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LIFE HISTORIES OF STONEFLIES (PLECOPTERA) IN THE RIO CONEJOS OF SOUTHERN COLORADO

R. Edward DeWalt¹,² and Kenneth W. Stewart¹

ABSTRACT.—Thirty-one stonefly species representing eight families were collected during the March 1987 to May 1990 study period. Genera represented by more than one species included Capnia, Utacapnia, Taenionema, Suwallia, Triszaka, Isogenoides, and Isoperla. Peak species richness was recorded on or near the summer solstice in 1988 and 1989. Climatic differences between years were reflected in nymphal development and emergence phenology of most species. New or important corroborative life history data are presented for 11 stonefly species of this assemblage. The hyporheic nymphal development of most chloroperlid species limited the number of early instars sampled and our capacity to interpret voltinism. Limited nymphal data suggested a univoltine-slow cycle for Plumpiperla diversa (Frison). Adults of Suwallia pallidula (Banks) and S. wardi (Banks) were present for an extended summer period, but the bulk of their respective emergence times was temporally separated. Isogenoides zionensis Hanson, Pteronarcella bailea (Hagen), and Pteronarcys californica Newport were all shown for the first time to have a 9–10-mo egg diapause, and all three species have a semivoltine life cycle. Skuwa americana (Klapálek) and Isoperla fulva Claassen were further confirmed to have univoltine-slow cycles. Univoltine-fast and univoltine-slow life cycles are reported for the first time in I. phalerata and I. quinquenectata, respectively. Regression analysis revealed that six of the eight abundant species had extended emergence patterns (slopes of <5%/d), while only two had synchronous patterns. Warmer spring and summer temperatures in 1989 increased the slopes for five of the eight species studied, but did not change their synchrony designation. Nine of 11 abundant species advanced their median emergence date in 1989 over 1988. This and the higher slope values are consistent with a hurried nymphal development and narrower emergence period due to the warmer thermal regime of 1989.

Key words: Plecoptera, life history, biodiversity, life cycle, Rocky Mountains.

Stoneflies (Plecoptera) are one of the integral and often dominant insect orders in stream ecosystems; therefore, they are important as biological indicators, as fish food, and as part of the energy and nutrient economy of streams (Stewart and Stark 1988). Taxonomy of the North American fauna is now well known; however, information on their life histories, local species richness, and ecology is still poorly understood (Sheldon and Jewett 1967, Stewart and Stark 1988). Precise life histories are known for <5% of the more than 575 North American species, and knowledge of stonefly life histories and ecology in southern Rocky Mountain streams is sparse. This has limited our ability to increase understanding of ecological relationships between cohabiting stonefly species in this region.

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One objective of this study was to determine richness of the stonfly assemblage of the Rio Conejos of southern Colorado, a large drainage that has not been previously studied. Second, we documented the important life history events of its dominant species for which sufficient individuals and observations could be gathered by intensive monthly sampling and by living streamside during spring and summer.

Research was patterned after the classic studies of Harper (1973a, 1973b) and Harper and Hynes (1972), who studied a substantial portion of the eastern Canadian fauna and addressed critical aspects of life histories such as egg development, diapause, and adult behaviors that are often overlooked. H. B. N. Hynes, in an address to the International Plecoptera Symposium (1992), emphasized the need for more attention to these aspects to support the eventual development of a paradigm of life history evolution within the Plecoptera. We have also adopted the approaches of Knight and Gaufin (1966), Harper and Magnin (1969), Sheldon (1972), Barton (1980), Ernst and Stewart (1985a, 1985b), and Hassage and Stewart (1990) in comparatively studying an assemblage of species. This report is the first to address, on a large scale, such an assemblage in a western North American stream since the works of Knight and Gaufin (1966), Sheldon (1972), and Stanford (1975).

METHODS

Study Stream

The Rio Conejos is located in the southern Rocky Mountains of south central Colorado. The river flows east to west for 145 km from its headwaters in the Rio Grande National Forest of the San Juan range to the Rio Grande 32 km northeast of Antonito, CO. Three sampling sites were established along the Rio Conejos to ensure access to at least one of them during the winter and to enhance collection of stonfly species that were not abundant at all sites. These were located at elevations between 2400 and 2600 m above sea level. The primary site (106°15'W longitude, 37°03'N latitude) consisted of a 1-km stretch located 24 km west of Antonito, Conejos County, CO, off Colorado highway 17. Sites two and three were located 22.5 km west of Antonito, also on highway 17, and 4 km north of Antonito at the Colorado highway 285 bridge, respectively.

Stream temperatures varied from below freezing during the winter months to near 20°C in August. Ice cover was common from December through March. Snowmelt began in April, usually leading to peak flows in June. Base flows were attained by late August and continued through the winter. Water released from Platoro Reservoir, 48 km upstream, augmented river flow during summer low-flow periods. Bottom substrates were characterized by large boulders, cobble, gravel, and sand. These were covered by a thin layer of silt in quiet water. Important organic substrates included the flooded coppices of willows and cottonwoods and their entrained leaf packs. Willow (Salix spp.), cottonwoods and aspens (Populus spp.), and alder (Alnus sp.) contributed to the riparian corridor.

Physical Conditions

Stream temperature was monitored at site one from June through August 1988 using a Ryan™ continuous recording thermograph. High, low, and mean daily stream temperatures were calculated from temperatures recorded at 0400, 0800, 1200, 1600, 2000, and 2400 h. Water temperatures were not recorded during 1989 due to equipment failure. However, summer air temperature highs and lows and rainfall were recorded (1300 h daily, mountain time) for both 1988 and 1989 at the Conejos Peak U.S. Weather Service reporting station at site one. Flow data for site two were gathered from Petsch (1987–90).

Nymphal Growth

Nymphs were collected monthly (except December due to poor weather conditions) at all sites from March 1987 to May 1988. Additional collections were made at irregular intervals until March 1990. Samples were collected by disturbing the substrate (mineral and organic) upstream of a BioQuip rectangular dipnet until debris clogged the net. The net was composed of a coarse, 1-mm mesh first stage, modified by the addition of a conical second stage of 153-μm mesh size. The latter collected even the smallest instars. A plankton bucket was attached to the second stage to facilitate sample removal. Contents of the plankton bucket and the coarse stage constituted a sampling unit and were stored in
70% isopropyl alcohol. The number of sampling units per month varied with the effort necessary to secure approximately 50 nymphs of all abundant species.

Nymphs were separated from sample debris with the aid of 4-10X magnification on a stereo-dissecting microscope, sorted to species when possible, and stored in 80% ethanol until measurement. Head capsule width (HCW, greatest distance across the eyes) was measured with a calibrated ocular micrometer fitted to a stereo-dissection microscope. Nymphs from all sites for the 3-yr sampling period were pooled by species and month of collection to increase the number of nymphs per month and to allow construction of more robust growth histograms. Gender of nymphs was assessed by a gap in the posterior setal margin of the eighth sternum of females (Stewart and Stark 1988) and by developing external genitalia of females. Sex-specific kite diagrams were constructed by placing male and female nymphs into 0.1- or 0.2-mm size classes. The frequency of these classes was converted to a percentage of the total number of nymphs (males + females + unsexed nymphs) collected for that month. Polygons were constructed for each month depicting the relative proportion of all nymphs at that size class.

Adult Emergence

Adults of winter- and early spring-emerging stoneflies were collected from bridge abutments, from shoreline debris, and under the cobble at streamside to provide a general emergence period for each species. Adults were also reared from preemergent nymphs.

A combination of sampling methods and observational procedures was used during the summers of 1988 and 1989 to evaluate emergence, duration of adult presence, and behavior of these species. Adult traps and methods included a 2.25-m² basal area BioQuip malaise trap, two 0.25-m² basal area floating emergence traps, pitfall traps, sweepnetting of streamside vegetation, exuviae collection, and day and night transect walks. Pitfall traps were emptied on alternate days, and the others were emptied daily between 0900 and 1100 h. All of these methods were used at site one; sweepnetting was employed at site three on several occasions.

The malaise trap was deployed among willow and cottonwood coppices, where its olivedrab coloration mimicked the surrounding vegetation. Flying, or crawling, adults intercepted by the trap ascended the screening into a dry apical collection chamber. Additionally, all adults on the trap mesh were collected using an aspirator.

Emergence traps were anchored over shallow riffles during the 1988 field season. Natural diurnal changes in water level and erratic discharges due to water release from Plateno Reservoir rendered these ineffective at times; therefore, their use was discontinued in 1989.

Pitfall traps consisted of 28.3-cm² modified aluminum soda cans that were buried flush in streamside substrates. A mixture of 70% ethanol and ethylene glycol (the latter to retard evaporation) was used as a preservative. In 1988, 12 traps were installed 1 m from the stream at 1-m intervals on an open beach with nearby vegetation. This was expanded in 1989 to three transects, each consisting of 30 cans set 1 m apart in transects 1 m, 5 m, and 8 m from the initial shoreline. These traps monitored not only adult presence of ground-traversing, brachypterous stoneflies, but also their potential to move laterally from the stream.

Sweepnetting was conducted over a 15 × 2-m willow and cottonwood riparian zone. The entire area was methodically swept, working from the base of each clump of vegetation upward. Exuviae removal was the only method used to assess emergence of Calessenia sabulosa (Banks) and was used for no other species. In 1988 exuviae were removed daily from the same 15 × 1-m area of cobble shoreline, and the frequency of each sex was noted. In 1989 the removal area was expanded to 30 × 1 m of shoreline area and up to 5 m into the water for collecting exuviae from emergent substrates.

Year and sex-specific kite diagrams of adult presence were produced for all abundant summer stoneflies by pooling all methods and expressing daily catches as a percentage of the total catch. Duration of emergence of Pteronarcys californica Newport would be greatly overestimated by including pitfall trap collections due to its synchronous emergence and since pitfall traps were emptied on alternate days.
Dates of first capture, 50% cumulative catch, and last collection, plus total duration of adult presence, were determined for the 11 most abundant species collected in the summers of 1988 and 1989. Emergence synchrony was estimated using linear regression of the cumulative percentage catch (all methods pooled) versus days since first capture. Slopes generated for each species were used as an index of synchrony. Steeper slopes indicated a more synchronous emergence. Slopes ≥ 5%/d were chosen to be indicative of synchronous emergence since species with these slopes emerged their entire population within a few days and had steep, j-shaped, cumulative emergence curves. Differences between slopes for 1988 and 1989 were tested using a modified t test (Zar 1984). Common slopes were calculated if no differences between years were noted. This was a purely descriptive approach designed to detect and compare patterns; therefore, it is not our aim to model emergence for the purpose of prediction, but only to describe patterns of emergence.

Since most adult collection methods employed in this study collected adults of unknown age, results reflected adult presence rather than, in the strictest sense, emergence. No attempt was made to discard old males and females using any index of age. However, patterns of adult presence should follow that of a true emergence pattern, and since longevity of most adults approached only 1 wk in the laboratory, we believe these results to be useful.

Behavioral observations were made from 0800 to 1300 h and from 2000 to 2300 h for several days during emergence of each species. Observations made during intervening hours produced little adult behavior. Timing of adult activities, their relative distance from the stream, and substrates on which activities took place were monitored by walking the stream margin, turning logs and rocks, and exposing leaf-entrained bases of marginal vegetation. Details of these observations have been narratively described for each species in this paper.

Fecundity and Egg Incubation

Eggs of several species were incubated in the laboratory to confirm proposed voltinism based on growth histograms. Eggs were placed into 1-cm-diameter dialysis tubing bags and reared in a Frigid Units Living Stream™, or they were stored in 100 × 15-mm plastic petri dishes in an environmental chamber. In both instances these were incubated at approximate stream temperature and light regime.

Fecundity was estimated from number of egg batches deposited, number of eggs per batch, and, for Skwala americana (Klapálek) only, total number of eggs remaining in the ovarioles. Females were housed at streamside in screened, glass containers and provided with moist cotton balls as a source of water. Alternatively, some species were reared in Denton and held under simulated streamside conditions in large cotton-stoppered shell vials.

RESULTS

Physical Conditions

Mean daily stream temperatures in 1988 increased from near 10°C in early June to 15°C in mid-July (Fig. 1). The stream cooled dramatically between 8 and 12 July. This coincided with cool, damp weather conditions (Fig. 2). Summer air temperature highs rarely exceeded 30°C in 1988, and rainfall occurred at regular intervals throughout the summer (Fig. 2). However, 1989 was marked by many days above 30°C with rainfall relegated to late July and August (Fig. 2). The mean monthly discharge of the Río Conejos during 1987–1989 fluctuated predictably. Peak discharge occurred typically in June but occurred in May during the warm, windy spring of 1989 (Fig. 3).

Species Richness

More than 13,000 nymphs and adults were studied over the 3-yr period. Among these
were 31 species (Table 1) in eight families. The Chloroperlidae, Perlodidae, and Capniidae were the most speciose families with six, seven, and seven species, respectively. Seven genera were represented by more than one species: Capnia, Utacapnia, Taenionema, Suwaltia, Triznaka, Isogenoides, and Isoperla (Table 1).

Peak species richness occurred on or near the summer solstice in both years (Fig. 4). Pattern differences existed between years, including an early waning and a more peaked distribution of species richness in 1989.

**Leuctridae**

*Paraleuctra vershina* Gaufin and Ricker. This was the only leuctrid found at our sites. No nymphs were recovered from the stream, indicating a probable hyporheic existence. Adults were abundant in riparian vegetation during June and July (Fig. 5). No variation in adult presence parameters was noted for *P. vershina* (Table 2). Emergence was classified as extended in both years, although slopes of these cumulative emergence curves were significantly different over the 2 yr (Table 3).

<table>
<thead>
<tr>
<th>Year</th>
<th>Average Temperature</th>
<th>Average Rainfall</th>
<th>Maximum Temperature</th>
<th>Minimum Temperature</th>
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</thead>
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<td>1988</td>
<td>20°C</td>
<td>50 mm</td>
<td>35°C</td>
<td>10°C</td>
</tr>
<tr>
<td>1989</td>
<td>22°C</td>
<td>55 mm</td>
<td>38°C</td>
<td>12°C</td>
</tr>
</tbody>
</table>

**Table 1.** Stonefiles collected from the Rio Conejos, Colorado, March 1987 through March 1990.

**Eubolognathia**

**Capniidae**

*Capnia coloradensis* Claassen³
*Capnia confusa* Claassen
*Capnia vernalis* (Newport)
*Isocapnia crinita* (Needham & Claassen)³
*Utacapnia logana* (Nebeke & Gaufin)³
*Utacapnia poda* (Nebeke & Gaufin)³

**Nemouridae**

*Amphinemura banksi* Baumann & Gaufin³
*Protaia besemetsa* (Ricker)³
*Zapada frigida* (Claassen)³

**Taeniopterygidae**

*Taenionema pallidum* (Banks)³
*Taenionema pacificum* (Banks)³
*Doellsia occidentalis* (Banks)³

**Systellognathia**

**Chloroperlidae**

*Paraperla frontalis* (Banks)³
*Plumoperla diversa* (Frison)³
*Suvellia lutea* (Banks)³
*Suvellia pallidula* (Banks)³
*Suvellia vardi* Kondratieff & Kirchner³
*Triznaka pintada* (Ricker)³
*Triznaka signata* (Banks)³

**Perlidae**

*Classenia sabulosas* (Banks)³
*Hesperoperla pacifica* (Banks)³

**Perlodidae**

*Isogenoides zionensis* Hanson³
*Isogenoides prob. coloradensis* (Hagen)³
*Isoperla fulva* Claassen
*Isoperla mormona* Banks³
*Isoperla phalerata* (Smith)³
*Isoperla quinquepunctata* (Banks)
*Stealia americana* (Klapalek)

**Pteronarcitidae**

*Pteronarcia badia* (Hagen)
*Pteronarcyia californica* Newport³

³ New drainage and county records.
Chloroperlidae

Representatives from two subfamilies inhabited the stream. The early- and mid-instar nymphs of the Chloroperlinae genera could not be reliably identified to genus. This necessitated the illustration of a portion of the nymphal growth of *Plumiperla diversa* (Frison) and *Triznaka signata* (Banks) as Chloroperlinae spp. (Fig. 6). Growth of reliably identified mid- to late-instar nymphs was illustrated separately.

*Paraperla frontalis* (Banks) (Paraperlinae). Nymphs were collected infrequently among marginal substrates during the colder months of the year. All were pale, very thin, and had eyes set far forward as described for mature nymphs (Stewart and Stark 1988). These limited data are presented for the first year of the presumed semivoltine growth pattern of this large chloroperlid (Fig. 6). Less than 10 adults were collected in early June during the 3-yr study.

*Plumiperla diversa* (Chloroperlinae). No adults were collected on which to base specific identity; however, nymphs of this genus are distinctive, and only *P. diversa* has been collected in this region (Baumann et al. 1977). Nymphs were identifiable to genus by March. Females were readily distinguished from males at this time. Growth continued through May when females attained a median HCW 9.6% larger than males. The limited nymphal data suggested a univoltine-slow life cycle for this species.

*Suwallia pallidula* (Banks) (Chloroperlinae). Only 59 nymphs of *Suwallia* spp. were collected from the Rio Conejos, even though adults were abundant. Nymphs were hyporheic until immediately prior to emergence. This habitat preference and our present inability to distinguish congeners of *Suwallia* nymphs precluded generation of meaningful histograms and designation of voltinism for either species. Adults of *Suwallia wardi* Kondratieff & Kirchner were consistently larger than *S. pallidula*. This trend followed in nymphs, too, with proposed female nymphs of *S. wardi* in June (peak emergence) being 22.0% larger

Fig. 5. Emergence of *Paraleuctra vepshina* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.
than the July (peak emergence) females of *S. pallidula*. Only two proposed male nymphs of the latter were collected over the 3-yr period.

Adults of *S. pallidula* were collected in July and August in both years (Fig. 7, Table 2). Slopes from regression models were different between years (*t* = −64.7, *p* < .0001), but below the 5%/d criterion. We categorized this species as an extended emitter (Table 3). The median emergence date was advanced by 2 wk in 1989 over that of 1988 (Table 2). The adult sex ratio over the two seasons was 13 ♀: 415 ♂. Six field-collected and laboratory-maintained females produced only one egg batch (Table 4).

*Sucalia wardi* (Chloroperlinae). This was the most abundant of the three *Sucalia* species collected from the Rio Conejos. Adults were first collected in late May or early June, reached 50% cumulative catch by mid-July, and disappeared from streamside by early August (Table 2). It had the longest mean duration of presence (66 d) for any stonefly studied on the Rio Conejos (Table 2). Like its congener, *S. wardi*’s 1989 date of median catch was advanced by 2 wk over that of 1988 (Table 2, Fig. 7). Emergence of *S. wardi* was extended, and no significant slope differences were noted between years (Table 3). No egg data were collected for this species.

Riparian vegetation was used by this large, yellow-green chloroperlida as a staging ground for adult behaviors. *Suwallia wardi* was active throughout the morning on sunny days and again for 2−3 h before sunset if conditions were warm and dry. During cool, rainy days the low vegetation was devoid of *S. wardi* or any other stonefly species.

*Triznaka signata* (Banks) (Chloroperlinae). Identifiable, late-instar nymphs were collected during a 5-mo period in the spring and summer. Nymphs of this univoltine-slow

<table>
<thead>
<tr>
<th>Species</th>
<th><em>n</em></th>
<th>First capture</th>
<th>50% catch</th>
<th>Last capture</th>
<th>Duration (d)</th>
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<tr>
<td><em>P. vershina</em></td>
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<td>35.0 ± 0.0</td>
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<td></td>
<td>58</td>
<td>1 June</td>
<td>17 June</td>
<td>7 July</td>
<td></td>
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<tr>
<td><em>S. wardi</em></td>
<td>467</td>
<td>6 June</td>
<td>10 July</td>
<td>15 August</td>
<td>66.0 ± 7.1</td>
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<tr>
<td></td>
<td>352</td>
<td>19 May</td>
<td>25 June</td>
<td>18 July</td>
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<tr>
<td><em>S. pallidula</em></td>
<td>276</td>
<td>30 June</td>
<td>28 July</td>
<td>23 August</td>
<td>44.5 ± 4.8</td>
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<tr>
<td></td>
<td>162</td>
<td>1 July</td>
<td>14 July</td>
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<tr>
<td><em>T. signata</em></td>
<td>682</td>
<td>9 June</td>
<td>23 August</td>
<td>12 July</td>
<td>59.0 ± 24.0</td>
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<td></td>
<td>2697</td>
<td>2 June</td>
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<td><em>C. sabulosa</em></td>
<td>356</td>
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<td>1195</td>
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<td><em>I. fulva</em></td>
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<td><em>I. phalerata</em></td>
<td>12</td>
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<td>22.5 ± 3.5</td>
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<td>18 June</td>
<td>25 June</td>
<td>8 July</td>
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<td><em>I. quinquepunctata</em></td>
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<td>14 July</td>
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<td>22 June</td>
<td>17 July</td>
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<td><em>P. californica</em></td>
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<td>6 June</td>
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<td>13 June</td>
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species were largely full grown by April (Fig. 6) with some degree of sexual dimorphism present at this time.

Adults first appeared in early June, reached 50% cumulative catch 2 wk later, and could no longer be collected by late August (Fig. 7, Table 2). Emergence was protandrous, but slightly female-skewed sex ratios dominated in both 1988 and 1989 (Fig. 7). Triznaka signata displayed the greatest variation in last date of capture and duration of presence of all stoneflies in the river (Table 2). It advanced its 1989 median emergence date by 9 d over that of 1988. Regression slopes indicated an extended emergence in both years (Table 3). Differences between slopes for 1988 and 1989 were significant ($t = -11.35, p < .0001$).

Attempts during the entire study to obtain eggs from laboratory-reared and -mated females were unsuccessful. The mean number of eggs from six females caught during oviposition flights was lower than any first batches for other stoneflies studied (Table 4). Although these females were held for a prolonged period of time, no additional egg batches were laid.

Adults were never seen emerging in the field, despite many hours of observation along the shoreline, day and night, in habitats where they were collected in abundance during the day. Adults inhabited marginal vegetation, where males were observed actively searching willow stems and leaves for females. No drumming was observed during the two summers of intensive fieldwork. Large flights of adults of both sexes took place just before dark, at which time females were observed ovipositing. Egg masses were dropped from up to 4–5 m above the stream.

**Perlidae**

*Claassenia sabulosa.* Although two perlids were present in the Rio Conejos (Table 1), only *C. sabulosa* was sufficiently abundant for growth and emergence interpretation. Nymphs of this species were found among larger rubble of midstream. The life cycle was semivoltine and appeared to require 3 yr of nymphal growth (Fig. 8). Recruitment occurred throughout the fall with possibly some additional recruitment in March from overwintering eggs. Eggs containing eyespots were recovered from the stream in October and November. Sexual dimorphism in both size and external genitalia occurred when nymphal size reached 2.2 mm HCW. The size disparity increased until the third year of growth when little overlap between the sexes remained.

A protandrous emergence began in mid-July in both years (Fig. 9, Table 2). Exuviae of this species were abundant throughout August, possibly into September. Emergence of *C. sabulosa* was extended and slopes were significantly different between years ($t = -10.7, p < .0001$, Table 3).

<table>
<thead>
<tr>
<th>Species</th>
<th>Slope</th>
<th>$R^2$</th>
<th>$p$</th>
<th>Synchrony</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. versina</em></td>
<td>3.0</td>
<td>.85</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>3.5*</td>
<td>.90</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>T. signata</em></td>
<td>1.5</td>
<td>.87</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>3.0*</td>
<td>.91</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>S. pallidula</em></td>
<td>2.5</td>
<td>.96</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>3.5*</td>
<td>.90</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>S. wards</em></td>
<td>2.2</td>
<td>.84</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>.85</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>C. sabulosa</em></td>
<td>2.8</td>
<td>.94</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>4.1*</td>
<td>.99</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>I. zionensis</em></td>
<td>7.5</td>
<td>.92</td>
<td>.0001</td>
<td>synchronous</td>
</tr>
<tr>
<td></td>
<td>7.9</td>
<td>.95</td>
<td>.0001</td>
<td>synchronous</td>
</tr>
<tr>
<td><em>P. badia</em></td>
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<td>.81</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td></td>
<td>4.4*</td>
<td>.92</td>
<td>.0001</td>
<td>extended</td>
</tr>
<tr>
<td><em>P. californica</em></td>
<td>13.3</td>
<td>.84</td>
<td>.004</td>
<td>synchronous</td>
</tr>
<tr>
<td></td>
<td>18.9*</td>
<td>.97</td>
<td>.103</td>
<td>synchronous</td>
</tr>
</tbody>
</table>

Table 3. Synchrony and linear regression statistics for the years 1988 (appears first) and 1989. Slopes between years were tested: * = significance .05–.01, ** = <.001 level or lower probability, and NT = not tested.
**Isogenoides zionensis** Hanson (Perlodinae: Perlodini). The large range in size of nymphs from July samples (Fig. 10) could not be accounted for by nymphs hatching from eggs laid by June-mated females. June eggs reared at simulated stream conditions hatched in March and April, 9–10 mo after oviposition. Therefore, at least some individuals of this species have a semivoltine life cycle with eggs diapausing over their first summer and winter. Early-instar nymphs were missed in benthic samples during their second spring, possibly due to high water or their occurrence deep in the substratum. Sexual dimorphism in size and morphology was apparent by July of the second year when nymphs approached 1.8 mm HCW (Fig. 10). This disparity increased steadily throughout the rest of their growth. Little overlap in size of the sexes existed by May prior to emergence.

The adult presence parameters of *I. zionensis* showed little variation over the 2 yr studied (Table 2). Emergence was not protandrous, but the sex ratio was heavily skewed towards males (Fig. 11). This species was one of two that emerged synchronously (Table 3). No difference in slope was found between years (t = 0.82, p > .2); therefore, a common slope of 7.6%/d was calculated.

Laboratory-reared females put nearly 75% of their total egg complement into a first batch (Table 4). Only one of four females produced additional batches.

Transformation of *I. zionensis* took place from 2030 to about 2200 h. Nymphs crawled away from the stream until they reached willows or other vegetation, then ascended <1 m vertically where they molted. Daylight activity began by 0700–0800 h at the base of small willow coppices, where adults were often found in emergent leafpacks. Adults ascended streamside willows as the sun rose. Drumming, mating, and egg batch formation took place from these perches. Females crawled to the tops of these willows and flew to the stream where they fluttered on the water to release their black egg masses. Most activity ceased by 1300–1400 h on days when air temperature reached near 25°C. On cloudy, cool days this ascendance did not occur. Most adults could then be found in the leaf-entrained bases of riparian vegetation. Drumming on willow stems
Table 4. Mean eggs per batch, number of batches, and mean total egg complement for nine species of stoneflies occurring in the Rio Conejos, Colorado.

<table>
<thead>
<tr>
<th>Species</th>
<th>Eggs / batch</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>n</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. pallidula</td>
<td></td>
<td>54.7</td>
<td>6</td>
<td></td>
<td></td>
<td>2</td>
<td>54.7 ± 26.6</td>
</tr>
<tr>
<td>T. signata</td>
<td></td>
<td>42.2</td>
<td>6</td>
<td></td>
<td></td>
<td>2</td>
<td>42.2 ± 17.4</td>
</tr>
<tr>
<td>C. sabulosa</td>
<td></td>
<td>2166.0</td>
<td>7</td>
<td>902.0</td>
<td>158.9</td>
<td>40.0</td>
<td>3188.0 ± 613.0</td>
</tr>
<tr>
<td>I. zionensis</td>
<td></td>
<td>588.0</td>
<td>4</td>
<td>327.0</td>
<td>185.0</td>
<td>1</td>
<td>843.2 ± 141.4</td>
</tr>
<tr>
<td>I. fulva</td>
<td></td>
<td>231.5</td>
<td>2</td>
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<td></td>
<td>1</td>
<td>231.5 ± 7.8</td>
</tr>
<tr>
<td>I. phalerata</td>
<td></td>
<td>703.0</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
<td>703.0</td>
</tr>
<tr>
<td>S. americana</td>
<td></td>
<td>884.7</td>
<td>6</td>
<td></td>
<td></td>
<td>2</td>
<td>884.7 ± 267.3</td>
</tr>
<tr>
<td>P. badia</td>
<td></td>
<td>339.0</td>
<td>30</td>
<td>58.4</td>
<td>56.8</td>
<td>4</td>
<td>351.0 ± 101.0</td>
</tr>
<tr>
<td>P. californica</td>
<td></td>
<td>393.0</td>
<td>4</td>
<td>191.3</td>
<td>94.3</td>
<td>4</td>
<td>318.8 ± 49.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>6</td>
<td>58.5</td>
<td>57.0</td>
<td></td>
<td>845.3 ± 90.5</td>
</tr>
</tbody>
</table>

*Total fecundity includes those eggs remaining in ovaries.

was observed at night, even when temperatures approached 10°C.

*Isoperla fulva Claassen (Isoperlinae).* We collected this species in benthic samples only occasionally, but enough individuals were obtained to allow a tentative interpretation of voltinism. Recruitment of nymphs was first detected in August (Fig. 12). These measured 0.4–0.8 mm HCW and grew at a slow rate throughout the fall until a winter decrease in growth rate. Their size increased dramatically after February, until emergence in June and July. This species conformed to a univoltine-slow growth pattern.

Adults were collected for the first time on 9 June in both years (Fig. 11, Table 2). Sex ratios for the small number of 1988 adults were approximately equal, but heavily skewed towards males in 1989. Numbers of adults collected in both years were too small to warrant an analysis of synchrony.

Fecundity was difficult to assess since few mature nymphs were available for rearing. One egg batch from each of two field-ovipositing females was collected (Table 4). Longevity of three field-collected adult females was 5.7 ± 0.58 d.

*Isoperla phalerata* (Smith) (Isoperlinae). Although the number of nymphs collected was small, no month supported more than one size class (Fig. 12). Therefore, we have tentatively proposed a univoltine-slow growth pattern for this species. Adults were taken from mid-June through mid-July (Table 2, Fig. 11). No assessment of synchrony was made for I. phalerata due to low numbers of adults captured. Females did not produce eggs in captivity. A single egg batch from a field-collected individual contained 703 eggs. Four field-caught females lived 11.3 ± 3.6 d past date of capture.

*Isoperla quinquepunctata* (Banks) (Isoperlinae). This species was more common at site
three. The data suggested that *L. quinquen punctata* had a univoltine-fast growth pattern. Recruitment occurred in January and February (Fig. 12), and growth was rapid from March through May. Sexual dimorphism in nymphal size was not as evident in this species as in its congeners. Emergence began in mid-June and lasted through much of July (Table 2, Fig. 11). No eggs were collected.

*Skwala americana* (Klapálek) (Perlodinae). This species displayed a univoltine-slow growth pattern and grew faster during summer and fall months than all other perlodids in the Rio Conejos (Fig. 13). Nymphs were recruited in June and increased their median HCW from 0.4 mm to about 2.8 mm by January. Growth was nearly completed by this time. Sexual dimorphism was apparent as early as August, and female nymphs reached a median HCW before emergence that was 21.4% greater than males. Female nymphs in April were found to contain fully sclerotized eggs in their oviducts; hence, this species is fully capable of mating and egg-laying immediately upon emergence.

Emergence was in April and early May when our sampling was still on a monthly basis; therefore, no detailed analysis of emergence phenology and synchrony can be offered. Adults were collected mainly from emergent logjam debris or under cobble at the stream margin.

Egg batches collected in mid-April from four laboratory-reared females hatched synchronously after a mean of 61.0 ± 7.3 d. This corroborates field collections of early-instar nymphs in June. Only a single egg batch was collected from each of six laboratory-reared females (Table 1).

Fig. 8. Growth of *Claassenia sabulosa* nymphs collected from the Rio Conejos, 1987–1990.

Fig. 9. Emergence of *Claassenia sabulosa* from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.

**Pteronarcyidae**

*Pteronarcella badia* (Hagen). This species was found to have a semivoltine growth pattern. Recruitment of nymphs began in March and April from eggs laid the previous June (Fig. 14). Many small nymphs were available in benthic samples by mid-April when they were at 0.2–0.4 mm HCW. This scenario was corroborated by laboratory incubation of several egg batches that hatched in March and April after a 9–10-mo diapause. Growth of nymphs was rapid throughout their first spring. Size differentiation among sexes was not apparent until August, a full 14 mo after oviposition. Median size of females just before emergence the following May was 21% greater than that of males.

Emergence began by early June, with slight protandry and a preponderance of males being collected (Fig. 15). Median emergence occurred in the third week of June in both years (Table 2). Emergence was extended (Table 3) and slopes were significantly different between years (t = −2.2, p < .05).

