSCA 1). **Washington Co.**, Fayetteville, 13 June 1950, N.B. Causey (FSCA 13); Cave Creek Valley, January 1956 (FSCA 2); and Prairie Cove, along AR Hwy. 1, M. Hite (FSCA 8).

**Louisiana:**  **Allen Par.**, 1 mile (1.6 km) N Reeves, along LA Hwy. 113, 20 February 1966, R.E. Tandy (FSCA 2). **Grant Par.**, Williana (FMNH 1). **Washington Par.**, 6 miles (9.6 km) SW Bogalusa, 21 January 1965, N.B. Causey (FSCA 2). **West Feliciana Par.**, Tunica Hills Nature Preserve, 27 February 1971, D.A. Rossman (FSCA 3). **St. Bernard Par.**, Harahan, 15 September 1944, FG. Werner (MCZ 32).

**Oklahoma:**  **McCurtain Co.**, off Hwy. 259A nr. Beaver's Bend St. Pk., 4 November 2004, C.T. McAllister (NCSM 14). New state record. **Texas:**  **Angelina Co.**, Lufkin, 22 August 1940, L. Hubricht (NMNH 1). **Bowie Co.**, ca. 7 miles (11.2 km) SW Texarkana and 5 miles (8 km) E Redwater, off US Hwy. 59 near NE corner of Wright Patman Lake, 11 December 2003, Z.D. Ramsey (NCSM 2). **Cass Co.**, ca. 6 miles (9.6 km) NE Atlanta, along FM Rd. 3129, 0.5 miles (0.8 km) N Bloomburg, 24 February 2004, Z.D. Ramsey (NCSM 1). **Newton Co.**, ca. 24 miles (38.4 km) N Newton, Canyon Rim.
Trail off TX Hwy. 87, 1.6 miles (2.6 km) N Jct. FM Rd. R255 and 10.2 miles (16.3 km) N TX Hwy. 63 [15R 0430457 3442649], 7 October 2004, R.M. Shelley (NCSM 1); and ca. 12 miles (19.2 km) NE Newton, Wild Azalea Trail off FM Rd. 1414, 6.7 miles (10.7 km) N Jct. TX Hwy. 87 [15R 0442598 3415623], 7 October 2004, R.M. Shelley (NCSM 1). **Rusk Co.**, 2.2 miles (3.5 km) E Mt. Enterprise, Griff Ross Trail off US Hwy. 84 [15R 034452 3532802], 6 October 2004, R.M. Shelley (NCSM 5). *New state record.*

There is also a sample with 8 females (MCZ) that was collected in September 1904 at "Anechar," New York, which is believed to be a missspelling for "Arrochar," a neighborhood in Staten Island, Richmond County; because it is around the same latitude as the northernmost records in Illinois, Indiana, and Ohio, we place a dot here in Figure 1. The species is not known definitely from central and western New York, or from a latitude north of Berrien County, Michigan.

**ACKNOWLEDGMENTS**

We thank the following professors, curators, and collection managers for providing access to or loaning specimens to the 2nd author: N.I. Platnick (AMNH), D. Summers (FMNH), G.B. Edwards (FSCA), K. Methven (INHS), L. Leibensperger (MCZ), T.L. Schieffer (MEM), J.P. Jass (MPM), J.A. Coddington (NMNH), J.K. Barnes (UAAM), R.W. Sites (UMO), and R.L. Hoffman (VMNH). We also thank J.A. Beatty for loaning samples in his private collection; J.T. McAllister III, C. Harris, J. Hollis, and J.E. Kessler for assistance in collecting; J. Hannik for placing the locality in New York; and H. Robison for advising us that "Argenta," Arkansas, is actually North Little Rock. The 1st author's fieldwork was supported in part by TAMU-T Faculty Senate Research Enhancement Grant 200900.

**LITERATURE CITED**


______. 1943b. On Mexican millipeds. Bulletin of the University of Utah 34(7) [Biological Series 8]:1–103.


Received 30 April 2004
Accepted 3 August 2004
Adult male pronghorn (*Antilocapra americana*) have never been reported defending fawns against predators (Marion and Sexton 1979, Byers 1997). Lipetz and Bekoff (1980) observed male pronghorn participating in coyote chases. However, they were uncertain of the motivation and suggested that males may only appear to participate in chases and may actually be trying to stop females from leaving their territories. I report here 2 instances in which an adult male pronghorn assisted female pronghorn in defending fawns against searching coyotes (*Canis latrans*) in Grand Teton National Park in northwestern Wyoming (43°39′N, 110°40′W).

