



12-31-1990

## Full Issue, Vol. 50 No. 4

Follow this and additional works at: <https://scholarsarchive.byu.edu/gbn>

---

### Recommended Citation

(1990) "Full Issue, Vol. 50 No. 4," *Great Basin Naturalist*. Vol. 50 : No. 4 , Article 20.

Available at: <https://scholarsarchive.byu.edu/gbn/vol50/iss4/20>

This Full Issue is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Great Basin Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact [scholarsarchive@byu.edu](mailto:scholarsarchive@byu.edu), [ellen\\_amatangelo@byu.edu](mailto:ellen_amatangelo@byu.edu).

---

**T H E**

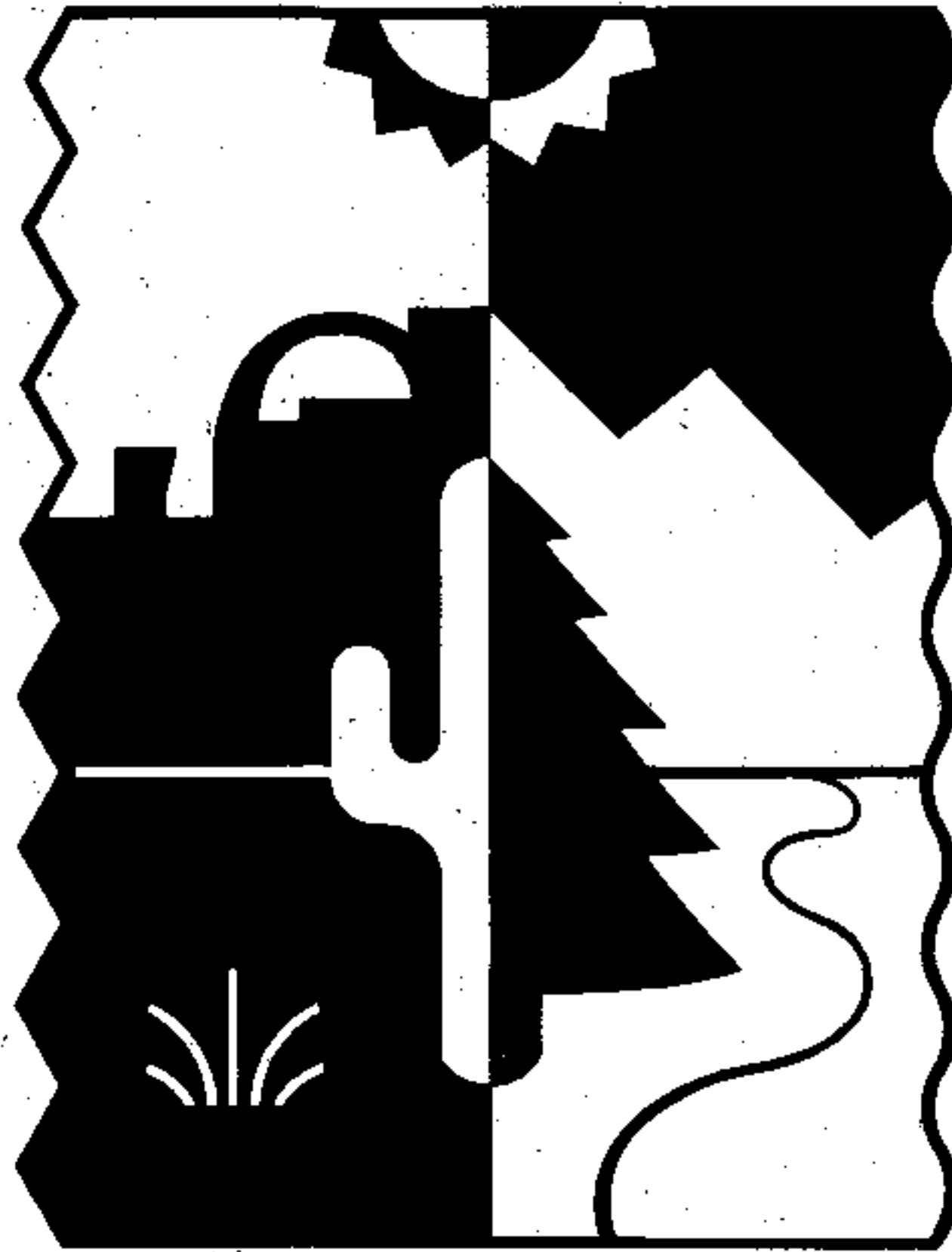
---

**G R E A T B A S I N**

---

**N A T U R A L I S T**

---



---

**VOLUME 50 № 4 — DECEMBER 1990**

---

**BRIGHAM YOUNG UNIVERSITY**

---

# GREAT BASIN NATURALIST

## Editor

JAMES R. BARNES

290 MLBM

Brigham Young University  
Provo, Utah 84602

## Associate Editors

MICHAEL A. BOWERS  
Blandy Experimental Farm  
University of Virginia  
Box 175  
Boyce, Virginia 22620

JEANNE C. CHAMBERS  
USDA Forest Service Research  
860 North 12th East  
Logan, Utah 84322-8000

JEFFREY R. JOHANSEN  
Department of Biology  
John Carroll University  
Cleveland, Ohio 44118

PAUL C. MARSH  
Center for Environmental Studies  
Arizona State University  
Tempe, Arizona 85287

BRIAN A. MAURER  
Department of Zoology  
Brigham Young University  
Provo, Utah 84602

JIMMIE R. PARRISH  
Department of Zoology  
Brigham Young University  
Provo, Utah 84602

**Editorial Board.** Richard W. Baumann, Chairman, Zoology; H. Duane Smith, Zoology; Clayton M. White, Zoology; Jerran T. Flinders, Botany and Range Science; William Hess, Botany and Range Science. All are at Brigham Young University. Ex Officio Editorial Board members include Clayton S. Huber, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications; James R. Barnes, Editor, *Great Basin Naturalist*.

The *Great Basin Naturalist*, founded in 1939, is published quarterly by Brigham Young University. Unpublished manuscripts that further our biological understanding of the Great Basin and surrounding areas in western North America are accepted for publication.

**Subscriptions.** Annual subscriptions to the *Great Basin Naturalist* for 1990 are \$25 for individual subscribers, \$15 for student and emeritus subscriptions, and \$40 for institutions (outside the United States, \$30, \$20, and \$45, respectively). The price of single issues is \$12. All back issues are in print and available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to the Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

**Scholarly Exchanges.** Libraries or other organizations interested in obtaining the *Great Basin Naturalist* through a continuing exchange of scholarly publications should contact the Exchange Librarian, Harold B. Lee Library, Brigham Young University, Provo, UT 84602.

## EDITORIAL PRODUCTION STAFF

JoAnne Abel .....	Technical Editor
Carolyn Backman .....	Assistant to the Editor
Heidi Larsen .....	Production Assistant

# The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY  
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 50

31 DECEMBER 1990

No. 4

Great Basin Naturalist 50(4), 1990, pp. 303–311

## LONGITUDINAL DEVELOPMENT OF MACROINVERTEBRATE COMMUNITIES BELOW OLIGOTROPHIC LAKE OUTLETS

Christopher T. Robinson<sup>1</sup> and G. Wayne Minshall<sup>1</sup>

**ABSTRACT.**—Benthic macroinvertebrates were collected at several sites downstream of three oligotrophic lake outfalls in July 1986. Total numbers, biomass, and species richness increased rapidly immediately downstream from the outlets, and then either stabilized or continued to increase downstream in parallel with benthic organic matter standing crops. Filter feeder densities showed an initial buildup and then decline downstream from the outlets. Variability in longitudinal patterns of other functional feeding groups among lake outlets was related to differences in food quantity and quality, and microhabitat.

An additional set of samples was collected at Pettit Lake outlet in August 1986. Species richness and total density peaked sooner under baseflow conditions in August than under spring runoff conditions in June. Distributions of all functional feeding groups, except filter feeders, also differed between the two periods, reflecting differences in the physical environment. We conclude that reduced lentic inputs of particulate organic matter seston and improved habitat suitability downstream are responsible for the progressive development of macroinvertebrate communities in oligotrophic lake outlets. These data imply the importance of the habitat template in the structuring of benthic communities.