Females generally laid only single egg batches, but a small number produced up to three egg batches (Table 4). Most females laid their first egg batch within 24 h of mating and often waited 2-d intervals before laying others. Longevity of seven females under simulated field conditions was 7.7 ± 4.2 d.

*Pteronarcella badia* emerged just after dusk and typically used willows, cottonwoods, and stream margin sedges as transformation sites. Males were observed actively searching the willows and drumming for females at night,
even when air temperatures were near 10°C. Adults entered the leaf-choked bases of willows as the night progressed and were often found the next morning in large mating aggregations under these debris. These individuals ascended the willows as the sun warmed the air at streamside. Drumming, mate searching, mating, and egg batching took place in mid-morning hours, while most activity ceased by 1200 h when air temperatures reached 22–25°C. Females oviposited by launching themselves from the tips of tall riparian shrubs toward the stream, where they would jettison their white egg mass a few meters above the surface of fast-flowing water.

_Pteronarcyis californica_ Newport. This species is commonly known as the salmonfly. Recruitment began in April (Fig. 16) after a 9–10 mo egg diapause. Nymphs grew to only about 1 mm HCW through their first year. Sexual differences in size and morphology were apparent by June of their second year, when they were nearly 1.5 mm HCW. Nymphs grew for two more years, by the end of which time preemergent females had attained a 20% larger median HCW than males. These data suggest a semivoltine life history of 4-yr duration for this species.

Adults were first found on 6 June during both years (Fig. 15, Table 2). Emergence was a highly synchronous event (Table 3). Slopes were not tested for significant differences due to small sample size.

Most laboratory-reared females produced five egg batches, but one individual produced seven (Table 4). Egg production lasted through 82% of the 15.0 ± 1.8 d (n = 4) average adult female life span.

![Fig. 10. Growth of _Isogenoides zionensis_ nymphs collected from the Rio Conejos, 1987–1990.](image)

![Fig. 11. Emergence of Perlodidae from the Rio Conejos, 1988 and 1989. Polygons indicate daily relative proportion of total catch.](image)

Adults utilized marginal vegetation, much as did _F. badia_, as a staging ground for mating and ovipositing. However, they tended to select the taller cottonwoods and Engelmann spruce rather than the shorter willows for their activities. Salmonflies oviposited by flying over the stream and dropping their salmon-colored or bluish egg masses (dimorphism in egg color was observed) from as high as 10 m. Ovipositing adults were heavily fed upon by opportunistic Eastern Robins (_Turdus migratorius_) and Steller’s Jays (_Cyanocitta stelleri_).

**DISCUSSION**

**Species Richness**

The Rio Conejos displayed a great diversity of Plecoptera. Twenty of the 31 species were evenly distributed among the Capniidae, the Chloroperlidae, and the Perlodidae. The only North American family not represented was the Peltoperlidae, which occurs transcontinentally, but not in latitudes below the northern Rocky Mountains (Baumann _et al._ 1977). Nearly all species collected were adapted for a montane existence and were characteristic of streams with high biotic integrity. Twenty-five species were both new drainage and county records (Baumann _et al._ 1977, Szczytko and Stewart 1979, Nelson and Baumann 1989; Table 1), though all of them had been previously reported from Colorado and neighboring New Mexico. This demonstrates that we have yet to adequately investigate the fine-scale diversity

Fig. 13. Growth of *Skwala americana* nymphs collected from the Rio Conejos, 1987–1990.

and distribution of this order of aquatic insects in at least some portions of the southern Rocky Mountains.

Responses to Altered Thermal Regime

We became aware of substantial climatic differences (Fig. 2) between the two summers when adults were intensively studied. Though no water temperatures were available for 1989, air temperatures (Fig. 2) and hydrologic data (Fig. 3) suggested that the stream warmed more quickly and attained peak summer highs much earlier than in 1988. Consequently, development of several species was hurried, which narrowed the window of time adults were present streamside. At the assemblage level of organization, this trend is demonstrated by the species richness pattern of Figure 4. The 1989 pattern was more peaked and greatly truncated over that of 1988. Species-level responses can be demonstrated by inspection of the flight diagrams for each species. Nine of the 11 species presented in Table 2 show increased median emergence dates. Additionally, slopes produced by linear regression that were different between years (Table 3) were always higher in 1989. This result was consistent with a hurried nymphal development and shorter emergence period for each species.

Life History Parameters

**Leuctridae**

*Paraleuctra vershina*. Harper (1973b) reports that most *Leuctra ferruginea* in an Ontario stream are semivoltine, but that some univoltine individuals exist. Huryn and Wallace (1987) propose a 2-yr life cycle for a composite of *Leuctra* spp., most of which were probably


**Chloroperlidae**

Most Chloroperlidae exhibit a univoltine-slow or fast growth pattern. *Haploperla brevis* (Banks) is widespread from Oklahoma to Quebec and west to Alberta, Canada. Ontario (Harper and Magnin 1969), Quebec (Harper et al. 1994), and Oklahoma (Ernst and Stewart 1985a) populations exhibited univoltine-fast growth with a 2–5-mo diapause, while Alberta populations were univoltine-slow (Barton 1980). European populations of *Chloroperla tripunctata* (Scopoli) (Elliott 1958), *Siphomonopera torrentium* (Pictet) (Elliott 1967), and *S. burmeisteri* (Pictet) (Benedetto 1973) also exhibited univoltine-slow growth. Species with semivoltine growth include *Svetltsa onkos* (Ricker) and possibly *Utaperla gaspiana* Harper and Roy (Harper 1973a, Harper et al. 1994), *S. mediana* (Banks) (Cushman et al. 1977), and *S. lateralis* (Banks) (Huryn and Wallace 1987).

*Paraperla frontalis*. Stanford and Gauvin (1974) presented some evidence for semivoltine growth of this species. Emergence for this species and for *P. wilsoni* Ricker occurs from May through July (Stewart and Stark 1988). Paraperlinae are rather robust chloroperlids that tend to be hyporheic for most of their nymphal development. Their larger size, the more stable stream temperatures in the hyporheic environment (Hendricks 1993), and the possibly low availability of some nutrients in the
hyporheic habitat (Stanford and Ward 1993) may have contributed to a preponderance of semivoltinism in this subfamily.

Plumiperla diversa. Stewart et al. (1990) reported a univoltine-slow cycle for this species on the North Slope of Alaska. Emergence occurred from May through September, with recruitment of nymphs from a direct hatch in July. Growth occurred through the summer months with most nymphs attaining maximum size before a winter quiescence. This assessment compared well with our limited data. Failure to collect adults was probably due to our infrequent sampling during their presumed early May emergence.

Suwallia pallidula and Suwallia wardi. No aspects of the life histories of either S. pallidula or S. wardi have been reported. The latter was recently described from a Colorado Front Range springbrook (Kondratieff and Kirchner 1990). It was one of the most abundant chloroperlids in the Rio Conejos. This suggests that its ecological tolerance is wide and that it may soon be found in a variety of streams in the southern Rocky Mountains.

Several explanations are possible for the heavily female-skewed sex ratio (13 $\delta$ : 425 $\varphi$) of S. pallidula adults. The most probable is a combination of limited use of emergence traps coupled with an inaccessible microhabitat of adult males, probably high in the vegetation. Parthenogenesis may also be possible, but it is exceedingly rare in stoneflies. Harper (1973a) reported that a few eggs of a perlid, Paragnetina media (Walker), hatched without fertilization. We did not attempt rearing of eggs from virgin females to check for parthenogenesis in either Suwallia spp. These sex ratios are a perplexing problem, compounded by the fact that 0 $\delta$ : 657 $\varphi$ of the closely related S. lineosa were caught during concurrent sampling on Massey Creek, a tributary of the Rio Conejos.

Triznaka signata. Hassage and Stewart (1990) studied the widely distributed T. signata in the Rio Vallecitos of northern New Mexico. They reported a univoltine-slow growth pattern, with which we concur. No study of the emergence of this species has previously been published.

Perlidae

Claassenia sabulosa. Hassage and Stewart (1990) and Barton (1980) report a merovoltine (>2 yr) growth pattern for New Mexico and Alberta populations of this species. No egg batches from the Rio Conejos hatched in our laboratory, but this Colorado population showed some evidence of an extended hatch leading to cohort splitting (Stewart and Stark 1988). Eggs may undergo a temperature-dependent quiescence as occurs in Dinocras cephalotes (Curtis) when fall temperatures decline to 8°C (Lillehammer et al. 1989). Presence of first-instar nymphs in the fall, eyed eggs in October and November, and more first-instar nymphs in March supported this contention.

Life histories have been reported for at least one species in every genus in the tribe Perlini, to which C. sabulosa belongs. All growth patterns involve 2–3 yr of development. Agnetina flavescens (Walsh), from an Ozark stream, exhibits a 2-yr life cycle, a short egg incubation period, and an extended emergence period.
(Ernst and Stewart 1985b). *Agneta capitata* (Pictet) was shown to have a 3-yr cycle, extended emergence, and a 40–80-d egg incubation period in Ontario (Harper 1973a). This range of incubation coupled with a long emergence promotes great differences in size of nymphs that ultimately prevents the separation of cohorts and determination of voltinism. This was also a problem for *C. sabulosa* in the Rio Conejos.

**Perlodidae**

This family contains over 115 species (Stark et al. 1986, Stewart and Stark 1988) in the Nearctic. Although life histories of only 26 species are known, a clear trend toward univoltine-slow cycles occurs among the subfamilies Isoperlinae and Perlodinae (Stewart and Stark 1988). Growth and emergence had not previously been studied for three of the seven perlodids in the Rio Conejos. These include *I. zionensis*, *I. quinquepunctata*, and *I. phalerata*.

**Isogenoides zionensis.** Few detailed life history studies of the genus have been reported (Stewart and Stark 1988). Barton (1980) suspected semivoltinism for an Alberta population of *I. colubrinus*, since two size classes of nymphs were collected in early May. Flannagan (1977) reported great body length variation in May for this species in another Alberta watershed but concluded a univoltine-slow cycle. Hilsenhoff and Billmeyer (1973) and Dossdall and Lehmkühl (1979) proposed univoltine growth patterns for the May–June-emerging *I. frontalis* in Wisconsin and Saskatchewan streams, respectively, based on samples taken a few months of the year. Semivoltinism, as reported for *I. zionensis* in the Rio Conejos, may also occur in its congeners, but this will be confirmed only when detailed studies using small mesh nets, frequent sampling, and egg rearing have been conducted.

**Isoperla spp.** Of the three *Isoperla* whose partial growth patterns are presented here, only *I. fulva* has been previously reported. Hassage and Stewart (1990) reported a univoltine-slow cycle, with a June emergence in the Rio Vallecitos of New Mexico. We concur with the New Mexico study. Our results agree well with reviews of *Isoperla* biology, summarized for 12 Nearctic species through 1987 (Stewart and Stark 1988). Ten species were univoltine-slow, while only two were univoltine-fast.

In more recent literature Stewart et al. (1990) reported univoltine-slow growth for *I. petersoni* Needham & Christenson of Alaska. Additionally, Harper et al. (1994) added as univoltine-slow *I. francesca* Harper and *I. montana* (Banks) from Quebec populations. These and our Rio Conejos work bring to 17 the Nearctic *Isoperla* species known to exhibit univoltine-slow cycles, while only three species appear to be univoltine-fast. *Isoperla grammatica* (Poda) and *I. difformis* (Klapálek) (Malmqvist and Sjöström 1989) and *I. obscura* (Zetterstedt) studied by Ulfstrand (1968) are univoltine-slow in the Palearctic.

Up to seven species of *Isoperla* commonly occur in streams in North America (Stewart and Stark 1988); conversely, in Scandinavia rarely more than two species occur simultaneously (Malmqvist and Sjöström 1989). Congeneric species of aquatic insects often partition resources along one or more resource gradients (Grant and Mackay 1969). Though only small numbers of adults were collected, a pattern of successive emergence of *I. fulva*, *I. quinquepunctata*, and *I. phalerata* was clear in the Rio Conejos. Fifty percent cumulative catch dates for *I. fulva*, *I. phalerata*, and *I. quinquepunctata* were 22 June, 28 June, and 14 July, respectively, for 1988. These dates for 1989 were 18 June, 25 June, and 5 July. Temporal segregation brought about by a gradual change in dominance (Illies 1952) of these species may have accounted for the pres-ent coexistence of these stoneflies.

**Skwala americana.** Two other studies reported univoltine-slow cycles with emergence from February through April for this species in northern New Mexico and central Colorado (Short and Ward 1980, Hassage and Stewart
1990). Skwala curvata (Hanson) of California also exhibited a univoltine-slow cycle, with emergence in April and May (Sheldon 1972). Other Arcynopterygini with univoltine-slow growth include Frisonia picticeps (Hanson) in California (Sheldon 1972), Megarceps signata (Hagen) in Utah (Cather and Gaufin 1975), and Perlinoidea aurea (Smith) in California and Alberta (Radford and Hartland-Rowe 1971, Sheldon 1972).

Sheldon (1972) estimated average total fecundity of S. curvata to be near 1780 eggs for preemergent nymphs. This is much greater than that proposed for S. americana from the Rio Conejos. He used interocular width as an index to predict fecundity. Conversion of interocular width to HCW likely involves a factor of 2X, which would make S. curvata the larger of the two stoneflies. This largely accounts for differences in fecundity. Mutch and Pritchard (1986) reported that S. americana (as S. parallela) had a warm, stenothermal egg development.

Most species in this family have conserved the life history traits that Lillehammer et al. (1989) proposed as ancestral. These traits include univoltine-slow cycles, temperature-dependent growth, and direct egg development. Isoperla quinquepunctata and I. zionensis have likely abandoned all of these except temperature-dependent growth.

Pteronarcyidae

Pteronarcella badia. Gaufin et al. (1972) reported that a 2-yr life cycle was possible for this species in Utah; however, S. Perry et al. (1987) and Stanford (1975) reported a univoltine life history in Montana. No eggs were reared in either Montana study, and it is apparent from their growth histograms that early instars were missed entirely. Therefore, semivoltine life history is most probable throughout its range.

Nymphs of this species are more likely to be found aggregated on filter paper leaf models than alone (Hassage et al. 1988). We have also observed nymphs aggregating under margin cobble immediately before emergence. Adults aggregate in leaf debris at the base of willow and cottonwood coppices at the Rio Conejos. This behavior may be attributable to the transformation and nighttime refuge sites being contagiously distributed. Hassage et al. (1988) also postulated that aggregation in P. badia lowers individual risk to predation.

Pteronarceps californica. The egg diapause plus 38-mo nymal life span places total life span of this population at 4 yr. This is one of the longest-lived aquatic insects known to occur in the Nearctic. Additionally, this species is perhaps our most synchronously emerging stonefly.

Two- to 3-yr life cycles with a 9–10-mo egg diapause occur in other Pteronarceps such as P. dorsata (Barton 1980), P. proteus (Holdsworth 1941a, 1941b, W. Perry et al. 1987), and P. scottii in the southern Appalachian Mountains (Folsom and Manuel 1983). However, Lechleitner and Kondratieff (1983) detailed a 1-yr life history for P. dorsata in Virginia.

Multiple-year life histories are common among larger species of the Pteronarcyidae (Stewart and Stark 1988). Accompanying this long nymphal growth, and perhaps contributing to it, is another life history trait, long egg diapause. Univoltine growth patterns and direct egg development are ancestral patterns, while the semivoltine growth and diapause of P. badia and P. californica are derived traits (Lillehammer et al. 1989). Future studies of egg incubation in lower latitudes of North America will enable us to outline the range of responses of which Pteronarceps and Pteronarcella are capable.

Unanswered Questions

Several largely unanswered questions persist about the life histories of stoneflies in and along the Rio Conejos. We have found that nymphs of many chloroperlids are not available in surface sediments until just prior to emergence. They must be hyporheic in their habitat choice. Second, chloroperlids of the present study did not readily produce eggs in captivity, and those incubated never hatched. We can still ask many questions about their life histories. The answers would require a detailed study of the hyporheic habitat of an open-sediment stream like the Rio Conejos. This study should concentrate only on the chloroperlids, since they are generally abundant and diverse. Such a study would still fit within the comparative study approach of Sheldon (1972), but the guild would involve hyporheic chloroperlids.

To settle the dilemma of aberrant sex ratios in this family, studies must concentrate on the presence of male nymphs in the stream. In this way the search for adult males whose
whereabouts are unknown need not take place, since both sexes of nymphs presumably enjoy a similar microhabitat. If no male nymphs are located, then incubation of eggs from virgin females should be conducted to confirm the possibility of parthenogenesis.

An exciting observation we made during the study was that of basking in the sun of nearly all adults of summer-emerging species. Most displayed a remarkably consistent pattern of ascendency of riparian vegetation beginning at about 0800 h. Activity usually ceased by 1300 h when air temperatures were hottest. This ascendency culminated for females in egg batching and oviposition flights, while males used these riparian staging grounds for mate searching, drumming, and mating. Stoneflies should be investigated for potential to benefit from basking, an unreported phenomenon for Plecoptera.

ACKNOWLEDGMENTS

We thank the Conejos Peak District of the U.S. Forest Service for providing lodging and laboratory space during the study. Special thanks go to J. B. Moring for his help with sample collection and D. Ziegler for providing some fecundity data for *P. badia*. This project was partially funded by faculty research funds of UNT and a National Science Foundation grant, BSR 8308422, to KWS.

LITERATURE CITED


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POLLINATOR SHARING BY THREE SYMPATRIC MILKVETCHES, INCLUDING THE ENDANGERED SPECIES ASTRAGALUS MONTII

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ABSTRACT—Insects visiting flowers of the endangered Heliotrope milkvetch, Astragalus montii, were compared with those visiting two common sympatric congeners, A. kentrophyta and A. miser, on three sites in the Wasatch Plateau of central Utah for 2 yr. We recorded 27+ species of bees, most of which were uncommon, visiting the three species. All three species were primarily visited by native bees of the genera Osmia (15 species) and/or Bombus (4 species). Most Osmia species visited the three species of Astragalus indiscriminantly, bumblebees preferred A. miser and avoided A. montii. Our hypothesis that A. montii flowers would receive fewer total bee visits and be visited by fewer bee species than their common congeners was rejected: A. montii was intermediate to the two common species in its attractiveness to bees. Also rejected was our hypothesis that the greater similarity between A. montii and A. kentrophyta in flower size, flower morphology, and microhabitat would be associated with greater similarity of flower visitors than either had with A. miser. The data suggest that, rather than competing with each other for pollinators, the three species of Astragalus facilitate each other’s visitation rates.

Key words: Astragalus, milkvetch, endangered plant, reproduction, pollination, facilitation, bee diversity, conservation, Fabaceae, Osmia.

Many insects such as dipterans and lepidopterans use flowers only as fuel stations (Elton 1966); they collect nectar and burn it as they search for suitable spots to lay eggs. Such insects may merely pass through areas where flowers are sparse. Bees, in contrast, are central-place foragers (Orians and Pearson 1979) that must consistently reap profits in both nectar and pollen, for they forage not simply to underwrite their own movements, but to provide food to rear their progeny as well (Stephen et al. 1969). Because bees are under strong, selective pressure to be profitable foragers, they are attracted to dense patches of flowers (Heinrich 1976, 1979; Thomson 1982). Bumblebees, for example, quickly recognize and exploit particularly rewarding flower patches (Heinrich 1976, 1979); other bees probably do so also.

Density-dependent foraging behavior by bees has important implications for certain rare plants. Rabinowitz (1981) distinguished seven types of rarity in plants using the following three criteria: (1) local abundance, (2) habitat specificity (narrow or wide), and (3) geographic range (large or small). Those species with both narrow habitat specificity and small local populations (regardless of geographic range) are sparse and likely to attract foraging bees only incidentally. We expect such species to be pollinator-vulnerable and, therefore, to be highly self-compatible and perhaps primarily self-pollinating (Karron 1987). It is less clear whether plants in other categories of rarity, especially endemics (Rabinowitz 1981, Kruckberg and Rabinowitz 1985), are also pollinator-vulnerable. Endemics have narrow habitat specificity but may be locally abundant.

One such endemic, the rare Heliotrope milkvetch, Astragalus montii Welsh, is limited to a few isolated populations in limestone gravel outcrops on the Wasatch Plateau of central Utah at about 3350 m. There it grows with two common congeners, A. kentrophyta var. tegetarius (S. Wats.) Dorn, hereafter A. kentrophyta, and A. miser var. oblongifolius (Ryd.) Cron., hereafter A. miser. In all three species, seed production requires, or is increased by, pollinator visits to flowers (Geer and Tepedino 1993). Information on the identity and biology of these pollinators is important, for A. montii occurs on rangelands that are grazed by domestic livestock and sprayed with insecticides to control grasshoppers. Successful management of this rare species requires

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knowledge of how such spraying may affect its pollinators.

In this report we compared composition and abundance of pollinator fauna of A. montii with those of its two sympatric congeners. Because there may be wide variation in a species' pollinators between years and sites (Tepe-dino and Stanton 1981. Herrera 1990, Eckhart 1992), we censused pollinators of A. montii and its congeners for 2 yr at three sites. We hypothesized that A. montii would (1) attract fewer individual pollinators, (2) have lower pollinator species diversity than its two common congeners, and (3) share more species of flower visitors with A. kentrophysa than with A. miser because similarity in plant and flower size, flowering time, and microhabitat is greater with the former than with the latter.

Species and Study Areas

All three species of Astragalus are small perennial herbaceous legumes. A. montii is restricted to three mountaintops on the Wasatch Plateau in central Utah. Although Isely (1983) proposed that A. montii be reduced in status to a variety of A. limnocharis Barneby, it was listed as endangered under the Endangered Species Act in 1987 as A. montii and remains so (Anonymous 1991). Therefore, we refer to this taxon as A. montii.

A. kentrophysa and A. miser are widespread species that occur with A. montii at three sites on two of the mountains; the third mountain is less accessible and was not included in the study. A. kentrophysa is widespread and abundant in the Rocky Mountains, mostly between 2280 and 3650 m. A. miser, one of the most common species of Astragalus in the Rocky Mountains, is locally abundant from sagebrush foothills to the spruce-fir belt (Barneby 1989). The three species co-occur at 3250 to 3350 m in an Engelmann spruce (Picea engelmannii Parry)/subalpine fir (Abies lasiocarpa [Hook.] Nutt.) community. A. montii and A. kentrophysa are intermingled in limestone gravel outcrops where A. miser is found only occasionally. A. miser is most abundant nearby where soil is deeper and less rocky. A. montii and A. miser occur at similar local densities on Heliotrope Mountain (9.3 ± 0.1/m² and 12.6 ± 8.3/m²; Geer unpublished data). There are fewer A. kentrophysa (2.6 ± 0.8/m²; Geer unpublished), but individuals cover more ground than do those of its congeners. The three species overlap in bloom time for about 3 wk (Fig. 1).

Heliotrope milkvetch is a subacaulescent plant 1–5 cm tall that arises from a branched caudex. Flowers are deep purple with white wingtips. There may be a dozen to a hundred or more flowers (7.8 ± 1.5 mm long, N = 10; Geer unpublished) per plant, two to eight per raceme (Barneby 1989). It does not appear to reproduce vegetatively (personal observation). In 1989 and 1990 A. montii commenced flowering with final snowmelt beginning as early as June and continuing for about 4 wk until mid-July (Fig. 1).

The common species A. kentrophysa started to flower approximately 1 wk before A. montii and continued to flower through early August. It is prostrate, with stems that fork repeatedly and closely to form low convex cushions covered with small blue-white to purplish flowers (6.6 ± 1.2 mm long, N = 10; Geer unpublished), only two per raceme (Barneby 1989).

The other common congener, A. miser, commenced flowering 1–2 wk after A. montii and continued flowering until September. It is taller (2–20 cm) than A. montii or A. kentrophysa. Flowers are larger (11.4 ± 1.4 mm long, N = 11; Geer unpublished) and vary in number per raceme (3–15; Barneby 1989) and in color; flowers may be white, pink, or lavender.

All Astragalus species have papilionaceous blossoms composed of a showy standard or banner petal, a keel that protects the joined stamens and pistil, and two wings that, along with the keel, typically serve as a landing platform (Kalin Arroyo 1981). To trip A. miser flowers, bees land on the keel and force their way under the banner (personal observation) as they do for other species of Astragalus (Green and Bohart 1975, Faegri and van der Pijl 1979). Visitors to A. montii or A. kentrophysa spread the wing petals with their midlegs and take nectar, or comb pollen from the anthers to their abdominal pollen baskets with their forelegs (personal observation). Stylar hairs (termed a brush mechanism) aid in the collection of pollen by transporting it from the keel outward (Kalin Arroyo 1981).

Sexual reproduction by A. miser and A. kentrophysa requires insects to transfer pollen; A. montii is capable of unassisted self-pollination (autogamy). However, fruits produced autogamously by A. montii may be inferior in
quality to those produced by geitonogamous or xenogamous hand pollinations, or open-pollinated control treatments (there are fewer seeds per fruit and seeds are smaller; Geer and Tepedino 1993). Thus all three species probably benefit from insect visitation.

**METHODS**

Insect visitors were collected for about 3 wk in 1989 and for 2 wk in 1990 at the following three sites, starting when *A. montii* was in peak bloom: the head of Mill Stream on Ferron Mountain (HMS), south side of Heliotrope Mountain (SSH), and east end of Heliotrope Mountain (EEH). In 1990 collections from all three *Astragalus* species were made only at the SSH site because only two insect collectors were available instead of four, as in 1989. We concentrated on the SSH site in 1990 to make the number of collector hours there equivalent to the 1989 effort. In 1990 visitors to *A. kentrophyta* were collected at the SSH and HMS sites, and visitors to *A. miser* were collected at the SSH and EEH sites. Following are approximate direct distances between sites: HMS to SSH = 3.6 km, HMS to EEH = 2.4 km, and EEH to SSH = 1.2 km.

Pollinators were collected with a standard butterfly net and killed in cyanide jars. Cold temperatures, strong winds, and frequent precipitation (snow and rain) prohibited pollinators from flying during all but brief windows of calm, sunny weather; so opportunistic collection was necessary to ensure an adequate sample size. Collections were made from all three species contemporaneously, whenever weather permitted (i.e., temperatures >13°C, little wind, and no precipitation). Initially, sight identification of some taxa was attempted so as to reduce impact on the pollinator community. It soon became obvious that it was impossible to identify *Osma* and other individuals without laboratory examination. Subsequently, all flower visitors were collected whenever possible. Few insects other than bees visited the flowers.

Diversity of bee visitors to each *Astragalus* species was calculated using Simpson's diversity index, \( D = 1 - \Sigma_{i=1}^{P} (P_i)^2 \), where \( P_i \) is the proportion of individuals that belong to each bee species (Southwood 1978). Simpson's index gives little weight to rare species and more weight to common ones. Similarity of the bee fauna visiting *Astragalus* species was estimated using Czekanowski's similarity index: \( C_s = N J / (a + b + \ldots + n) \), where \( N \) is the number of plant species being compared, \( J \) is the number of bee species shared by those plant species, and \( a, b, \ldots, n \), are the total number of bee species visiting each plant species (Southwood 1978). \( C_s \) is based on species presence alone. We also calculated \( C_p \), which adjusts for the number of individuals per species (Southwood 1978). The indices range from 0 (no similarity) to 1.0 (complete similarity). They were calculated between pairs of species and among all three species.

Probable pollinators of the three *Astragalus* species were ascertained by examining flower visitors and recording areas of their bodies on which pollen was found. Specimens were then relaxed and pollen was removed using an insect pin or by dabbing it with acid-fuchsin gel (Beattie 1971). The pollen was placed on a glass slide with acid-fuchsin gel, warmed until liquid, and a cover slip applied (modified from Faegri and Iverson 1964). One slide per leg or two slides per abdomen were made for each insect. All slides were viewed at 100X magnification and the pollen compared to a pollen reference collection of species in bloom at the study sites.

**RESULTS**

Bees were scarce at the study sites in both years (Table 1, Appendices I, II). Bee visitors per plant species ranged from about 0.5 to just over 3 per hour; a small number considering that many flowers of each species were being monitored. Bee numbers were higher in 1990;
when categorized by site and *Astragalus* species visited, six of seven categories had more individuals per hour in 1990 than in 1989.

The initial hypothesis, that *A. montii* would have fewer individual flower visitors than would its common congener, received little support (Table 1, Appendices I, II). In 1989 there was little difference among species in visitors per person hour at SSH. At EEH *A. montii* flowers were visited more often than the other species. Conversely, at HMS *A. montii* flowers received the fewest visits. In 1990 comparisons of number of visitors among all three *Astragalus* species could be made only at the SSH site where *A. montii* had an intermediate number of visitors per hour. At EEH *A. montii* again had more visits per hour than *A. kentrophyta*, and at HMS it had fewer visits per hour than *A. miser*.

The prediction that species richness and species diversity of bees visiting the three *Astragalus* species would be lowest for *A. montii* was also provisionally rejected. The number of species captured on *A. montii* commonly exceeded those captured on the other species, both when more hours were spent collecting from *A. montii* than the other species (1989 SSH) and when collecting hours were equal (1990 HMS; Table 1). Only once, when fewer hours were spent collecting on *A. montii* than on the other *Astragalus* species (1989 HMS), was *A. montii* visited by the fewest species of bees. When all sites were considered, total number of species collected on *A. montii* in 1989 exceeded those captured on *A. kentrophyta* and equaled those captured on *A. miser* (Table 2). In 1990 more species were caught visiting *A. montii* than the other two species, but this difference is probably because we collected at three sites for *A. montii* but at only two for each of the other two species.

Calculations using species diversity, D', also failed to yield expected trends (Table 2). In 1989 diversity of visitors to flowers of *A. montii* was very similar to diversity recorded for *A. kentrophyta* and *A. miser*. Comparisons for 1990 are more tenuous because of the differences among species in number of sites sampled. However, diversity of flower visitors was highest for *A. miser* and similar for *A. montii* and *A. kentrophyta*. Diversity in 1990 was generally lower than in 1989, although number of individuals captured was greater.

The most frequent visitors to these *Astragalus* species in both 1989 and 1990 were *Osmia* bees (Table 3). For the small-flowered *A. montii* and *A. kentrophyta*, in both years >70.0% of all visitors were *Osmia* bees. Only for *A. miser* in 1990 did the percent *Osmia* visitors drop below 50%. *A. miser* was more frequently visited by bumblebees, especially at SSH. The abundance of bumblebees caused SSH to have the lowest percentage of *Osmia* individuals recorded at any site in both years. Even so, *Osmia* bees were always more than 60% of the total flower visitor fauna recorded in any site-year.

Because of greater similarities in flower size, color, and microclimate, we expected *A. montii* and *A. kentrophyta* to have more visitors in common than either did with *A. miser*. This was not true in either year. The three pairings of *Astragalus* did not differ much in the number of bee species they shared, though results

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**Table 1.** Number of person hours spent collecting and number of bee individuals collected or observed visiting flowers of *Astragalus montii* (Asmo), *A. kentrophyta* (Aske), and *A. miser* (Asmi) at three sites on the Wasatch Plateau in 1989 and 1990. SSH = south and east side Heliotrope Mountain, respectively; HMS = head of Mill Stream, Ferron Mountain.

<table>
<thead>
<tr>
<th></th>
<th>SSH</th>
<th></th>
<th>EEH</th>
<th></th>
<th>HMS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asmo</td>
<td>Aske</td>
<td>Asmi</td>
<td>Asmo</td>
<td>Aske</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hours</td>
<td>24</td>
<td>8</td>
<td>10</td>
<td>30</td>
<td>24</td>
</tr>
<tr>
<td>Individuals</td>
<td>28</td>
<td>9</td>
<td>10</td>
<td>30</td>
<td>19</td>
</tr>
<tr>
<td>Individuals/hour</td>
<td>1.2</td>
<td>1.1</td>
<td>1.0</td>
<td>1.0</td>
<td>0.8</td>
</tr>
<tr>
<td>Species</td>
<td>7</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hours</td>
<td>30</td>
<td>15</td>
<td>15</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Individuals</td>
<td>57</td>
<td>7</td>
<td>35</td>
<td>40</td>
<td>24</td>
</tr>
<tr>
<td>Individuals/hour</td>
<td>1.9</td>
<td>0.5</td>
<td>2.3</td>
<td>3.3</td>
<td>2.0</td>
</tr>
<tr>
<td>Species</td>
<td>10</td>
<td>5</td>
<td>11</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>


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GREAT BASIN NATURALIST | Volume 55
TABLE 2. Number of individuals, number of species, and species diversity (D) of bees found visiting three species of *Astragalus* at three sites on the Wasatch Plateau. In 1989 collections were made for each species at all three sites; in 1990 collections were made at all sites for *A. montii*, but at only two sites for the other two species. For comparative purposes, collection data for the latter two species are shown in 1989 for all three sites and for only the two sites collected at in 1990. D = Simpson’s diversity index.