The 1st instance occurred on 16 June 2001 while I was conducting a focal observation of a radio-collared female pronghorn to determine the survival status of her fawn. At 1015 MST the female became extremely agitated when she noticed a coyote searching the vegetation 50 m away from her. The pronghorn immediately ran toward the coyote, repeatedly charging it in an attempt to drive it away from the area. A solitary adult male pronghorn had been browsing approximately 0.4 km from the female. When the female began charging the coyote, the male ceased feeding, trotted toward the female, and joined in the chase (1017 MST). The 2 pronghorn succeeded in displacing the coyote 0.5 km from its location at the beginning of the encounter, whereupon it adopted a defensive, reclining posture in a shallow irrigation ditch (1045 MST). For the next hour both pronghorn alternately stood next to, and circled, the reclining coyote. The pronghorn finally moved about 30 m away, and the male pronghorn bedded down (1150 MST). The coyote took this opportunity to leave the ditch and began moving directly away from the pronghorn. The female pronghorn immediately re-initiated the chase (1205 MST), and the male promptly stood and followed. The 2 pronghorn pursued the coyote for over 1 km, at which point all 3 animals left my range of view (1225 MST).

Both pronghorn remained out of sight for nearly an hour before returning concurrently to the vicinity of the pre-encounter location of the female (1330 MST). The male began browsing, while the female commenced the vigilant behavior characteristic of mothers with hidden fawns (Byers 1997). At 1426 MST, the female reunited with her fawn, which had been hiding less than 100 m from the area where the coyote had been searching.

The 2nd instance occurred on 8 June 2004 while I was observing 2 females (~200 m apart; hereafter female A and female B) to identify the bedsite locations of their fawns to capture the fawns for radio-collaring. I already knew the bedsite location of 1 fawn belonging to female A because I had collared the fawn earlier that same day (1018 MST). At approximately 1130 MST, female A reunited with her uncollared fawn and allowed it to nurse. Approximately 15 minutes later (1145 MST), female B also reunited with an uncollared fawn and allowed it to nurse. At this point I knew the locations of 3 fawns, the fawn I had previously radio-collared plus the 2 uncollared fawns that had recently nursed and had subsequently reclined at new bedsites.

At 1210 MST, 2 coyotes approached within 150 m of the bedsite of the uncollared fawn belonging to female A. Female A noticed the coyotes and ran toward them. Female B also noticed the coyotes and ran to join female A.
Together, the 2 females began charging at the coyotes in an attempt to drive them from the area. A solitary adult male pronghorn that had been browsing in the vicinity of female A (100 m away) trotted toward the 2 females (1215 MST). The 3 pronghorn adopted a triangular formation, with the male at the apex and the females flanking the male on either side. The male pronghorn took up the primary defense, charging at the coyotes with his head lowered. Whenever a coyote succeeded in getting past the male, the female on that side would step forward to assist in the defense. All 3 pronghorn kept up the harassment for nearly an hour, at which point the coyotes left the area (1310 MST).

That defense of fawns by male pronghorn has not previously been reported is perhaps a result of both the isolation of females that tends to occur at parturition and the difficulty in knowing whether hidden fawns are present when male pronghorn are observed harassing coyotes. Why male pronghorn engage in fawn defense is a different issue. Variation in lifetime reproductive success among pronghorn males is largely a result of differences in offspring survival (Byers 1997). Consequently, in areas where fawn mortality is chiefly attributable to predation, reproductive males might increase their own fitness by defending from predators fawns they sired. However, for this to be a satisfactory explanation of the interactions I described, males would either have to recognize their offspring or have a high probability of being in areas where females bore their offspring. Evidence in support of these suppositions is weak given the ephemeral nature of social groups, which, as is the case with most polygynous ungulates, precludes determination of paternity (Sinclair 1979, Berger 1986, Byers 1997).

Several alternatives might also explain why male pronghorn engage in fawn defense. First, nonpaternal males might protect fawns as a form of future reproductive investment because opportunities for mating increase with a greater number of surviving females. This idea suggests that males should defend female rather than male fawns. In the 2nd observation reported above, the 2 fawns closest to the coyotes were a male and a female. Whether the male pronghorn was defending the male or female fawn, or both, is unknown. Second, if coyotes that are recipients of male-directed aggression are more hesitant to attack pronghorn in the future, then the behavior might be explained by a purely selfish model. However, previous harassment did not appear to deter coyotes from future interactions with pronghorn (Lipetz and Bekoff 1980). Third, male pronghorn may only appear to harass coyotes and may actually be trying to stop females from leaving their territories (Lipetz and Bekoff 1980). This latter supposition appears unlikely as there was no effort by the 2 females involved in the 2nd incidence to leave the area, and the aggression exhibited by the male pronghorn was clearly directed at the coyotes.