Studies on the macroinvertebrate fauna in the outlet streams of meso- and eutrophic lakes have focused on the fate of lentic plankton or on longitudinal distribution of filter feeders in relation to progressively declining amounts of lake seston (Chandler 1937, Reif 1939, Cushing 1963, Maciolek and Tunzi 1968, Sheldon and Oswood 1977, Statzner 1978, Mackay and Waters 1986, Morin and Peters 1988). No comparable studies have been published for outlet streams of oligotrophic lakes. We hypothesized that streams draining oligotrophic mountain lakes would contain low levels of lake seston and that the invertebrate community would develop gradually as instream and adjacent riparian (allochthonous detritus) food sources developed. As a corollary, we expected that dense benthic filter feeder populations would not develop below the outlet or would dissipate

rapidly as the limited seston resource was rapidly utilized. Our ultimate aim was to use the oligotrophic lake outlet invertebrate community as an analogue to low-head hydroelectric diversions to determine the distance required for recovery to prediversion community conditions under the "worst case scenario" of total elimination of invertebrate drift.

### METHODS

#### Description of Study Sites

Studies were conducted during 8–15 June 1986 on three lake outlet streams located within the Stanley Basin of central Idaho (115°00'W longitude, 44°07'N latitude). Specifically, the streams drained Yellowbelly Lake, Stanley Lake, and Pettit Lake. Both the Yellowbelly Lake outlet stream and the Pettit Lake outlet stream flow into Alturas Lake

<sup>1</sup>Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209.

TABLE 1. Physical measurements characterizing the three lake outlet streams at each transect for the preliminary lake outlet study (June 1986).

TRANS*	DIST (m)	%	W (m)	D (m)	V (cm/s)	SUB (cm <sup>3</sup> )	LRIP (m)	RRIP (m)
Yellowbelly Lake outlet			Temp = 13 C					
1	10	1	10	.70	49	275	7	7
2	20	1	13	.67	58	186	7	7
3	40	1	15	.44	54	77	8	7
4	80	1	12	.49	97	333	8	6
5	160	1	8	.55	87	657	8	13
6	400	1	20	.45	63	50	5	15
Stanley Lake outlet			Temp = 10.2 C					
1	30	1	12	.86	72	109	10	2
2	220	1	10	.50	122	1691	20	15
3	240	1	8	.51	135	337	8	20
4	280	1	15	.59	110	229	5	15
5	360	1	13	.62	96	497	35	8
6	600	1	NA	.54	115	83	25	40
7	1000	1	18	.50	109	167	16	20
Pettit Lake outlet			Temp = 14.8 C					
1	10	1	15	.65	50	8	15	25
2	20	1	15	.51	55	3	15	50
3	40	1	15	.56	77	385	15	10
4	80	1	10	.62	90	299	2	15
5	160	1	15	.46	93	323	15	10
6	400	2	12	.44	137	358	10	12
7	900	2	14	.47	109	281	2	6

\*TRANS = transect, DIST = distance downstream from lake outlet, % = percent gradient, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, LRIP = width of riparian zone on left side of stream, RRIP = width of riparian zone on right side of stream. N = 5 for D, V, and SUB for each transect.

Creek, which flows into the Salmon River. Stanley Lake Creek flows into Valley Creek before entering the Salmon River near the town of Stanley, Idaho. The three outlet streams were chosen because of their relatively pristine conditions and the large size of the lakes. Motor boat usage occurs on Pettit and Stanley lakes during summer. In addition, Pettit Lake has summer homes situated on the east side. Yellowbelly Lake is accessible primarily by foot.

Seven transects were located on each stream at geometrically increasing points downstream from the lake outlet (Table 1), but only six transects were placed at Yellowbelly Lake outlet because of a fish migration barrier located further downstream. The barrier altered the natural geomorphology of the stream by backing up and slowing streamflow for 100 m. Below the barrier the stream gradient greatly increased, thus again interfering with placement of transect 7. A fish migration barrier was located at Stanley Lake about 200 m downstream of the lake outlet. This barrier backed up streamflow to within 70 m

of the lake. Here, transect 1 was placed 30 m downstream from the outlet and the remaining transects (2–7) starting 20 m below the barrier (about 220 m from the actual lake outlet, Table 1). Pettit Lake had a fish migration barrier located about 120 m downstream from the lake outlet. The barrier had no obvious effects on the natural streamflow; thus transect distances were left unmodified.

Physical measurements at each transect included percent gradient, stream width, mean stream depth, mean channel velocity, dominant substratum size, and width of the riparian zone on each side of the stream (Table 1). Temperature was recorded at midday for each stream. Generally, all three streams were similar in gradient (1–2%), stream width (10–15 m), stream depth (45–65 cm), mean stream velocity (70–120 cm/s), dominant substratum size (about 200 cm<sup>3</sup>), and riparian width (about 15 m) (Table 1). Yellowbelly Lake outlet stream had relatively slower channel velocities, probably due to the migration barrier below transect 6. The effect of the barrier also is evident in the reduction of the



TABLE 2. Comparison of physical measurements in the Pettit Lake outlet stream at each transect for both June (J) and August (A) 1986. Distances, gradients, and riparian zone widths remained the same on both dates (see Table 1).

TRANS*	W (m)		D (m)		V (cm/s)		SUB (cm <sup>3</sup> )		Q (m <sup>3</sup> /s)	
	J	A	J	A	J	A	J	A	J	A
1	15	9	.65	.16	50	29	8	6	4.88	0.42
2	15	9	.51	.24	55	27	3	2	4.21	0.58
3	15	10	.56	.21	77	26	385	430	6.47	0.55
4	10	8	.62	.23	90	33	299	380	5.58	0.61
5	15	8	.46	.25	93	37	323	688	6.42	0.74
6	12	6	.44	.24	137	40	358	822	7.23	0.58
7	14	6	.47	.31	109	21	281	896	7.17	0.39

\*TRANS = transect, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, Q = mean streamflow. N = 5 for each transect.

dominant substrate size at transect 6 (Table 1). Stanley Lake outlet had a lower temperature than either Yellowbelly or Pettit Lake outlet streams (Table 1).

Pettit Lake outlet was chosen for a more extensive analysis in August 1986. The stream differed physically between the two study periods (Table 2). Mean stream width (by 4–5 m), mean stream depth (by 20–30 cm), mean channel velocity (by 30–100 cm/s), and mean streamflow (by 0.4–0.6 m<sup>3</sup>/s) were lower in August than in June (Table 2). The dominant substratum size increased in August (by 12%–219%) except at transects 1 and 2, where the substratum was predominantly coarse sand (Table 2). This change in dominant particle size could be attributed to the restricted area for sampling during low flows.

### Collection Methods

Five macroinvertebrate samples were collected at each transect using a modified Hess net (210  $\mu$ m mesh). Five additional benthic samples were collected from each transect at Pettit Lake outlet in August 1986. The circular net was placed firmly on the stream bottom, and a railroad spike was used to disturb the substratum within the net to a depth of 10 cm. Large cobbles were scrubbed by hand and removed for inspection of invertebrates. The contents of the net were collected, preserved in 10% formalin, and returned to the laboratory for analysis.

In the laboratory the invertebrates were hand-picked, identified, and enumerated using a dissecting microscope (8X). Chironomids were identified to family. Macroinvertebrate biomass (dry mass) was determined by drying the samples at 60 C and weighing. The remaining debris from each sample was used