<table>
<thead>
<tr>
<th>Astragalus species</th>
<th>Individuals</th>
<th></th>
<th>Species</th>
<th></th>
<th></th>
<th>D&lt;sup&gt;1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3 sites</td>
<td>2 sites</td>
<td>3 sites</td>
<td>2 sites</td>
<td>3 sites</td>
<td>2 sites</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>montii</td>
<td>63</td>
<td>—</td>
<td>13</td>
<td>—</td>
<td>0.87</td>
<td></td>
</tr>
<tr>
<td>kentrophyta</td>
<td>39</td>
<td>28</td>
<td>9</td>
<td>8</td>
<td>0.79</td>
<td>0.81</td>
</tr>
<tr>
<td>miser</td>
<td>38</td>
<td>28</td>
<td>13</td>
<td>11</td>
<td>0.88</td>
<td>0.87</td>
</tr>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>montii</td>
<td>113</td>
<td>—</td>
<td>13</td>
<td>—</td>
<td>0.62</td>
<td></td>
</tr>
<tr>
<td>kentrophyta</td>
<td>—</td>
<td>31</td>
<td>—</td>
<td>7</td>
<td>—</td>
<td>0.60</td>
</tr>
<tr>
<td>miser</td>
<td>—</td>
<td>59</td>
<td>—</td>
<td>12</td>
<td>—</td>
<td>0.79</td>
</tr>
</tbody>
</table>

<sup>1</sup>In 1989 only individuals that were collected were used in calculations, because uncaught *Osmia* individuals were not identifiable to species.

TABLE 3. Percent visitors that were *Osmia* bees to the flowers of three *Astragalus* species (abbreviations as in Table 1). Data shown grouped by species across sites, and by site across species, for 2 yr. For comparative purposes, 1989 data are shown in entirety (3 sites or 3 species) or only for the 2 sites or 2 species sampled in 1990.

<table>
<thead>
<tr>
<th></th>
<th>Asmo</th>
<th>Aske</th>
<th>Asmi</th>
<th>SSH</th>
<th>EEH</th>
<th>HMS</th>
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<td>----</td>
<td>----</td>
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<td>----</td>
</tr>
<tr>
<td>1989</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 (sites/species)</td>
<td>88.9</td>
<td>71.8</td>
<td>73.7</td>
<td>62.3</td>
<td>88.1</td>
<td>76.5</td>
</tr>
<tr>
<td>2 (sites/species)</td>
<td>—</td>
<td>75.6</td>
<td>64.3</td>
<td>—</td>
<td>85.7</td>
<td>87.0</td>
</tr>
<tr>
<td>1990</td>
<td>93.8</td>
<td>74.2</td>
<td>47.5</td>
<td>62.6</td>
<td>87.5</td>
<td>95.0</td>
</tr>
</tbody>
</table>

varied somewhat with year and with index used (Table 4). In 1989 the three pairings of *Astragalus* species had about the same number of bee species in common. In 1990 *A. miser* and *A. montii* had about twice the number of species in common as did the other pairings. Neither coefficient of similarity, C<sub>0</sub> or C<sub>1</sub>, consistently supported the hypothesis; in 1989, but not 1990, C<sub>0</sub> and C<sub>1</sub> were highest for the *A. montii*–*A. kentrophyta* comparison.

Many bees visiting *Astragalus* flowers carried pollen on their bodies: 43% of the bees captured, primarily females of the genus *Osmia*, had been collecting pollen. Pollen loads comprised primarily *Astragalus* pollen (all means >80%; Table 5). It is unknown whether loads commonly contained more than one species of *Astragalus* because pollen grains could not be distinguished to species with the light microscope.

Our observations of foraging bees suggest some interspecific movement. In 1989 few *Osmia* individuals flew between *A. montii* and *A. miser* or *A. kentrophyta*; of 74 interplant movements only two were interspecific. In 1990, 4 of 21 observed interplant movements were between species. Interspecific visits occurred most commonly where species grew intermingled.

**DISCUSSION**

Two hypotheses make predictions about the abundance and diversity of visitors to the flowers of rare plants. For entomophilous plants, Levin and Anderson (1970), Straw (1972), and Karron (1987) proposed that pollinators should be more flower constant to abundant plant species than to rare ones, that this differential flower constancy would result in more successful reproduction by “majority” species than by “minority” species, and that over time minority species would become extinct because of dwindling recruitment or would evolve some method of self-reproduction (Levin 1972). A corollary of this hypothesis is that both the number and diversity of visitors to the flowers of rare plants should be lower than they are to abundant ones.
Table 4. Number of bee species (S) collected on each Astragalus species, and number of species shared (C) and similarity indices for each pairing for each year. \( C_s \) = Czekanowski's similarity index for bee species presence-absence; \( C_i \) = index weighted by individuals captured.

<table>
<thead>
<tr>
<th>Astragalus species pair</th>
<th>S</th>
<th>C</th>
<th>( C_s )</th>
<th>( C_i )</th>
<th>S</th>
<th>C</th>
<th>( C_s )</th>
<th>( C_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>montii</td>
<td>13</td>
<td>6</td>
<td>0.50</td>
<td>0.34</td>
<td>13</td>
<td>7</td>
<td>0.56</td>
<td>0.37</td>
</tr>
<tr>
<td>miser</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>montii</td>
<td>13</td>
<td>6</td>
<td>0.55</td>
<td>0.43</td>
<td>13</td>
<td>4</td>
<td>0.40</td>
<td>0.35</td>
</tr>
<tr>
<td>kentrophyta</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>kentrophyta</td>
<td>13</td>
<td>5</td>
<td>0.45</td>
<td>0.43</td>
<td>12</td>
<td>3</td>
<td>0.32</td>
<td>0.53</td>
</tr>
<tr>
<td>miser</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All three species</td>
<td>20</td>
<td>4</td>
<td>0.35</td>
<td>0.27</td>
<td>21</td>
<td>3</td>
<td>0.28</td>
<td>0.30</td>
</tr>
</tbody>
</table>

In contrast, the facilitation hypothesis (reviewed by Rathcke 1983) predicts that rare species growing with attractive, more abundant species may actually reproduce more successfully because the latter draw many more pollinating insects into the area than would otherwise be present. If so, rare and abundant sympatric species should have similar visitor diversity, and visitor abundances should reflect respective frequencies of the plants. This study indirectly assessed the importance of facilitation and competition. A direct assessment is difficult because (1) the experiments necessary to distinguish between alternatives cannot be conducted when the "plant protagonist" is protected by the Endangered Species Act; and (2) A. montii did not occur in the absence of its congeners on our study sites, so visitation rates of "facilitated" and "unfacilitated" populations could not be compared.

Our results supply consistent, though indirect, support for the facilitation hypothesis. Except for bumblebees, which foraged almost exclusively from large-flowered A. miser, bees did not discriminate against A. montii but rather seemed to treat all three Astragalus species as one taxa. First, A. montii did not consistently attract fewer visitors per hour than did the other species. Indeed, visitation rates to A. montii were higher than to the other species in three of six site-years (Table 1). Second, neither species richness nor species diversity of pollinators was consistently lower for A. montii than for the other species (Table 2). In fact, an equal or greater number of species visited A. montii than visited the others in both years. And finally, bees were observed moving between species on individual foraging trips. Gross (1992) also reported that bees foraging on closely related legumes commonly moved between species. Thus, there was no detectable rare species disadvantage and no evidence that endemics, at least those growing in close proximity to abundant congeners, are pollinator-vulnerable.

The shared microhabitat and similarities in flower size and morphology of A. montii and A. kentrophyta led us to expect that facilitation would be more likely between these two species and, therefore, that they would have more visitors in common than either would with A. miser. For example, Thomson (1978, 1981, 1982) found that, in two-species mixtures, the degree of intermingling and the similarity in structure and appearance of congeners' flowers determined the importance of competition and mutualism. The more similar the flowers, the more likely that visitation rates to rare species would be bolstered by the presence of abundant species and the more likely that visitors would be shared. Our data supported this expectation for 1989 but not for 1990 (Table 4). In 1990 \( C_s \) for the A. montii--A. kentrophyta comparison was intermediate to the other comparisons; for \( C_i \) it was lower than the other comparisons. Thus, results for the similarity analyses also tend to support the hypothesis that most bees do not distinguish among these Astragalus species when foraging and that the Astragalus species tend to facilitate each other's visitation rates.

Only bumblebees seem uninfluenced by Astragalus flowers in the aggregate. They clearly preferred flowers of A. miser and avoided those of the other Astragalus species. Flowers of A. miser are large, probably more rewarding, and provide a landing platform from
TABLE 5. Percent Astragalus pollen grains in pollen loads, and location of pollen loads carried by bees collected on three Astragalus species at three sites on the Wasatch Plateau in 1989 and 1990.

<table>
<thead>
<tr>
<th>Astragalus species</th>
<th>Number of pollen loads</th>
<th>Mean % Astragalus pollen (+SE)</th>
<th>Location of pollen</th>
</tr>
</thead>
<tbody>
<tr>
<td>montii</td>
<td>45</td>
<td>82 ± 4</td>
<td>Abdomen 42 Legs 3</td>
</tr>
<tr>
<td>miser</td>
<td>19</td>
<td>90 ± 1</td>
<td>19</td>
</tr>
<tr>
<td>kentrophyta</td>
<td>5</td>
<td>95 ± 1</td>
<td>5</td>
</tr>
</tbody>
</table>

which large, energy-demanding bumblebees can readily forage. Other large-flowered Astragalus species also attract numerous large bees such as bumblebees (Bombus spp.) and anthophorids (Green and Bohart 1975, Sugden 1985, Karron 1987). In comparison, bumblebees seemed unable to land on the small, weakly supported A. montii flowers which are borne above the foliage; they did occasionally exploit the tiny A. kentrophyta blossoms while perched on the foliage of that cushion plant.

Factors other than flower abundance can influence the flight path of foraging bees. Because bees are central-place foragers (Orians and Pearson 1979), travel time and energy expended between flower patches and nest are also important. Thus, bees may patronize a flower patch because of its proximity to their nest, even though flowers are more abundant elsewhere. For example, Osmia bees mated and nested at the sheltered EEH site where relatively few A. kentrophyta or A. miser plants grew; the population of A. montii was small but dense. Nevertheless, bees visited flowers at least as frequently at EEH as at the other, more flower-rich, sites (Tables 1, 2). Thus, suitability of nesting habitat at EEH, rather than Astragalus flower abundance, may best account for the abundance of bees there. The effect of wild bee nesting sites on seed production of surrounding vegetation is poorly studied and warrants additional attention.

Rigorous subalpine communities of the Wasatch Plateau, with frequent high winds, thunderstorms, and below-freezing temperatures during the blooming season, support a surprisingly rich bee fauna. In 2 yr we collected 27+ bee species foraging on Astragalus flowers during 2–3 wk (Appendices I, II). These bees are invaluable pollinators of native plants both rare and common. Their welfare must also be considered in management plans for rare plants. Land managers must eliminate losses of bees to insecticide applications made for rangeland grasshoppers and minimize physical damage to nest sites. The present insecticide-free buffer zone (currently 4.5 km) around rare plant populations should continue to be maintained. Areas where bees nest in soil should also be protected from livestock trampling, off-road vehicle use, and foot traffic (Sugden 1965). Such diversity, comparable to or greater than that of other subalpine areas in North America (Moldenke and Lincoln 1979), is to be marveled at and preserved.

ACKNOWLEDGMENTS

We are grateful to the many people who assisted in this study. Etta Sechrest and Mike Cram were reliable field and laboratory assistants. John Healey, Don Riddle, and Bob Thompson of the U.S. Forest Service and Larry England, U.S. Fish and Wildlife Service, helped in a variety of ways, from locating plant populations to putting a roof over our heads. The manuscript was constructively reviewed by M. Barkworth, K. Harper, and E. Sugden. This study was funded as part of the APHIS Grasshopper IPM Project. It is Journal Paper #4436 from the Utah Agricultural Experiment Station.

LITERATURE CITED


Received 29 April 1993
Accepted 2 June 1994

APPENDIX I. Species of bees collected and observed visiting flowers of A. montii (Asmo), A. miser (Asmi), or A. kentrophyta (Aske) at three sites in 1989. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Bee species</th>
<th>SSH 1–21 June</th>
<th>EEH 14–25 June</th>
<th>HMS 14–22 June</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asmo</td>
<td>Aske</td>
<td>Asmi</td>
</tr>
<tr>
<td>ANDRENIIDAE</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andrena transnigra Vier.</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andrena spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(1)
APPENDIX I. Continued.

<table>
<thead>
<tr>
<th>Bee species</th>
<th>SSH 1–21 June</th>
<th>EEH 14–25 June</th>
<th>HMS 14–22 June</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asmo</td>
<td>Aske</td>
<td>Asmi</td>
</tr>
<tr>
<td><strong>APIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus bifarius Cr.</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus flavifrons Cr.</td>
<td></td>
<td>(0/2)</td>
<td></td>
</tr>
<tr>
<td>Bombus huntii Greene</td>
<td></td>
<td>(0/2)</td>
<td></td>
</tr>
<tr>
<td>Bombus nevadensis Cr.</td>
<td></td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td><strong>HALICTIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucyphlaeus nigricans (Vierock)</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>MEGACHILIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthidium tenellum Ckll.</td>
<td>(2)1/0</td>
<td>(1)</td>
<td>(1)1/2(1)</td>
</tr>
<tr>
<td>Megachile spp.</td>
<td>(1/0)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma cyanopoda Ckll.</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma hardii White</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma longula Cr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma nigricans Cr.</td>
<td>0/1</td>
<td>0/4</td>
<td>0/2</td>
</tr>
<tr>
<td>Osma aff. nigricans</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma paradisica Sanh.</td>
<td>1/0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma penstemonis Ckll.</td>
<td></td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td>Osma pilae Ckll.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma pusilla Cr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Osma sladenae Sanh.</td>
<td>2/0</td>
<td>1/0</td>
<td>4/0</td>
</tr>
<tr>
<td>Osma sladenae &amp;tor alpestris</td>
<td>0/2</td>
<td>0/3</td>
<td>0/2</td>
</tr>
<tr>
<td>Osma tanneri Sanh.</td>
<td>1/3</td>
<td>1/2</td>
<td>0/1</td>
</tr>
<tr>
<td>Osma spp.</td>
<td>(5/9)</td>
<td>(1/4)</td>
<td>(0/3)</td>
</tr>
</tbody>
</table>

APPENDIX II. Species of bees collected and observed visiting flowers of A. montii (Asmo) at three sites and A. miser (Asmi) and A. kentrophyta (Aske) at two sites each in 1990. Entries represent number of males/females collected. Observations are in parentheses. Site abbreviations as in Table 1.

<table>
<thead>
<tr>
<th>Visitor</th>
<th>SSH 19 June–4 July</th>
<th>EEH 19–29 June</th>
<th>HMS 21–29 June</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asmo</td>
<td>Aske</td>
<td>Asmi</td>
</tr>
<tr>
<td><strong>ANDRENIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andrena nigricans (Ashm)</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Andrena transnigra Vier.</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>APIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apis mellifera L.</td>
<td>0/1(5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus bifarius Cr.</td>
<td></td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td>Bombus flavifrons Cr.</td>
<td>0/1</td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td>Bombus huntii Greene</td>
<td></td>
<td>0/3(6)</td>
<td></td>
</tr>
<tr>
<td>Bombus nevadensis Cr.</td>
<td></td>
<td>0/3(5)</td>
<td></td>
</tr>
<tr>
<td><strong>MEGACHILIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthidium tenellum Ckll.</td>
<td>1/0(2)</td>
<td>2/0</td>
<td></td>
</tr>
<tr>
<td>Hoplitis fulgida Ckll.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megacile melanophaea Smith</td>
<td>2/0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megacile pershirta Ckll.</td>
<td>1/0</td>
<td></td>
<td></td>
</tr>
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</table>
### Appendix II. Continued.

<table>
<thead>
<tr>
<th>Visitor</th>
<th>SSH 19 June–4 July</th>
<th>EEH 19–29 June</th>
<th>HMS 21–29 June</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asmo</td>
<td>Aske</td>
<td>Asmi</td>
</tr>
<tr>
<td><strong>Megachilidae (continued)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia longula</em> Cr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia montana</em> Cr.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia aff. nigrifrons</em></td>
<td>0/1</td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td><em>Osmia paradisca</em> Sanh.</td>
<td>1/0</td>
<td>0/2</td>
<td>3/0</td>
</tr>
<tr>
<td><em>Osmia penstemonis</em> Ckll.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia pusilla</em> Cr.</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia sculleni</em> Ckll.</td>
<td>1/0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia sladeni</em> Sanh.</td>
<td>8/16</td>
<td>7/8</td>
<td>3/6</td>
</tr>
<tr>
<td><em>Osmia subaustralis</em> Ckll.</td>
<td>4/0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Osmia tanneri</em> Santh.</td>
<td>9/1</td>
<td>1/0</td>
<td>1/0</td>
</tr>
</tbody>
</table>
FACTORS AFFECTING SELECTION OF WINTER FOOD AND ROOSTING RESOURCES BY PORCUPINES IN UTAH

Dave Strickland,1,2, Jerran T. Flinders1,3, and Rex G. Cates1

ABSTRACT.—Ecological and phytochemical factors potentially affecting winter dietary discrimination by porcupines (Erethiszon dorsatum) in the mountain brush zone of Utah were studied. Porcupines utilized gambel oak (Quercus gambelii) as their primary winter food and roosting resource. Big-tooth maple (Acer grandidentatum) was the most common tree species in the study area but was rarely utilized by porcupines. Conifer species were used as a food and roosting resource significantly less often than they occurred in the study area, despite thermal advantages provided by their relatively dense canopies. Oak feed trees were successfully separated from conifer feed trees by discriminant analysis 100% of the time. Oak trees were correctly classified as feed and nonfeed trees 71% of the time. Gambel oak contained higher amounts of crude protein, fiber, and tannins, but was lower in ether extract fractions and fatty acid content than conifers. A layer of adipose tissue used as an energy reserve by porcupines may have relaxed energy intake demands sufficiently to permit them to concentrate on a diet of oak tissue, which is high in protein, rather than a high-fat conifer diet. A diet relatively high in protein may have facilitated digestion of food material high in fiber. Temperature did not affect selection of tree species used for roosting. Rock and snow caves were utilized infrequently and the study population ranged widely. Three of 15 study animals were eaten by predators.

Key words: porcupine, Erethiszon dorsatum, gambel oak, Quercus gambelii, dietary selection, mountain brush zone, predation.

Porcupines (Erethiszon dorsatum) roost and feed in canopies of deciduous trees and shrubs for extended periods during winter in much of western North America (Oveson 1983, Craig and Keller 1986, Switzer and Berger 1992). Apparent localized interspecific and intraspecific preferences for food and shelter resources by porcupines imply that chemical and/or physical advantages are available to them. Further, since snow caves, rock dens, and cover in canopies of coniferous tree species likely offer increased thermal advantages in the form of energy savings to porcupines (Clarke and Brander 1973, Roze 1987, 1989), their dependence on a deciduous food and roosting resource (which does not offer those advantages) further strengthens the implication that chemical and/or physical selective advantages are realized by dietary selection. Predator avoidance may also be an important force in food and roost tree selection. The objective of this research was to investigate physical, phytochemical, and ecological agents involved in selection of gambel oak by porcupines in south central Utah.

STUDY AREA

The study was conducted in the mountain brush zone near the mouth of Spanish Fork Canyon in north central Utah. Elevations at the study site range from 1650 to 2073 m. The general exposure is northern, and terrain is steep. Overstory woody vegetation is dominated by gambel oak (Quercus gambelii) and big-tooth maple (Acer grandidentatum). Aspen (Populus tremuloides), chokecherry (Prunus virginiana), Douglas fir (Pseudotsuga menziesii), white fir (Abies concolor), and mountain maple (Acer glabrum) are also represented in the woody flora. The climate in Spanish Fork Canyon during the winter of 1984–85 was not atypical. Data from the Spanish Fork U.S. Climatological Station, located approximately 5.5 km from the study site, indicate that temperatures were slightly colder and precipitation was slightly higher than average (U.S. Climatological Data for Utah 1984–85). Coyote (Canis latrans) and mountain lion (Felis concolor) tracks were frequently encountered in the study area. Private access into the study area allowed observation.
of a porcupine population relatively free from human disturbance.

Methods

Fieldwork

We conducted fieldwork from late December 1984 through April 1985, at which time the study population had shifted from a diet of inner bark (phloem and cambium) of woody vegetation to herbaceous vegetation. The study area was systematically searched by researchers on snowshoes. Study animals were captured by hand, usually while they were still in tree canopies. This was accomplished by grasping distal guard hairs at the posterior end of the tail between thumb and forefinger and pulling the tail taut. The captured animal was then secured by grasping the tail with the free hand using a backward stroking motion to flatten the quills. Fifteen porcupines, 10 females and 5 males, were instrumented with radio transmitter collars (Telonics, Inc.). Animals were located daily by triangulation, and visual sightings were made on each animal approximately weekly.

Percent occurrence of woody species was calculated from point-quarter measurements using the feed/roost tree as the center point (Cottam and Curtis 1956). Percent occurrence of woody species vs. percent utilization of each feed tree species was compared using chi-square analysis to test whether feed tree selection was random. Diameter at breast height (dbh), species, and distance from the feed tree center point were recorded for the nearest woody stem in each quadrant. Point-quarter measurements were repeated using the nearest neighbor nonfeed tree of the same species as the center point. Tissues from feed and nonfeed trees were collected to investigate possible differences in chemical makeup. Tissue samples from feed trees were collected where fresh bark removal indicated the roosting animal had foraged. Samples from nearest neighbor nonfeed trees were taken from branches at the same height and with a diameter similar to those from corresponding feed trees. Bark samples were frozen and analyzed for dietary components. Results from those analyses reasonably approximated values reported for gambel oak (Smith 1957, Kufeld et al. 1981, Welch 1989). Location, slope, aspect, snow depth, and climatic conditions were recorded at each feed tree site. High and low temperature readings were taken daily at an elevation of 1597 m, as well as from the Spanish Fork climatological station.

Laboratory and Statistical Methods

Tissues from feed and nonfeed trees were analyzed for protein and phosphorus using the auto analyzer semiautomated method #12 for feeds (Horwitz 1980). Calcium, magnesium, potassium, and sodium content were determined by the atomic absorption method #2 for plants (Horwitz 1980). Sulphur content was determined by a wet-ash process using nitric and perchloric acid. Crude fiber was determined by the acid detergent fiber and lignin #21 method (Horwitz 1980). An evaluation of crude fat was made using the direct method (Horwitz 1980) on a Lab Con soxlet extractor. A limited number of tissue samples were analyzed on a Hewlett Packard model 5995 gas chromatograph/mass spectrometer (GCMS) for fatty acids and terpenes. Tannin content was measured by the radial diffusion method (Hagerman 1987) with quebracho tannin being the standard, and by astringency (Gambiel et al. 1985). Soluble carbohydrates were determined according to daSilveira (1978). Urine samples of captive porcupines on a strict diet of gambel oak were analyzed for calcium and phosphorus content when laboratory results indicated the Ca/P ratio in the tissue of food materials was greater than expected. Eight oak tissue samples were chosen at random and retested for calcium and phosphorus content according to Horwitz (1980) on a Beckman DU-30 spectrophotometer.

Differences between oak, white fir, and Douglas fir feed and nonfeed trees were statistically analyzed to help discern foraging patterns used by instrumented porcupines. Chemical and ecological factors were evaluated for between-species differences using two-sample t tests, and for within-species differences with paired t tests (Minitab 1982). Statistical results are reported at the p < .05 and p < .1 levels. Chi-square analysis was used to determine if utilization of feed tree species by porcupines differed from the expected. Discriminant analysis using backward elimination and forward selection (SAS 1985) was used to determine chemical and ecological factors that best discriminate between tree species, and between feed and nonfeed trees of the same species.
RESULTS

Oak and white fir feed trees were larger than nonfeed trees of the same species \((p < .05)\), Table 1\). Herbivory by porcupines in deciduous species occurred in the canopies of large trees or in shrubs where branch diameters were relatively small. In coniferous species herbivory was also concentrated in the canopy rather than on the tree bole. Only two instances of chipping bark off the bole to expose the inner bark were noted in our study, both on deciduous tree species. There were no trends correlating calendar date or temperature to selection of feed tree species. Douglas fir feed trees contained greater amounts of crude protein than Douglas fir nonfeed trees \((p < .05)\). Crude protein content of both conifer species was less than that of oak trees (Douglas fir \(p < .05\), white fir \(p < .1\)). Total tannins (as measured by radial diffusion) were higher in oak than in conifers (Douglas fir \(p < .1\), white fir \(p < .05\)). Astringency (protein binding capacity) was not comparable among species but was greater for white fir feed trees than nonfeed trees \((p < .1)\). Ether extract fractions were lower in oak than in conifers \((p < .05)\) and lower in white fir than Douglas fir \((p < .1)\).

Tissue from Douglas fir contained less crude fiber than tissue from oak and white fir \((p < .05)\), and Douglas fir feed trees contained still less than nonfeed trees \((p < .1)\). Water content was lower in oak tissue than in conifer tissue \((p < .05)\). Oak contained higher levels of potassium and calcium than Douglas fir \((p < .05)\). White fir was also higher than Douglas fir in calcium \((p < .05)\). Magnesium levels for oak were greater than for either conifer species \((p < .05)\). White fir and oak tissue had higher pH values than tissues from Douglas fir \((p < .05)\). Oak feed trees were higher in sodium salts than Douglas fir feed trees \((p < .1)\). Calcium-phosphorus ratios for feed trees were higher in oak than in Douglas fir \((p < .05)\). The calcium-phosphorus ratio for oak is well above acceptable limits for mineral absorption by mammals.

### Table 1. Mean values for factors tested for possible effects on porcupine herbivory.

<table>
<thead>
<tr>
<th></th>
<th>Oak (1)</th>
<th>White fir (2)</th>
<th>Douglas fir (3)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nonfeed</td>
<td>Feed</td>
<td>Nonfeed</td>
</tr>
<tr>
<td></td>
<td>tree</td>
<td>tree</td>
<td>tree</td>
</tr>
<tr>
<td><strong>n = 48</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance from conifer (m)</td>
<td>—</td>
<td>207</td>
<td>—</td>
</tr>
<tr>
<td>Distance to feed tree, same sp. (m)</td>
<td>—</td>
<td>35.2</td>
<td>—</td>
</tr>
<tr>
<td>Wind speed (mph)</td>
<td>—</td>
<td>5.7</td>
<td>—</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>—</td>
<td>33.5</td>
<td>—</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>—</td>
<td>1779.2</td>
<td>—</td>
</tr>
<tr>
<td>Dbh (cm)</td>
<td>*13.2</td>
<td>16.5</td>
<td>*25.4</td>
</tr>
<tr>
<td>Crude fiber (%)</td>
<td>43.3</td>
<td>44.2</td>
<td>43.6</td>
</tr>
<tr>
<td>Protein (%)</td>
<td>4.9</td>
<td>5.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Phosphorus (%)</td>
<td>0.033</td>
<td>0.039</td>
<td>0.087</td>
</tr>
<tr>
<td>Ether extract fractions (%)</td>
<td>9.0</td>
<td>9.11.3</td>
<td>15.7</td>
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<tr>
<td>Water</td>
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<tr>
<td>Potassium (%)</td>
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<tr>
<td>Calcium (%)</td>
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<td>2.8</td>
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<tr>
<td>Magnesium (%)</td>
<td>0.137</td>
<td>0.1429.3</td>
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<tr>
<td>Sodium (ppm)</td>
<td>51.1</td>
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<tr>
<td>Sulfur (%)</td>
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<tr>
<td>pH</td>
<td>4.7</td>
<td>4.7</td>
<td>4.7</td>
</tr>
<tr>
<td>Tannins (radus in cm)</td>
<td>30.5</td>
<td>29.6</td>
<td>17.5</td>
</tr>
<tr>
<td>***Astringency (mg/g fw)</td>
<td>85.8</td>
<td>83.0</td>
<td>*48.7</td>
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<tr>
<td>Sodium salts (%)</td>
<td>2.9</td>
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<td>3.0</td>
</tr>
<tr>
<td>Soluble carbohydrates (%)</td>
<td>16.02</td>
<td>16.20</td>
<td>—</td>
</tr>
<tr>
<td>FAA (GCMS count units)</td>
<td>827.905</td>
<td>399.239</td>
<td>2,609.969</td>
</tr>
</tbody>
</table>

* Superscript values indicate differences between species at the \(p < .1\) level or less. 1 = oak, 2 = white fir, 3 = Douglas fir.
* Values different between feed and nonfeed trees of the same species at or below \(p < .1\).
** Multiple locations in the same tree responsible for different \(n\) values used in calculations of chemistry and climatic data. Climatic data \(n\) values are the same as reported in Table 3.
*** Not comparable across species boundaries.

\(n\) values for factors below dashed line not as reported for rest of column. Not statistically comparable due to smaller sample size.
(Underwood 1966). High calcium-phosphorus ratios have also been reported by Masslich (1985) for aspen (Populus tremuloides) tissue utilized by beaver. After an independent test of feed tree tissue confirmed the high ratio, we tested the mineral content of feces and urine from captive porcupines on an oak diet. Calcium-phosphorus ratios from fecal material were 10:1, while ratios from urine were approximately 221:1.

Tissue samples from feed trees were analyzed by GCMS primarily as a check on ether extract fractions. The small sample size did not permit statistical analysis, but trends showing lower fatty acid content in oak than in conifers concurred with our observation of lower ether extract fractions in oak. The amount of fatty acids was lower in oak than in either conifer species.

Discriminant analysis correctly classified feed trees as either conifer or oak 100% of the time (Table 2). Six factors were important contributors to the model. Conifer feed trees had higher amounts of phosphorus and a greater ether extract fraction than oak feed trees. Alternatively, oak feed trees were higher in protein, calcium, tannins, and magnesium. Although tannins entered into the model, they were not a significant contributor. These differences between oak and conifer feed trees generally are in agreement with differences in Table 1. The classification of oak feed and nonfeed trees was less successful (71%, Table 2). Oak feed trees were significantly higher in sodium and fiber than nonfeed trees, while nonfeed trees were higher in water content.

Porcupines used gambel oak as a food source more often than it occurred in the study site (p values listed in Table 3). Six of 15 animals were found roosting and feeding exclusively in oak, while 9 roosted and fed in conifer species at least once. Snow depths and temperatures were analyzed for the winter period before the main snowmelt (judged to be 18 March). Average snow depths at porcupine location sites for that time period were 0.60 m. Maximum snow depth was 1.20 m (median 0.65 m). Mean minimum temperature for the night previous to locating study animals was -10°C; the extreme low was -27°C. Mean temperature for the night previous to locating animals in rock or snow caves was -12°C. There was no statistical difference between the minimum nightly temperature previous to locating porcupines in station trees compared to locating porcupines in rock or snow dens.

There were approximately 7.0 porcupines/km² in the study area. Radio-collared animals were far ranging and did not utilize a single den or station tree as a base from which to launch foraging expeditions. Rather, they roosted and fed in a single tree for one to several days and then moved to another roost and feeding tree. Death loss due to predation and other causes limited only 3 of 5 male and 6 of 10 female porcupines instrumented with radio transmitting devices for the entire winter. This sample size made statistical analysis of home ranges unreliable. Several animals spent the winter in relatively small areas, but most had relatively large, overlapping home ranges. Male home range extremes were 6.8 and 47.5 ha. Extremes for females were 9.2 and 61.8 ha. One female’s home range overlapped those of three males and at least four other females. Movements of up to 400–500 m between relocations of some of the larger, mature animals were not uncommon. Some juvenile animals had reduced home ranges and movements, which generally agrees with observations by Roze (1989). Mean distance from oak feed trees to a potential conifer feed tree was significantly less (p < .05) than the distance of an average move by a porcupine from an oak feed tree to any other feed tree (Table 1).

Three of 15 porcupines (20%) were eaten by predators in a 4-mo period. Tracks in the snow indicated that one porcupine was pursued, worried, and killed by two coyotes. The other two porcupines eaten by predators died late in the season on south-facing slopes bare of snow; neither the cause of death nor carnivore species could be positively determined. Carcasses of two other porcupines that died presumably of starvation and/or exposure during the course of the study were not scavenged by coyotes.