A fuller understanding of the underlying cause(s) of male-directed aggression toward coyotes will require further investigation. Irrespective of the cause, the observations reported here demonstrate that male pronghorn, in addition to females, do defend fawns from predators.

This work was funded by the Biological Resources Division of the U.S. Geological Survey under Cooperative Agreement 01CRAG0031, and Earth Friends Foundation. I thank Joel Berger for discussions and Mike Oehler, Becky Pierce, and an anonymous reviewer for helpful comments.

**Literature Cited**


Received 5 February 2004
Accepted 28 October 2004
In the western U.S., deciduous woody species along riparian systems provide important ecological functions. For example, they stabilize stream banks and impart hydraulic resistance during overbank flows, enhance deposition of organic matter and fine sediment on floodplains, support general food webs of aquatic and riparian organisms, moderate water temperatures and microclimates, and recruit large wood (National Research Council 2002b). Measures of biodiversity, biomass, and number of rare species are often much greater in riparian habitats than on adjacent uplands (Knopf et al. 1988). Deciduous woody species on upland sites provide for watershed protection, aesthetics, wood fiber, and habitats that also help support a wide variety of wildlife and avian species (Bartos 2001, National Research Council 2002a).

Despite their significance to western ecosystems, deciduous woody species have been in decline (Braatne et al. 1996, Kay 1997, Bartos 2001). Many western riparian systems have been diminished in total area (Swift 1984) while many that remain often have been altered or degraded by various human activities and land uses (Wigington and Beschta 2000).

While the causes of loss and alteration of woody species during a period of increasing Euro-American influence are multiple, high levels of herbivory from domestic ungulates have often degraded ecosystem structure and function. Such degradation includes impacts to habitats of numerous species of vertebrates and invertebrates, various food web interactions, and nutrient cycling (Fleischner 1994, Braatne et al. 1996, Belsky and Blumenthal 1997, Donahue 1999, Rooney and Waller 2003). Even where land has been set aside within the National Park system, native ungulates sometimes have had significant impacts on vegetation (National Research Council 2002a). Thus, there is an increased need for restoration of deciduous woody species at landscape scales. Such restorations would be facilitated if reference sites existed that were relatively unimpacted by ungulate herbivory (i.e., refugia) since they (1) can provide an understanding of vegetation dynamics without the effects of herbivory, (2) help define the degree and extent of degradation in woody plant communities for other portions of a landscape, (3) may assist in setting restoration priorities, and (4) may provide important “targets” for restoration programs.

In landscapes that have experienced the effects of widespread and sustained herbivory from ungulates (either domestic or wild), refugia from browsing can be created with fenced exclosures (Brookshire et al. 2002, Sarr 2002), provided that sufficient seed or bud banks remain. Unfortunately, such exclosures are seldom available. Yet, even within a heavily browsed landscape we suggest there will often exist scattered refugia sites with deciduous woody species; such sites are often small in area but may contain a relatively diverse plant community structure and composition. Where such refugia have persisted is notable as they typically occur in locations where there are multiple impediments to ungulate access. The importance of these sites is that they provide a glimpse of the potential structure and composition of plant communities where ungulate herbivory is not of overriding significance and may represent an initial approximation of what other areas in a landscape might become if herbivory levels were reduced or curtailed. Because refugia are often visually different (e.g., high contrast, taller plants, higher plant
densities) relative to the general landscape, they are typically easy to locate. In the following discussion, we identify numerous types of “impediments” to browsing that have contributed to the maintenance of refugia.

Several studies have described the role of natural physical barriers to animal movement in creating refugia. At the microsite scale, Rooney (1997) described how herbaceous vegetation growing on the tops of boulders escaped deer browsing. Schreiner et al. (1996) discovered shrub refugia behind log barriers created by fallen conifers in Olympic National Park. They found several species of shrubs in these refugia that successfully produced flowers and fruit unlike the majority of the shrubs growing nearby in the open. They concluded that these refugial shrub patches may provide critical seed sources for recolonization of the floodplain by species that might otherwise be absent. Ripple and Larsen (2001) found that fallen conifers killed by the 1988 fires in Yellowstone National Park could be dense enough to provide local refugia, allowing aspen recruitment with high levels of ungulate browsing nearby (Fig. 1). Beschta and Ripple (2005) identified increased cottonwood recruitment occurring between highways and terrain features such as steep slopes and rivers that reduced the presence of animals. Larsen and Ripple (2003) discovered a lack of aspen recruitment across the northern range in Yellowstone National Park except for stands growing in the midst of scree deposits. They concluded that the scree protected the aspen from ungulate browsing. The scale of the refugia in the above case studies ranges from 1 to several thousand square meters. Yet, physical barriers also have been described at much larger scales where terrain features such as mesas and buttes impeded ungulate access and created refugia (Jameson et al. 1962, Ambos et al. 2000).