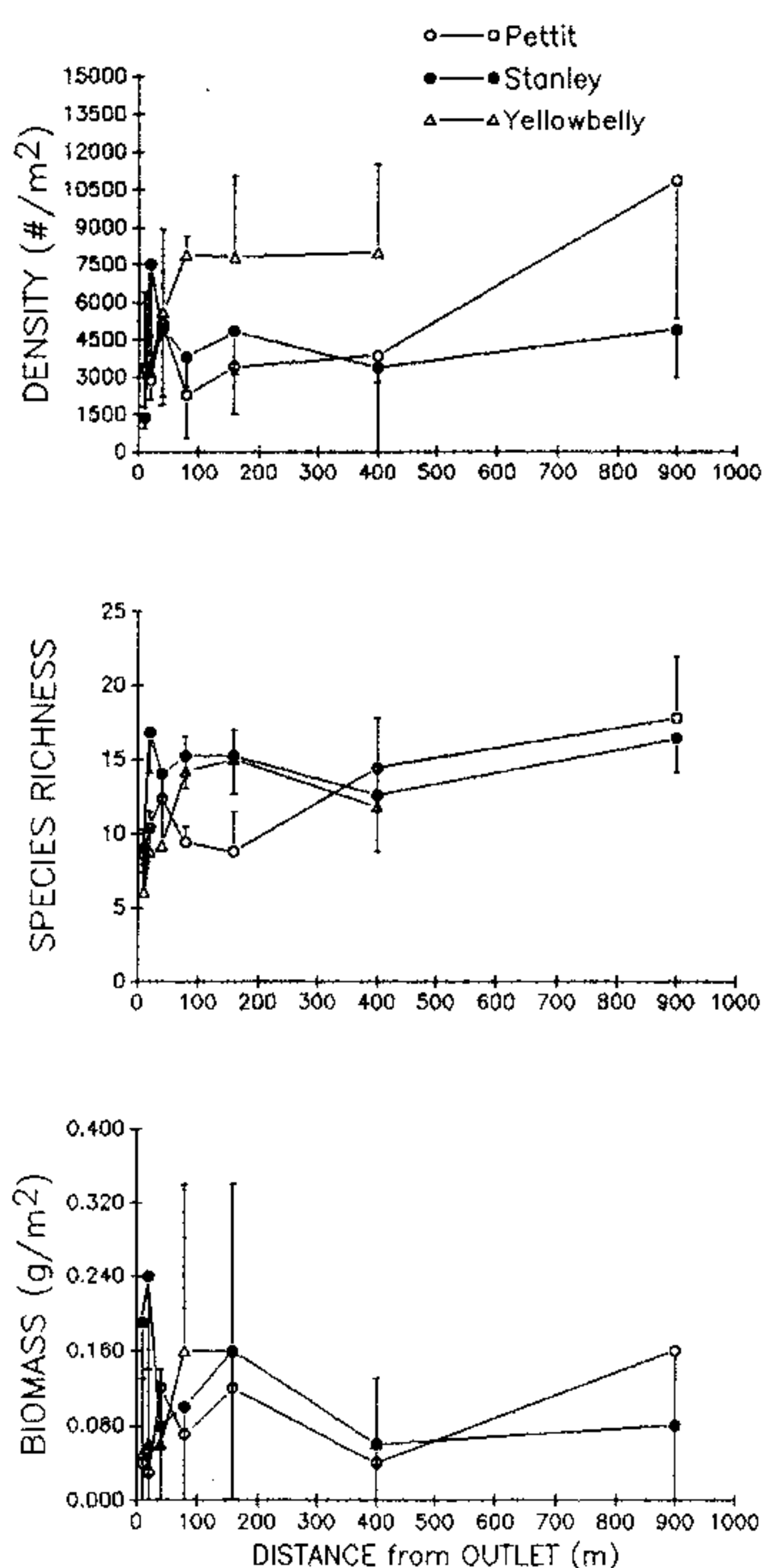


Fig. 1. Macroinvertebrate density, biomass, and species richness in three lake outlet streams in June 1986. Vertical bars indicate  $\pm 1$  standard deviation.

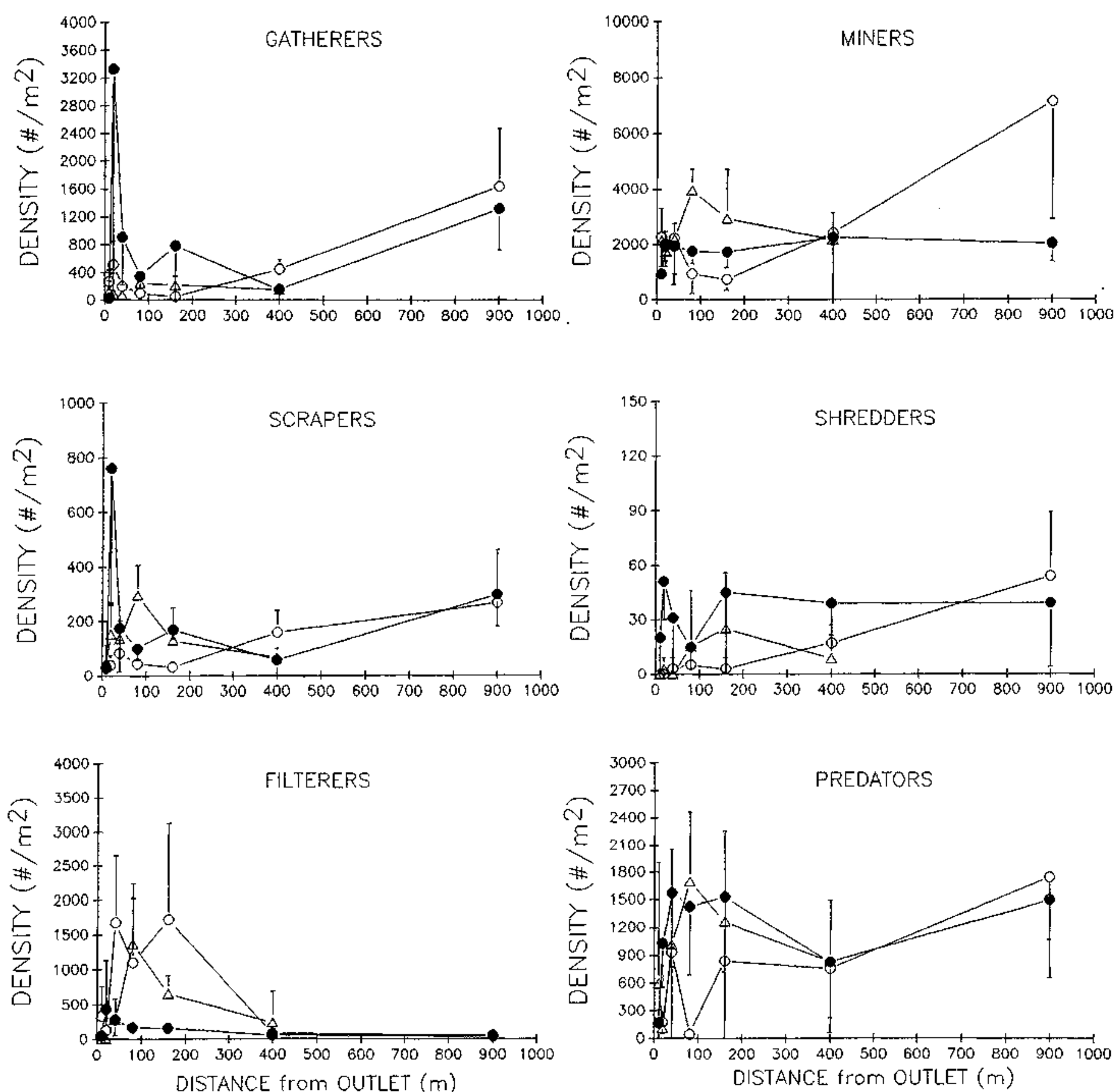


Fig. 2. Macroinvertebrate density by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent  $\pm 1$  standard deviation.

to determine the amount of benthic organic matter (AFDM). The sample was dried at 60 C, weighed, ashed at 550 C, rehydrated, redried at 60 C, and reweighed.

## RESULTS

### Community Analysis

Macroinvertebrate density and biomass increased rapidly immediately below the outlets and then plateaued or, as in the case of Pettit and Stanley, decreased before stabilizing (Fig. 1). Total density and biomass at Stan-

ley and Yellowbelly Lake outlets plateaued within 40 m. Yellowbelly Lake outlet had densities twice those of Pettit and Stanley Lake outlets, although biomass was similar among sites. This was probably in response to greater food availability as reflected in differences in organic matter standing crops between the two locations (Fig. 1). Macroinvertebrate density in Pettit Lake outlet was lower than that in the two other outlets at 80 m, but showed a relatively rapid increase to levels exceeding those of Stanley Lake outlet at transect 7.