DISCUSSION

Chemical Factors

Dietary alternatives in the form of different feed tree species, with significantly different chemical makeup, were available to the study population. In winter, vegetative oils have the potential to be the most important source of energy for porcupines. Data from ether extract fractions derived from feed tree tissues indicate
that gambel oak, the major food source of our animals, had lower values of ether extract fractions than tissues from conifers. Evaluation of fatty acids by GCMS confirmed that fatty acid content was higher in conifer tissue. Additional research on known digestible fractions is needed, but until data indicating otherwise are presented, we will operate under the premise that for porcupines conifers provide a greater source of usable fats than do oaks. Discriminant analysis was used to determine if, when all variables were taken together, there would be general support from this analysis with the t test. Significant differences found by these analyses comparing oak and conifer feed trees were in agreement (Tables 1, 2). Phosphorus and the ether extract fraction were higher in conifer feed trees compared to oak feed trees, and protein, calcium, tannins, and magnesium were higher in oak feed trees. Discriminant analysis was less successful in classifying feed and nonfeed trees within oak (Table 2). An important reason for this less successful classification was that the cloning nature of oak was emphasized by the point-quarter method. This method may have resulted in selecting nonfeed trees from the same clone as the feed tree. Future research should involve delineating the boundary of the clone and selecting a nonfeed tree from a clone different from the feed-tree clone.

Conifer roost sites also offer greater thermal advantages than deciduous roost sites (Clarke and Brander 1973, Roze 1989). Despite multiple options, porcupines depended heavily on an oak diet low in fats and associated thermal advantages but higher in tannins. The advantage of the oak diet may well be that it is higher in protein. High levels of crude fiber (e.g., cellulose) reduce the digestibility of crude protein in monogastrics (Glover and Duthie 1958a, 1958b). Therefore, herbivores on a high-fiber diet would be expected to maximize the intake of crude protein to compensate for a low digestibility rate. Implications of a diet high in calcium and tannins are less clear, but it is possible that porcupines may deal with high levels of calcium in their food material by concentrating calcium in the urine. Tannins function as protein binding agents (Rhoades and Cates 1976). It is now evident that some insects can circumvent tannins through a higher gut pH and the presence of surfactants (Bernays 1981, Martin and Martin 1984, Martin et al. 1985). However, pH values for the mid-caecum (6.6), and the pyloric (1.8) and esophageal (3.2) regions of the stomach of a laboratory porcupine on a diet of oak were consistent with gut pH for monogastrics of comparable size (Hume 1982).

Oveson (1983) measured subcutaneous adipose concentrations on the rump of porcupines and reported a thickness of 15.1 mm (± 2.6 mm) in early winter. By late February and early March fat reserves were virtually nonexistent. A similar phenomenon was observed by Sweitzer and Berger (1993) in Nevada, where porcupine body condition decreased significantly throughout the winter season. Those authors suggested the change in body mass was an indication that porcupines depleted energy reserves early in the winter and were stressed nutritionally during late winter. The heavy accumulation of fat serves as an energy reserve for porcupines to draw upon throughout the winter, allowing them to concentrate on a food source relatively high in crude protein. The reduced capabilities of protein digestibility associated with a high-fiber diet may have encouraged our study animals to maximize dietary protein by selecting oak.

Porcupine herbivory was generally noted on small branches. In large trees porcupines fed high in the canopy where limbs are smaller.
We observed only two instances in which porcupines chipped bark of large tree boles and fed on tissue from large dbh limbs or trunks. Selection of larger feed trees by porcupines may be related to the texture of bark and ease of climbing (Roze 1989) rather than chemistry.

**Deciduous Food and Roosting Resource**

Roze (1989) discussed the thermal advantages of dens and/or conifer roost trees in relation to maintenance of a core body temperature. Citing Irving et al. (1955) and Clarke (1969), he indicated that the critical external temperature below which porcupines must increase their metabolic rates to maintain a core body temperature is a range between -12 and -4°C. He suggested dens are temperature-averaging devices that protect porcupines against convective and radiational heat loss. Station trees provide thermal advantages to porcupines (Clarke and Brander 1973) and may serve as a substitute for rock caves and snow dens. However, none of these are requisite to porcupine survival. Roze (1989) noted that porcupines may spend winters in trees away from dens and that in every report the tree species have been evergreens.

Our data conflict with this observation. Porcupines throughout western North America are able to survive using a variety of deciduous species as food and roost tree resources. Despite the prominence of literature concerning dens and conifer station trees, use of a deciduous food and roosting resource without dependence on caves or snow dens is not an anomaly for porcupines. Craig and Keller's (1986) study site in southern Idaho was at an elevation of 1525–2089 m in desert shrub habitat. Animals in this study were not observed using dens during the winter or following runways in feeding areas. They remained in the tops of hawthorne (Crataegus douglasii) thickets or utilized other deciduous food sources throughout the winter. Switzer and Berger (1993) identified buffalo-berry (Shepherdia argentea), willow (Salix spp.), bitterbrush (Purshia tridentata), and juniper (Juniperus osteosperma) as primary winter food sources of porcupines in Nevada. We have also observed the extensive use of hackberry (Celtis occidentalis) and green ash (Fraxinus pennsylvanica) by porcupines as a food and roosting resource in the Sand Hills of Nebraska and the Missouri River Breaks of South Dakota. Caves and conifers (except plantation forests and eastern red cedar [Juniperus virginiana]) are not available in the Sand Hills (Swinehart 1989). Oveson (1983) reported that a porcupine remained virtually motionless while perched in a gambel oak tree for a 24-h period when the ambient temperature was as low as -37°C. During a 13-d period from 30 January through 11 February, when the mean low temperature was -17°C, 3 of 25 (12%) locations of our study animals were in conifers, 4 (16%) were in rock or snow caves, and 18 (72%) were in oak. Although porcupines did select trees with a larger dbh as roosting/feeding sites, they were also often found in smallish shrubs even though large trees were readily available. It is therefore difficult to link possible benefits presumed to be available to porcupines that roost in larger trees, such as protection from the elements or from predators, to the selection shown by animals in this study.

Despite the availability of snow caves, dens, and conifer species that could provide thermal advantages, the study population was heavily
dependent on gambel oak for a roosting and feeding resource. Considering that this reliance was during a season of energetic stress, it is likely that remaining motionless in the canopy of oak trees to conserve energy while exploiting a high-protein food source is an adaptive strategy.

Movements and Predation

The availability of conifer feed trees was not limiting since the average distance between locations of study animals was significantly greater than the mean distance of a move from any roost tree to a conifer roost tree (Table 1). It does not appear that spatial relationships of the various feed tree species played a role in feed tree selection by our study population. The relatively large overlapping winter home ranges of animals in this study differ from reports of other researchers. Home ranges for porcupines in northwestern Minnesota were small enough to be reported in square meters (Tennessee and Oring 1985). Curtis (1941), Dodge (1967), Brander (1973), Roze (1987, 1989), and others have documented that porcupines move short distances from dens to feed trees, sometimes along permanent trails in the snow. Craig and Keller (1986) and Smith (1979) also reported reduced ranges in the winter. However, Dodge and Barnes (1975) did not indicate a similar restriction in winter movements. Roze (1987) suggested the reason may be crusty snows that bear the weight of the animals. Porcupines in our study did adeptly toboggan on crusty snows down extreme slopes in an attempt to avoid capture. However, one female moved over 450 m in fresh snow. Trails in powdery snow were often direct and suggested that a destination may have been predetermined.

Common use of oak and conifer feed trees by different porcupines occurred several times during the study, sometimes concurrently. Hedging in the canopies of gambel oak trees indicated that some trees were used consistently over time by porcupines while others were not. Consistent foraging in common trees over time may indicate a learned behavior such as that described by Glander (1981) for howler monkeys, but we hesitate to attribute it to such because porcupine young-of-the-year were usually separated from their mothers during the winter. It is possible that some young accompanied their mothers for limited periods in the winter or that more subtle cues were used to transfer the information.

Long movements between feed trees in dense oak cover by some study animals suggest that predator-prey relationships may have influenced movements. Sweitzer and Berger (1992) found that habitat use was related to the age or size class of porcupines, presumably in response to increased risk of predation to smaller porcupines. Our observations generally agree with their findings. Mountain lion and coyote tracks were seen regularly in the study area. Both species are known to prey on porcupines (Keller 1935, Robinette et al. 1959, Towell and Meslow 1977, Maser and Rohwedler 1983). The strong urine scent at station trees or dens makes porcupines readily detectable. Mountain lions are capable of knocking porcupines from the canopies of trees (Taylor 1935). If long moves decreased the predictability of mountain lions locating porcupines in station trees, it would be an adaptive strategy. However, long moves expose porcupines to terrestrial predation by mountain lions, coyotes, and wolves (Canis lupis, which are now exterminated from the study area) and would presumably be nonadaptive. Since ample forage exists throughout the study site and long moves to locate food resources do not appear to be a dietary necessity, long movements may be an adaptive strategy to avoid arboreal predation by mountain lions. This hypothesis deserves further examination.

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Literature Cited


Minta, W. 1982. Release 82.1. Copyright, Penn State University, State College, PA.


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HISTORIC EXPANSION OF JUNIPERUS OCCIDENTALIS
(WESTERN JUNIPER) IN SOUTHEASTERN OREGON

Richard F. Miller¹ and Jeffery A. Rose¹

ABSTRACT.—The chronology of Juniperus occidentalis (western juniper) expansion in eastern Oregon, the effect of plant canopy and interspace on J. occidentalis seedling establishment and growth rates, and the age of J. occidentalis maximum reproductive potential were determined. Measurements were recorded in twenty-two 0.4-ha plots established in sagebrush-grassland communities and six 0.1-ha plots in Populus tremuloides (quaking aspen) communities. J. occidentalis began increasing during the 1880s in stands containing trees >130 yr old. Relatively steady establishment ensued into the 1950s and then began to progress at a geometric rate in the 1960s. J. occidentalis encroachment into aspen stands began between 1910 and 1920. The largest proportion of juvenile trees established beneath Artemisia species in sagebrush-grassland communities. J. occidentalis trees appeared to reach full reproductive potential at >50 yr of age. The ratio of male:female trees increased from 1:7 in scattered J. occidentalis stands to 3:8 in closed stands. The initiation of J. occidentalis encroachment during the late 1800s coincides with optimal climatic conditions for Juniperus berry production and establishment, reduced fire-return intervals, and heavy livestock grazing. The accelerated increase in J. occidentalis expansion since 1960 may be due to the continued absence of fire, abundant woody plant cover, and the large increase in J. occidentalis seed production.

Key words: western juniper, Juniperus occidentalis, expansion, Great Basin, intermountain shrub steppe, aspen, Populus tremuloides, succession.

One of the most pronounced plant community changes in the 20th century has occurred in the juniper and pinyon-juniper woodlands, a major vegetation type characterizing the Intermountain Region. These woodlands, sometimes described as pygmy forests, currently occupy 17 million ha throughout this region (West 1988). Juniperus occidentalis ssp. occidentalis Hook. (western juniper) is considered the Northwest representative of the pinyon-juniper zone in the Intermountain Region (Franklin and Dynnes 1973) and occupies over 1 million ha (Dealy et al. 1978) in eastern Oregon, southwestern Idaho, and northeastern California (Cronquist et al. 1972). This subspecies of J. occidentalis is found primarily north of the polar front gradient (Neilson 1987; parallel to the Oregon and Nevada border; latitude 42°) where temperatures are cooler, summer precipitation decreases, and winter precipitation increases (Mitchell 1976).

Relict juniper woodlands, tree-age class distribution, fire scars, and historical documents indicate presettlement pinyon-juniper and juniper woodlands were usually open, savannah-like (Nicol 1937, West 1988), or confined to rocky surfaces or ridges (Cottam and Stewart 1940, Barney and Frishknecht 1974, Hopkins 1979, Johnson and Simon 1987). J. occidentalis began increasing in both density and distribution in the late 1800s (Burkhardt and Tisdale 1976, Young and Evans 1981, Eddleman 1987), invading Artemisia tridentata subsp. vaseyana (mountain big sagebrush), Artemisia arbuscula (low sagebrush), Populus tremuloides (quaking aspen), and riparian communities. Although J. occidentalis is long lived (Vasek 1966, Lanner 1984), less than 3% of the woodlands in Oregon are characterized by trees >100 years old (USDI-BLM 1990). In 1825, Ogden observed only occasional J. occidentalis (reported as cedars) growing on hillsides while traveling through the Crooked River drainage in central Oregon (Rich et al. 1950). Today, these hillsides are covered by dense J. occidentalis woodlands. In a nearby area J. W. Meldrum's 1870 survey notes describe a gently rolling landscape covered with an abundance of perennial bunchgrasses and a wide scattering of J. occidentalis trees (Caraher 1977). Today, J.

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occidentalis densities on this site range between 125 and 250 ha\(^{-1}\). In Silver Lake, Oregon, J. occidentalis density increased from 62 ha\(^{-1}\) in 1890 to over 400 ha\(^{-1}\) by 1970 (Adams 1975). On another site in central Oregon where trees were absent prior to 1880, J. occidentalis increased to 1018 ha\(^{-1}\) by 1980 (Eddleman 1987). Recent expansion is similar to increases in other Juniperus species throughout western United States (Ellis and Schuster 1968, Tausch et al. 1981, West 1984, Tausch and West 1988).

The objectives of our study were to (1) describe the chronology of J. occidentalis expansion during the past several centuries in southeastern Oregon, (2) determine the effect of plant canopy and interspace on J. occidentalis seedling establishment and growth rates, and (3) determine the age when J. occidentalis reaches maximum reproductive potential.

METHODS

Study Area

The study area is located on Steens Mountain in southeastern Oregon, approximately 80 km south of Burns. This isolated volcanic fault-block, which lies in the extreme northwest Basin and Range Province (Fenneman 1931), is about 80 km long and oriented in a northeast direction (Baldwin 1981). The elevation of Steens Mountain ranges from 1265 to 2949 m, with a steep east-facing escarpment and a gentle west-facing slope. Climate is cool and semiarid, characteristic of the northern Great Basin. Annual precipitation at the lower elevations averages 220–280 mm, increasing to ≥ 700 mm at higher elevations (NOAA 1993). Most moisture is received as snow in November, December, and January and as rain in March through June.

J. occidentalis woodlands on Steens Mountain form a discontinuous belt between 1450 and 2100 m in elevation. Severe winter conditions probably restrict J. occidentalis from expanding into higher elevations (Billings 1954, Mehringer 1987). Limited distribution below 1500 m is possibly due to a combination of late spring frosts (Billings 1954) and limiting moisture. Tree canopy cover varies from open to 30% cover, except on mesic P. tremuloides sites where J. occidentalis cover approaches 100%. However, based on age structure and canopy leader growth, tree canopies are still actively expanding on the majority of sites measured. Early observations on Steens Mountain indicate the landscape contained only scattered stands of J. occidentalis (Griffiths 1902). Since 1900 the abundance of J. occidentalis pollen in the Steens Mountain area has increased five-fold (Mehringer and Wigand 1990).

Plant communities characteristic of J. occidentalis woodlands are Artemisia tridentata ssp. vaseyana/Festuca idahoensis (Idaho fescue), Artemisia arbuscula/F. idahoensis, and P. tremuloides. P. tremuloides communities on Steens Mountain range in elevation from 1760 to 2400 m. At lower elevations, in the J. occidentalis woodland belt, P. tremuloides stands form long, narrow communities along north aspects, which capture windblown snow and runoff.

Plot Layout

Plot locations were selected in an attempt to reflect sagebrush-grassland communities in different stages of J. occidentalis invasion on the west slope of Steens Mountain. Old stands on the rocky outcrops, which make up only a small percentage of present-day woodlands, were not measured. Sites selected support, or have the potential to support, sagebrush-grassland communities. Currently these sites are occupied by varying numbers and sizes of J. occidentalis dominance, creating a woodland structure of dispersed, intermediate, and closed tree stands (Table 1). Twenty-two 0.4-ha plots were located within the J. occidentalis belt of Steens Mountain; they ranged from 1500 to 2000 m in elevation and were distributed 32 km along the mountain range. Plots were situated along an elevation gradient representing communities from the lower- to upper-elevation J. occidentalis woodland belt. Dominant understory vegetation in the dispersed and intermediate plots was A. tridentata ssp. vaseyana and Festuca idahoensis (13 stands), A. arbuscula and F. idahoensis (4 stands), and A. tridentata ssp. vaseyana (2 stands). Understory vegetation in the closed stands (n = 3) comprised a few remnant deep-rooted perennial grasses, skeletons of dead A. tridentata ssp. vaseyana, and 70% bare ground (EOARC data file).

An additional six 0.1-ha plots were established in six separate P. tremuloides stands. Three stands were in advanced stages of J. occidentalis invasion with few to no adult P.
tremuloides trees and dead *P. tremuloides* trunks on the ground. The remaining three stands were characterized by a dominant *P. tremuloides* overstory and an understory of young *J. occidentalis*. Elevation for the *J. occidentalis*-*P. tremuloides* plots ranged from 1930 to 2000 m, all with a similar northeast aspect.

**Measurements**

Prior to sampling, string was stretched along the contour of each 0.4-ha plot at 1-m intervals to keep track of measured trees. *J. occidentalis* density (trees ha \(^{-1}\)) was recorded for trees <0.5 m tall, defined as adult, across the entire plot. Tree height, minimal and maximal crown diameters, and basal area just above the trunk swell at the stem base near the litter layer were recorded. Tree height was measured with a tape for trees <2 m and a clinometer for trees >2 m tall. Tree canopy cover was estimated by adding crown area measurements of all trees for each plot. Similar measurements were recorded on juvenile trees (defined as trees ≤ 0.5 m tall), but only those on the lower left quarter (0.1 ha) of each 0.4-ha plot. Current-year *J. occidentalis* seedlings (any plant with cotyledons still attached) were not recorded. Establishment location of each juvenile tree was recorded: beneath the canopy of *J. occidentalis*, *Artemisia*, other shrubs, tussock grass, or in the interspace. Less than 1% of juveniles were located beneath other shrubs or grasses; therefore, only *J. occidentalis*, *Artemisia*, and interspace are reported.

*J. occidentalis* is considered submonoeocious (Vasek 1966). Male and female reproductive status was determined by estimating abundance of cones and berries for each tree. Abundance was ranked in four classes: (0) absent, (1) scarce, (2) obvious but not abundant, and (3) abundant.

In each plot a 10-tree subsample was randomly selected for aging in each of four height classes: (1) <0.5 m, (2) 0.5–1.8 m, (3) 1.8–3 m, and (4) >3 m. In several of the dispersed plots, sample size for trees >3 m was smaller than 10, due to a lack of trees. We also sampled all old trees on plots when they occurred (n = 0–5 ha \(^{-1}\)). Old trees were easily identified by their growth form, containing rounded tops and heavy limbs, and lacking strong terminal leader growth (Burkhardt and Tisdale 1969). A cross section was removed approximately 30 cm above ground level from each tree >0.5 m tall and at ground level for trees ≤ 0.5 m, and then brought back to the lab for aging. Two radii from each cross section were polished, stained, and counted. Age was estimated by averaging both radii and adding 10 yr to correct for the 30-cm base. Mean differences between radii were 4% for trees >50 yr and 1% for trees ≤ 50 yr of age. Adams (1975) reported that growth-ring characteristics of *J. occidentalis* are useful in dendrochronological studies. The presence of false and missing rings was similar to that for *Pinus ponderosa*. Over 1200 trees were aged and approximately 14,000 counted and measured. In the six *P. tremuloides* stands, density of both *J. occidentalis* and *P. tremuloides* and age and height for *J. occidentalis* were measured across the entire 0.1-ha plot.

Evidence indicated minimal *J. occidentalis* mortality has occurred on Steens Mountain during the past 120 years. We observed very few dead or dying trees for all age classes (excluding seedlings), except where individual *J. occidentalis* trees had been cut or burned. Mortality of *Juniperus* species rapidly declines following the seedling stage (Van Pelt et al. 1990). *Juniperus* has few pests that prove fatal to the tree (Lanner 1984). We avoided recently cut or burned stands, which constituted a small percentage of *J. occidentalis*-occupied stands. Where remains of dead trees were observed, we noted they persisted for a long period of time. By recutting several stumps adjacent to one of our plots and aging and matching ring widths with adjacent live trees, we determined these trees were harvested around 1920. Others have also observed the persistence of *Juniperus* stumps (Young and Budy 1979).
Statistical Analysis

Height growth data for adult trees were analyzed using a randomized complete block design in PROC GLM of SAS (SAS 1986). Means were separated using Duncan's Multiple Range Test at $p \leq .05$ level. A split-plot design was used in the analysis of juvenile height growth. Main plots were sites and subplots were location of establishment (interspace, *Artemisia, J. occidentalis*). A Duncan's Multiple Range Test was used to separate the means.

Results

Little change in *J. occidentalis* density appeared to occur between the early 1700s and the 1880s (Fig. 1). We encountered old trees (standing trees $>130$ years old, large stumps, and burned-out trunks) on several *A. arbuscula* flats and *A. tridentata* ssp. *vaseyana* communities. However, data indicated presettlement tree densities in these *Artemisia* communities were $\leq 5$ trees ha$^{-1}$, suggesting very open *J. occidentalis* stands. The first evidence of an increase in tree densities occurred in the 1880s, with relatively steady establishment ensuing into the 1950s, similar to that observed by Tausch and West (1988). In the 1960s *J. occidentalis* establishment began occurring at a geometric rate.

Closed *J. occidentalis* stands, which once supported *A. tridentata* ssp. *vaseyana*, were characterized by an abundance of adult trees ($\geq 3$ m tall), a tree canopy cover of 18–28% (Table 2), and the presence of a few old trees (130+ yr; 2 to 5 ha$^{-1}$). *J. occidentalis* densities began increasing in these stands between 1878 and 1890. In the intermediate *J. occidentalis* stands, trees $>130$ yr were rare. Tree canopy cover ranged from about 8 to 16%, and densities of adult trees varied from 35 to 100 ha$^{-1}$. Trees $<3$ m in height, particularly juveniles, were abundant. *J. occidentalis* expansion in these sagebrush-grassland communities began between 1890 and 1910. In the dispersed stands few trees were $>60$ yrs old, and we aged no trees $>100$ yr. Tree canopy cover was usually $<5\%$ in the dispersed stands and densities of large adult trees $<35$ ha$^{-1}$. Invasion of *J. occidentalis* into these sagebrush-grassland communities began after 1930.

Greatest densities of *J. occidentalis* trees measured on Steens Mountain occurred in *P. tremuloides* sites (Table 3). In the late stages of *J. occidentalis* succession on these sites, tree canopy cover approached 100%. Live *P. tremuloides* occurred only on one of the three sites, and almost all trees were $<0.5$ m tall. In the remaining two stands only the remnants of large *P. tremuloides* trunks decaying in the understory were present. *J. occidentalis* invasion in these *P. tremuloides* sites began between 1910 and 1920. No *J. occidentalis* trees

![Graph](https://example.com/graph.png)

Fig. 1. Years of establishment for *juniperus occidentalis* trees on Steens Mountain, Oregon ($n = 1200$).
Table 2. General description of closed, intermediate, and dispersed *Juniperus occidentalis* stands on Steens Mountain in *Artemisia tridentata* ssp. *vaseyana* and *A. arbuscula* communities, and the percentage of juveniles located beneath *J. occidentalis*, *Artemisia*, and interspace. Canopy cover, basal area, and density means are followed by range in parentheses ( ).

<table>
<thead>
<tr>
<th># sites</th>
<th>Canopy cover %</th>
<th>Basal area (m²ha⁻¹)</th>
<th>Adults &gt;0.5 m ht</th>
<th>Juveniles &lt;0.5 m ht</th>
<th>J. occidentalis</th>
<th>Artemisia</th>
<th>Interspace</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. tridentata ssp. <em>vaseyana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>closed</td>
<td>6</td>
<td>22 (18-28)</td>
<td>5.2 (3.1-9.8)</td>
<td>296 (217-496)</td>
<td>580 (118-1236)</td>
<td>86⁴</td>
<td>9b</td>
</tr>
<tr>
<td>intermediate</td>
<td>5</td>
<td>6 (5-10)</td>
<td>1.8 (0.5-4.7)</td>
<td>95 (50-165)</td>
<td>815 (335-1423)</td>
<td>20b</td>
<td>58b</td>
</tr>
<tr>
<td>dispersed</td>
<td>2</td>
<td>2 (1-3)</td>
<td>0.4 (0.2-0.6)</td>
<td>52 (31-70)</td>
<td>185 (96-290)</td>
<td>3b</td>
<td>50b</td>
</tr>
<tr>
<td>A. arbuscula</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>closed</td>
<td>3</td>
<td>15 (12-20)</td>
<td>3.5 (1.8-5.4)</td>
<td>158 (74-247)</td>
<td>99 (20-198)</td>
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<td>67a</td>
</tr>
<tr>
<td>intermediate</td>
<td>3</td>
<td>6 (4.5-6.7)</td>
<td>1.8 (0.4-3.2)</td>
<td>104 (77-153)</td>
<td>375 (167-790)</td>
<td>11b</td>
<td>61a</td>
</tr>
</tbody>
</table>

1Sites of establishment means (%) followed by similar lowercase letters are not significantly different between establishment sites within *J. occidentalis* stand maturity classes (p ≤ .05).

> 80 yr were encountered. In stands with a *P. tremuloides* overstory, *P. tremuloides* density of small shoots was greater than that of *J. occidentalis*. However, *P. tremuloides* size classes between 0.5 m and large adults were absent, indicating a lack of *P. tremuloides* stand rejuvenation. On these sites *J. occidentalis* invasion began between 1930 and 1940.

Height growth for young *J. occidentalis* trees (<20 yr) across all sites averaged 2.9 cm yr⁻¹. Based on growth rates and height of trees between 10 and 20 yr of age (n = 200) across all *Artemisia* sites, 90% of trees 15 yr old were < 1 m tall (64% were <0.5 m tall). Surprisingly, height growth rates of juvenile trees did not significantly differ between *A. arbuscula* and *A. tridentata* ssp. *vaseyana* communities. However, location of establishment within communities significantly influenced growth rates of young *J. occidentalis* trees (Table 4). Trees establishing beneath an *Artemisia* canopy grew faster than young trees growing in the interspace.

Shrub and tree canopies also significantly influenced location of *J. occidentalis* seedling establishment in *Artemisia* communities. The largest proportion of juvenile trees was usually located beneath canopies of *A. tridentata* ssp. *vaseyana* or *A. arbuscula* and *J. occidentalis* (Table 2). Less than 20% of juveniles across all 22 *Artemisia* sites established in the interspace.

On Steens Mountain, for trees >0.5 m tall, 32% expressed predominantly only male or only female characteristics, 38% both male and female, and 30% contained neither fruits nor cones. *J. occidentalis* trees producing abundant crops of cones or berries were either male or female dominant. No trees were measured which contained an abundant crop of both berries and cones. Fifty-five percent of *J. occidentalis* trees with an abundant crop of berries contained no male cones. The remaining 35% contained only a scarce number of cones. The majority of trees producing abundant crops of male cones contained only scarce numbers of berries. Approximately 75% of trees producing heavy crops of berries or cones were >50 yr old. Trees <20 yr old expressing reproductive effort were rare and produced only a few cones or berries. The ratio of trees producing large crops of cones versus berries (cones:berries) increased from 1.7 in the scattered *J. occidentalis* stands to 3.8 in the closed stands.

**Discussion**

Low densities and limited distribution of *J. occidentalis* trees >130 yr and limited numbers of dead trees or old stumps suggest *J. occidentalis* has greatly expanded on Steens Mountain during the past 100 yr. Distribution of old trees was generally limited to rocky ridges and *A. arbuscula* communities. Old trees were found only occasionally growing in deeper, well-drained soils such as *A. tridentata* ssp. *vaseyana* grassland communities and were absent in *P. tremuloides* communities. In northeastern California, Barbour and Major
TABLE 3. Mean densities (6 ha-1) followed by range in () of Populus tremuloides and Juniperus occidentalis in P. tremuloides sites.

<table>
<thead>
<tr>
<th>Stage of succession</th>
<th>P. tremuloides</th>
<th>J. occidentalis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Juvenile</td>
</tr>
<tr>
<td>Late (n = 3)</td>
<td>17</td>
<td>1316</td>
</tr>
<tr>
<td></td>
<td>(0-50)</td>
<td>(0-3662)</td>
</tr>
<tr>
<td>Intermediate (n = 3)</td>
<td>1060</td>
<td>6553</td>
</tr>
<tr>
<td></td>
<td>(476-1670)</td>
<td>(5266-9450)</td>
</tr>
</tbody>
</table>

(1977) found a similar distribution of old and young J. occidentalis trees. A. tridentata ssp. voseyana and A. arbuscula communities, which contained a low density of J. occidentalis trees prior to settlement, were the earliest sites to initiate an increase in J. occidentalis. Dates of initial establishment of closed and intermediate stands were similar to periods of early stand development reported by Young and Evans (1981) in northeastern California and Eddleman (1987) in central Oregon.

Expansion of J. occidentalis coincides with Euro-American settlement in this portion of the Great Basin. Although no direct cause-and-effect relationship can be drawn, we hypothesize that climate, altered fire frequencies, and grazing in the late 1800s were primary factors initiating the recent expansion of J. occidentalis. Following the end of the Little Ice Age in the mid 1800s (Bryson 1989), winters became more mild and precipitation increased above the present long-term average in the northern half of the Great Basin between 1850 and 1916 (Antevs 1948, Graumlich 1985). Mild, wet winters and cool, wet springs promote vigorous growth in J. occidentalis (Earle and Fritts 1986, Fritts and Xiangdig 1986).

Presettlement fire-return intervals in A. tridentata ssp. voseyana communities have been reported to vary from 15 to 25 yr (Houston 1973, Burkhardt and Tisdale 1976, Martin and Johnson 1979). Burkhardt and Tisdale (1976) concluded that fire-frequency intervals of 30-40 yr would be adequate to keep J. occidentalis from invading a sagebrush-grassland community. Following settlement, frequency of fire in sagebrush grasslands has greatly declined. The reduction of fine fuels by high densities of domestic livestock greatly reduced the potential for fire in the Intermountain Shrub Region (Burkhardt and Tisdale 1976, West 1988). Griffiths' (1902) observations of the overgrazed landscape on Steens Mountain support this hypothesis. Fires set by Native Americans also declined in the 19th century due to large reductions in their populations caused by European diseases (Thompson 1916, Cressman 1981) and relocation to reservations in the 1870s.

The invasion of conifers into P. tremuloides communities is a common occurrence throughout the western U.S. However, conifers reported to typically invade P. tremuloides stands are species adapted to more mesic sites such as Pinus contorta (lodgepole pine), P. ponderosa, Pseudotsuga menziesii (Douglas-fir), Abies concolor (white fir), Abies lasiocarpa (subalpine fir), Picea engelmannii (Engelmann spruce), and Picea pungens (blue spruce) (Bartos 1973, Mueggler 1985). Invasion of the more drought-tolerant J. occidentalis into P. tremuloides stands is not well documented.

P. tremuloides is frequently considered a fire-induced species, replaced by less fire tolerant conifers (Baker 1925, Daubenmire 1943, Mueggler 1976). Prior to settlement, lightning and human-set fires probably helped maintain many P. tremuloides communities. However, the occurrence of fire in P. tremuloides stands in the Rocky Mountains has been greatly reduced since the late 1800s (Jones and DeByle 1985). Mueggler (1985) suggested the combination of fire suppression and heavy grazing in P. tremuloides communities may favor the establishment of conifers.

An increase in Artemisia cover may also enhance the invasion of J. occidentalis. As a sagebrush-grassland community shifts towards a greater dominance of shrubs, the number of safe sites for J. occidentalis seedling establishment increases. Others have also reported the majority of J. occidentalis seedlings established beneath Artemisia canopies (Burkhardt and Tisdale 1976, Eddleman 1987). In west Texas, J. pinchottii frequently establishes beneath mesquite plants (McPherson et al. 1988).
Table 4. Mean growth rates for juvenile Juniperus occidentalis trees (2-30 yr old) in three different establishment sites.

<table>
<thead>
<tr>
<th>Establishment site</th>
<th>cm yr⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artemisia</td>
<td>3.3A</td>
</tr>
<tr>
<td>J. occidentalis</td>
<td>2.7AB</td>
</tr>
<tr>
<td>Interspace</td>
<td>2.4B</td>
</tr>
</tbody>
</table>

Means followed by similar uppercase letters are not significantly different (p ≤ .05).