It is important to recognize that the widespread loss of major predators such as wolves (*Canis lupus*) early in the 20th century allowed ungulates to browse with a reduced threat of predation. In addition to the often widespread effects of domestic ungulates, woody plant communities can be profoundly affected by native ungulates when top predators are removed from ecosystems (Leopold et al. 1947, Terborgh et al. 1999, Ripple and Larsen 2000, Beschta 2003, Soulé et al. 2003) and evidence is growing on the importance of predator conservation because of cascading effects upon lower trophic levels (Smith et al. 2003, Ripple and Beschta 2004). Refugia created through risk-sensitive foraging involve predator/prey interactions whereby areas of low browsing intensity occur, either in conjunction with existing physical barriers or independent of them. Changes in prey behavior due to the presence of predators are referred to as predation-risk effects. These behavioral modifications include changes in habitat use, patch selection, and choices of feeding sites (Lima and Dill 1990). This process can produce low populations of herbivores in a predator’s core use area, thus creating refugia for woody browse species through lower herbivory. For example, in response to the presence of predators, researchers have documented increased concentrations of ungulates in buffer zones away from both mammalian predators (Mech 1977, White et al. 1998, Ripple et al. 2001) and human hunters (Laliberte and Ripple 2003).

Predation-risk effects on prey animals, in combination with varying terrain conditions, can also create “invisible impediments” to browsing and have apparently been caused by sport hunters as well as wolves. For example, St. John (1995) concluded that aspen stands within 500 m of roads were less impacted by wild ungulates than those farther away, suggesting that elk adjusted their foraging behavior to avoid human contact and possible predation by humans. Other researchers found that aspen were heavily browsed on U.S. Air Force land that was utilized year-round by a large elk population but where sport hunting was not permitted. Conversely, this property is surrounded by national forest land where hunting is allowed and the aspen stands were minimally browsed (McCain et al. 2003).

Ripple and Beschta (2003) proposed that, following the reintroduction of wolves in Yellowstone National Park, a “terrain fear factor” has been playing an important role in the selective release of cottonwood and willow from long-term browsing suppression by elk. In their predation-risk hypothesis, they suggested that elk would increasingly forage at sites that allow early detection, avoidance, and successful escape from wolves. They found cottonwood and willow to be releasing at potentially high-risk sites with limited visibility of approaching wolves and/or with terrain impediments to escape from an attack, such as...
high terraces, steep cutbanks, and nearby gul- 
lies (Fig. 2).

There are several limitations to the use of 
refugia as reference sites. Because they are 
typically of limited size and spatial distribu-
tion, their locations may not be representative 
of the broader landscape (i.e., different abiotic 
conditions, geographically or topographically 
biased). In such situations they provide little 
opportunity for developing statistical inferences. 
Refugia may maintain certain rare species, but 
in some cases overall community composition 
and functioning can be different from the larger 
landscape in need of restoration. Information 
identifying the historical level of ungulate use 
often is lacking for these sites, and levels of 
browsing may be occurring, of which a certain 
amount would represent a natural condition 
(e.g., Schreiner et al. 1996). Finally, a total lack 
of browsing (such as a fenced exclosure) might 
represent atypical conditions for pre-European 
plant communities.

Realizing the potential limitations of local 
refugia as examples of these conditions, we 
nevertheless suggest that the identification 
and use of refugia can be important in under-
standing the role of ungulate herbivory on 
western landscapes and their potential for re-
covery. We propose 3 situations where refugia 
for deciduous woody browse species are likely 
to persist: (1) Where the browsing is predomi-
nantly from domestic ungulates, physical bar-
riers to site access will control the occurrence 
of refugia. (2) Where wild ungulates are pre-
sent but natural predators are not, both physi-
cal barriers and predation risk associated with 
human hunting will tend to control the occur-
rence of refugia. (3) Where natural predators 
have a significant presence, physical barriers 
and terrain features that affect the perceived