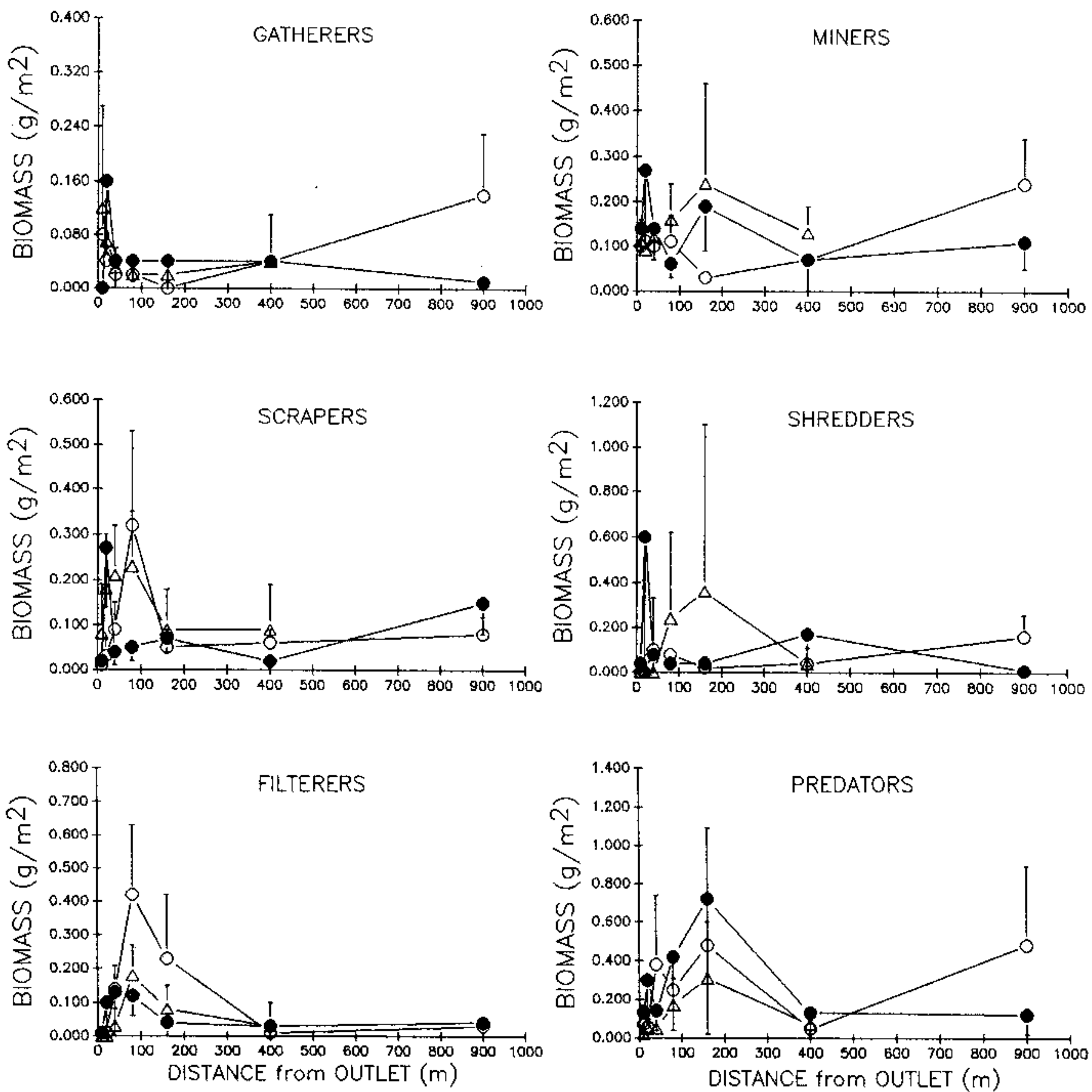


Fig. 3. Macroinvertebrate biomass by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent  $\pm 1$  standard deviation.

Species richness increased immediately downstream from each lake outlet (Fig. 1). Pettit and Stanley Lake outlets showed slight declines in richness 20–80 m downstream, although there was a tendency, best seen at Pettit, to progressively add species with increasing distance from the lake.

#### Functional Feeding Group Analysis

**STANLEY LAKE OUTLET.**—The density and biomass of gatherers, scrapers, filterers, and predators each showed patterns comparable to that of total density and biomass (Figs. 2, 3). An exception was the extended high abun-

dance of predators at 40–160 m. Shredder density downstream of 160 m showed a resurgence to high values observed at 20 m rather than a maintenance of values comparable to those found at 80 m as occurred for total density. Miners did not show the marked peak at 20 m seen for total numbers and for other functional feeding groups. Miners, such as chironomids, have been found to be abundant in lentic sediments, which may explain their lack of response immediately below lake outlets.

**PETTIT LAKE OUTLET.**—Gatherer, scraper, and miner density and biomass all showed



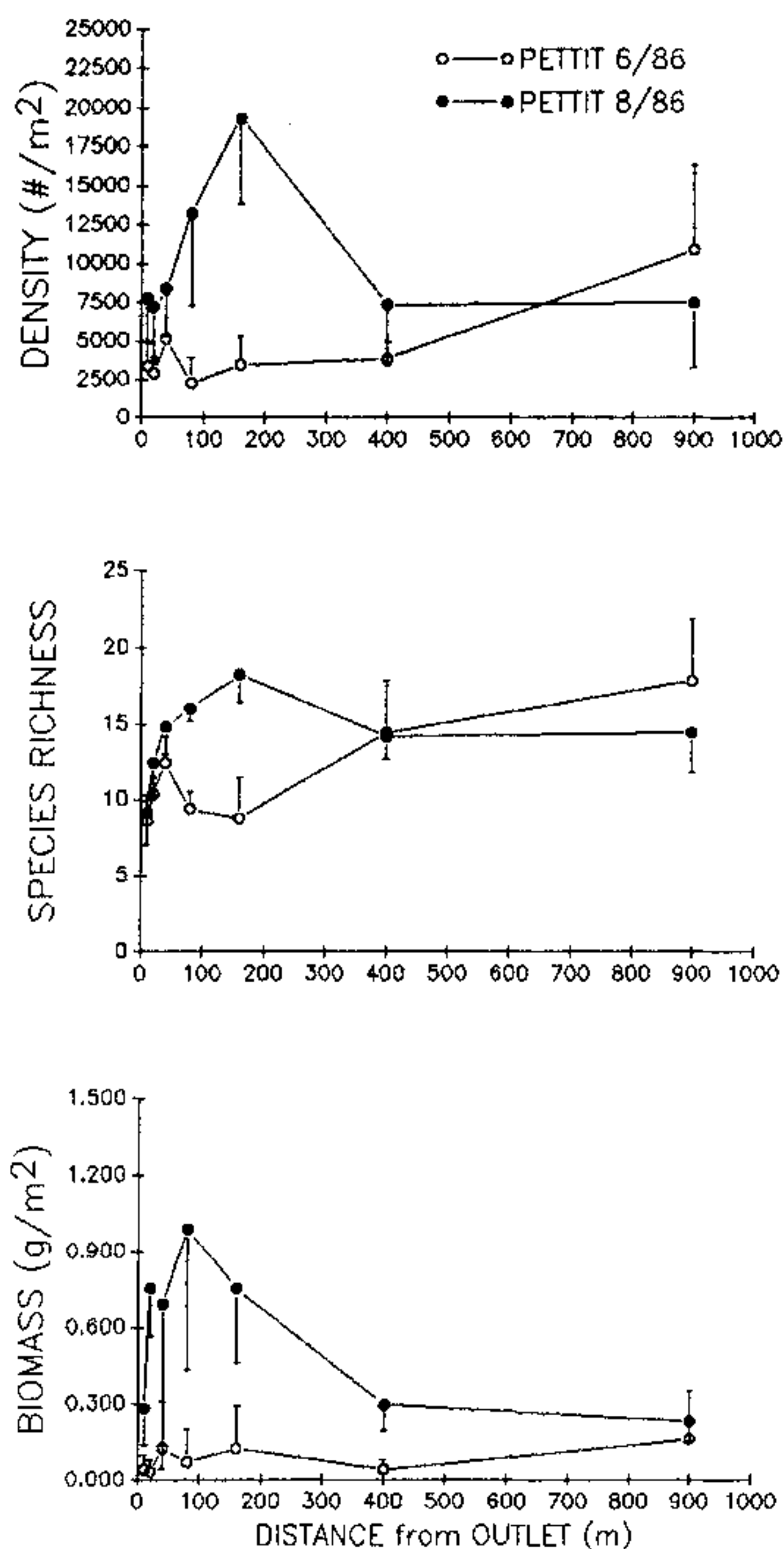


Fig. 4. Macroinvertebrate species richness, density, and biomass in Pettit Creek in June and August 1986. Bars represent  $\pm 1$  standard deviation.

patterns similar to those of total density and biomass. Filterer density and biomass peaked at 40 and 160 m (Figs. 2, 3). Predators showed an accentuated recovery in numbers at 160 m and continued high levels at 400 m in contrast to the pattern for total numbers. Predator biomass followed the pattern observed for filterer biomass (Fig. 3).

**YELLOWBELLY LAKE OUTLET.**—The density and biomass of gatherers, filterers, and predators showed patterns similar to those of total density and biomass. However, the predator biomass deviated from the general trend by decreasing downstream of the 80-m transect

(Figs. 2, 3). Filterer density and biomass peaked shortly below the outlet as was found at Pettit Lake outlet. The high filterer density and biomass were at a single location (80 m) rather than over an extended stretch (40–160 m) as at Pettit. Greater current velocity and substrate size may have facilitated colonization by filterers at 80 m at Yellowbelly Lake outlet (Table 1).