Shading by nurse plants may benefit J. occidentalis seedlings (Johnsen 1962) by reducing summer surface temperatures by 45–57% of bare ground surface temperatures (Burkhardt and Tisdale 1976). Enhanced growth rates of young trees growing beneath A. tridentata ssp. vaseyana suggest microclimates beneath shrub canopies are more beneficial than conditions in the interspace. Burkhardt and Tisdale (1976) reported J. occidentalis seedling growth rates were correlated positively with Artemisia and correlated negatively with bare ground.

*J. occidentalis* approached full reproductive potential near 50 yr. As *J. occidentalis* densities increased, the proportion of trees became predominantly male across sites. Highly fecund female trees appeared to be most important in open stands where *J. occidentalis* was actively expanding. In central Oregon, Eddleman (1984) observed that trees in the interior woodlands were strongly dominated by male cone production while trees growing in the open produced more female cones. He also reported trees did not produce significant quantities of fruit until 50–70 yr of age.

Conclusion

Optimal climatic conditions around the turn of the century, reduced fire return intervals, and the indirect effect of livestock through the reduction of fine fuels and an increase in *Artemisia* cover are probably primary factors that have contributed to the rapid expansion of *J. occidentalis* in southeast Oregon during the late 1800s and early 1900s. The accelerated increase in *J. occidentalis* density and invasion during the last 30 years into new communities is probably largely due to the continued absence of fire, abundant woody plant cover, and the large increase in *J. occidentalis* seed rain.

Acknowledgments

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Literature Cited


Dealy, J. E., J. M. Geist, and R. S. Driscoll. 1978. Western juniper communities on rangeland of the


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RANGELAND ALPHA DIVERSITIES: HARVEY VALLEY, LASSEN NATIONAL FOREST, CALIFORNIA

Raymond D. Ratliff

ABSTRACT.—Monitoring diversity usually begins by estimating alpha diversity of a plant community on a specific site. The objectives of this study were to provide alpha diversity benchmarks and to determine whether rangeland community basal cover characteristics explained variation in diversity estimates. Plant and surface component cover percentages were estimated on 51 plots (representing four vegetation types) on the Lassen National Forest, CA. Each plot was sampled with 30 random, 102 basal point transects. Jackknife procedures were used to compute means and standard errors for Margalef’s diversity index \( D_m \), which stresses species richness, and Simpson’s index \( D_s \), which stresses species dominance. Within vegetation types, \( D_m \) and \( D_s \) did not rank all plots in the same order. Highest \( D_m \) values occurred with the most species. Highest \( D_s \) values occurred with comparatively few species but more uniform cover. With either index, average diversity declined from the meadow to grassland to open shrub-grass to timber-bunchgrass types. All possible subset regressions of diversity on the basal cover characteristics were computed. Portions of the variance accounted for by the best models were too low to allow prediction of \( D_m \) and \( D_s \). The relation of alpha diversity to rangeland health is discussed.

Key words: ecology, plant communities, Margalef’s index, Simpson’s index, monitoring, basal cover.

Biological diversity (hereafter called diversity) involves ecological processes, structures, and functions and may occur at any spatial scale (Society of American Foresters 1992). Diversity refers to variety and abundance; it is variety or multiforality—of different forms or kinds (Stein and Urdang 1966). There are alpha, beta, and gamma diversities (Whittaker 1972). Alpha diversity is the variety that occurs within a plant community of a specific site. A site or stand is defined as an individual unit that is homogeneous in vegetation, soil, topography, microclimate, and history (West 1993). Beta diversity is the variety of communities along a gradient (e.g., topography, soil acidity, or moisture regime) or on a given site through time. Gamma or large-scale diversity is the variety of plant communities, or the total number of species present, or both in a specific geographic area (e.g., grazing allotment or watershed).

Diversity has two components, richness and evenness (Ludwig and Reynolds 1988, Magurran 1988). Richness refers to variety (numbers) of species, for example. Evenness refers to equality (abundance or numbers) of species botanical composition, for example.

Diversity may or may not follow traditional concepts of succession and increase from pioneer to climax plant communities or decrease with rangeland deterioration. Over large areas diversity may be higher if communities are at several seral stages than if the entire area is at a single seral stage. Within specific sites physical/chemical factors or intense competition or both may work to reduce diversity (Odum 1959). Absence of an expected species may be due to frequent disturbances, a low immigration potential, an immature soil, or an inhospitable moisture regime (del Moral and Wood 1988).

Nevertheless, because it may change with the kind of management, diversity should be assessed as part of range health evaluations. Diversity indices provide information that may not be immediately apparent from basic measures of the plant community such as cover and composition. High diversity of plant species is important in maintaining processes and flow pathways for energy and nutrients within and among communities. Higher diversity implies a greater number of occupied niches (Whittaker 1972).

Protecting or enhancing diversity, or both, are goals commonly set by policy or law. West

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1This article was written and prepared by U.S. government employees on official time; it is therefore in the public domain and not subject to copyright.
2Pacific Southwest Research Station, USDA Forest Service, 2081 E. Sierra, Fresno, CA 93710.
(1993) gave four reasons for having diverse plant communities: a sense of moral obligation to living things, an aesthetic appreciation of nature, economic benefits possible from them (e.g., the gene pool for cultivated crops), and the important array of services they provide (e.g., maintaining oxygen levels and cycling nutrients).

A major cause of rangeland deterioration is selective grazing of preferred plants and sites in similar patterns each year (Hormay 1970). Even with conservative grazing, populations of preferred plants on preferred sites may disappear, thereby reducing the overall diversity of vegetation. If such populations are ecotypes (Odum 1959), the ability of the species to recapture site resources is reduced.

Because nature abhors a vacuum, other species may increase or invade as those preferred by livestock decrease in abundance (Dyksterhuis 1949). As a result, plant species diversity may be higher rather than lower under grazing, at least initially. As preferred species decrease and less preferred ones increase, their abundances tend to become more even (Dyksterhuis 1949). With continued deterioration, species not previously able to compete tend to invade and become established and thereby increase species richness. The new plant community, though possibly comprising more species that are more evenly abundant, may cover less total area, and higher diversity may be associated with greater amounts of bare soil.

Increasingly, land managers are asked to monitor and determine change in diversity. Monitoring diversity usually starts with an estimation of alpha diversity for plant communities on specific sites. Such estimates are rare for rangelands. To derive the greatest benefit from monitoring efforts, managers must know what constitutes high and low diversity in given situations. They need to know how diversity changes when other commonly estimated properties of the site change (e.g., litter cover and amount of bare soil).

Seldom will examples of pristine or climax plant communities be available for developing diversity guides. Current plant communities represent the sums of all past influences. Current vegetation and site characteristics, therefore, must serve as benchmarks from which to develop guides and evaluate future change.

The objectives of this study were (1) to provide local rangeland managers with indices of alpha diversity from plant communities to use as guides of expected diversity for similar sites, and (2) to question whether variation in basal cover percentages of common and important indicators of rangeland health could explain variation in diversity. Although the findings are specific to the study area, it is hoped they may assist others dealing with questions of plant species diversity on rangelands.

**Methods**

**Study Plots**

During 1964 and 1965, 51 plots were established on the Harvey Valley and neighboring grazing allotments of the Lassen National Forest, CA (Ratliff et al. 1972). The plots were either 0.1 ha or 0.2 ha and unevenly distributed among meadow (8), open grassland (13), open shrub-grass (12), and timber-bunchgrass (18) vegetation types. These plots were used for evaluating range condition (health) at Harvey Valley relative to the neighboring allotments.

Meadows ranged from ephemeral lake sites with hardpans to deep, organically rich soil of drainage bottoms. Open grasslands included those dominated by shorthair sedge (Carex exsera) and those where shorthair sedge had been replaced by grasses. Open shrub-grass areas included silver sagebrush (Artemisia cana), black sagebrush (A. arbuscula), big sagebrush (A. tridentata), and bitterbrush (Purshia tridentata) subtypes. The timber-bunchgrass types were all in second-growth ponderosa pine (Pinus ponderosa). Some of them had bitterbrush and big sagebrush along with grasses in the understory.

**Data Collection**

Data used to estimate alpha diversity on each plot were actual point contacts (hits) with plant bases or soil surface components (gravel, litter, rock, bare soil, and large woody debris) and shrub crown area. A hit on a shrub was recorded when a point contacted the shrub crown or was within its projected crown area at the soil surface. For each plot 3060 hits were recorded, consisting of 102 points (in regularly spaced 3-point quadrats) on each of 30 randomly placed transects. Points in a quadrat
were at 23-cm centers and projected vertically. Within transects, quadrat spacing was either 0.6 m or 0.9 m, depending upon plot width. Basal cover percentages (proportions of the surface occupied by different plants and surface components) were calculated from the hits and summarized (Ratliff et al. 1972).

**Diversity Indices**

Two indices of diversity were used: (1) Margalef's \( D_m = (S - 1)/\ln N \), where \( S \) is the number of species and \( N \) is the total number of individuals (hits) for all species and (2) Simpson's

\[
D_S = 1/D, \quad D = \sum \frac{n_i(n_i - 1)}{s}
\]

\( N(N - 1) \) and \( n_i \) is the number of individuals (here the percentage cover) of the \( i \)th species (Maguran 1988). \( D_m \) was selected for its simplicity and because it stresses the species richness component. \( D_s \) was selected because it is well known and stresses the species evenness (dominance) component. In addition, these indices were selected because they do not require testing assumptions regarding the underlying distributions of species abundance.

An overall estimate of diversity was computed for each plot using each index. Then 30 new diversity estimates were computed using the jackknife procedure. This procedure consisted of deleting each transect in turn from the data set. From each new estimate and the overall estimate, a pseudovalue (related form) was computed. From the pseudovalues, means and standard errors for the two indices were derived for each plot. Use of the jackknife procedure to improve estimates of diversity and provide a way of calculating confidence intervals was suggested by Maguran (1988).

**Basal Cover Relationships**

Contributions of basal cover of various characteristics to the variance in estimates of alpha diversity were examined. Characteristics for each plot were basal covers of grasses, grasslike herbaceous plants, forbs, shrubs, and soil surface components. All possible subset regressions of \( D_m \) and \( D_s \) on the characteristics were computed using the Mallows' Cp criterion of the REG procedure (a multiple linear regression program) of the SAS Institute, Inc. (1982). Subset regression models explaining most variation in the indices were selected for study. The Pearson correlation matrix was computed, using the correlations (CORR) module of SYSTAT (Wilkinson 1989), to help assess the influence of individual characteristics on the indices.

**Results**

**Alpha Diversity Indices**

Diversity indices and basal cover values are available for all 51 plots. Here, only those plots within each vegetation type ranking lowest

<table>
<thead>
<tr>
<th>Veg. type</th>
<th>No. of species</th>
<th>Species</th>
<th>Composition percentage</th>
<th>Margalef's Mean</th>
<th>Margalef's SE</th>
<th>Simpson's Mean</th>
<th>Simpson's SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>MD</td>
<td>6</td>
<td>Eleocharis palustris</td>
<td>52</td>
<td>1.0</td>
<td>0.2</td>
<td>2.8</td>
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<tr>
<td></td>
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<td>Deschampsia caespitosa</td>
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<td>4.0</td>
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<td>0.2</td>
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<tr>
<td></td>
<td>14</td>
<td>Juncus balticus</td>
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<td>1.9</td>
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<td>Purshia tridentata</td>
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<td>1.1</td>
<td>0.2</td>
<td>4.7</td>
<td>0.4</td>
</tr>
</tbody>
</table>

1Highlighted values are the highest and lowest for each index within vegetation types.
2Vegetation types follow Ratliff et al. (1972): MD = meadow, GR = open grassland, SG = open shrub-grass, TB = timber-bunchgrass.
Fig. 1. Meadow diversity benchmarks: (a) Eleocharis palustris-, (b) Deschampsia caespitosa-, and (c) Juncus balticus-dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.
and highest for $D_m$ and $D_s$ are specifically discussed. Those plots are considered diversity benchmarks for their vegetation types in and near the Harvey Valley allotment.

**Meadow.**—$D_m$ in the meadows was lowest on a plot with just six species and demonstrated the effect of lack of richness (Table 1). The site was an ephemeral lake meadow (Fig. 1a) where dominant species covered 3.3% of the surface. Among the meadow plots, percentage litter cover was lowest and percentage bare soil was highest (Table 2).

$D_m$ was highest, but $D_s$ was lowest on a meadow with 19 species. That finding demonstrated the effect of good variety with uneven abundance. The site was a basin meadow, possibly an ancient lake (Fig. 1b). There the dominant species covered 5.7% of the surface. Only one species, among the others, contributed as much as 5% to the composition. Percentages of litter and bare soil were higher and lower, respectively, than averages for the meadow plots (Table 3).

$D_s$ was highest on a plot with 14 species. The site was a groundwater-fed meadow (Fig. 1c). Evenness in species abundance with moderate variety was demonstrated. Four species (including the dominant) each constituted more than 10% of the composition but less than 1% of the basal cover. Only one species, among the others, contributed less than 1% to the composition. Total live plant cover was below average, but percentages of litter and soil cover were well above and below the averages, respectively.

**Grassland.**—Both $D_m$ and $D_s$ were lowest on grassland plots, with nine species (Figs. 2a, 2b), respectively. Shorthair sedge was the main contributor to the composition. In the case of $D_m$, three species each contributed 5% or more, and five species each contributed 1% or less. In the case of $D_s$, only one species, other than shorthair sedge, contributed as much as 5% of the composition. For the plot with low $D_m$ the evenness component was better, litter cover was higher, and bare soil cover was lower than for the plot with low $D_s$.

$D_m$ was highest on a plot with 19 species (Fig. 2c). Shorthair sedge, Idaho fescue (*Festuca idahoensis*, 20%), and Sandberg bluegrass (*Poa sandbergii*, 9%) were main contributors to the composition. Sixteen species contributed less than 5% each. Among the grassland plots, this plot had the highest live plant cover and was well above average in litter cover and well below average in percentage of bare soil.

Idaho fescue dominated the plot with highest $D_s$ (Fig. 2d). Four of the other 10 species present each made up more than 10% of the composition; two species each made up about 6%. While the evenness component of diversity was good and total live plant cover was

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Plant groups$^1$</th>
<th>Surface components$^2$</th>
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<td></td>
<td>1.6</td>
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</table>

$^1$gr = grasses, gl = graminoid herbaceous plants, bl = broadleaf herbaceous plants (forbs), sh = shrubs, dp = dead attached cover, lp = live plant cover (gr + gl + bl + sh).

$^2$Gr = ground, Li = litter, Ro = rock, So = soil, Wo = large woody debris.

$^3$Types follow Bertliff et al. (1972), and plot order is the same as in Table 1.

$^4$t = less than 0.1% of basal cover.
above average, Idaho fescue covered only 3% of the surface and litter cover was well below but bare soil was well above average.

**SHRUB-GRASS.**—Both indices were lowest on an open shrub-grass plot where big sagebrush contributed over 95% of the composition (Fig. 3a). Only one other species, bottlebrush squirreltail (*Sitanion hystrix*), made up as much as 1%, and only five species occurred on that plot. This finding demonstrates the effects of both low variety and low evenness on diversity. Among the shrub-grass plots, this plot was second highest in total live plant cover (nearly all sagebrush), highest in grass cover, and lowest in bare soil. This suggests soil loss and formation of pavement.

Black sagebrush dominated the plot with highest $D_m$ (Fig. 3b). Of the 17 species on that plot, 12 of them each contributed less than 3% of the composition. The plot was above average in both litter and soil cover, but lowest in total live plant cover.

The plot with highest $D_s$ (Fig. 3c) had just 11 species and was dominated by false phlox (*Leptodactylon pungens*). Five other species combined contributed nearly 62% of the composition. Among the shrub-grass plots, this plot was well below average in litter cover but highest in bare soil.

**TIMBER-BUNCHGRASS.**—Both indices were lowest (Fig. 4a) on a timber-bunchgrass plot with seven species. Bitterbrush contributed over 80% of the composition. Three species contributed 2% or more and three species contributed less than 1% of the composition. While total live plant cover was above average, litter was near average and bare soil was well below average; there were few species, and they were unevenly abundant. This plot was similar in diversity to the shrub-grass plot with $D_m$ and $D_s$ both low.

$D_m$ was highest on a plot with 13 species (Fig. 4b). Nine of them contributed 1% or less of the composition, thereby demonstrating that high evenness is not required when variety is the main component of diversity considered. Big sagebrush dominated the understory and covered 4.3% of the surface. Litter cover was well above and bare soil was well below average for the timber-bunchgrass plots.

By contrast, $D_s$ was highest on a plot with just six species (Fig. 4c). Ross sedge (*Carex rossii*) contributed most of the composition (0.6% of the surface cover), three species contributed 15-26% each, and two species contributed 3% each, thereby demonstrating that high variety is not required when evenness is the main component of diversity considered. Percentages of soil and litter cover were near average for the timber-bunchgrass plots.

**Beta Diversity Indices**

Statistical comparisons of diversity among communities and vegetation types were not made. Nevertheless, average values for both indices declined from meadow to grassland to open shrub-grass to timber-bunchgrass types (Table 3).

Relative plot ranking (high to low diversity) depends on the index used, and inconsistent ranking by $D_m$ and $D_s$ was expected. Among the open shrub-grass and timber-bunchgrass types only two plots ranked the same, those with lowest diversity by both indices. Rankings by $D_m$ and $D_s$ were the same for 3 of the 8 meadow plots and 2 of the 13 open grassland plots.

**Basal Cover Relationships**

Meadow and grassland plots had higher average diversity indices than open shrub-grass
or timber-bunchgrass plots, but lower average percentages of live plant cover (Table 3). Total live plant cover was largely a property of shrub cover because projected crown hits were incorporated into the data base.

Significant portions of variances in the diversity indices (all 51 plots included) were accounted for by variation in percentages of some basal cover characteristics. Forty-seven percent of the variation in $D_m$ and 27% of the variation in $D_s$ were explained by the best models (Table 4).

$$D_m = a + \text{grb}_1 + \text{glb}_2 + \text{shb}_3 + \text{Grb}_4 + \text{Sob}_5 + \text{Wob}_6 + \text{error}$$

and

$$D_s = a + \text{shb}_1 + \text{Grb}_2 + \text{error},$$

where $a$, gr, gl, sh, Gr, So, and Wo are explained in Table 4; and the (b)’s are the coefficients.

Although gravel and bare soil were included in the model for $D_m$, they did not significantly correlate with $D_m$. Also, while in the model for $D_s$, gravel was not significantly correlated with $D_s$.

Individually, correlation with $D_m$ was positive for grasses ($r = .471$) but negative for grass-like plants ($r = -.014$), shrubs ($r = -.320$), and wood ($r = -.348$). Correlation of $D_s$ with shrubs was negative ($r = -.507$), also.

Fig. 2. Open grassland diversity benchmarks: (a, b, c) Carex exserta- and (d) Festuca idahoensis–dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.
DISCUSSION

Alpha Diversity

Many diversity indices are available to the land manager. Although a particular diversity index may be preferred, it is generally best to use one that stresses species richness and one that stresses evenness (dominance), such as $D_m$ and $D_n$, respectively. Doing so allows the manager to consider both components of diversity. The richness component of diversity may increase at the expense of the evenness component, or vice versa. Also, those indices that stress richness and those that stress evenness tend to be poorly correlated (Magurran 1988).

Beta Diversity

Data used in this study represent single-time samples and were not designed to estimate beta diversity. Testing for differences in diversity using such data was not considered reliable (West and Reese 1991).

Nevertheless, diversity indices for different but closely similar plots or communities, when computed by the same methods, should be nearly equal. With time or different treatment, wide divergence of the indices may occur.
Fig. 3. Open shrub-grass diversity benchmarks: (a) *Artemisia tridentata*, (b) *A. arbuscula*, and (c) *Leptodactylon pungens*-dominated plots; Eagle Lake Ranger District, Lassen National Forest, CA.
Fig. 4. Timber-bunchgrass diversity benchmarks: (a) *Purshia tridentata*–, (b) *Artemisia tridentata*–, and (c) *Carex rossii*–dominated plots, Eagle Lake Ranger District, Lassen National Forest, CA.
Permanent plots represent a resource for assessing beta diversity responses to land management practices. Although sampling a site to include within- and between-season variation is desirable, doing so is seldom possible, given time and monetary constraints. As an alternative, one might restrict sampling to times when selected species indicators are in specific phenologic stages (e.g., budding or flowering).

### Basal Cover

Because of the usual dominance of a single species and because that species tends to occupy high proportions of an area, reductions in diversity indices with increases in shrub cover may be expected.

Both diversity indices may be related positively or negatively to characteristics of basal cover or to soil properties. Nevertheless, $D_m$ was related to a greater number of characteristics than $D_s$, suggesting that $D_m$ may be the more desirable index for comparing plant communities of different sites or plant communities present through time on a given site.

### CONCLUSIONS

For similar communities we can expect plant species diversity to be highest in the meadow and lowest in the pine-bunchgrass types. High and low values of Margalef’s and Simpson’s diversity indices are available for benchmark plots of different vegetation types in and near the Harvey Valley allotment. Diversity indices for and averages among 51 plots are available by vegetation types.

The influence of species richness on $D_m$ was clearly evident. $D_m$ tended to be highest with the greatest numbers of species. Frequently that occurred when one species was clearly dominant and the others contributed little plant cover. The influence of evenness in abundance on $D_s$ was clearly evident. $D_s$ tended to be highest when species were more or less evenly abundant. Frequently that occurred with relatively few species. Few species with one contributing a high percentage of the composition produced low values of both indices. Situations with many species, all contributing equally to the composition, were not encountered, but such situations should give high values of $D_m$ and $D_s$.

Higher diversity did not necessarily mean greater plant cover or greater forage cover or more litter or less bare soil. While some relationships between diversity and basal cover values were significant, coefficients of determination were too low to allow either of the best models to be used to predict diversity.

Neither index should be relied on apart from other information for evaluating rangeland health. Nevertheless, plants capture the sun’s energy and pass it as food for other organisms, and a high degree of plant diversity may equate with high diversity in other parts of the biotic community.

### LITERATURE CITED


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**Table 4. Best model multiple linear regression coefficients, tests of significance (T), and probabilities of significance (P) for Margalef’s and Simpson’s diversity indices; Eagle Lake Ranger District, Lassen National Forest, CA, 1964–65.**

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1Regression coefficient


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EFFECTS OF SALINITY ON ESTABLISHMENT OF POPULUS FREMONTII (COTTONWOOD) AND TAMARIX RAMOSISSIMA (SALTCEDAR) IN SOUTHWESTERN UNITED STATES

Patrick B. Shafroth1, Jonathan M. Friedman1, and Lee S. Ischinger1

ABSTRACT.—The exotic shrub Tamarix ramosissima (saltcedar) has replaced the native Populus fremontii (cottonwood) along many streams in southwestern United States. We used a controlled outdoor experiment to examine the influence of river salinity on germination and first-year survival of P. fremontii var. todasenii (Rio Grande cottonwood) and T. ramosissima on freshly deposited alluvial bars. We grew both species from seed in planters of sand subjected to a declining water table and solutions containing 0, 1, 3, and 5 times the concentrations of major ions in the Rio Grande at San Marcial, NM (1.2, 10.0, 25.7, and 37.4 meq l¬1, 0.11, 0.97, 2.37, and 3.45 dS m¬1). Germination of P. fremontii declined by 35% with increasing salinity (P = .008). Germination of T. ramosissima was not affected. There were no significant effects of salinity on mortality or above- and belowground growth of either species. In laboratory tests the same salinities had no effect on P. fremontii germination. P. fremontii germination is more sensitive to salinity outdoors than in covered petri dishes, probably because water scarcity resulting from evaporation intensifies the low soil water potentials associated with high salinity. River salinity appears to play only a minor role in determining relative numbers of P. fremontii and T. ramosissima seedlings on freshly deposited sandbars. However, over many years salt becomes concentrated on floodplains as a result of evaporation and salt extrusion from saltcedar leaves. T. ramosissima is known to be more tolerant of the resulting extreme salinities than P. fremontii. Therefore, increases in river salinities could indirectly contribute to decline of P. fremontii forests by exacerbating salt accumulation on floodplains.

Key words: exotic species, Tamarix ramosissima, Populus fremontii, river salinity, seedling establishment, Rio Grande, riparian vegetation, Bosque del Apache National Wildlife Refuge.

In the last century the exotic shrub saltcedar (Tamarix ramosissima Ledebour) has spread throughout southwestern United States, where it now dominates many riparian ecosystems (Bowser 1958, Robinson 1965). In many areas T. ramosissima has replaced stands dominated by the native Fremont cottonwood (Populus fremontii Wats.; Campbell and Dick-Peddie 1964, Ohmart et al. 1977), decreasing the habitat of Neotropical migrant birds (Anderson et al. 1977, Cohan et al. 1978) and altering fluvial processes (Graf 1978, Blackburn et al. 1982). Understanding the factors controlling establishment of T. ramosissima and P. fremontii can aid in managing these species.

Successful invasion by Tamarix in the Southwest has been attributed to many factors. Much of the early spread probably resulted from the coincidental timing of clearing of P. fremontii stands by early settlers and the availability of Tamarix seed (Campbell and Dick-Peddie 1964, Harris 1966, Horton and Campbell 1974, Ohmart et al. 1977). Subsequent spread resulted largely from effects of damming and channelizing southwestern watercourses. Reductions in the magnitude of high flows and associated reductions in channel movements decreased the formation of bare, moist alluvial bars, which provide ideal P. fremontii seedling habitat (Ohmart et al. 1977, Stromberg et al. 1991). Smaller peak flows have also reduced leaching of salts from floodplain soils (Busch and Smith in press), perhaps favoring the salt-tolerant Tamarix (Everitt 1980, Brotherson and Winkel 1986, Jackson et al. 1990). Flow regulations that have altered the historical timing of peak flows may have inhibited P. fremontii regeneration because of its short period of seed dispersal and viability in early summer (Horton 1977, Everitt 1980), but they have enhanced Tamarix regeneration because of its abundant seed production throughout the growing season (Merkel and Hopkins 1957, Tomanek and Ziegler 1962, Warren and Turner 1975, Horton 1977). Finally, successful invasion of T. ramosissima has been attributed to its superior ability to resprout following fire (Busch and Smith 1993).

1National Biological Survey, Midcontinent Ecological Science Center, Fort Collins, CO 80525-3490.
We conducted experiments to examine the influence of river salinity on germination, survival, and growth of *Populus fremontii* var. *wislizenii* (Rio Grande cottonwood) and *T. ramosissima* on freshly deposited alluvial bars, the principal habitat for seedling establishment of both species. Field observations have suggested that *P. fremontii* is more negatively affected by high salt concentrations than *T. ramosissima* (Brotherson and Winkel 1986, Anderson 1989). Laboratory studies have confirmed this difference by exposing seedlings and cuttings of these species to varying concentrations of NaCl and CaCl₂ (Jackson et al. 1990, Siegel and Brock 1990). Two factors potentially confound the relationship of laboratory studies to field conditions. First, the mix of salts found in riparian ecosystems typically includes many constituents other than Na, Ca, and Cl. In many plants, salinity effects result from toxicity of specific ions as opposed to osmotic stress (Greenway and Munns 1980). Second, moisture availability is lower and more variable in the field than in these laboratory studies. This factor is important because low soil water potential caused by high salinity is exacerbated by low soil moisture content. We addressed these concerns by exposing *T. ramosissima* and *P. fremontii* seedlings to four different concentrations of a mix of salts designed to mimic ion concentrations in the Rio Grande. The experiment was conducted outdoors in planters subjected to a controlled water-table drawdown. Experimental conditions were designed to simulate alluvial bars along the Rio Grande in central New Mexico, where once-extensive *P. fremontii* forests have largely been replaced by *T. ramosissima* thickets (Campbell and Dick-Peddie 1964). Our outdoor experiments were supplemented by studies of germination under similar salinity treatments in the laboratory.

**Methods**

Seedling establishment experiments were conducted outdoors in 1993 near Fort Collins, CO, at latitude 40°35' north, longitude 105°5' west, and elevation 1524 m. Twelve 122 × 92-cm (diameter × depth) epoxy-lined steel tanks contained six 30 × 100-cm planters made of PVC pipe. Holes 1.26 cm in diameter were drilled into the lower 10 cm of each planter to allow water exchange, and the planters were filled to 92 cm with washed coarse sand (approximately 6% gravel [>2000 μm], 75% sand [=300–2000 μm], 16% fine sand [>75–300 μm], and <1% silt and clay).

Four salinity treatments were each replicated in three tanks (12 tanks total). Each tank contained three planters of *P. fremontii* var. *wislizenii* and three of *T. ramosissima*. Thus, the experimental unit for each species was a group of three planters within a tank. To avoid pseudoreplication, responses were measured as the mean value of the three planters. The results for the two species were analyzed as separate, completely randomized experiments with four treatments and three replicates per treatment.

The tanks were filled with water from the Cache la Poudre River (a snowmelt stream low in dissolved solids), and solutions containing multiples (0, 1, 3, and 5 times) of the mean concentration of all major ions in the middle Rio Grande were made. These four solutions constitute treatments 0x, 1x, 3x, and 5x. Mean ion concentrations were derived from eight measurements from the conveyance channel at San Marcial, NM, between October 1989 and September 1991 (U.S. Geological Survey 1991, 1992). The following salts were added to make treatment 1x: 309.9 mg l⁻¹ CaSO₄·2H₂O; 302.4 mg l⁻¹ NaHCO₃; 122.0 mg l⁻¹ MgCl₂·6H₂O; 70.1 mg l⁻¹ NaCl; 13.9 mg l⁻¹ K₂SO₄. Because the coarse sand substrate was low in nutrients (cf. Segelquist et al. 1993), 15 mg l⁻¹ of Fisons Technigro fertilizer (16% N, 17% P, 17% K) was added to every tank.

At the time of planting and for 1 wk thereafter, the water level was 10 cm below the soil surface. A 3.5-cm-week⁻¹ drawdown rate was applied for the remainder of the growing season (17 June to late September). Water-table drawdowns are associated with summer declines in discharge along western streams. The 3.5-cm-week⁻¹ drawdown rate was selected because a previous study (Segelquist et al. 1993) indicated that it is within the optimal range for establishment and growth of plains cottonwood (*Populus deltoides* ssp. monilifera).

Flowering panicles of *T. ramosissima* were collected on 17 May at the Bosque del Apache National Wildlife Refuge (latitude 33°46' north, longitude 106°54' west, elevation 1375 m). The panicles were air-dried for 48 h to enhance opening of seed capsules. Collected material was shifted through a series of soil
screens until clean samples of seeds were obtained. Catkins of *P. fremontii* were collected at the Bosque del Apache on 1 June. The catkins were air-dried for 72 h to enhance opening of seed capsules. Capsules were placed between soil screens and seeds were separated from the cotton and capsules using forced air. Seeds of both species were sealed in plastic containers and refrigerated at 5°C (Zasada and Densmore 1977). On 10 June, 100 *P. fremontii* seeds were planted in each of three planters per tank, and 200 *T. ramosissima* seeds were planted in each of the other three planters.

Electrical conductivity (EC) and temperature were measured using a Yellow Springs Instrument Co., Inc., Model 33 S-C-T meter, and pH was measured using a Corning 105 hand-held pH meter in conjunction with a Corning ATC temperature probe and a Corning general purpose combination electrode. EC was measured weekly in every tank beginning 12 June (17 measuring dates). Whenever EC was measured, a representative water temperature for that day was determined by averaging the temperature values from five randomly selected tanks. All EC measurements were corrected for temperature and reported at 25°C. Fourteen weekly measurements of pH were made beginning 30 June. On 16 June, 14 July, 18 August, and 17 September, water samples from one randomly selected tank per treatment were analyzed to determine concentrations of Ca, Mg, Na, K, CO₃, HCO₃, Cl, SO₄, and NO₃. Ca, Mg, Na, and K were determined by inductively coupled plasma emission spectroscopy (ICP; EPA method 200.0, United States Environmental Protection Agency 1983); CO₃ and HCO₃ were determined by titration (EPA method 310.1, United States Environmental Protection Agency 1983); Cl, SO₄, and NO₃ were determined by ion chromatography. Concentrations are reported in meq L⁻¹ to facilitate comparison of our solutions to solutions in other studies and because meq L⁻¹ can be related easily to electrical conductivity, which is commonly reported in the context of salinity studies.