Fig. 1. Protected aspen sprouts growing among coarse woody debris on the Blacktail Plateau in Yellowstone National 
Park (example of a physical barrier to browsing). See Ripple and Larsen (2001) for details on aspen recruitment in loca-
tions where dead trees have created a jackstraw barrier to ungulate movement. In 2003 the aspen sapling to the left of 
the white pole was approximately 4 m tall (see arrow), while aspen sprouts growing nearby outside the woody debris 
were less than 1 m tall.
predation risk of prey animals at varying spatial scales will influence the number, size, and spatial distribution of refugia. While the occurrence of refugia may be sufficiently common in some landscapes to provide adequate reference sites for restoration purposes, additional sites could be targeted for livestock or native ungulate exclusion using fenced enclosures to ensure a full portfolio of reference sites. In some extreme cases, refugia might be the only places where certain native species still occur, and these sites can serve as important genetic repositories. We suggest that identification of refugia across watersheds and landscapes is needed to better understand reference conditions for woody browse species that may have existed prior to the widespread influences of domestic ungulates and the effects of native ungulates where major predators have been extirpated.

The authors thank Daniel Sarr, 2 anonymous reviewers, and an associate editor for providing helpful comments on an early draft of this paper.

**Literature Cited**


Received 3 January 2004
Accepted 28 June 2004
Few studies have evaluated the impacts of flooding on riparian bird communities (Brown and Johnson 1987, Knopf and Sedgwick 1987). Most research has focused on inundation of the riparian zone rather than structurally devasting flooding events. Floods in mountain streams are often brief and catastrophic, due to rapid movement of water, coarse sediment, and woody debris down steep slopes and channels (Swanson et al. 1998). Here, we describe the effect of a catastrophic flooding event on riparian bird communities in west central Idaho and northeastern Oregon. This event provided us with an opportunity to compare bird communities at riparian sites before and after flood damage. Specifically, we investigated whether overall bird abundances and individual species abundances differed at sites pre- (1995, 1996) and post-flood (1997, 1998).

We conducted our research along tributaries to the Snake River in the Hells Canyon reach, situated in west central Idaho and northeastern Oregon. Moderate to steep slopes characterize the area. Grasslands and upland shrub habitat are interspersed and found upslope of the riparian zone. White alder (Alnus rhombifolia) was the most common tree species found in the riparian communities sampled. Other common tree and shrub species included netleaf hackberry (Celtis reticulata), rocky mountain maple (Acer glabrum), hawthorn (Crataegus spp.), blue elderberry (Sambucus cerulea), poison ivy (Toxicodendron rydbergii), and chokecherry (Prunus virginiana).

In 1995, as part of a larger study (Turley and Holthuijzen 2000), we established 288 bird survey plots in homogenous patches of Forested Wetland and Scrub-Shrub Wetland habitat cover types along 57 tributaries to the Snake River. Riparian vegetation cover types generally followed the classification system described by Cowardin et al. (1979) and modified for Habitat Evaluation Procedures (HEP; U.S. Fish and Wildlife Service 1981). Each plot was permanently marked and coordinates were established using a Global Positioning System (Geo Explorer II, Trimble Navigation Limited, Sunnyvale, CA). During January 1997, twenty-seven plots located in 8 tributaries experienced high to severe flooding disturbance. Flood damage was patchy within a tributary, with damaged or even completely denuded patches interspersed with undamaged ones. Vegetation at 8 plots was categorized as “highly disturbed” and at 19 plots as “severely disturbed.” In “highly disturbed” plots most herbaceous, small- and larger-diameter woody species were impacted, whereas at “severely disturbed” plots nearly all vegetation was removed.

In 1995 we measured shrub and tree cover at 13 of 27 plots that were flooded in 1997; these 13 plots were resampled in 1998 (6 highly disturbed and 7 severely disturbed). We used the line-intercept method (Müller-Dombois and Ellenberg 1974) to determine percent canopy cover for the shrub and tree layers. Tree and shrub canopies, identified to species, were projected vertically to the tape, and the length of line segments covered by woody plant species was recorded (Hays et al. 1981). We used simple paired t tests to evaluate percent tree and shrub canopy cover pre- and post-flood. Average percent shrub cover was higher before flooding in 1995 (80.3%) than after flooding in 1998 (20.4%; 1-tailed paired t test: \( t = 4.90, P < 0.001 \)). Likewise, average percent tree cover was higher before
flooding (77.6%) than after flooding (33.6%; $t = 5.04$, $P < 0.001$).

Riparian zones along tributaries of the Snake River are generally narrow. We sampled available tributaries where the riparian zone was at least 40 m in width. We used fixed-radius plots (20-m plots) and conducted point counts at each plot. From 1995 through 1998, we intended to survey each plot twice during the breeding season (May and June). However, in May 1995 only 4 plots were established and surveyed. In May 1997 we surveyed only 5 plots because many plot markers washed away during the flood and had to be reestablished. During May 1996 and 1998 and June 1995–1998 point counts were conducted at all 27 plots. Hence, we conducted 31 surveys in 1995, 54 in 1996, 32 in 1997, and 54 in 1998.