In general, the density and biomass of shredders followed the pattern seen for benthic organic matter at all three lakes. This was the “expected” pattern for all functional groups, based on the assumption of a lake outlet stream gradually accruing food downstream from allochthonous sources. Deviations from this pattern, especially by filter feeders, suggest “contamination” of the water by lake plankton. This was least evident at Stanley Lake outlet and most pronounced at Pettit Lake outlet. However, even at Pettit Lake outlet filter feeder populations declined rapidly within 160–400 m, indicating depletion of this material (Figs. 2, 3). Scraper density and biomass suggest that, for the most part, autochthonous sources of food were low, as would be expected for the headwater streams we were attempting to simulate. Yellowbelly Lake outlet at the 20-m transect is a notable exception. Although there were some minor deviations, data for density and biomass of functional feeding groups showed similar patterns (Figs. 2, 3).

#### Seasonal Study of Pettit Lake Outlet

Longitudinal patterns of total density, biomass, and species richness were somewhat different in August from those found in June (Fig. 4). Animal density, biomass, and species richness peaked sooner in August than in June and were not significantly different downstream of the 400 m transect. Total density and biomass increased downstream to 160 m, declined markedly for the next 240 m, and then stabilized in August (Fig. 3). The peak in abundance 40–200 m downstream of the lake outlets in August suggests greater production occurring at this time of year, possibly due to increases in stream temperature, solar radiation, and lentic inputs.

Longitudinal distributions of all functional feeding groups except filterers and scrapers differed in August from those in June (Figs. 5, 6). Filterer density and biomass peaked early

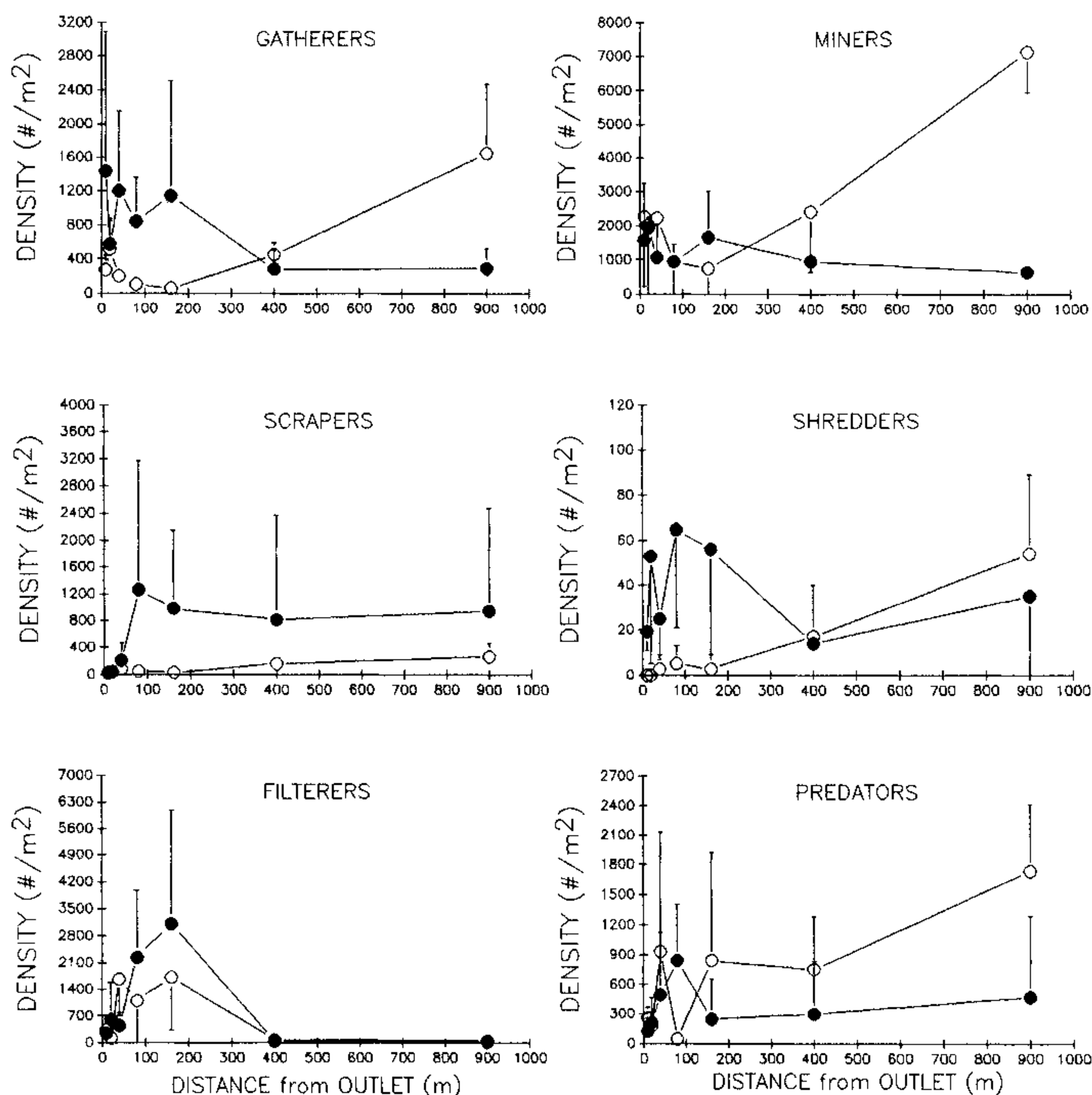


Fig. 5. Macroinvertebrate density by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent  $\pm 1$  standard deviation.

and then virtually disappeared from the community downstream for both sampling dates. Gatherers, miners, and shredders increased in abundance (density and biomass) downstream of the outlet in June, whereas gatherers, miners, and shredders had high densities through 160 m and then decreased to low values at 400 and 900 m in August. Gatherer, miner, and shredder biomass was similar among transects in August. Scrapers peaked in biomass at 80 m in June but displayed similar biomass values among transects in August (Fig. 6). The main difference in predator abundance between the two dates was the

reduced peak at 40 m and the decrease at 80 m in June that was absent in August (Figs. 5, 6).

## DISCUSSION

The results support our hypothesis of a gradually developing stream community (greater numbers/m² and taxonomic complexity) with progressive distance downstream of a lake outlet. The distance required for the development of full community potential (i.e., the recovery distance following complete interception of incoming drift) could not be determined precisely and seems to vary