On 29 September 1993 (day 112) we measured the shoot length of every living seedling. We harvested all live seedlings in early October. To harvest, we lifted a planter and laid it horizontally in a water-filled basin. The planter was then slowly lifted upside down, leaving the substrate column and seedlings in the basin. We gently separated seedlings from the sand and water and measured total length of every harvested seedling. Mean root lengths were determined by subtracting the mean shoot length for a planter from the mean total length in that planter. Roots and shoots were separated for both species, and *P. fremontii* leaves were stripped from the stems. Roots, shoots, and leaves were dried at 60°C for 72 h and weighed.

One-way analysis of variance (SAS Institute, Inc. 1990) was used to assess the significance of treatment differences within the two species for five variables: percent of planted seeds alive at the end of the experiment ("end-of-season survival"), shoot length, root length, per-plant aboveground biomass, and per-plant root biomass. For all variables the mean value of the three planters in a tank was the unit of analysis. The arcsine transformation was applied to end-of-season survival values to meet the equal variance assumption (Snedecor and Cochran 1980).

Data from the Colorado Climate Center were used to determine the difference between precipitation and open-pan evaporation (adjusted with pan coefficient = 0.73) for the period 1 June–30 September 1993 in Fort Collins. Evaporation at Fort Collins exceeded precipitation by 26.2 cm during this period. The same calculation was made for the Bosque del Apache using data from the Western Regional Climate Center for the years 1975 through 1990. Precipitation data are from the Bosque del Apache National Wildlife Refuge, and open-pan evaporation data are from Socorro, NM (latitude 34°35’ north, longitude 106°53’ west, elevation 1399 m; pan coefficient = 0.73). Growing-season evaporation at the Bosque del Apache exceeded precipitation by an average of 40.6 cm; n = 16, maximum = 51.0 cm, and minimum = 32.3 cm during these 16 years.

We performed laboratory germination experiments in January 1994. Five 25-seed replicates of five salinity treatments were completely randomized for both *T. ramosissima* and *P. fremontii*. Seeds were sowed in 7.5-cm petri dishes containing a Whatman #3 filter and 7 ml of a treatment solution. Petri dishes were placed in a Percival Model 1-35 biological incubator after sealing the dish tops with Parafilm. Temperature in the incubator was 20°C throughout the experiment, and petri dishes were exposed to 16 h of light and 8 h of darkness each day. Four of the treatment solutions
were the same as those used in the establishment experiment (0, 1, 3, and 5 times the concentration of the Rio Grande at San Marcial, NM); the fifth solution contained 7 times the concentration of the Rio Grande. Germinants in every petri dish were counted after seven days. A seed was considered germinated if it exhibited expanded cotyledons and an elongated radicle. The arcsine transformation was applied to percent germination values to meet the equal variance assumption, and one-way analysis of variance was performed on the transformed values (SAS Institute, Inc. 1990). When germination equaled 100%, the proportion was counted as \((n - 0.25)/n\), where \(n\) is the number of seeds planted (Snedecor and Cochran 1980).

## Results

EC and pH in the tanks varied little within treatments over the course of the experiment (Table 1). Mean temperature in the tanks was 21.7°C (standard error = 0.8, \(n = 17\)). Concentrations of measured chemical constituents in different treatments did not increase proportionally to the quantities of salt originally added, indicating that salts (especially CaCO\(_3\)) precipitated at higher concentrations (Table 1). Nevertheless, concentrations increased across treatments, with total concentrations ranging from 0.7 meq l\(^{-1}\) (0.11 dS m\(^{-1}\)) in treatment 0x to 37.4 meq l\(^{-1}\) (3.45 dS m\(^{-1}\)) in treatment 5x (Table 1).

For *P. fremontii* there was a significant treatment effect \((P = .003)\) on end-of-season survival, but not on any of the four measured growth variables (Table 2). End-of-season survival was negatively associated with increasing salinity: survival was greatest in treatment 0x and lowest in treatment 5x. Because the end-of-season survival variable combines germination and mortality, we analyzed the arcsine-transformed number of seedlings 7 d after planting (germination), and the arcsine-transformed difference between germination and end-of-

### Table 1. Chemical analysis of tank water for four treatments in the outdoor establishment experiment in Fort Collins, CO. For ion concentrations \((n = 4)\), minimum and maximum values are presented in parentheses below treatment means. For electrical conductivity \((n = 51)\) and pH \((n = 42)\), means ± 1 standard error are presented.

<table>
<thead>
<tr>
<th>Factor</th>
<th>0x</th>
<th>1x</th>
<th>3x</th>
<th>5x</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ca (mmol l(^{-1}))</td>
<td>0.36 (0.20, 0.52)</td>
<td>1.82 (1.71, 2.00)</td>
<td>4.02 (3.49, 4.83)</td>
<td>4.54 (3.02, 7.02)</td>
</tr>
<tr>
<td>Mg (mmol l(^{-1}))</td>
<td>0.11 (0.08, 0.16)</td>
<td>0.60 (0.46, 0.75)</td>
<td>1.65 (1.47, 1.97)</td>
<td>2.62 (2.28, 2.97)</td>
</tr>
<tr>
<td>Na (mmol l(^{-1}))</td>
<td>0.17 (0.09, 0.28)</td>
<td>4.85 (4.41, 5.11)</td>
<td>13.87 (11.91, 15.49)</td>
<td>22.24 (19.33, 24.65)</td>
</tr>
<tr>
<td>K (mmol l(^{-1}))</td>
<td>0.08 (0.06, 0.09)</td>
<td>0.26 (0.20, 0.34)</td>
<td>0.51 (0.44, 0.55)</td>
<td>0.79 (0.72, 0.90)</td>
</tr>
<tr>
<td>HCO(_3) (mmol l(^{-1}))</td>
<td>1.04 (0.92, 1.44)</td>
<td>3.92 (3.24, 4.44)</td>
<td>8.34 (7.29, 9.96)</td>
<td>9.60 (5.87, 15.74)</td>
</tr>
<tr>
<td>Cl (mmol l(^{-1}))</td>
<td>0.10 (0.07, 0.14)</td>
<td>2.47 (1.88, 2.82)</td>
<td>7.10 (6.96, 7.31)</td>
<td>12.12 (10.88, 13.21)</td>
</tr>
<tr>
<td>SO(_4) (mmol l(^{-1}))</td>
<td>0.04 (0.04, 0.05)</td>
<td>1.66 (1.32, 1.86)</td>
<td>5.06 (4.76, 5.32)</td>
<td>7.73 (7.13, 8.33)</td>
</tr>
<tr>
<td>NO(_3) (mmol l(^{-1}))</td>
<td>0.03 (0.002, 0.08)</td>
<td>0.03 (0.006, 0.09)</td>
<td>0.05 (0.01, 0.08)</td>
<td>0.06 (0.02, 0.15)</td>
</tr>
<tr>
<td>Total cations (meq l(^{-1}))</td>
<td>1.2 (0.7, 1.6)</td>
<td>10.0 (9.2, 10.8)</td>
<td>25.7 (23.8, 26.7)</td>
<td>37.4 (34.5, 41.5)</td>
</tr>
<tr>
<td>EC (dS m(^{-1}))</td>
<td>1.09 ± 0.03</td>
<td>0.97 ± 0.11</td>
<td>2.37 ± 0.23</td>
<td>3.45 ± 0.39</td>
</tr>
<tr>
<td>pH</td>
<td>7.54 ± 0.03</td>
<td>8.10 ± 0.02</td>
<td>8.29 ± 0.02</td>
<td>8.05 ± 0.03</td>
</tr>
</tbody>
</table>
season survival (mortality). There was a significant treatment effect on germination \((P = .008)\), but not on mortality \((P = .45)\), indicating that the effect on end-of-season survival was predominantly due to lower germination at higher salt concentrations. For *T. ramosissima* there were no significant treatment effects (Table 2).

Although *P. fremontii* germination in outdoor tanks was significantly decreased at high salinity, laboratory germination was not similarly affected even at seven times the salinity of the Rio Grande, total concentration 48.4 meq l\(^{-1}\) (4.56 dS m\(^{-1}\); Table 3). There was a significant positive effect of increasing salinity on *T. ramosissima* germination \((P = .03)\) (Table 3).

**DISCUSSION**

The absence of a negative effect of salinity on *P. fremontii* germination in the laboratory at concentrations as high as 48.4 meq l\(^{-1}\) (4.56 dS m\(^{-1}\)) is consistent with results of earlier studies. Jackson et al. (1990) found that *P. fremontii* germinated in the laboratory at salinities of 0, 27, and 106 meq l\(^{-1}\) using a mixture of NaCl and CaCl\(_2\), but not at 319 meq l\(^{-1}\) or above. Siegel and Brock (1990) observed higher percent germination of *P. fremontii* in the laboratory in NaCl solutions of 0, 25, and 50 meq l\(^{-1}\) than at 100 meq l\(^{-1}\) and above. Therefore, *P. fremontii* is no more sensitive to the mix of salts present in the Rio Grande than to NaCl and CaCl\(_2\) solutions of equal strength. Tests at higher salinities with the same ionic ratios were not possible with our Rio Grande mix because of low solubilities of some of the constituent salts. The decrease in *T. ramosissima* germination at low salinity in the laboratory (Table 3) is consistent with the finding by Jackson et al. (1990) that germination increases between 0 and 106 meq l\(^{-1}\).

Our results indicate that a given water salinity may negatively affect germination of *P.
fremontii seeds under ambient conditions but not under laboratory conditions. This may have resulted from an interaction between the effects of salinity and soil moisture content, or from vapor-pressure deficit differences. In outdoor planters, but not laboratory petri dishes, evaporation of water may have resulted in lower soil moisture and higher salt concentration at the soil surface. These factors would both tend to reduce soil water potential, thereby increasing plant water stress. Because the difference between evaporation and precipitation is somewhat greater at the Bosque del Apache than in Fort Collins, the effect of salinity might be stronger at the Bosque, especially in dry years. Finally, greater vapor-pressure deficits in the field relative to the laboratory may have exacerbated plant water stress.

Salinity appears to be a relatively minor factor regulating numbers of P. fremontii and T. ramosissima seedlings on freshly deposited sandbars along the Rio Grande. The only significant effects of increasing salinity were a small decrease in P. fremontii germination in outdoor planters and a small increase in T. ramosissima germination in the laboratory. There were no significant effects on survival after germination or above- or belowground growth for either species, even at water salinities several times that of the Rio Grande. The presence of abundant seedlings of P. fremontii and T. ramosissima on sandbars along the Rio Grande in most years is consistent with our results.

Although salinity may play only a minor role in the colonization of newly deposited alluvial bars by T. ramosissima and P. fremontii, this factor can become more important over time. Over many years salt becomes concentrated on some floodplains as a result of evaporation and salt extrusion from T. ramosissima leaves. EC readings as high as 10.0 dS m⁻¹ have been reported in floodplain sediment at the Bosque del Apache (John Taylor, Bosque del Apache National Wildlife Refuge, personal communication), and soil salinity levels as high as 60,000 mg l⁻¹ occur on floodplain sites along the lower Colorado River (Jackson et al. 1990). Soil EC above 2.0 dS m⁻¹ can reduce the growth of P. fremontii pole plantings (Anderson 1989). T. ramosissima has been shown to be less susceptible than P. fremontii to many of the negative effects of higher salinities (Brotherson and Winkle 1986, Jackson et al. 1990). Tamarix species avoid harmful effects of salts through extrusion from leaves and cellular compartmentation (Berry 1970, Kleinkopf and Wallace 1974, Waisel 1991).

Our results could be applied to efforts to revegetate riparian areas from seed. Riparian revegetation in the Southwest has largely consisted of planting poles or potted shoot cuttings. Although these approaches have been successful in some areas (Anderson et al. 1990), they can cost up to $10,000 per hectare (Ohmart et al. 1988). Furthermore, they require the destruction of parts of existing trees, and often entire trees or stands. Finally, these approaches may require importing cuttings or poles adapted to different site conditions. One alternative is regeneration of native cottonwoods and willows using natural seedfall (Friedman 1993, John Taylor personal communication). This approach generally involves clearing and irrigating an area so that seeds from nearby trees can colonize it. Our results suggest that water as saline as 37.4 meq l⁻¹ (EC 3.45 dS m⁻¹) can be used to grow P. fremontii from seed on sand (Tables 1, 2). However, care must be taken to prevent long-term salt accumulation through evaporation (e.g., through periodic flooding to flush salts) and to avoid sites with preexisting high salinity. Use of water with low salinity can help prevent negative effects on P. fremontii and may decrease the

<table>
<thead>
<tr>
<th>Treatment</th>
<th>0x</th>
<th>1x</th>
<th>3x</th>
<th>5x</th>
<th>7x</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cottonwood</td>
<td>90.4</td>
<td>96.0</td>
<td>96.0</td>
<td>92.8</td>
<td>96.0</td>
<td>1.2</td>
<td>35</td>
</tr>
<tr>
<td>Saltcedar</td>
<td>69.6</td>
<td>68.8</td>
<td>78.4</td>
<td>84.8</td>
<td>84.0</td>
<td>3.3</td>
<td>03</td>
</tr>
</tbody>
</table>

TABLE 3. Percent germination of Populus fremontii and Tamarix ramosissima seedlings exposed to five salinity treatments in covered petri dishes. High and low replicate values are given below the treatment mean (n = 5). Treatment effects were analyzed by completely randomized one-way ANOVA using arcsine-transformed data.
germination rate of *T. ramosissima* (Table 3). However, in a restoration effort along the Cache la Poudre River, *T. ramosissima* became established in large numbers along with *P. deltoides* in spite of use of water of low salinity (Douglas Gladwin, National Biological Survey, personal communication). Therefore, low salinity will not prevent establishment of *T. ramosissima* from seed when moisture, a bare sediment, and a seed source are present.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


BOWSER, C. W. 1958. Introduction and spread of the undesirable tamarisks in the Pacific southwestern sec-

tion of the United States and comments concerning the plants’ influence upon the indigenous vegetation. Pages 12–16 in Symposium on Phreatophytes. American Geophysical Union, Sacramento, CA.


SALINITY EFFECTS ON *Populus* AND *Tamarix*  65


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Accepted 12 August 1994
The following list of names and types in *Hedysarum* L. was prepared preliminary to submittal of a summary revision to the Flora North America Project. The genus *Hedysarum* L., as here interpreted for American taxa extends from the Bering Strait to Newfoundland and Vermont, and from the Polar Sea and the Canadian Arctic Archipelago south through the mountains and plains of western North America to Oklahoma, New Mexico, Arizona, and Nevada. Excluded from this treatment are those taxa originally included in *Hedysarum*, which are now interpreted as belonging to other genera, i.e., to *Desmodium*. The genus in the restricted sense consists of two complexes, i.e., those with leaflets thickened and veins obscured (the *boreale* complex) and those with relatively thin leaflets in which the veins are rather readily apparent (the *alpinum* complex). The earliest taxon within *Hedysarum alpinum* complex is that by Michaux (1803), who established the trinomial *Hedysarum alpinum americana* Michx. The *boreale* complex was initiated by Nuttall (1818) with the publication of *H. boreale*.

Taxa in the two complexes demonstrate remarkable morphological and geographical parallelism. Each consists of additional taxa separable generally into two geographical subgroups juxtaposed at or near the 50th parallel of latitude (somewhat north of the Canada-U.S. boundary). North of that parallel lies most of *H. boreale* ssp. *mackenzii* (Richards) Welsh, and most of *H. alpinum* sensu stricto. To the south occurs *H. occidentale* Greene, most of *H. sulphurescens* Rydb., limited extensions of *H. alpinum* L., and most of *H. boreale* ssp. *boreale*. Glacial events during the Pleistocene have been suggested as having separated the subsets, allowing them to achieve the degree of morphological and genetic integrity of the present populations. The present juxtaposition is suggested to have resulted by expansion of the respective entities into areas previously occupied by glaciers.

The rather large number of names involved in the genus is indicative of variation inherent in the various taxa. Flower size, plant size, leaflet size, and pubescence are features variable in both complexes. Apparent correlation of two or more of these features has served as justification for several names. Indeed, when one observes dwarf, large-flowered plants in either complex, there appears to be a compelling need for their recognition. However, much, if not all, of the variation is haphazard, or the attempt at segregation devolves to use of a single characteristic, such as presence or absence of pubescence, which fails also. There are few truly diagnostic characteristics once the two complexes are separated. The taxonomist ultimately must rely on a series of varying features to identify a particular specimen. Fortunately, the taxa are, with some notable exceptions, disjunct from each other. If the disjunction is not apparent from examination of a distribution map, it is often apparent in the field where the plants grow in different habitats. For example, the range of yellow-flowered *H. sulphurescens* apparently overlaps that of pink-purple-flowered *H. occidentale* in large part; yet, they seldom occur together, and only an exceptional intermediate is known.

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There are, in spite of gross similarities of the taxa within the respective complexes, few recorded intermediates.

Adding to the difficulties of interpretation of the North American materials is the interrupted circumboreal distribution of *H. alpinum*, a species with several close allies in Siberia. The initial interpretation by Michaux of North American *H. alpinum* as being taxonomically different ("H. alpinum: americanum") from that of the Old World has paraded apparition-like through most subsequent treatments of the genus. Unpublished work by Northstrom (1974) refuted the claim to difference between Siberian and American phases of the species, at least as far as broad categories were concerned. The claim that North American materials constitute a separate entity is likewise refuted by comparison of specimens from Siberia and North America in the present study. Other workers have asserted that large-flowered, low-growing plants of the species are identical with substantial Asian taxa [i.e., *H. hedyarioides* (L.) Schinz & Thellung (Astragalus hedyarioides L.)]. Such claims were investigated by Northstrom (1974), who determined that there is little basis for such assertions. Evidence to support the conspecific nature of the supposed entities is apparent when localities of such supposed taxa in western Alaska are examined and plants with larger flowers are found to occur within populations having small flowers, and that flower size within the species in a broad sense forms a continuum. And, occasional tall specimens within the *alpinum* complex also bear large flowers.

Another factor leading to the creation of a large number of synonyms was the early mis-interpretation of specimens of *H. alpinum* under the name *H. boreale*. This switching of names, while not uniquely a problem in this genus, became of great importance to those workers who encountered the genus piecemeal and treated the variants as though they had not already been named. It was not helpful, perhaps, that the most ardent authors of western American plant names should be involved with the genus (i.e., Edward L. Greene, Per Axel Rydberg, and Aven Nelson). Greene, as the record indicates, was prone to name the same species several times in this and other genera, not recognizing, or possibly not caring, that he was renaming the same taxon.

Still another trend resulting in the formation of inconsequential names was the well-intentioned effort to provide epithets for specimens differing in insubstantial ways, i.e., the naming of white-flowered or teratological specimens as formae.

The following list is thought to be exhaustive for *Hedysarum* names in North America. Pertinent types have been received on loan through the kindness of curators of herbaria cited with the specimens. Abbreviations for herbaria are those standard ones cited in Index Herbariorum. Type information is presented below in dual format for some taxa, with type information (type locality) as recorded with the protologue cited first and label data of the type specimen (type) cited second where there is a substantial difference in the two accounts.


*Basionym:* *H. boreale var. albiflorum* Macoun

= *H. sulphureascens* Rydb.

**Hedysarum alpinum** L., Sp. Pl. 750. 1753.

Type locality: "Habitat in Siberia" (Linnaeus i.c.).

Type: Possible lectotype 921.54 LINN (microfiche BRY!).

**Hedysarum alpinum var. americanum** Michx., Fl. Bor. Amer. 2: 74. 1803.

= *H. alpinum* L.


Type locality: "In borealibus Canadæ, et in catarmecis montum alleganhis."

Type: "Hedys. J ii p. 74–75, Herb. Ms" (isotype NY!).

There is a mounted half herbarium sheet at NY Torrey! bearing a large portion of a stem with a leaf and mature, strigose fruit of *H. boreale var. boreale*. This specimen is apparently superfluous (probably having been added later when additional material became available to Dr. Torrey from western American collections), but more pertinent to the present case the sheet also has an attached fragment envelope on which is written the type information noted above. The envelope contains a portion of an inflorescence, a flower, and several immature loment segments. The segments are glabrous, have a definite winged margin, and are identifiable as *H. alpinum* L. It is probable that the specimen from which the fragments were removed is with the Michaux herbarium at P.

Continued recognition of the American materials of *H. alpinum* at any infraspecific rank is fraught with difficulties; there are no diagnostic features known that will allow segregation of the American specimens from the Asiatic ones.
**Hedysarum alpinum var. americanum f. albiflorum** (Standl.) Fern., Rhodora 35: 275. 1933.

Basionym: *H. americanum* f. albiflorum Standl.

= *H. alpinum* L.

The publication by Fernald (1933) recognizes white-flowered plants from Newfoundland.

**Hedysarum alpinum var. grandiflorum** Rollins, Rhodora 42: 233. 1940.  
Type: "Newfoundland, Pistolet Bay, Messy and turfy trap cliffs and talus, Anse aux Sauvages, M. L. Fernald, K. M. Wiegand and Bayard Long 29625, August 11, 1925;" holotype GHI!  
Paratype: "Newfoundland, Region of Port a Port Bay, No. 10849. In humus or turf on the limestone tablet, altitude 200-300 m., Table Mountain, M. L. Fernald and H. St. John, July 16 & 17, 1914" (CAN! BM!).

This name is based on large-flowered (about 16 mm long), low-growing specimens from Newfoundland. There are other similar plants scattered through most of the distribution of *H. alpinum* in North America, but they are more consistently represented in frigid or other inhospitable arctic or subarctic sites. Even in the type series cited with the protologue there is considerable variation. The paratype cited above differs significantly from the holotype specimen; it is much taller and has flowers of a size intermediate with those of specimens more usual for var. *alpinum* in a more strict sense. Indeed, the low-growing, larger-flowered phase appears to be a phenotypically recurring recombinant form within a complex exhibiting much variation in flower size and other features. However, size of flower is not always correlated with plant height or flower number. All possible combinations of flower size, flower number, and plant height are represented in the species as a whole. It is possible to write a key that will separate these plants, but it seems that such a key will not then be segregating natural taxa.

Basionym: *H. philosocia* A. Nels.  
= *H. alpinum* L.

**Hedysarum alpinum var. philosocia** (A. Nels.) Rollins, Rhodora 42: 224. 1940.  
Basionym: *H. philosocia* A. Nels.  
= *H. alpinum* L.

Basionym: *H. alpinum var. americanum* Michx.  
= *H. alpinum* L.

= *H. alpinum* L.  
Synonym: *H. albiflorum* (Macoun) Fedtsch.  
Type: "Alaska: Davidson Glacier, July 4, 1929, William S. Cooper & Frances E. Andrews 95 (Herb. Field Mus. No. 598,264, type"); holotype Fl!

White-flowered specimens occur sporadically through populations of taxa with generally pink-purple flowers. Their recognition at any taxonomic rank is probably moot, and the publication of the taxon by Standley (1930) is therefore inconsequential.

= *H. boreale* ssp. mackenzii (Richards.) Welsh

= *H. alpinum* L.  
Type: Alaska, Cape Nome, Blaisdell s.n. summer 1900 (lectotype selected here: GHI, isotype type US!).

Specimens on which *H. auriculatum* is based were distributed from the California Academy of Sciences herbarium with collection information recorded on labels of that institution. The only known specimens in contemporary collections are those at GH and US. The two specimens consist of almost identical branches of *H. alpinum*, with both flowers and fruit, although that at GH is designated on the label as a duplicate of the type, which was presumably at CAS prior to the San Francisco earthquake early in this century. Fire resulting from that devastating tragedy destroyed much of the early Academy herbarium.

= *H. boreale* Nutt. var. boreale

Intended type: "Flora of Colorado. Plants the Gunnison Watershed, Cimarron, June 28. Stems in large clusters 8 in. to 1 1/2 ft. on dry open slopes. Collected in 1901 by C. F. Baker, No. 274" (NDG!).

Evidently the name was never published by E. L. Greene but was cited as a synonym of *H. pabulare* A. Nelson by Rydberg in his Flora of Colorado. The intended type has three mounted stems showing flowers and maturing fruit; they are stigisose both on herbage and on the leaves. The plants differ in no material way from a great many specimens from Colorado. Perhaps Greene also realized as much.

**Hedysarum boreale** Nutt., Gen. N. Amer. Pl. 2: 110. 1816.  
Type locality: North Dakota, "around Fort Mandan, on the banks of the Missouri," Nuttall (l.c.).  
Type: "Hedysarum boreale—Sources of the Missouri," Nuttall (probably late June) 1811; holotype BM!  
The name *H. boreale* was early transferred to the concept of *H. alpinum*, and part of the synonymy reflects attempts by various authors to resolve the apparent lack of a name for this wide-ranging and highly variable species. Nuttall (Torrey and Gray 1838) named the species a second time, as *H. canescens*, based on specimens from along the Snake River in present Idaho taken in 1834. He was in the vicinity of Fort Hall, Idaho, from 14 July to 6 August 1834 (McKelvey 1955: 602). Whether he noted the similarity between earlier- and later-named materials is not known. It seems likely that
he did not have authentic material of the earlier-named taxon at hand for comparison with his collections on the 1834 Wyeth expedition. The type at BM, a solitary flowering stem, is mounted with several flowering stems of _H. alpinum_ of unknown collector.

**Hedysarum boreale var. albiflorum** Macoun, Cat. Canad. Pl. 1: 510. 1884. non nud.

= _H. sulphureescens_ Rydb.

_Syn._ *H. albiflorum* (Macoun) Fedtsch.

Type locality: “This form is peculiar to the foothills and drier mountain slopes, and is abundant from the Kananaskis through the Rocky Mountains to the Columbia valley at Donald, Lat. 51° (Macoun). Eastern summit of the North Kootanie Pass, Rocky Mountains” (Lc.).


There is no description aside from the designation “albiflorum” proposed as an epithet. The only other information provided by Macoun aside from that related with the locality data is the statement: “This fine plant is closely related to _H. boreale_, but is certainly distinct.” The name is regarded as a nomen nudum. The collection by Dawson is, nevertheless, an excellent flowering example of _H. sulphureescens_, and the Macoun sheet consists of two plants with both flowers and immature to mature fruits, both also _H. sulphureescens_. The indication by Macoun of relationship of var. _albiflorum_ to _H. boreale_ reflects the general misapplication by many American botanists of _H. boreale_ to the _alpinum_ complex in North America, of which _H. sulphureescens_ is a portion. Macoun used the number 533 for several collections of _Hedysarum_ taken from 1883 to 1885.

**Hedysarum boreale var. cinerascens** (Rydb.) Rollins, Rhodora 42: 234. 1940.

_Basionym:_ *H. cinerascens* Rydb. et _H. canescens_ Nutt. in seq.

= _H. boreale_ Nutt. var. _boreale_.

**Hedysarum boreale var. cinerascens f. album** Boivin, Naturaliste Canad. 87: 34. 1960.

= _H. boreale_ Nutt. var. _boreale_.

Type: “Canads, Saskatchewan, Maple Creek District, Eastend, hillside along river valley, 19 July 1980, R. C. Russell 5 5075” (holotype at DAO).


_Basionym:_ *H. flavescens* Coutt. & Fisher

= _H. sulphureescens_ Rydb.

**Hedysarum boreale var. gremiale** (Rollins) Northstrom & Welsh, Great Basin Nat. 30: 125. 1970.

_Basionym:_ *H. gremiale* Rollins


_Basionym:_ *H. mackenzii var. leucanthum* Greene

= _H. boreale_ ssp. _mackenzii_ (Richards.) Welsh

**Hedysarum boreale ssp. mackenzii** (Richards.) Welsh, Great Basin Nat. 28: 152. 1968.

_Basionym:_ *H. mackenzii_ Richards.

**Hedysarum boreale var. mackenzii f. niveum** (Boivin) Boivin, Naturaliste Canad. 93: 433. 1966.

_Basionym:_ *H. mackenzii var. mackenzii f. niveum* Boivin

= _H. boreale_ ssp. _mackenzii_ (Richards.) Welsh

**Hedysarum boreale var. oboratum** Rollins, Rhodora 42: 235. 1940.

= _H. boreale_ Nutt. var. _boreale_.

Type: Nevada. Elko County, Thorpe Creek, E of Lamolile, 25 July 1926, H. H. Price 188 (holotype photo RMI).

**Hedysarum boreale f. proliferum** (Dore) Boivin, Naturaliste Canad. 94: 630. 1967.

_Basionym:_ *H. mackenzii f. proliferum* Dore

= _H. boreale_ ssp. _mackenzii_ (Richards.) Welsh

**Hedysarum boreale var. utahense** (Rydb.) Rollins, Rhodora 42: 235. 1940.

_Basionym:_ *H. utahense* Rydb.

= _Hedysarum boreale_ Nutt. var. _boreale_.

**Hedysarum canescens** Nutt., in Torr. & Gray, Fl. N. Amer. 1: 357. 1838. Not _H. canescens_ L.

_Basionym:_ *H. cinerascens* Rydb.; _H. boreale var. cinerascens* (Rydb.) Rollins

= _H. boreale_ Nutt. var. _boreale_.

Type locality: Idaho, “Plains of the Rocky Mountains, particularly near Lewis’ River,” Nuttall (Lc).


The specimen at PH (which is mounted on a sheet with two other superficial collections) bears the date “July 12,” with the incorrect year date 1833 obviously added later. Nuttall was with the Wyeth Expedition in 1834, and on 12 July was a short distance east of where Fort Hall would be constructed subsequently. Despite the existence of the earlier-named _H. boreale_, with which _H. canescens_ is synonymous, this name or its substitudes would be featured prominently in 19th-century accounts of the genus in the American West. There are two of Nuttall’s specimens on the sheet at GH, each provided with a label—both with flowers and both representing the same taxon. The label information consists of the following: “Hedysarum * canescens. H. mackenzii? R. Mts.,” and _Hedysarum * canescens_ R. Mts.” Since no additional locality
information or date accompanies the labels, the status as exact duplicates is unknown. It seems likely that both were included within the concept of *H. canescent* by Nuttall, and both can be regarded as isotypes. There is a second possible isotype of *H. canescent* at BM. "Hedysarum mackenziiz? Fort Hall, Prairie, common. Aug." It lacks the usual for Nuttall’s labels, and his name is not in evidence, but the handwriting appears to be his.

**Hedysarum carnulorum** Greene, Pittonia 3: 212. 1897.
= *H. boreale* Nutt. var. *boreale*
Type locality: "Common in clayey soil about the mouth of the Canon of the Arkansas, in southern Colorado" (Greene 1e.).
Type: Colorado, Fremont Co., "Plants of Colorado, Canon City, 8 Sept. 1896. Edw. L. Greene" (lectotype here designated: NDGI, 2 isolectotypes also NDGI).

While no specimens were cited with the original description, the three specimens so named in Greene’s handwriting at NDG are most certainly type material. All bear the same date and locality information. The specimen bearing the “Greenennum Herbarium” number 35866 is here chosen as lectotype; the others, 35687 and 35688, are considered isolectotypes. The lectotype has both flowers and fruit; the other two are in fruit and flower (with immature fruit), respectively. All have strigose herbage and lomentas. Usual flowering time for the species is April to late July. Is it possible that the species flowered again following late summer rains at Canon City in September 1896?

= *H. boreale* Nutt. var. *boreale*
Basionym: *H. canescent* Nutt.
Syn: *H. boreale* var. *cinerasces* (Rydb.) Rollins

This material was retained by Northstrom (1974) at varietal rank. The taxon stands on the sole character of pubescence, and a plotting of the distribution of hairy versus glabrous plants demonstrates much overlap. The specimens can be separated, but do they represent taxa?

**Hedysarum flavescens** Coult. & Fisher, Bot. Gaz. 18: 300. 1893, non Regel & Schmalz.
Basionym of: *H. sulphurescens* Rydb.
Type: Montana, near Helena, May 1892, F. D. Kelsey s.n. (holotype F!).

It is unfortunate that the epithet *flavescens* was occupied; it fits well the description of flower color in this taxon. Many of the Kelsey collections are in the U.S. National Museum (Eilens 1985), but the type of *H. flavescens* is at F, where Coulter’s herbarium is deposited.

**Hedysarum greguale** Rollins, Rhodora 42: 230. 1940.
= *H. boreale* var. *greguale* (Rollins) Northstrom & Welsh
Type: Utah, Uintah County, "ca 14 mi W. of Vernal, 16 June 1937," R. C. Rollins 1733 (holotype GHI, isotypes BM!, US!, CAS!, UTC!, MONTU!, PHI!, F).

This taxon stands on the feature of lateral spines on the loment segments; it is otherwise indistinguishable from plants of var. *boreale* by which it is surrounded (Northstrom and Welsh 1970).

= *H. occidentale* Greene
Type: "Mountain woods near head waters of Jocko River, Montana,—flowers pale purple, W. M. Canby 93, July 15, 1883" (holotype NY!).