We conducted point counts following standard protocols (Ralph et al. 1995) to minimize bias and make bird detectability rates as consistent as possible. Fixed-radius point counts are effective in providing indices of abundance between treatments (Petit et al. 1995). We chose 10-minute counts to maximize species detection since travel time between plots was often greater than 15 minutes (Buskirk and McDonald 1995, Dawson et al. 1995, Ralph et al. 1995). Radii of less than 50 m reduce bias due to vegetation structure and observer limitations, and maximize species detections (Petit et al. 1995). We excluded birds flying over the plots from further analyses. Surveys began up to 30 minutes before sunrise and were completed no later than 5 hours after sunrise. Bird surveys were not conducted during inclement weather conditions such as strong winds (>20 km ⋅ hour$^{-1}$) or rain (Robbins 1981).

We calculated the relative abundance of each bird species individually and all bird species combined as the total number of individuals observed divided by the number of times a plot was surveyed during pre- and post-flood periods. Relative abundances were calculated only for species observed on at least 5 plots, either pre- or post-flood. Because relative abundance estimates were not normally distributed, we used the Wilcoxon matched-pairs signed rank test to compare relative abundances of individual species and pooled across all species between pre- and post-flood periods (Zar 1984). Also, we classified all bird species observed into foraging guilds for bird community analysis (Table 1).

Forty bird species were observed at the plots. Bird species richness was highest in 1996 (23 species) and lowest in 1997 (15 species). Overall relative bird abundances declined, but not

### Table 1. Number of plots at which a species was observed and relative abundance (birds/count and standard errors) of 8 bird species at 27 plots in Hells Canyon, Idaho and Oregon, 1995–96 and 1997–98.

<table>
<thead>
<tr>
<th>Species</th>
<th>Foraging guild</th>
<th>Number of plots</th>
<th>Relative abundances</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lazuli Bunting</td>
<td>LCF</td>
<td>10</td>
<td>15</td>
<td>0.29 (0.06)</td>
</tr>
<tr>
<td>(Passerina amoena)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow-breasted Chat</td>
<td>LCF</td>
<td>5</td>
<td>4</td>
<td>0.11 (0.04)</td>
</tr>
<tr>
<td>(Icteria virens)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-capped Chickadee</td>
<td>LCG</td>
<td>9</td>
<td>3</td>
<td>0.24 (0.08)</td>
</tr>
<tr>
<td>(Poecile atricapilla)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>LCG</td>
<td>9</td>
<td>2</td>
<td>0.20 (0.05)</td>
</tr>
<tr>
<td>(Dendroica petechia)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nashville Warbler</td>
<td>LCG</td>
<td>6</td>
<td>0</td>
<td>0.09 (0.04)</td>
</tr>
<tr>
<td>(Vermicola ruficapa)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spotted Towhee</td>
<td>GF</td>
<td>13</td>
<td>12</td>
<td>0.24 (0.06)</td>
</tr>
<tr>
<td>(Pipilo maculatus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-eyed Vireo</td>
<td>UCG</td>
<td>6</td>
<td>8</td>
<td>0.11 (0.04)</td>
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<tr>
<td>(Vireo olivaceus)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American Dipper</td>
<td>RBG</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>(Cinclus mexicanus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All birds</td>
<td></td>
<td></td>
<td></td>
<td>2.04 (0.25)</td>
</tr>
</tbody>
</table>

b A total of 81 surveys were conducted pre-flood and 86 surveys post-flood.
c Red-eyed Vireos relative abundances are based on June surveys, the only time the species was observed.
significantly, between pre- and post-flood periods ($P = 0.197$; Table 1). Relative abundance of lower-canopy foragers (Lazuli Bunting [Passerina amoena] and Yellow-breasted Chat [Icteria virens]), a ground forager (Spotted Towhee [Pipilo maculatus]), and an upper-canopy gleaner (Red-eyed Vireo [Vireo olivaceus]) was similar between pre- and post-flood periods ($P > 0.20$; Table 1). Relative abundance of Yellow Warblers (Dendroica petechia) and Nashville Warblers (Vermivora ruficapilla), lower-canopy gleaners, was higher pre-flood than post-flood (Yellow Warbler: $P = 0.004$; Nashville Warbler: $P = 0.032$). Relative abundance of American Dippers (Cinclus mexicanus) was higher post-flood than pre-flood but was not significant ($P = 0.062$). Relative abundance of Black-capped Chickadees (Poecile atricapilla) was lower post-flood than pre-flood, but was not significant ($P = 0.078$).