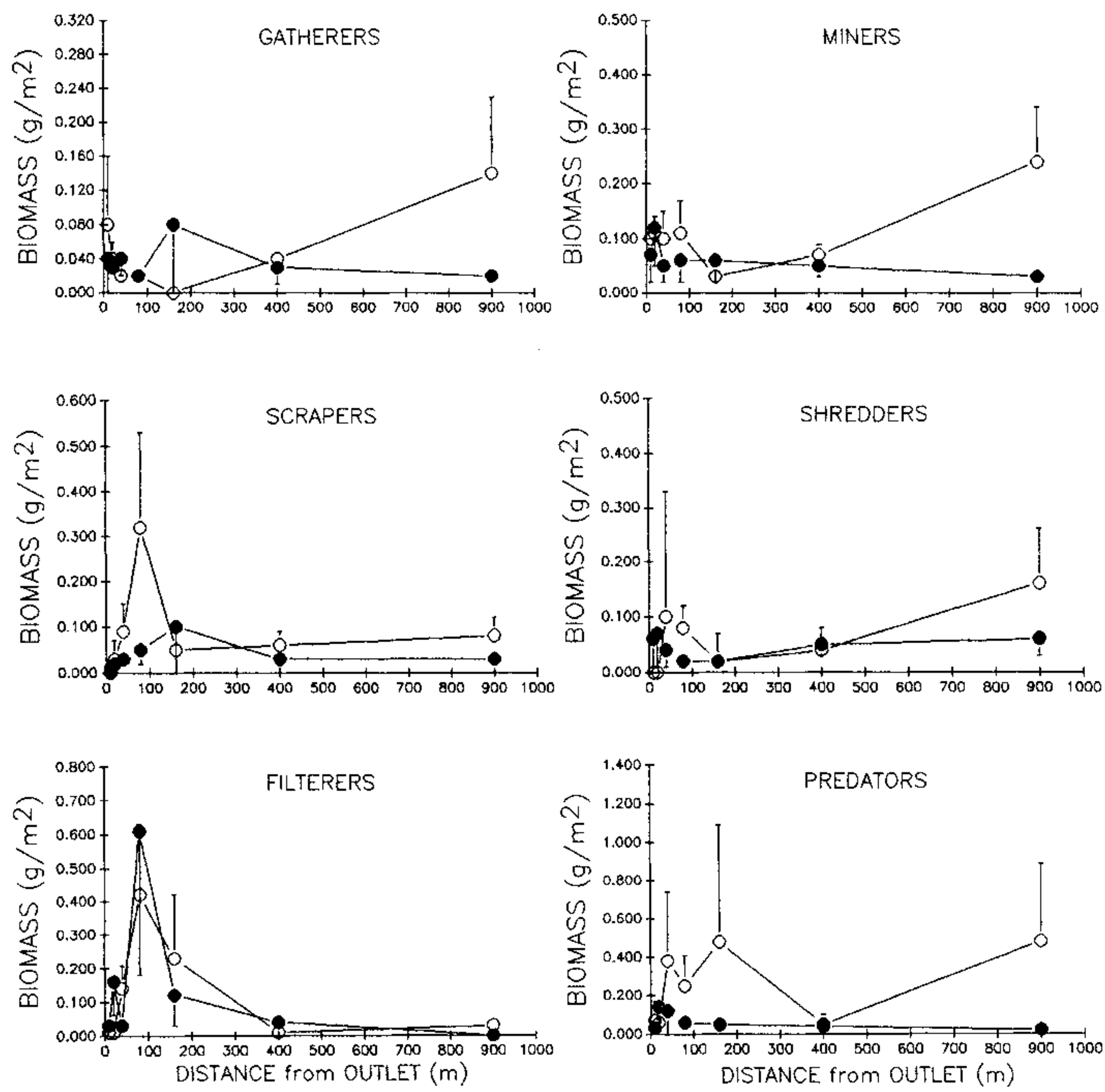


Fig. 6. Macroinvertebrate biomass by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent  $\pm 1$  standard deviation.

widely depending on the particular stream and time of year. In June, during a period of relatively high discharge, "recovery," measured in terms of species richness and total density, ranged from 20 m at Stanley Lake to over 900 m at Pettit Lake. During near base flow conditions in August, community development in Pettit Lake seemed to be much more rapid than in June, peaking somewhere between 160 and 400 m. These data suggest that community development is impeded under conditions of high flow. Additional measurements should be made in several outlet streams having unaltered flows and channels so that the full distances required for recovery

during each season and the factors responsible for the different rates of community development among streams can be established. Our results also show a restricted distribution by filter feeders. The decline from peak numbers below the outlet was more rapid than reported by Sheldon and Oswood (1977), thus supporting our prediction that oligotrophic lakes will show more limited supplies of seston and consequently a more restricted distribution of filter feeders in their outlet streams than meso- or eutrophic lakes. In addition, we found that filter feeder abundances increased from low numbers immediately below the outlet to peak numbers some

distance (40–80 m) downstream. This differs from the progressive downstream decrease in filter feeder abundance modeled by Sheldon and Oswood (1977) and may have been overlooked by them because they sampled no closer than 25 m below the lake outlet. A parabolic relationship of filterer density with distance rather than a negative linear regression may be due to suboptimal environmental (e.g., velocity) or biotic conditions near the outlet. Current velocities in Pettit Creek were less near the outlet (26–29 cm/s) than further downstream (33–40 cm/s) and may not have met the needs of filterers for feeding or respiration. Further, changes in substratum characteristics occurred within 40 m of the lake outlet (Table 1). Mackay and Waters (1986) suggest that changes in filterer abundances between the impoundments they studied may be due to a greater abundance of attachment sites.

Our data contribute a spatial dimension to the recolonization of stream benthos by macroinvertebrates. These data suggest the importance of the habitat templet in the structuring of benthic communities. This implies faster recovery or community development in streams below lake outlets in which adequate structural habitat is present. These data suggest that low-head hydro installations can impact macroinvertebrate communities by reducing the structural attributes of the habitat templet.

#### ACKNOWLEDGMENTS

We are grateful to B. Jamison, J. Mann, and C. Nelson for their help in the field and in the

laboratory throughout the course of this project. We also thank D. Bosen, S. Danamraj, D. Goetsche, S. Hart, E. Hitchcock, S. Minshall, D. Misner, L. Reed, C. Richards, and T. Tiersch for their assistance. Funding for the project was provided by the U.S. Fish and Wildlife Service.

#### LITERATURE CITED

- CHANDLER, D. C. 1937. Fate of typical lake plankton in streams. *Ecological Monographs* 7: 445–479.
- CUSHING, C. E. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. *Transactions of the American Fisheries Society* 92: 216–219.
- MACIOLEK, J. A., AND M. G. TUNZI. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream system. *Ecology* 49: 60–75.
- MACKAY, R. M., AND T. F. WATERS. 1986. Effects of small impoundments of hydropsychid caddisfly production in Valley Creek, Minnesota. *Ecology* 67: 1680–1686.
- MORIN, A., AND R. H. PETERS. 1988. Effects of microhabitat features, seston quality, and periphyton on abundance of overwintering black fly larvae in southern Quebec. *Limnology and Oceanography* 33: 431–446.
- REIF, C. B. 1939. The effect of stream conditions on lake plankton. *Transactions of the American Microscopical Society* 58: 398–403.
- SHELDON, A. L., AND M. W. OSWOOD. 1977. Blackfly (Diptera: Simuliidae) abundance in a lake outlet: test of a predictive model. *Hydrobiologia* 56: 113–120.
- STATZNER, B. 1978. Factors that determine the benthic secondary production in two lake outflows—a cybernetic model. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 20: 1517–1522.

*Received 15 September 1990*

*Revised 20 November 1990*

*Accepted 28 January 1991*





## SPATIAL PATTERN AND INTERFERENCE IN PIÑON-JUNIPER WOODLANDS OF NORTHWEST COLORADO

Charles W. Welden<sup>1,2</sup>, William L. Slauson<sup>1</sup>, and Richard T. Ward<sup>1</sup>

**ABSTRACT.**—The local spatial arrangement of the coniferous trees *Pinus edulis* and *Juniperus osteosperma* was mapped in two woodland stands and measured in two shrub-dominated stands in the semiarid Piceance Basin of northwest Colorado. In the woodlands, small trees were often clumped, while medium and large trees were either randomly or uniformly dispersed. Significant regressions were obtained between a tree's basal area or canopy area and the area of its Dirichlet domain (the region closer to it than to any other tree). Both findings from the woodland stands accord with results obtained by other workers in other vegetation. Like earlier workers, we interpret these patterns to indicate density-dependent mortality and density-dependent depression of growth rates among the trees in the woodlands. In contrast, the trees in the shrub-dominated stands are located at random with respect to each other. However, they are strongly associated with shrub cover. Apparently, tree seeds arrive in these stands primarily by long-distance dispersal, and the establishment of seedlings is more likely in the shade of shrubs.

Since plants are sessile and their growth is plastic, their arrangement in space and their sizes can reflect the history of their interactions with each other and with the environment. With long-lived, slow-growing plants, studying pattern may be the only feasible way to discover which processes and interactions are important in determining community structure.

We used some of the methods compared by Goodall and West (1979) to study the local spatial arrangement (pattern) of the small coniferous trees *Pinus edulis* and *Juniperus osteosperma* in four stands in the semiarid Piceance Basin of northwest Colorado. Our goals were twofold. First, we wished to determine whether the differences between methods Goodall and West (1979) detected in artificial populations are borne out in more complex real populations. Second, we wished to infer the processes that influence the establishment of seedlings and the growth and mortality of plants.

### STUDY AREA

The Piceance Basin occupies about 3000 km<sup>2</sup> in Garfield and Rio Blanco counties of northwest Colorado. Elevations range from 1707 to 2743 m (Tiedeman and Terwilliger 1978). The climate is semiarid with average

annual precipitation ranging from 28 cm in the northwest to 63.5 cm in the southeast. About half of the annual total falls as snow and most of the remainder as rain in late-summer thunderstorms. In the short term, precipitation is unpredictable and variable (Wymore 1974).

The average annual temperature is 7 C at 1825 m (the elevation of the only permanent weather station in the basin), with a minimum monthly average in January of -5.9 C and a maximum monthly average in July of 20.3 C. The average annual temperature decreases by approximately 0.85 C for every 100 m increase in elevation. Both temperature and precipitation are strongly influenced by local topography (Wymore 1974).

We studied the spatial patterns of *Pinus edulis* Engelm. and *Juniperus osteosperma* (Torr.) Little (piñon and Utah juniper). Nomenclature follows Goodrich and Neese (1986). *P. edulis* and *J. osteosperma* are small coniferous trees common throughout the western United States, where they form mixed stands, often with an understory of scattered grasses, forbs, and shrubs. They commonly attain heights of 6–8 m, and both reproduce by seed. *P. edulis* usually possesses a single stem, while *J. osteosperma* is often multistemmed.

The vegetation of the basin includes shrublands and woodlands of various floristic

<sup>1</sup>Department of Biology, Colorado State University, Fort Collins, Colorado, USA 80523.