The type specimen consists of a folded plant some 75 cm tall bearing leaves and flowers, and a stem fragment bearing immature fruit. Mature flowers are about 16 mm long, on the short side of the variation in *H. occidentale*, but the fruit, even though immature, is of the size and form of that species.

**Hedysarum leucanthum** (Greene) Greene, Pittonia 3: 213. 1897.
Basionym: *H. mackenziiz* var. *leucanthum* Greene
= *H. boreale* ssp. *mackenziiz* (Richards.) Welsh

= *H. boreale* ssp. *mackenziiz* (Richardson) Welsh

Evidently Dr. William Jackson Hooker sent representative material obtained by John Richardson, botanist with the Franklin expedition, to the Philadelphia Academy and to John Torrey and Aza Gray. Collections from the Franklin expedition demonstrate the variability represented in a rather large set of specimens, each matched by modern collections of the taxon. The second sheet cited at CH is doubly mounted with a mere fragment presumed to have come from the Franklin expedition in the lower portion and a second fragmentary collection by Burke (apparently a phase of *H. boreale*) from the Rocky Mountains. The latter material is not a portion of the type of *H. mackenziiz*.

= *H. boreale* Nutt. var. *boreale*
Type locality: Canada: "Saskatchewan: W. P. Fraser, Langham, river valley, June 12 and 26, 1938" (l.c.)
Type: "Hedysarum Mackenziiz Richards. River valley, Langham, Sask., W.F[rasers], June 12 & 26, 1938" (holotype DAO!).

Boivin (l.c.) cites the revisionary treatment of Rollins (1940) as indicating that *H. mackenziiz* var. *mackenziiz* has flowers 18–21 mm long, but with
some 16–20 mm. Prairie plants from Saskatchewan and Alberta, however, have flowers 13–15 mm long. These latter plants are the basis of his var. **fraseri**. The type of var. **fraseri** represents *H. boreale* ssp. **boreale** var. **boreale**, which is present along the plains and foot slope of the Rocky Mountains, and has flowers of the size indicated for the variety.

**Hedysarum mackenzii** var. **leucanthum** Greene, Pittonia 2: 294. 1892.
- Basionym of: *H. leucanthum* (Greene) Greene
- = *H. boreale* ssp. **mackenzii** (Richards.) Welsh
- Type locality: "On the Porcupine River, northern Alaska, Mr. J. J. Turner" (Greene Lc.).
- Type: "Plants of Alaska, collected on the Porcupine River, 1891, Mr. J. Turner" (holotype NDG!).

Greene (1892) notes that this is "far more than an albino state of *H. Mackenzii*; perhaps identical with some asiatic species; but the plants were just coming into flower when gathered, in that there is no trace of the loment." He later (1897) elevated it to species rank. However, except for white flowers, which occur with some frequency in the species, the plant differs in no respect from numerous other plants from the arctic range of the taxon generally.

- Basionym of: *H. boreale* var. **mackenzii** f. **niveum** (Boivin) Boivin
- = *H. boreale* ssp. **mackenzii** (Richards.) Welsh
- Type: "Yukon Territory: J. W. Abbott 17a, Pine Creek, sandy land, June 7, 1946" (holotype DAO!).
- The collection consists of five flowering stems of *H. boreale* ssp. **mackenzii**, all with white flowers. The condition of white flowers is occasional throughout the subspecies and hardly worthy of taxonomic consideration.

- Basionym of: *H. pabulare* A. Nels.
- = *Hedysarum boreale* Nutt. var. **boreale**

- = *H. boreale* ssp. **mackenzii** (Richards.) Welsh
- Syn: *H. leucanthum* (Greene) Greene

- Basionym of: *H. boreale* f. **proliferum** (Dore) Boivin
- = *H. boreale* ssp. **mackenzii** (Richards.) Welsh
- Type: "Plants of Alaska. A single clump in shallow soil over broken rock (growing beside common petaliferous plant, cf. 4983). North Side of Tanana River, Mile 277, Richardson Highway, 64°10'N, 145°32'W, W. J. Cody & P. J. M. Webster 4984, June 3, 1959" (holotype DAO!).

This name is based (Dore 1959) on a teratological specimen of *H. boreale* ssp. **mackenzii**, a recurring variant induced by a pathogen, likely a smut fungus. Teratology occurs in several if not all boreal legumes native to Alaska. In certain of those instances the inflorescence typically elongates, flowers become erect on attenuated pedicels, petals are deformed, and the ovary is typically exerted from the flower. In some specimens at least the ovary is filled with black spores. The type specimen of *f. proliferum* exhibits another variant than that typically encountered. The inflorescence is shortened and modified flower buds are in tight clusters. Whether elongate or compact, specimens on which such aberrations are based are not taxa, and the need to name them is therefore moot.

- Basionym: *H. canescens* Nutt.
- = *H. boreale* Nutt. var. **boreale**

**Hedysarum marginatum** Greene, Pittonia 4: 138. 1900.
- = *H. occidentale* Greene
- Type locality: "Mountains above Cimarron, southern Colorado, collected by the writer, 30 Aug. 1896; also near Pagosa Springs, Colo., 26 July, 1899, C. F. Baker" (Greene Lc.).
- Type: "Plants of Colorado, Near Cimarron, 30 Aug. 1896, Edw. L. Greene" (lectotype NDG!, here chosen); "Plants of Southern Colorado, Pagosa Springs, 26 July 1899, C. F. Baker" (syntypes NDG!, NY!, RM!, GH!, R!).

The lectotype collected by Greene is in fruit; syntypes at NDG and NY have both flowering and fruiting branches. In both the loment articles are markedly winged and strigose; herbage is strigose also (see Greene 1900).

**Hedysarum occidentale** Greene, Pittonia 3: 19. 1896.
- Type locality: "Olympic Mountains, Washington, 1890, C. V. Piper" (Greene Lc.).
- Type: "Washington, "Olympic Mts., G. V. Piper 905, flowers 11 August 1890, fruit 30 Sept. 1900" (holotype NDG!).

Greene (1896) provides a description and a short note: "Plant like *H. boreale* when in flower, though with broader leaflets and widely different fruit." A second sheet from the Olympic Mountains at NDG, Piper 2227 (August 1895), has the epithet "occidentale" in Greene's hand, but it was not cited by him. It is much better material than the type. For a long time the name *H. boreale* was included within the concept of *H. alpinum*. It is likely that Greene was under a similar misconception. The general aspect of *H. occidentale* (i.e., conspicuously veined leaflets and large loments with prominently reticulate venation), which occurs from Vancouver Island, British Columbia, and the Olympic Peninsula, Washington, disjunctly eastward to northern and eastern Idaho, western Montana, western Wyoming, northeastern Utah, and montane southern Colorado, is that of *H. alpinum*; and it differs generally in the manner indicated by Greene.

The most distinctive feature separating most, if not all, specimens of *H. occidentale* from *H.
alpinum is the much larger, rather conspicuously wing-margined loment segments. Flowers are generally larger, often much larger. However, plants from the Absaroka Range of northwestern Wyoming approach H. alpinum in occasionally having small flowers, but when collected at maturity, the fruit is that of H. occidentale. Additional collections might demonstrate that H. alpinum per se is indeed in the Absarokas. Large-flowered plants of H. alpinum, mainly of frigid sites in the arctic, approach the size of flowers of some H. occidentale specimens, but the fruit there is that of H. alpinum.


Type: Utah, Carbon County, "ca 14 mi due ENE of Helper, Soldier Creek, 30 June 1977, Welsh & Taylor 15256" (holotype BRY; isotype at NY).

The syndrome of characters associated with this taxon is shared individually elsewhere within the species as a whole. However, specimens from Duchesne, Carbon, and Emery counties, Utah, and Gunnison County, Colorado, are recognizable by their large, thick, ovate to ovate-lanceolate, yellow-green leaflets, and large pale flowers. Plants are known from rather xeric sites in pinyon-juniper and mountain brush communities, whereas plants of the type variety are mainly of more mesic sites. Although the taxon is segregated on weak diagnostic features, it seems to be at least a trend worthy of taxonomic recognition. It has long been known in collections.


= H. boreale Nutt. var. boreale

Type: Wyoming, Wind River, Dubois, A. Nelson 732, 1894 (lectotype here designated RM!).

This name is based on several Wyoming, Colorado, and Utah syntypes: i.e., M. E. Jones 5592, Soldier Summit, Utah, in 1894, POM?, BM, F!; Snake River, Wyoming, A. Nelson 3496, 19 August 1899 RM!, Wyoming, Natrona Co., Bates Creek, L. N. Goodding 201, 5 July 1901, RM!, F!


= H. boreale Nutt. var. boreale

Type: Wyoming, Teton County, along the Snake River, 31 July 1932, L. O. Williams 975 (holotype RM; isotypes GH!, CAS!).


Basionym: H. alpinum var. phylloscia (A. Nels.) Rollins; H. alpinum ssp. phylloscia (A. Nels.) Love & Love

= H. alpinum L.

Type: Wyoming, Albany County, Head of Crow Creek, Laramie Mountains, 1896, A. Nelson 2034; holotype RM!

Material from the Black Hills of South Dakota and from southeastern Wyoming is morphologically similar and has been recognized as belonging to a taxon that survived south of the major glacial events of the Pleistocene. The main diagnostic criterion is, however, loment pubescence. That feature is inconstant within the southern material and often is present in plants far beyond its supposed range (which has been plotted to include plants as far north as the 50th parallel). Recognition of plants at any taxonomic rank is, therefore, problematical.


= H. boreale Nutt. var. boreale?

I have been unable to find any reference to this taxon aside from its citation by Rollins (1940).


Yellow to yellowish flowers easily distinguish this entity, which shares the peculiar loment features of H. occidentale. The species ranges from the southern British Columbia-Alberta Rockies south through north central Washington, northern Idaho, western Montana, and northwestern Wyoming.


= H. alpinum L.

Type: Alaska, Nome, Dr. F. E. Blaisdell s.n. summer 1900 (lectotype NY! here designated; isolotype GH!).

Type material is low, about 2–2.5 dm tall, has mature flowers about 12 mm long, and has fruit the size and conformation of H. alpinum. It is identical for all practical purposes with material named by Eastwood simultaneously as H. curvatum and taken at the same place and time by the same collector in 1900.


= H. occidentale Greene

Type: Wyoming, "In draws of the foothills, Evanston, A. Nelson 7198, 14 June 1900" (holotype RM; iso- tyopes RM!, NY!, GH!).

Type sheets uniformly bear thick, lanceolate to lance-ovate leaflets similar to var. canone, but with flowers of typical H. occidentale. Plants from southwest Wyoming are not uniformly of the uintahense type, but vary from one population to another, with most being similar to traditional H. occidentale.


= H. boreale Nutt. var. boreale

Type: Utah, Salt Lake County, "vicinity of Salt Lake City, Utah," Leonard 55, 26 May 1883 (holotype NY!).

The type consists of two complete stems and a fragmentary branch; it is typical of the material
growing through much of Utah and elsewhere in the West.

REFERENCES


GREENE, E. L. 1892. New or noteworthy species.—XIV. Pittonia 2: 293–296.


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WHIPWORM (TRICHURIS DIPodomys) INFECTION IN KANGAROO RATS (Dipodomys SPP): EFFECTS ON DIGESTIVE EFFICIENCY

James C. Munger1 and Todd A. Slichter1

ABSTRACT.—To determine whether infections by whipworms (Trichuris dipodomys [Nematoda: Trichurata: Trichuridae]) might affect digestive efficiency and therefore energy budgets of two species of kangaroo rats (Dipodomys microps and Dipodomys ordii [Rodentia: Heteromyidae]), we compared the apparent dry matter digestibility of three groups of hosts: those naturally infected with whipworms, those naturally uninfected with whipworms, and those originally naturally infected but later deinfected by treatment with the anthelmintic Ivermectin. Prevalence of T. dipodomys was higher in D. microps (53%) than in D. ordii (14%). Apparent dry matter digestibility was reduced by whipworm infection in D. microps but not in D. ordii. Although a statistically significant effect was shown, its small magnitude indicates that whipworm infection is unlikely to have a biologically significant impact on the energy budgets of host kangaroo rats.

Key words: parasite, digestive efficiency, whipworm, kangaroo rat, Trichuris, Dipodomys, energy budget.

Parasites inhabiting the gastrointestinal tract of a host may reduce the efficiency of the organs they inhabit either through direct competition for nutrients or through damage to absorptive surfaces. Because decreased digestive efficiency may reduce the rate of energy input into a host, gastrointestinal parasites have the potential to cause a change in host energy allocation (e.g., reduced activity or reduced reproduction), and thereby impact the ecology of the host (Munger and Karasov 1989).

Tapeworm infections have a measurable effect on digestive efficiency, but a biologically unimportant effect on the energy budget of host white-footed mice (Peromyscus leucopus; Munger and Karasov 1989). The present study was designed to determine if infection by a nematode, the whipworm Trichuris dipodomys, has a substantial effect on one aspect of the energy budget, digestive efficiency, of host kangaroo rats (Dipodomys microps and D. ordii).

MATERIALS AND METHODS

Our study site, located 2 km N of Murphy, Owyhee County, ID, is in desert scrub habitat with sandy loam substrate. Primary shrub species of the study area are Artemisia spinescens, Artemisia tridentata, Atriplex canescens, Atriplex confertifolia, Atriplex spinosa, and Chrysothamnus nauseosus. Six rodent species were captured at the site, Ammospermophilus leucurus, Neotoma lepida, Perognathus flavus, Peromyscus maniculatus, and two species of kangaroo rats, Dipodomys ordii and Dipodomys microps. Dipodomys ordii ranges from 42 to 72 g and consumes a diet consisting primarily of seeds (Zeveloff 1988). Dipodomys microps is larger, 72–91 g, and is unique among kangaroo rats in that it relies heavily on leaves of Atriplex confertifolia for forage (Kenagy 1972, Zeveloff 1988). Both species are liable to infection by the whipworm Trichuris dipodomys, a nematode that inhabits the cecum of infected hosts (Grundmann 1957, Whitaker et al. 1993).

On the study site we established a 13 × 13 grid of 169 Sherman live traps baited with millet and placed at 15 m intervals. During two trapping sessions, 14–22 June and 15–18 August 1990, kangaroo rats (30 individuals of D. microps and 85 of D. ordii) were captured and brought into the laboratory. Fecal specimens from each animal were analyzed for the presence of parasite eggs by standard centrifugal flotation techniques using saturated sucrose solution (Pritchard and Kruse 1982). Six infected but untreated animals from the June experiment were included in the pool of animals used in the August experiment. The few animals that failed to thrive in the lab were removed from the experiment; data from a
total of 29 *D. microps* individuals and 56 *D. ordii* were analyzed.

Each month’s set of captures was subjected to the following protocol:

(1) Kangaroo rats were acclimated to a diet of millet seed for 3–11 d.

(2) A pretreatment feeding trial was performed: Animals were placed in wire-bottomed cages with a measured amount of whole millet seed. At the end of 5 d, fecal pellets were separated from spilled food and dried >24 h at 50°C. Initial digestive efficiency of each animal was measured as apparent dry matter digestibility (i.e., the proportion of mass consumed but not lost as waste), which was calculated as \((M_{FO} - M_{FE}) / M_{FO}\), where \(M_{FO}\) and \(M_{FE}\) are the mass of food consumed and feces produced, respectively.

(3) Half of the infected animals were then injected subcutaneously with a solution of Ivermectin (a systemic anthelmintic; Ivomec brand, from MSD AGVET, Rahway, NJ). Figure 1 gives sample sizes of treatment groups. June captures received, on each of two consecutive days, a 0.2-cc injection of Ivermectin in 40% glycerol formal and 60% propylene glycol; each injection delivered ca 350 μg Ivermectin / kg body mass. Controls received equal-volume injections of the glycerol formal–propylene glycol carrier. This dosage had little effect on the presence of whipworm eggs in feces of injected animals. Therefore animals received 8 d later a second set of two injections, each of 0.15 cc and delivering ca 2 mg Ivermectin / kg body mass; control animals received the carrier. August captures received, on each of two consecutive days, an injection of 0.15 cc volume delivering ca 2 mg Ivermectin / kg body mass. Control animals received the carrier. To control for possible side effects of Ivermectin, half of the uninfected animals captured in August were also injected with a solution of Ivermectin.

(4) Two days after each set of injections a posttreatment feeding trial was conducted using techniques in (2) above. Only results of the pretreatment feeding trials and feeding trials following the 2-mg Ivermectin / kg body mass injection will be presented below.

**RESULTS AND DISCUSSION**

Adult worms (seven of each gender) taken from a *Dipodomys microps* at our site were identified as *Trichuris dipodomys*. Although some minor morphological differences from the original species description (Read 1956) do exist, perhaps as a result of geographical variation, the specimens most closely match Read’s description of *T. dipodomys* (A. Shostak personal communication). Measurements of several key morphological characters are as follows (\(X \pm SD\)): total length: \(\delta 25.6 \pm 0.8\) mm, \(\varphi 41.3 \pm 2.9\) mm; hindbody length: \(\delta 12.7 \pm 0.4\) mm, \(\varphi 23.7 \pm 1.9\) mm; spicule length: 850 ± 85.1 μm; egg length: 64.8 ± 5.0 μm; egg width: 33.5 ± 1.0 μm. Voucher specimens were deposited with the University of Alberta Parasite Collection (#’s UAPC11464 and UAPC11465). Although we did not identify whipworms from *D. ordii*, we are confident they are *T. dipodomys*; the type host for *T. dipodomys* is *D. ordii*, and *T. dipodomys* is known only from *D. ordii* and *D. microps* (Whitaker et al. 1993).

**Prevalence in Host Species.**

*Trichuris dipodomys* occurred at substantially higher prevalence in *D. microps* than in *D. ordii* (Table 1), a result similar to that of Grundmann (1957). We can speculate as to three possible explanations for this pattern. The first is that eggs produced by adult worms in *D. microps* may become embryonated more easily than those in *D. ordii*. Freshly produced fecal pellets of *D. microps* appear moistier than those of *D. ordii* (Munger personal observation), probably because of the higher amount of green or leafy vegetation in the diet of *D. microps*. If moisture is necessary for embryonation of the eggs (as is implied by Parry 1968),
moister feces may lead to higher embryonation rates and therefore higher prevalence among *D. microps*. The second explanation is that social and burrow use behavior may differ between these species. For example, perhaps *D. microps* individuals visit one another’s burrows (and thereby become exposed to parasite eggs) at a substantially higher frequency than do *D. ordii*. Also, *D. microps* inhabits a mound up to 2 m in diameter while *D. ordii* inhabits less substantial individual holes. Studies of another system of two species of kangaroo rats has shown that the larger, mound-inhabiting *D. spectabilis* uses its burrow system for prolonged periods, while the smaller *D. merriami* rotates among several burrows (Jones 1989). This latter behavior would tend to reduce reinfection of individuals; it would be interesting to see if behaviors differ similarly between *D. microps* and *D. ordii*. The third explanation is that resistance to infection may differ between these two host species.

### Effects on Digestive Efficiency

Apparent dry matter digestibility (ADMD) of millet seed was quite high, >95% on average (Table 2), a figure comparable to that found by Schrieber (1979) for granivorous rodents. Injection of Ivermectin did not appear to affect ADMD of animals uninfected by whipworms, an effect that might occur through the removal of other symbionts, or through some direct effect (proportional change in ADMD, \( \bar{X} \pm SE \); untreated: \(-0.0043 \pm 0.0035\), treated: \(-0.0058 \pm 0.0037\)). Therefore, in the following analyses all naturally uninfected animals are combined into one class.

The effect of whipworm removal on ADMD was analyzed with a two-way analysis of variance (ANOVA). One factor analyzed was the treatment: deinfected (naturally infected but treated with Ivermectin) vs. infected (naturally infected but not treated with Ivermectin) vs. naturally uninfected. The other factor was species. Experimental period (July vs. August) was included as a blocking factor. The dependent variable in the analysis was proportional change between pretreatment and posttreatment ADMD ([post–pre]/pre); this measure should be more sensitive than posttreatment ADMD in expressing treatment effects because it takes account of initial differences in ADMD among hosts.

Although there were no statistically significant main effects of treatment or species on ADMD, there was a significant interaction between these factors (Table 3), indicating that the two host species differ in their response to treatment. This difference between species was explored using a separate ANOVA for each species, which revealed that treatment with Ivermectin had a significant effect on change in ADMD in *D. microps*, but not in *D. ordii* (Table 4, Fig. 1). A Tukey’s *a posteriori* multiple sample test revealed that, within *D. microps*, the change in ADMD of the deinfected group differed significantly from the change in ADMD of both the infected group and the uninfected group. These results can be interpreted as showing that the deinfected group had 1.9% higher ADMD than the other two groups.

**Table 1.** Infection of two species of kangaroo rat with the nematode *Trichurus dipodomys*.

<table>
<thead>
<tr>
<th></th>
<th><em>D. microps</em></th>
<th><em>D. ordii</em></th>
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<tr>
<td></td>
<td>Infected</td>
<td>Uninfected</td>
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<tr>
<td>June trapping</td>
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<td>5</td>
</tr>
<tr>
<td>August trapping</td>
<td>6</td>
<td>9</td>
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**Table 2.** Effects of whipworm infection on apparent dry matter digestibility (ADMD). Standard errors are in parentheses. Figures on change between initial and final feeding trials, as well as sample sizes, are in Figure 1. See text for a description of treatments.

<table>
<thead>
<tr>
<th></th>
<th>Deinfected</th>
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<th>Uninfected</th>
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<td></td>
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<tr>
<td>Initial ADMD</td>
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<td>.965 (.0029)</td>
<td>.955 (.0103)</td>
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<td>Final ADMD</td>
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<td>.950 (.0026)</td>
<td>.953 (.0052)</td>
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<td><em>Dipodomys ordii</em></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Initial ADMD</td>
<td>.967 (.0107)</td>
<td>.957 (.0076)</td>
<td>.961 (.0022)</td>
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<tr>
<td>Final ADMD</td>
<td>.955 (.0034)</td>
<td>.958 (.0037)</td>
<td>.957 (.0014)</td>
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</tbody>
</table>

**Table 3.** Effects of whipworm infection on apparent dry matter digestibility (ADMD). Standard errors are in parentheses. Figures on change between initial and final feeding trials, as well as sample sizes, are in Figure 1. See text for a description of treatments.

**Table 4.** Effects of whipworm infection on apparent dry matter digestibility (ADMD). Standard errors are in parentheses. Figures on change between initial and final feeding trials, as well as sample sizes, are in Figure 1. See text for a description of treatments.
TABLE 3. *F* values and probability values (*P*) from three-way analyses of variance on effects of species, month, and treatment (deinfected, infected, or uninfected) on apparent dry matter digestibility (ADMD).

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<td>.48</td>
<td>9.11</td>
<td>.003</td>
<td>.00</td>
<td>.95</td>
</tr>
<tr>
<td>Error</td>
<td>77</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

Note: *F* values are derived from three-way analyses of variance on effects of species, month, and treatment (deinfected, infected, or uninfected) on apparent dry matter digestibility (ADMD).

Table 4. Results from one-way analyses of variance on the effect of treatment (deinfected, infected, and uninfected) on % change in dry matter digestibility in *D. microps* and *D. ordii*.

<table>
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<tr>
<th>Species</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th><em>F</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
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<td><em>D. microps</em></td>
<td>Treatment</td>
<td>2</td>
<td>.00106</td>
<td>4.64</td>
<td>.019</td>
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<tr>
<td></td>
<td>Error</td>
<td>27</td>
<td>.000229</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. ordii</em></td>
<td>Treatment</td>
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<td>.00034</td>
<td>1.21</td>
<td>.31</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>52</td>
<td>.01442</td>
<td></td>
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In the lab, Sara Murray and Aaron Munger helped in the field. Discussion with Mary Price was helpful, as were comments from anonymous reviewers. This research was supported by an Intramural Faculty Research Grant from Boise State University.

**Literature Cited**


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LOCAL DISTRIBUTION AND FORAGING BEHAVIOR OF THE SPOTTED BAT \textit{(Euderma maculatum)} IN NORTHWESTERN COLORADO AND ADJACENT UTAH

Jay F. Storz

ABSTRACT.—This study investigated local distribution and foraging behavior of the spotted bat \textit{(Euderma maculatum)} in Dinosaur National Monument, Colorado-Utah, by monitoring audible echolocation calls. The occurrence of this species was verified in a variety of habitat types in canyon bottoms and other relatively low elevation sites, indicating that the animals are widely distributed and locally common in the area. Foraging spotted bats concentrated flight activity in the open-air space above meadows and occasionally exploited near-canopy habitat (within 8 m of foliage). Bats began to forage shortly after dark, and activity levels were relatively constant throughout the night. Foraging spotted bats attacked airborne prey every 2.15 min on average. Consistent with published observations, spotted bats maintained exclusive foraging areas. Distinct vocalizations indicating agonistic encounters occurred when a bat encroached on the foraging area of a conspecific.

Key words: spotted bat, Euderma maculatum, Colorado, Utah, Dinosaur National Monument, foraging, habitat use, attack rates, echolocation.

The spotted bat \textit{(Euderma maculatum)} is widely distributed across western North America and apparently exists in low population numbers throughout its range (Fenton et al. 1987). The species is rare in collections, and viable populations have been documented in only a few widely separated localities (Watkins 1977, O’Farrell 1981). Findings presented here and those of Navo et al. (1992) indicate that \textit{E. maculatum} is locally common in canyon bottoms and other low-elevation sites in Dinosaur National Monument, Colorado-Utah, and occurs throughout a diverse range of habitat types.

Population studies (e.g., Leonard and Fenton 1983) in south central British Columbia have demonstrated that foraging spotted bats exhibit considerable habitat specificity; radiotracking in this same area (Wai-Ping and Fenton 1989) has demonstrated that individuals are faithful to specific sites over several consecutive nights. However, no clear association between foraging activity and any specific habitat conditions is apparent. In British Columbia, spotted bats forage over clearings in ponderosa pine (\textit{Pinus ponderosa}) forests, open fields, and marshes (Leonard and Fenton 1983, Wai-Ping and Fenton 1989). There is little information about foraging habitat throughout the remainder of the geographic range of \textit{E. maculatum}.

The purpose of this study was (1) to investigate local distribution of \textit{E. maculatum} by monitoring echolocation calls, (2) to identify and describe foraging habitat, and (3) to make a preliminary examination of spatial and temporal patterns of habitat use by spotted bats in the study area.

METHODS

This study was conducted in the canyon bottoms and other relatively low elevation sites in Dinosaur National Monument (109°W, 40°31'N), northwestern Colorado and northeastern Utah, from 17 May to 9 June 1993. Navo et al. (1992) provided a description of the physiography and vegetation of Dinosaur National Monument. In each study site where spotted bats occurred, I monitored movement patterns and foraging behavior by listening to the low-frequency (15–9 kHz; Leonard and Fenton 1984) echo-location calls of this species, which are clearly audible to the unaided human ear (Woodworth et al. 1981).

As reported previously (Navo et al. 1992), \textit{E. maculatum} is readily identifiable because it has the lowest-frequency echolocation calls of...
any bat species in the study area. *Nyctinomops macrotis* and *Idionycteris phyllotis* also produce orientation sounds that are partly audible to humans, with frequencies of 25–17 kHz for *N. macrotis* (Fenton and Bell 1981) and 24–12 kHz for *I. phyllotis* (Simmons and O’Farrell 1977). These two species inhabit southern parts of the Colorado Plateau and the Great Basin (Milner et al. 1990, Tumlison 1993), but neither is known to occur as far north as Dinosaur National Monument, extralimital records of *N. macrotis* notwithstanding (Milner et al. 1990). To further ensure correct call identification, I referred to recordings of known *E. maculatum* calls. I also visually identified free-flying individuals (based on conspicuous white venter and large ears) at close range in the beam of a high-intensity flashlight after locating the animals by listening to orientation sounds. It should be noted that *I. phyllotis* is often buff-colored ventrally and therefore could be visually misidentified as *E. maculatum* in areas of sympathy.

**Sampling Locations**

To investigate the ecological distribution of *E. maculatum*, I sampled 15 sites at 12 locations representative of common low-elevation habitat types in the area (Fig. 1). Riparian sites (Jenny Lind Rock, 1603 m; Echo Park, 1553 m; Split Mountain Gorge, riverbank and sandbar, 1439 m) are characterized by wide channels and reaches of calm water bounded by steep sandstone cliffs. Isolated stands of boxelder (*Acer negundo*) and cottonwood (*Populus fremontii*) line the riverbanks along with thickets of tamarisk (*Tamarix* sp.).

Orchid Draw (1484 m) and Red Wash (1537 m) are dry desert washes characterized by rabbitbrush (*Chrysothamnus nauseosus*), sagebrush (*Seriphidium tridentata*), greasewood (*Sarcobatus vermiculatus*), and shadscale (*Atriplex confertifolia*), with tamarisk dominating drainage bottoms.

Echo Park Meadow (1548 m) and Pool Creek (1635 m) are both open meadows with dominant ground cover of cheatgrass (*Antisantha tectorum*), various bunchgrasses, and isolated clumps of boxelder. Echo Park Meadow encompasses an area of ca 18 ha, bounded by the Green River to the west and high (150–230 m) sandstone cliffs on remaining sides. The meadow at Pool Creek (ca 8 ha) is situated at the mouth of a narrow canyon; boxelder and cottonwood form a dense, continuous canopy over much of the adjacent creek.

Remaining locations consist of a moist meadow (Hog Canyon, 1635 m), open sagebrush shrublands (Rainbow Park, 1488 m; Island Park, 1512 m), and a narrow canyon with thick riparian vegetation (Jones Hole, 1585 m).

**Sampling Methods**

At all locations I remained at a single site during each night of sampling. By pacing from a boxelder, which served as a focal point of bat foraging activity in Echo Park Meadow, I estimated that calls of *E. maculatum* were detectable at a distance of roughly 100 m. Therefore, the area sampled at each site is here defined as the air space within a hemisphere of radius 100 m. On several nights periods of high wind and/or rain reduced this range of detectability, with an attendant underestimation of bat activity. Furthermore, sites differed slightly in levels of background noise from nearby streams, the amount of obstructive vegetation, and various atmospheric conditions such as relative humidity, all of which affect the propagation of sound (Lawrence and Simmons 1982).

Study sites were situated either at the mouths of canyons or draws in the middle of open areas where movement patterns of bats could best be assessed and the range of detectability was maximized. In locations characterized by expansive terrain (open meadows or shrublands), I monitored two different sites separated by >300 m on consecutive nights to assess uniformity of activity levels over large areas. All sites were monitored from 2000 to 0200 h with the exception of Echo Park Meadow, which was monitored from 2000 to 0400 h for seven consecutive nights (19–26 May) to assess temporal patterns of foraging activity.

At locations where I observed high levels of foraging activity (e.g., Echo Park Meadow and Pool Creek), bat activity was quantified by timing the duration of individual foraging sessions and recording the number of feeding buzzes (the increased rate of echolocation pulse repetition associated with attacks on airborne prey; Griffin et al. 1960). Following Leonard and Fenton (1983), the occurrence of feeding buzzes indicates foraging activity, and a foraging session is defined as the time during which a single spotted bat hunted continuously within the study site. To permit comparison
of relative levels of activity throughout the night, the time spent by spotted bats in the study site was totaled for every 15-min period sampled. Sampling periods during which heavy rain occurred were not considered.

To assess spatial patterns of habitat use, I described the foraging flights of spotted bats into a minicassette recorder and noted flight patterns and use of available foraging space relative to a near-canopy habitat zone (within 8 m of tree canopies) and an open-area zone (the clutter-free air space over the open meadow). These habitats correspond to habitat zones 1 and 4, respectively, proposed by Aldridge and Rautenbach (1987). I recorded the duration of foraging activity occurring within each zone as well as the number of bats simultaneously present within the study site and interactions between them.

I recorded the number of feeding buzzes heard during each foraging session for each night of observation at Echo Park Meadow and Pool Creek for the purpose of calculating attack rates (feeding buzzes/min) of foraging spotted bats. I considered only those foraging sessions of duration >3 min during which all feeding buzzes produced by a single individual within the study site could be counted accurately.

At other locations where I observed only transient occurrences of foraging or commuting spotted bats, activity was quantified by recording the number of bat passes (sensu Fenton 1970) per 15-min sampling period.

RESULTS AND DISCUSSION

I observed spotted bats in 13 of 15 sites sampled (Table 1). At 8 of these locations I observed only commuting bats. Passes of commuting spotted bats occurred sporadically throughout the night. At locations where two separate sites were monitored on consecutive nights, the number of passes remained fairly constant (passes/night: Echo Park, 5, 4; Hog Canyon, 5, 6; Island Park, 6, 10), and directions of travel appeared similar for bats on both nights.