Brown and Johnson (1987) evaluated the impacts of high-water releases on bird species nesting in the zone of inundation along the Colorado River in the Grand Canyon. They reported that, similar to our findings, several species exhibited declines attributed to nest inundation and loss of habitat, while other species experienced unexpected increases. Likewise, Knopf and Sedgwick (1987) found that populations of Brown Thrashers (Toxostoma rufum) and Spotted Towhees, both foraging and nesting on or near the ground, did not significantly decline during a flood year that inundated an area along the South Platte in Colorado. Declines, however, were reported the year following the flood. Knopf and Sedgwick (1987) suggested that site tenacity may explain the similarity in pre-flood bird densities and those during a flood year; unsuccessful nesting is a likely result of riparian zone inundation, which in turn brought about lower densities in the year following flooding. In other habitats time lags in bird response to disturbance also were observed probably due to site tenacity of breeding individuals (Wiens and Rotenberry 1985). In Hells Canyon lower-canopy gleaners may have been displaced, presumably to areas that provided sufficient foraging and nesting substrates. Yellow Warbler and Nashville Warbler prefer early successional habitats such as thickets or open forest with shrubby undergrowth (Williams 1996, Lowther et al. 1999). Because the shrub understory was either greatly reduced or absent at our flood-damaged sites, habitat was unavailable and both species were not observed in 1998 (Table 1). Other foraging guilds did not decline and some species appeared to show site tenacity. During both 1997 and 1998, the Red-eyed Vireo was observed in small clumps of live alders in tributaries that had been otherwise scoured of vegetation (Turley personal observation), exhibiting apparent site tenacity. Two common species, Lazuli Bunting (lower-canopy forager) and Spotted Towhee (ground forager), were often observed in upland habitat adjacent to riparian habitats in Hells Canyon (Turley and Holthuijzen 2000) and were the 2 most frequently observed species at flood-damaged sites. These species and other lower-canopy foragers, as well as ground foragers, may be able to forage outside the riparian zone and remain at a site even with reduced riparian habitat available.

The American Dipper, a riparian bottom feeder, had highest abundances the 2nd year following flooding disturbance. This bird species was uncommonly observed in the study area. Of 288 riparian plots we sampled (Turley and Holthuijzen 2000), the American Dipper was observed at only 8 plots: 1 plot in 1995, 6 plots in 1997 and 1998 with flooding damage, and 1 plot in 1998 with mild flooding disturbance (Turley unpublished data). Lamberti et al. (1991) found that debris-flow disturbance of riparian vegetation opened up the canopy, resulting in increased light levels in the stream, which led to several years of increased primary productivity by aquatic plants and increased secondary productivity in communities of invertebrates that graze on aquatic vegetation. Thus, American Dippers may have responded to increased densities of aquatic insects.

Response of birds to flooding likely depends on the disturbance magnitude of the flood and life history traits of the individual species. Riparian patches within a tributary that remain intact and even disturbed patches may provide foraging and nesting habitat for some bird species during the recovery of the system. Also, adjacent upland habitat may provide foraging habitat for some riparian species. At our sites where average percent shrub cover declined from 80.3% to 20.4% and average percent tree cover declined from 77.6% to 33.6%, we found that flooding damage displaced lower-canopy gleaners whereas other guilds continued to use the sites.
We gratefully acknowledge all research assistants involved in this study. A. Moser, Idaho Power Company, and 2 anonymous reviewers provided valuable comments on earlier versions of the manuscript. The research was funded by Idaho Power Company, an IDACORP Company.

LITERATURE CITED

BROWN, B.T., AND R.R. JOHNSON. 1987. Fluctuating flows from Glen Canyon Dam and their effect on breeding birds of the Colorado River. Glen Canyon Environmental Studies, GCES/23/87, Bureau of Reclamation, Upper Colorado Region, Salt Lake City, UT.


Received 14 July 2003
Accepted 12 October 2004

You gotta read this book. Since you are already browsing a review in this journal, you are almost certainly the audience to whom it is directed (natural historians and conservationists broadly defined) and you will appreciate the style. In this book Dr. Lott tells enough about the natural history of bison to whet the generalist’s appetite and yet to engage the specialist in thinking in broader concepts. I learned more of the basics of buffalo, a term he prefers to bison in many applications, than I thought I would ever need. But now I feel I better understand the history of this animal that filled the grassland sea of the continent’s midsection.