<sup>2</sup>Present address: Department of Biology, Southern Oregon State College, 1250 Siskiyou Boulevard, Ashland, Oregon, USA 97520-5071.

compositions. Piñon-juniper woodlands (as described in Tiedeman and Terwilliger 1978) have open canopies dominated by *P. edulis* and *J. osteosperma* and occur on broad, flat ridge tops at elevations between 1890 m and 2170 m, where soils are shallow, rocky, light brown, sandy loams (Entisols). Shrublands dominated by *Artemisia tridentata* Nutt. (sagebrush flats) often occur on the same ridges as do piñon-juniper woodlands, at roughly the same elevations, but where soils are finer and deeper. Where piñon-juniper woodlands abut sagebrush flats, zones of intermediate vegetation are often found. In these intermediate areas, the vegetation is dominated by *Artemisia*, with small, scattered individuals of *P. edulis* and *J. osteosperma*. Few of the trees overtop the shrubs.

We studied two piñon-juniper woodlands (stands A and B), which were dominated by mature *P. edulis* and *J. osteosperma*, with little shrub understory. The canopies in these stands are not closed, but individual canopies sometimes abut or overlap. It is known from others (Fowells 1965) and from personal observation that the roots of these trees usually extend beyond the canopy. Thus, neighboring trees which do not seem to be competing for light may nonetheless be competing belowground for water or nutrients. These stands lie at elevations of 2164 m and 1890 m, which approximate the elevational limits of this vegetation in the basin. Stand A slopes 1.5° and faces to the northwest (N62°W). Stand B slopes 3.0°, facing to the north-northwest (N22°W).

Stands C and D are intermediate between piñon-juniper woodlands and sagebrush flats. None of the trees in these stands is as large as the largest trees in the piñon-juniper woodlands, although many bear cones and are thus sexually mature. These stands occupy ridge tops at elevations of 2164 m and 1981 m. Stand C slopes 4.5°, facing west (N80°W), and stand D slopes 6.5°, facing north (N5°W).

#### METHODS

Goodall and West (1979) reviewed pattern methods based on analyses of artificial populations. They compared the statistical powers of the methods, that is, the probabilities of rejecting a false null hypothesis. With large samples, all the tested methods gave results

reflecting the true dispersion pattern of artificial populations, with powers approaching 100%. With smaller samples, however, methods differed in power. We used those having the greatest power with small samples: the variance/mean ratio (Clapham 1936) among quadrat methods, and the indices of Hopkins (1954) and Pielou (1959, 1960, 1961) among distance methods (see descriptions below). We also compared the frequencies of quadrats containing exactly 0, 1, 2, . . . plants with the expected Poisson distribution by a chi-squared goodness-of-fit test.

In addition to these methods, we included a measure of pattern that uses information not only about the locations of plants but also about their sizes. The Dirichlet domain (or Thiessen or Voronoi polygon) of a plant comprises all the points closer to that plant than to any other (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984). Its size thus represents the area more easily accessible to the plant than to its neighbors and may represent the amount of resources captured or sequestered by a plant, or potentially more available to it than to its neighbors. This in turn may influence the plant's growth and fitness and indicate what effect, if any, its neighbors have on it. To detect whether this is the case, we regressed the areas of plants' Dirichlet domains on the sizes of the plants.

The variance/mean ratio test (Clapham 1936) is based on the expectation that, in a randomly dispersed population, the frequency distribution of quadrats containing exactly 0, 1, 2, 3, . . . individuals approximates the Poisson distribution. One property of this distribution is that its mean and variance are equal, and their ratio therefore unity. The distribution of this ratio in large samples is approximately normal, with a mean of 1 and a standard deviation of  $(2/n-1)^{1/2}$  (Goodall and West 1979), where  $n$  is the sample size (number of quadrats). In regularly dispersed populations the ratio is less than 1, in aggregated ones greater.

Hopkins's (1954) index A is based on the expectation that, in a randomly dispersed population, the average distance from randomly located points to the nearest plant equals the average distance between plants and their nearest neighbors. Hopkins proposed the ratio of these two averages as his index:



$$A = (\sum P_i^2) / (\sum I_i^2)$$

where  $P_i$  and  $I_i$  are the sums of equal numbers of distances from random points to the nearest plant and from randomly selected plants to their nearest neighbors, respectively. In a randomly dispersed population, the expected value of  $A$  is 1, and for large samples its frequency distribution is approximately normal. Values of  $A$  larger than 1 indicate aggregation, less than 1 regularity.

Pielou (1959, 1960, 1961) developed two distance methods to measure pattern. The first uses a sample of distances from randomly located points to the nearest plant and an independent estimate of plant density. From these a statistic,  $\alpha_p$ , can be calculated as follows:

$$\alpha_p = \pi(D)\omega_p$$

where  $D$  is the density of the plants,  $\omega_p$  is the mean squared point-to-plant distance, and  $\pi$  is the trigonometric constant.

The second method (Pielou 1960) uses a sample of distances from randomly chosen plants to their nearest neighbors. A statistic  $\alpha_i$  is calculated in the same way as  $\alpha_p$ , substituting the mean squared plant-to-plant distance for the mean squared point-to-point distance. Pielou (1959) provides tables of confidence intervals and significance levels for values of  $\alpha_i$  and shows how they may be used to interpret  $\alpha_p$  (Pielou 1960).

We mapped the location of each *Pinus edulis* and *Juniperus osteosperma* 10 cm tall or taller in parts of stands A and B. The mapped area in stand A was 2250 m<sup>2</sup>; in stand B it was 2500 m<sup>2</sup>. We checked the accuracy of the maps by comparing plant-to-plant distances calculated from map coordinates to the same distances measured in the field. The greatest difference was about 10 cm.

We classified plants into three height-classes. Small plants were 10 cm to 1 m tall, medium plants between 1 m and 3 m tall, and tall plants were taller than 3 m. The tallest trees in our stands were about 5 m tall. Small plants were not mapped in about one-third of stand A.

For each *P. edulis* in these stands we measured one canopy diameter in an arbitrary direction and estimated the area of its canopy as if it were circular. The living canopies of *J. osteosperma* were often interrupted by

dead branches. We measured the living portions of their canopies and summed the areas estimated from these. Basal areas were calculated for both species from stem diameters measured at ground level. For multi-stemmed plants, the basal areas of all living stems were summed.

We measured the dispersion patterns of the plants on these maps, using both quadrat and distance methods. Small plants were sampled with quadrats 2.5 m on a side (in map scale), medium and tall plants with quadrats 5 m on a side. Quadrats were placed at the intersections of a regular grid of lines 5 scale-meters apart; thus every point on the map was included in exactly one quadrat of a given size. There were 100 large and 400 small quadrats in stand B. Stand A was more irregular, encompassing 90 large and 230 small quadrats.

The spatial dispersions of each size class and species were measured separately and pooled. That is, the null hypothesis of random spatial dispersion was tested by five indices for small *P. edulis*, small *J. osteosperma*, all small plants, medium *P. edulis*, medium *J. osteosperma*, all medium plants, tall *P. edulis*, tall *J. osteosperma*, all tall plants, medium and tall *P. edulis* combined, medium and tall *J. osteosperma* combined, and all medium and tall plants combined.

We constructed Dirichlet domains (Honda 1978, Jack 1967, Mead 1971, Mithen, Harper, and Weiner 1984) for the plants by drawing lines connecting each plant to its immediate neighbors, and then constructing perpendicular bisectors of these lines (Fig. 1). Note that we did not weight the distance from a plant to the bisector by the size of the plant, and thus there is no necessary correlation between the size of a plant and the size of its Dirichlet domain. We estimated the areas of the Dirichlet domains by cutting the polygons from the maps and weighing them. We regressed the areas of the Dirichlet domains on the basal areas, and separately on the canopy areas, of their plants. Regressions on basal areas were compared to regressions on canopy areas, with and without logarithmic transformation, by graphical analysis of residuals.