Availability of cliff roosting sites has been suggested as a limiting factor in the distribu-
tion of *E. maculatum* (Easterla 1973). The abundance of high cliffs in Dinosaur National Monument as well as transient occurrences of commuting bats throughout a variety of widely separated low-elevation sites (Navo et al. 1992, this study) suggests that suitable roosting habitat is widespread throughout the area. However, information about microclimate requirements of this species is needed to fully assess actual availability of suitable roost sites.

I observed foraging spotted bats by sight and sound at five locations, three of which (Echo Park, Orchid Draw, Red Wash) involved only transient occurrences of bats that were observed executing steep dives and other abrupt flight maneuvers coincident with feeding buzzes as they passed through the area. I observed a single spotted bat foraging over a sand-and-gravel bar at Echo Park, but activity levels at this location were lower than those reported by Navo et al. (1992), who sampled this same site previously. Fairly high levels of activity occurred at Orchid Draw and Red Wash (Table 1), and I heard three feeding buzzes at each site. However, because spotted bats apparently capture prey opportunistically while commuting to specific foraging sites (Wai-Ping and Fenton 1989), observations of foraging bats passing through an area cannot be considered indicative of habitat preferences.

At Echo Park Meadow, spotted bats first arrived at the study site at 2123 h ± 11 min Mountain Daylight Time (n = 6 rain-free evenings), always after dark, and remained active throughout the night (Fig. 2). Spotted bats foraged within the study site for 6.22 ± 2.40 min out of every 15-min sampling period between 2100 and 0400 h (n = 2490 min; Fig. 2), and foraging sessions lasted 5.48 ± 2.74 min (n = 187). At Pool Creek, spotted bats hunted within the study site for 6.82 ± 5.03 min out of every 15-min sampling period between 2100 and 0200 h (n = 525 min), and foraging sessions lasted 8.97 ± 8.78 min (n = 30). These activity levels offer strong evidence that open meadows represent important foraging habitat for *E. maculatum* in this area.

Comparatively low levels of activity were recorded at riparian sites adjacent to Echo Park Meadow (Echo Park, Jenny Lind Rock). Because no physiographic barriers are present that might restrict accessibility to the bats, it appears that open water courses do not represent foraging areas of choice. These observations agree with those of Leonard and Fenton (1983), who reported that in British Columbia spotted bats foraged in forest clearings and open fields to the exclusion of a nearby river.

The temporal pattern of foraging activity in Dinosaur National Monument is similar to that reported from British Columbia (Leonard and Fenton 1983), where spotted bats were active throughout the night. Because radiotracking (Wai-Ping and Fenton 1989) has demonstrated that individual spotted bats hunt on the wing >300 min per night, reports of apparent peaks in nightly activity (which have been especially pronounced in mistnetting studies, e.g., Easterla 1973) are likely artifacts related to the proximity of sampling sites to diurnal roosts and/or drinking sites.

At Echo Park Meadow and Pool Creek, foraging spotted bats typically flew in large circular or elliptical orbits at heights of 10–30 m above the ground. In 1088.8 min of observation of foraging spotted bats at Echo Park
Meadow, 81.5% of activity occurred over the open meadow, which constituted roughly 85% of the site, while 18.5% of activity occurred within 8 m of the foliage of fully leafed boxelders at mid- to upper-canopy level. Such activity consisted of bats circling closely above and around individual trees or isolated clumps of trees. I rarely observed bats within 0.5 m of the canopy, and I never observed hovering flight or other evidence of foliage gleaning. In 290.8 min of observation of foraging spotted bats at Pool Creek, all activity occurred over the open meadow, although a much larger percentage of the study site area comprised canopies of boxelder and cottonwood than at Echo Park Meadow.

The predilection of E. maculatum for foraging over open terrain in Dinosaur National Monument agrees with the pattern observed in previous studies (e.g., Woodworth et al. 1981, Leonard and Fenton 1983). Low-frequency echolocation calls and long intercall intervals suggest that spotted bats use a foraging strategy based on long-range prey detection and high-level flight (Simmons and Stein 1980, Woodworth et al. 1981, Barclay 1986). This strategy likely is best suited to open areas (Neuweiler 1984). Although I never directly observed these bats gleaning prey from foliage during this study, observations of near-canopy foraging contrast with those of other workers (e.g., Wai-Ping and Fenton 1989) who have reported that this species never attacked insects near foliage or any other type of surface. Information about individual variability in foraging behavior is needed before drawing conclusions about variability between populations related to different ecological conditions.

At both Echo Park Meadow and Pool Creek, there were 118 instances in which two or three E. maculatum were present within the study site simultaneously. Leonard and Fenton (1983, 1984) estimated that spotted bats in British Columbia maintain a distance of at least 50 m between adjoining foraging areas and suggested that this spacing is accomplished through a combination of mutual avoidance and active monitoring of encroachments by conspecifics. This same system appears to be operating at foraging areas in Dinosaur National Monument. Consistent with observations of Leonard and Fenton (1983), foraging spotted bats often produced agonistic vocalizations when the 50-m buffer zone was breached by an intruding bat. Such vocalizations sounded qualitatively different from feeding buzzes and occurred only during close-range encounters between conspecifics. Information about known individuals and resource availability is needed to elucidate the role of agonistic interactions in the foraging ecology of E. maculatum.

During this study I heard a total of 247 feeding buzzes, and never more than one per min from the same individual. In a sample of 37 foraging sessions, spotted bats attacked an insect every 2.15 min on average (0.466 ± 0.294 attacks/min, range 0.16–0.94; n = 152 feeding buzzes). These rates generally agree with values reported in previous studies (Leonard and Fenton 1983, Wai-Ping and Fenton 1989), further confirmation that this species attacks prey at a rate much lower than is typical of bats that forage from continuous flight (Barclay 1985, Hickey and Fenton 1990).

Density of clutter in an environment imposes differential constraints on the maneuverability and perceptual capacities of bats, thereby determining the accessibility of different habitats by influencing foraging efficiency (Neuweiler 1984, Aldridge and Rautenbach 1987, Fenton 1990). Spotted bats appear to forage preferentially in open areas, which may be
related to the use of a long-range foraging strategy (Barclay 1986), and the ability to exploit edge situations may reflect a measure of behavioral flexibility in this regard. Because spotted bats are obviously not greatly restricted in foraging habitat with regard to vegetation associations (Wai-Ping and Fenton 1989, Navo et al. 1992), structural features of the environment related to density of clutter may be more predictive of habitat suitability and the use of available foraging space. However, information on individual variability is needed before drawing conclusions about the foraging strategy of this species.

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LITERATURE CITED


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THE CHRYSOOTHAMNUS-ERICAMERIA CONNECTION (ASTERACEAE)

Loran C. Anderson

ABSTRACT.—The genus Chrysothamnus (Asteraceae) contains 16 species. Recently, 4 species were transferred to Ericameria, and the remaining 12 were left in Chrysothamnus. The remaining species are now transferred to Ericameria as E. albida, E. depressa, E. eremobia, E. graminea, E. filifolia (formerly C. greenii), E. humilis, E. linifolia, E. molesta, E. pulchella, E. pulchelloides (a fossil species), E. spatulata, E. caseyi, and E. viscidiflora. Section alignments are given, and some infraspecific combinations are also made.

Key words: Chrysothamnus, Ericameria, rabbitbrush, nomenclature transfers.

The Asteraceae are a relatively young group, and yet they have experienced rapid evolution into a great number of species. One result is that many taxa appear more distant morphologically (phenotypically) than they actually are genetically, and, conversely, some taxa may appear more closely related than they are. These situations have created havoc amongst taxonomists in their attempts to circumscribe genera. This is particularly evident in the tribe Astereae. In 1894, E. L. Greene stated:

In North America the Astereae are excessively numerous, and no natural assemblage of plants has seemed to present such difficulties to the systematist; and the widest conceivable diversities of opinion as to the limits of genera have found expression among botanists when undertaking to classify them.

The situation continues a century later.

The genus Haplopappus was thought to be an unnatural, polyphyletic assemblage by many (e.g., Shinners 1950, Anderson 1966, Johnston 1970, Turner and Sanderson 1971, Clark 1977, Urbatsch 1978). Nevertheless, because there was no suitable taxonomic reorganization of the group, I continued to describe new taxa in Haplopappus (Anderson 1980a, 1983b), even though the species would probably be placed in some other genera at a later date. Recently, additional data have contributed to a clearer understanding of the relationships in this and related groups (Morgan and Simpson 1992), and several genera have been recognized for North American Haplopappi.

In a 1976 presentation at national meetings, I discussed the close affinity of Chrysothamnus with woody elements of Haplopappus and suggested that the Asiris-Ericameria-Macronema complex of Haplopappus probably should be included in Chrysothamnus. But, given the state of knowledge at that time, I deferred. In 1990, Nesom reorganized Ericameria as a genus to include Asiris and Macronema. Recently, based on occurrences of intergeneric hybrids (Anderson and Reveal 1966, Anderson 1970) and DNA data (Morgan and Simpson 1992), Nesom and Baird (1993) transferred four species of Chrysothamnus into Ericameria (C. nauseosus and C. parryi of section Nauseosus and C. paniculatus and C. teretifolius of section Punctati). They continued to recognize Chrysothamnus as a distinct (but smaller) genus and gave arguments for separating the two.

A problem in separating Ericameria and Chrysothamnus (sensu Nesom and Baird) is the occurrence of hybrids (Anderson 1970, 1973) between C. nauseosus (their Ericameria) and C. albida (their Chrysothamnus). After studying a specimen of only one of the three collections involved, Nesom and Baird (1993) devalued the connection by stating that "the plant in question [is] characteristic of C. nauseosus, and we identify it as C. nauseosus, finding no strong reason to implicate C. albida in its parentage." They stated that achenes of C. albida are linear and consistently producing 10 slightly raised nerves, whereas those of C. nauseosus are narrowly obovate with 5–7 nerves. Actually, achenes of both species can be characterized as being narrowly cylindrical. The number of vascular bundles (associated with the nerves) in the achenes averages approximately 7 and

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ranges from 5 to 10 (but mostly 6–8 in Ash Meadows) for *C. albidus* (Anderson 1970, 1973), whereas achene bundle number in *C. nauseosus* ranges from 5 to 12 (but is restricted to 5 for those in Ash Meadows).

The interspecific hybrid examined by Nesom and Baird (Beatley 11894, KSC) was studied anatomically by Anderson (1973); its hybridity is indicated by low pollen fertility and by morphological intermediacy between the two species in its revolute leaves, in vascular bundle number in the ovary wall, in corolla lobe length, and in anther appendage length. It has secreteory canals in the ovary wall and glandular trichomes on the corolla tube (like *C. nauseosus*, unlike *C. albidus*) and ovary wall (unlike *C. nauseosus*, like *C. albidus*). Further, progeny from one of my *C. albidus* garden plants also has low pollen fertility and looks intermediate between its seed parent and *C. nauseosus* (Anderson 1970). Its flowers have secreteory canals in the ovary wall and glandular trichomes on the corolla tube but lack glandular trichomes on the ovary wall; those three features are characteristic of *C. nauseosus* but not of *C. albidus* (the seed parent), clearly suggesting hybridity. If existence of interspecific hybrids is used to justify transferring *C. nauseosus* to *Ericameria*, then this feature also argues for bringing the remainder of *Chrysothamnus* into *Ericameria*.

The warranted position of *Chrysothamnus teretifolius* in *Ericameria* is taken by Nesom and Baird (1993: 80) because, like many *Ericameria* species (sensu strictum), that species has the tendency for the “resiniferous ducts that are almost always distinctly associated with the phyllary midvein to expand near the apex of the phyllary.” This characteristic also occurs in many species of *Chrysothamnus* (sensu Nesom and Baird) as illustrated for *C. vaseyi* (Anderson 1963: 660) and cannot be used to distinguish the two groups. I have observed adjacent populations of *C. viscidiflorus* subsp. *puberulus* in which plants of one had prominently enlarged resin ducts at the phyllyary tips and plants of the other did not.

With the transferral of four species from *Chrysothamnus* to *Ericameria*, Nesom and Baird (1993) separate the two newly structured genera with six criteria. (1) Leaves 3-nerved for *Chrysothamnus* and 1-nerved for *Ericameria*—but many of their *Ericameria* have prominently 3-nerved leaves. Hall and Clements (1923) used nerve number to distinguish *C. nauseosus* ssp. *graveolens* from ssp. *consimilis* (so the character is variable even within a species). Many of the latter group, such as *C. albidus*, *C. greenei*, and some forms of *C. viscidiflorus*, appear to have 1-nerved leaves. Actually, all species of *Ericameria* and *Chrysothamnus* have trilacunar, 3-trace nodal anatomy (personal observation); thus, the character of 1 versus 3 nerves is a matter of perception, not of fact. (2) Leaf margins ciliate in the former and never in the latter—but *C. albidus*, *C. eremobius*, and *C. viscidiflorus* subsp. *planifolius* of the former have entire leaf margins; also in that group, *C. pulchellus* subsp. *pulchellus* has entire leaf margins, whereas subsp. *baileyi* has ciliate leaf margins, and some populations of *C. gramineus* and *C. vaseyi* have entire leaf margins, but others do not. *Ericameria* (sensu Nesom 1990) has several species that have leaves with ciliate leaf margins, fairly prominent in *E. cooperi* and less so in several other species (e.g., *E. cerinum*, *E. nana*, *E. phhitidis*, and *E. zionis*). (3) Corollas more or less abruptly broadened from the tube into the throat with long, recurving or coiling lobes in the former and corollas tubular with short, erect or spreading lobes in the latter—but corollas of *C. spathulatus* (of the latter) have relatively broad tubes that lack noticeably flaring throats, *C. humulis* (of the former) has tubular corollas with short, erect lobes (Anderson 1964: 226), and *C. nauseosus* ssp. *ceruminosus* (of the latter) has corollas that are abruptly broadened from the tube into the throat with long, spreading lobes. (4) Style appendage collecting hairs merely papillate in the former, whereas they are long and sweeping in the latter—but *C. albidus*, *C. molestus*, *C. pulchellus*, and certain populations of *C. viscidiflorus* (all of the former) have style appendages with moderately long, sweeping hairs. Diversity in collecting hairs is greater in *Chrysothamnus* (sensu Anderson 1986) than Nesom and Baird (1993) imply and does not fall into two groups. Collecting hair length may be correlated with other floral features; namely, the corollas, style lengths, and pollen volumes of the former group (Anderson 1966) are generally smaller than those of the latter. (5) Involutar bracts in vertical files in the former (caveat noted) and usually not in vertical files in the latter—but, perhaps the most strongly aligned bracts occur in *C. nauseosus*
ssp. arenarius (of the latter). (6) Achenes glandular with nonresinous nerves in the former and eglandular (with duplex hairs) and resinous nerves in the latter—but only five species of the former have glandular achenes (in some they are hidden by duplex hairs) and the other seven do not, having either glabrous achenes or achenes with duplex hairs exclusively (Anderson 1970, 1983a), and many have resin canals associated with the bundles of the achenes, admittedly fewer than in those of the latter but well developed in C. molestus of the former. Also, C. paniculatus (of the latter grouping) lacks resin canals in its achenes (Anderson 1970). None of these six sets of characteristics can be used to consistently separate the two groups.

Clearly, Chrysothamnus (sensu Anderson 1986, not Nesom and Baird 1993) is fairly homogeneous and should not be dismembered. If some are to go into Ericameria (and DNA data suggest they should), then all should go into Ericameria. Therefore, the remaining 12 species of Chrysothamnus are transferred to Ericameria, and new combinations are made here.


9c. Ericameria pulchella subsp. pulchella var. eliator (Standl.) L. C. Anders., comb. nov. Basionym: Chrysothamnus eliator Standl., Proc. Biol. Soc. Wash. 26: 118. 1913. This variety with uniformly pubescent leaves occurs sporadically in a few populations of the typically glabrous-leaved subspecies pulchella and does not warrant a higher taxonomic status than this quadrinomial affords.


12b. Ericameria viscisiflora subsp. viscisiflora var. latifolia (D. C. Eaton) L. C. Anders., comb. nov. Basionym: Linosyris viscisiflora var. latifolia

12c. Eriocameria viscidaflora subsp. viscidaflora var. stenophylla (A. Gray) L. C. Anders., comb. nov. Basionym: Bigelowia douglasi var. stenophylla A. Gray, Proc. Amer. Acad. Arts 8: 646. 1873. Chrysothamnus stenophyllus (A. Gray) E. Greene, Erythea 3: 94. 1895. These quadriniums (12b and 12c) identify sporadic but rather distinctive morphotypes that occur in the northern regions of this subspecies (for distinct distinction between subspecies and variety, see Anderson 1980b).


Nesom and Baird (1993) suggest the Chrysothamnus taxa that I have just transferred to Eriocameria should be placed in a restructured genus to include elements of Hesperodoria, Petradoria, and Vanclevea. They conclude that chloroplast DNA data (Suh 1989) show Petradoria to be integrally related to the Solidago lineage and far removed from Eriocameria. However, they note that neither Suh (1989) nor Morgan and Simpson (1992) sampled any taxa of Chrysothamnus sensu Nesom and Baird. These taxa need DNA profiles determined because they certainly do not make a morphologically compatible grouping with Petradoria or Vanclevea. For example, Petradoria (Anderson 1963) has radiate heads with disk flowers that lack stigmatic areas on the style branches and have abortive ovaries, and Vanclevea (Anderson and Weberg 1974) has large turbinate heads with many phyllaries, many flowers, and a tardily deciduous pappus of paleaceous awns—none of these conditions are found in Chrysothamnus sensu Nesom and Baird. The cohesiveness of Chrysothamnus sensu Anderson is further illustrated in that C. spathulata twigs emit odor similar to that of C. nauseosus (Anderson 1964: 227).

Two alternate taxonomies are now available: one for Chrysothamnus as a genus (Anderson 1986) or as a component of Eriocameria (Nesom and Baird 1993, and here); both are preferable to merging some elements of Chrysothamnus with Petradoria or Vanclevea.

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The literature contains little information regarding mating chases and copulation in any of the western chipmunks (Tamias, subgenus Neotamias). Callahan (1981) reported mating chases for Merriam's (T. merriami) and dusky chipmunks (T. obscurus), but noted (unpublished) that both copulating pairs were partly concealed by foliage. Larson (1981) described two copulations for Merriam's chipmunk, but a careful reading suggests that one of these was a mounting attempt by an immature male and the other was observed from a considerable distance. Best and Granai (1994) found no references on this subject other than Callahan (1981) and Larson (1981).

There has been some speculation and difference of opinion regarding reproductive isolating mechanisms in parapatric species of western chipmunks. Blankenship and Brand (1987) reported differences in vocal behavior between Tamias merriami and T. obscurus at Black Mountain (Riverside County, CA) and noted a possible role in reproductive isolation. One of us (JRC), however, had previously conducted a more extensive study of vocal behavior in these two cryptic species at Black Mountain from 1975 to 1980. Vocalizing individuals were collected to confirm species identity, and sonograms were prepared and measured; yet no statistically significant vocal differences were found (Callahan 1981, and in preparation). Ecological, olfactory, and mechanical barriers to hybridization also have been suggested (Callahan 1977, 1981, Patterson 1984). These hypotheses cannot be tested without more data on chipmunk reproductive behavior. Accordingly, this note provides the first detailed description of western chipmunk copulation that has been published, to the best of our knowledge. Comparative data for other western chipmunk species would be of interest.

The observation was made 1 April 1994 in a wooded residential area in Idyllwild, Riverside County, CA (elevation 1590 m), between 1000 and 1130 h. The habitat is mixed-conifer forest dominated by incense cedar (Calocedrus decurrens), yellow pine (Pinus ponderosa), live oak (Quercus chrysolepis), and black oak (Q. kelloggii), with a sparse understory of chaparral shrubs. When the observer arrived at 1000 h, six to seven Merriam's chipmunks, many of them males, were running over, around, and through a large woodpile while performing conspicuous leaping maneuvers. No agonistic interaction was observed. It was not possible at this stage to identify the female(s) or to tell in which direction the "chase" was headed. The overall effect was somewhere between a Sciurus-like mating chase (e.g., Thompson 1977), in which several males follow one female, and a lek, involving male display. The chase covered an area 13–15 m in diameter but centered on the woodpile and a nearby heap of smaller pine branches.

After about 20 min, one chipmunk (later identified as female) ran up on one of the piled branches. A second chipmunk approached and they ran around for a few seconds. The female stopped on a branch and the other chipmunk, a male, ran up beside her. Her entire right side was in contact with her left side for about 1 sec, during which he made a nuzzling motion with the right side of his face on the rear left portion of her face. The expected nasal/genital contact was not observed, but the pair had been out of sight for a short time previously and this could have occurred. The female then jumped to another branch, which was 5 cm in diameter and 20 cm above the ground, sloping at a 25° angle so that the female was facing downhill. Copulation then occurred only 2 m from the observer (who was inside a parked vehicle).

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The female crouched on the branch as if resting. The male jumped to that branch and quickly grasped the female from the rear with his forelimbs around her pectoral region. The female's tail was deflected to the side and slightly raised, and the male's tail was extended to the rear. Copulation consisted of four series of pelvic thrusts. Each series (except the last) lasted about 4 sec and comprised an estimated 12–24 thrusts, at a rate of 3–6 per sec. Each series of rapid thrusts was followed by a short resting period, during which the male stopped thrusting and brushed his face (mouth, nose, and chin) from side to side 2–4 times against the back of the female's neck. The fourth and last series of thrusts was shorter than the first three. The male then released his grip on the female, dismounted, and ran off into the woodpile. The female, who had remained motionless during the act, remained on the branch about 1 sec and then also ran to the woodpile. The entire copulation lasted about 18 sec.

Although several male chipmunks participated in the chase, none of them approached the copulating pair. No chipmunks were heard vocalizing during the mating chase or copulation. We did not note any pre-mating vocal display or Lockrufe by the estrous female (Callahan 1981), but we were not present on the days when the display (if any) would have taken place. The Tamias vocal display has been reported for a few species of chipmunks by Callahan (1981), Blake (1992), and others. It is not clear whether this vocal display is universal or occurs only at low population densities, when the female benefits by attracting more distant males.

No further copulations were seen, but as many as seven male chipmunks continued to run around the same woodpile for another hour. The level of activity appeared to decrease, and there were none of the prodigious leaps seen earlier. The group then gradually dispersed as individuals headed for an adjacent area where other chipmunks were heard giving occasional “chipper” vocalizations (not the long series of chips that characterizes the Lockrufe).

The behavior described above suggests that scent glands play a key role in reproductive behavior of this species. Larson (1981) and others have noted that male chipmunks have scent glands near the chin and angle of the jaw (oral glands) that become enlarged during the breeding season. Scent marking is prevalent in sciurids, but usually this means marking the ground or a branch, not marking another animal. The “nuzzling” and “brushing” behavior of the male Merriam's chipmunk, before and during copulation, suggests that he was scent marking the female.

Conspecific marking has been described for various mammals, such as rabbits (Mykytowycz 1965), but not for sciurids. Gurnell (1987) describes “face-wiping” behavior by various tree squirrels, but only in the context of substrate marking and (in Paraxerus) self-grooming; his description of copulation in Sciurus and Tamiasciurus says nothing about the male marking the female. With reference to olfactory communication in ground squirrels, Halpin (1984) wrote that “there is no experimental evidence that conspecific marking ... actually occur[s] among the sciurids.”

Our observation indicates that conspecific marking does occur in Merriam's chipmunk as a component of reproductive behavior. Without experimental data, it is not possible to determine the significance of this marking. Pair bonding comes to mind, but there is no good evidence of long-term pair bonding in Merriam's or any other species of western chipmunk, despite many years of field observation. Other possibilities include the following: (1) the marking induces some required physiological state in the female; (2) the marking tells other males that the female has already mated (before the copulation plug forms and the message becomes redundant); or (3) the marking reinforces a short-term pair bond to ensure that subsequent copulations (if any) on the day of estrus will be with the same male. Larson (1981) indicated that the same estrous female sometimes copulates more than once.

Mortality from all causes is higher for male than for female chipmunks (Smith 1978), perhaps due in part to the dispersal and exposure associated with the breeding season (Callahan 1981). After incurring the risk of predation and expending considerable energy on the mating chase, it should be to the male's advantage to ensure that his genes are passed to all the female's offspring of the season.

**Literature Cited**


Mammalian Species 476: 1-9.


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ADDITIONAL RECORDS OF FLEAS (SIPHONAPTERA) FROM UTAH

James R. Kucera

Key words: Siphonaptera, fleas, Utah, Megabothris asio megacolpus, Euhoplospyllus glacialis lyxu.

Subsequent to the important work of Stark (1959), few publications have given flea collection records from Utah. These include Jellison and Senger (1976) and Kucera and Haas (1992); but most effort in this area has been that of Egoscube (1966, 1976, 1977, 1988, 1989).

Herein is presented information for 10 species of Siphonaptera for Utah. A number of important records were obtained from the flea collection at the Monte L. Bean (MLB) Life Science Museum, Brigham Young University, Provo, UT. Catalog numbers of host specimens deposited in the University of Utah Museum of Natural History (UU) mammal collection and flea specimens in the MLB Museum (BYU) insect collection are given in parentheses when available. Unless indicated otherwise, specimens were collected by me and are retained in my personal collection.

Carteret a clacata Good 1942


Few collections of this species are known from Utah (Tooele County: Stark 1959 [1♂], Egoscube 1976 [1 specimen, sex unknown]; Washington County: Jellison and Senger 1976 [2♂, 2♀♀]). It has also been collected in Clark County, NV (the type locality, Good 1942), and Mohave County, AZ (Augustson and Durham 1961). It is likely a nest flea of C. formosus.

Nearctopsylla brooksi (Rothschild 1904)


This species was previously known in Utah from a single collection in Sevier County (Stark 1959). It is usually found on weasels (Mustela spp.).

Nearctopsylla hyptaci (Rothschild 1904)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman campground, 2560 m (spruce-fir), 21 October 1990, 1♀ ex Sorex monticolus (UU #29163). Same locality, 28 October 1990, 1♀ ex Sorex monticolus (UU #29164).

Stark (1959) reported this species from Cache County. My collections extend the known range of this species further south in Utah along the Wasatch Cordillera. It is found on shrews (Sorex spp.) and Mustela spp.

Delotelis telegoni (Rothschild 1905)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman campground, 2560 m (spruce-fir), 21 October 1990, 1♂ ex Clethrionomys gapperi. Same date & locality, 1♀ ex Tamiasciurus hudsonicus nest. [The nest, about 3 m above ground level, also contained many red squirrel fleas (Orchopeas c. caedens). The squirrel probably carried this vole flea to its nest.] Same locality, 15 September 1991, 1♀ ex Peromyscus maniculatus. Same locality, 5 October 1991, 1♂ ex Clethrionomys gapperi.

1Associated Regional and University Pathologists, Inc., Salt Lake City, UT 84108. Address for correspondence: 3630 S. Sunset Circle, Murray, UT 84107-6630.
**Delotelis telegroni** has rarely been found in Utah; single specimens have been collected in Sanpete County (Stark 1959) and in Utah County (Egoscue 1988). It is significant that these collections were made in summer months (August 1951 and July 1985, respectively). Many more collections will likely be made if this species is searched for during the cooler months of the year. Also, it presumably would be profitable to search nests of Microtus and Clethrionomys for this species.

**Meringis shannoni** (Jordan 1929)

Eads et al. (1987) listed two collections of this species from Utah. The specimens are present in the BYU collection. However, the records are erroneous because the collection locality (Douglas County) does not exist in Utah. All other cited records of this species are from the states of Washington and Oregon, except a lone locality record in Humboldt County, NV (Lewis et al. 1988).

**Stenistomera hubbardi**

Egoscue 1968

This rare species was listed by Tipton and Saunders (1971) as occurring in Utah although no specific records were cited. Egoscue (personal communication) knows of no records from Utah, and no specimens were present in the MLB Life Science Museum, the main repository of Tipton's Utah collections. In addition to the type specimens from Oregon (Egoscue 1968), the only other published record of *S. hubbardi* is that of Lewis et al. (1988), also from Oregon. It is unlikely that the species has been collected in Utah.

**Megarthroglossus becki**

Tipton & Alred 1951

Salt Lake Co.: Wasatch Mts., mouth of Little Cottonwood Canyon, 1766 m (scrub oak), 3 December 1989; 1♂, 1♀ ex Neotoma cinerea nest.

The species has been collected only in Utah (Kane, Piute, Utah, and Wayne counties; Tipton et al. 1979) and Arizona (Augustson and Durham 1961). This is the northermost record known, some 37 km north of the type locality in the Wasatch Mountains. *Megarthroglossus becki* is a nest flea of woodrats, principally the bushy-tailed woodrat *Neotoma cinerea*.

**Megabothris asio megacolopus** (Jordan 1929)


The range of this boreal vole extends deep into south central Utah. Only two specimens are from Idaho, including one from Bear Lake County adjacent to Rich County (Baird and Saunders 1992). Collections from Ravalli and Beaverhead counties, MT, are documented (Holland 1950), and specimens from Ravalli County are present in the Natural History Museum, London (T. M. Howard personal communication). A point-mapped record roughly on the Utah-Wyoming border given in Haddow et al. (1983) is evidently meant to be Laketown because four specimens with the same collection data as the 22 August 1952 series are present in the Natural History Museum, London (Howard personal communication).

**Chaetopsylla stewarti** Johnson 1955


These specimens are the only ones known, other than the type series (from Cache County, Lewis and Lewis 1994). Weasels seem to be the preferred host.

**Euhoplopsyllus glacialis lynx** (Baker 1904)

Salt Lake Co.: Wasatch Mts., Big Cottonwood Canyon, vic. Redman Campground, 2550 m, 17 August 1988; 3♀♀, 1♂ ex Lepus americanus (UU #28674). Big Cottonwood Canyon, 2280 m, 30 August 1988, 1♀ ex Lepus americanus. Big Cottonwood Canyon, vic. Butler
Fork trailhead, 2182 m, 19 May 1991, 2♂♂ ex Lepus americanus.

Previously unknown in Utah, the nearest published records are for Ravalli County, MT (Kohls 1940), more than 570 km to the north. The type locality is Moscow, ID, about 790 km to the northwest (Baker 1904). This flea is consistently found on the snowshoe hare (Lepus americanus) and its predator, the lynx (Lynx canadensis). The form E. glacialis affinis is common in Utah and surrounding states on rabbits and jackrabbits (Sylvilagus spp. and Lepus spp. other than L. americanus). Questionable records of E. g. lynx from the states of Tamaulipas and Veracruz, Mexico (ex Sylvilagus floridanus and unidentified Sylvilagus sp.), are listed by Ayala et al. (1988).

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LITERATURE CITED


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CONTENTS

Articles

Life histories of stoneflies (Plecoptera) in the Rio Conejos of southern Colorado ........................................ R. Edward DeWalt and Kenneth W. Stewart 1

Pollinator sharing by three sympatric milkvetches, including the endangered species Astragalus montii ............. S. M. Geer, V. J. Tepedino, T. L. Griswold, and W. R. Bowlin 19

Factors affecting selection of winter food and roosting resources by porcupines in Utah ....................... Dave Stricklan, Jerran T. Flinders, and Rex G. Cates 29

Historic expansion of Juniperus occidentalis (western juniper) in southeastern Oregon .................................. Richard F. Miller and Jeffery A. Rose 37

Rangeland alpha diversities: Harvey Valley, Lassen National Forest, California ........................................ Raymond D. Ratliff 46

Effects of salinity on establishment of Populus fremontii (cottonwood) and Tamarix ramosissima (saltcedar) in southwestern United States ......................... Patrick B. Shafroth, Jonathan M. Friedman, and Lee S. Ischinger 58

Names and types of Hedysarum L. (Fabaceae) in North America ............................................................. Stanley L. Welsh 66

Whipworm (Trichuris dipodomys) infection in kangaroo rats (Dipodomys spp.): effects on digestive efficiency .......... James C. Munger and Todd A. Slichter 74

Local distribution and foraging behavior of the spotted bat (Euderma maculatum) in northwestern Colorado and adjacent Utah ................................. Jay F. Storz 78

The Chrysothamnus-Ericameria connection (Asteraceae) ..... Loran C. Anderson 84

Notes

Reproductive behavior in Merriam's chipmunk (Tamias merriami) .......................................................... Stephen B. Compton and J. R. Callahan 89

Additional records of fleas (Siphonaptera) from Utah ........... James R. Kucera 92