Clearly, Dr. Lott knows that of which he speaks, yet doesn’t flaunt it on the pages like the pompous academic most of us can become at times. As he unfolded story after well-woven story of these creatures and those with which they share (shared) the prairies, my eyes flew across the pages in anticipation of the next homey turn of words, like “from grass to gas and chips” to describe the digestion process of these ruminants. Or, “even when they’re getting serious, cows’ clashes seem more comic than cosmic. I’ve seen cows urinate thousands of times and wallow thousands of time, but only once have I seen a cow put urinating and wallowing together as a threatening bull would do.” Or, “It’s a sobering fact that 12 to 13 percent of a bottle of Dom Perignon Champagne is bacteria pee.” Or, in speaking of a particularly well-preserved 36,000-year-old bison that was frozen in blue coppery mud, “the tooth and claw marks in his hide were still so clear that Dale (Guthrie) could take an American lion’s skull, place its canine teeth on the marks left by the killer’s canines, and see a perfect match. Even the flesh was so well-preserved that when the corpse had yielded all it secrets Dale and his colleagues made an acceptable stew with a bit of the meat.”

Dr. Lott spent his earliest years on the National Bison Range in Montana, and by his own admission his first encounters were of bison not as symbols of the West, the squandering of a natural resource, or a conservation triumph. They were simply the animals he had seen most frequently as a youngster. The sense of wonder in this gray-haired youngster is still evident when he describes bulls fighting: “I once saw a bull somersaulted backward by such a charge: 2,000 pounds of bull flipped upside down like a lawn chair in a gust of wind.” You might think gems like this would only pepper the prose, but waits were short to the next one and were welcome to me, just as the words I’ve heard from master western storytellers huddled around smoky sagebrush fires on a hundred hillsides of the West.

I loved how the honest, open style flowed while facts were wound around each other to present an image of the objectivity that science needs. The openness might inspire skepticism in some about “observed reality” in these beasts, but that cynicism should disappear in respecting the mantra hymn of his flinty-jawed ecologist friend, Steve Minta: “Where’s the data?”, and all the lyrics just repeat the title. I believe Dr. Lott presents the data fairly, and those who want to check up on that can comb through the bibliography of reasonable length and coverage near the end of the book.

He also notes at length the several controversies that face the bison and its ecosystem, foremost the brucellosis dilemma of the Greater Yellowstone System and the potential loss of wild bison through introgression with domesticated bison he dubs “buffattle.” Recognizing that somehow wild buffalo, commercial buffalo, and commercial cattle need to share some...
Great Plains resources, he nonetheless laments, “The public is more than willing to lose money raising wild bison . . . and we should be willing to consider resolving this paradox: Bison bison is the only wild animal in the United States that is not allowed to live as a wild animal . . . anywhere in its original range.” Lest someone charge him with one-sidedness in his fascination with bison and his advocacy of their protection and restoration, he defuses with, “At bottom, wildlife management in our society uses biological knowledge to implement individual values as they are expressed through our political system. I am an expert on my own values, and I don’t hesitate to advocate them.” This is a clear enough statement on advocacy yet leaves the political implementation open to public debate.

Public debate occurred in the late 1800s and herds declined from millions of individuals to tens. Advocates for and against bison were vocal then. The Great Slaughter “choice” was taken then and the gene pool was bottlenecked severely. This narrowing has shaped the possibilities of what we can hope to accomplish with bison conservation now. Attitudes must be plumbed and a reasonable solution or solutions to the issues addressed soon. This book will serve well to popularize at least some of the possibilities. It should also be a model as each of us addresses our own advocacy issues in the conservation or eradication of our favorite plants, bugs, birds, and bacteria. You gotta read this book.

C. Riley Nelson
Department of Integrative Biology
Brigham Young University,
Provo, Utah 84602
rileynelson@byu

CONTENTS

(Continued from back cover)

Articles (continued)
Distribution of the millipede Virgoinulus minutus (Brandt, 1841): first records from Mississippi, Oklahoma, and Texas (Julida: Blaniulidae) . . . Chris T. McAllister, Rowland M. Shelley, Henrik Enghoff, and Zachary D. Ramsey

Notes
Defense of pronghorn fawns by adult male pronghorn against coyotes . . . Kim Murray Berger
Refugia from browsing as reference sites for restoration planning . . . . . . . . William J. Ripple and Robert L. Beschta
Impact of a catastrophic flooding event on riparian birds . . . . . . . . . . Natalie J. S. Turley and Anthonie M. A. Holthuijzen

Book Review
American bison, a natural history by Dale F. Lott . . . . . . . . . . . . . . . . . . C. Riley Nelson