In stands C and D we located every *P. edulis* and *J. osteosperma* 10 cm or more in height within a square 50 m on a side, noting whether it had become established under a plant canopy or in the open, based on observations of each



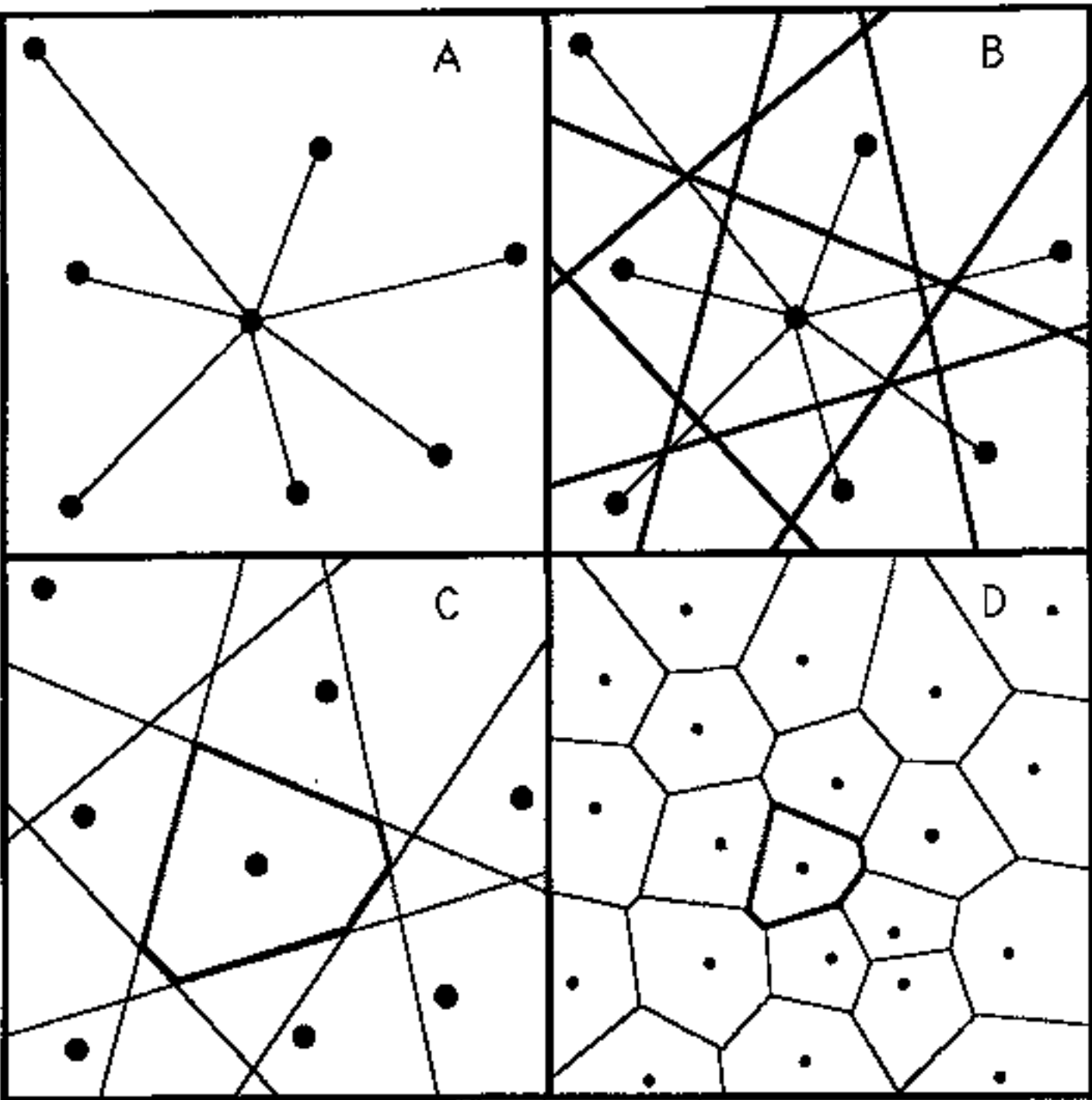


Fig. 1. Construction of Dirichlet domains.

a. Draw line segments connecting a focal plant to its neighbors.

b. Draw the perpendicular bisector of each line segment.

c. The Dirichlet domain is the region closer to the focal plant than all the perpendicular bisectors.

d. Repeat for each plant. The Dirichlet domain of each plant is the region closer to it than to any other plant.

tree's association with living or dead shrubs. We measured total plant cover of all species with two 50-m line intercepts. The association of *P. edulis* and *J. osteosperma* with plant cover was tested by a chi-squared test. We did not map these stands but measured distances between neighboring trees in the field. We used Pielou's alpha<sub>i</sub> to describe the spatial dispersion of the two tree species.

RESULTS

Table 1 shows the number of *P. edulis* and *J. osteosperma* in each stand and the corresponding numbers per hectare. Table 2 shows the five dispersion indices for the trees in stands A and B, and Table 3 the interpretations of these values. In the woodland stands (A and B) small plants tend to be clumped, and larger plants tend to be randomly or uniformly dispersed. The sequence from clumped to random to uniform is violated in only three instances (asterisks in Table 3). These violations may be the result of chance, since the tests for significance were all set at the 5% level and some spurious results are expected among such a large number of separate tests.

All log-log transformed regressions of Dirichlet domain areas on plant canopy areas and basal areas in stands A and B are significant at the 5% level, except for that of *J. osteosperma* in stand A (Table 4, Fig. 2). These regressions show that, on average, larger plants have larger Dirichlet domains and are correspondingly farther from their neighbors. The Dirichlet domains of small plants are more variable in area than those of larger plants. Logarithmic transformation of both variates improves the distribution of variates and residuals and produces reasonable conformity with the assumptions of regression, but it does not change the significance of the regressions. These results are similar to those of regressing the distance between a pair of neighboring plants on the sum of their sizes (Welden 1984, Welden, Slauson, and Ward 1988, cf. Fuentes and Gutierrez 1981, Gutierrez and Fuentes 1979, Nobel 1981, Phillips and MacMahon 1981, Pielou 1960,

TABLE 1. Stand censuses, divided by height categories (10 cm ≤ small < 1 m ≤ medium < 3 m ≤ tall) and by species. In parentheses are numbers per hectare.

		Small plants	Medium plants	Tall plants	Total
Stand A	<i>Pinus edulis</i>	61 (432)	56 (229)	67 (274)	184 (753)
	<i>Juniperus osteosperma</i>	26 (184)	12 (49)	39 (160)	77 (315)
Stand B	<i>P. edulis</i>	88 (352)	32 (128)	11 (44)	131 (524)
	<i>J. osteosperma</i>	86 (344)	9 (36)	41 (164)	136 (544)
Stand C	<i>P. edulis</i>	56 (224)	22 (88)	1 (4)	79 (316)
	<i>J. osteosperma</i>	7 (28)	7 (28)	0	14 (56)
Stand D	<i>P. edulis</i>	47 (188)	30 (120)	4 (16)	81 (324)
	<i>J. osteosperma</i>	34 (136)	46 (184)	17 (68)	97 (388)

TABLE 2. Values of dispersion indices in stands A and B. Indices are identified in the text and these values are interpreted in Table 4. A dash indicates that the test could not be performed.

Stand	Distance methods						Quadrat methods			
	$\alpha_p$		$\alpha_i$		A		$\chi^2$		var/mean	
	A	B	A	B	A	B	A	B	A	B
<i>P. edulis</i>										
Small	0.93	1.04	1.12	0.84	0.83	1.21	12.2	25.0	1.27	1.98
Medium	0.98	1.23	1.15	0.66	0.85	1.83	5.97	—	1.72	1.60
Medium and tall	1.00	0.74	1.04	0.97	0.96	1.38	2.90	2.16	1.48	1.28
Tall	0.84	0.38	0.88	0.91	0.95	0.42	0.17	—	1.10	0.89
<i>J. osteosperma</i>										
Small	1.03	1.36	1.04	1.07	0.99	1.27	—	29.4	1.52	1.15
Medium	0.61	1.06	0.84	0.64	0.72	1.65	—	—	1.04	0.86
Medium and tall	0.73	0.93	1.09	1.29	0.78	0.73	0.24	2.12	0.96	0.86
Tall	0.73	0.73	1.18	1.39	0.75	0.54	0.24	1.10	0.97	0.82
Species combined										
Small	1.25	1.29	0.79	0.86	1.58	1.50	18.1	8.18	1.62	1.65
Medium	1.17	1.58	0.96	0.54	1.22	2.94	2.28	10.9	1.44	2.22
Medium and tall	1.06	0.86	0.94	1.14	1.12	0.92	4.35	0.91	1.34	1.19
Tall	0.92	0.74	0.98	1.13	0.78	0.59	0.60	3.76	1.04	0.95

TABLE 3. Pattern analyses of stands A and B. C indicates that the plants are clumped, R that they are randomly dispersed, U that they are uniformly dispersed. All indicated nonrandom dispersions are significant at the 5% level. A dash indicates that the test could not be performed. Asterisks denote contradictions to the general trend of C – R – U with increasing plant size.

Stand	Distance methods						Quadrat methods			
	$\alpha_p$		$\alpha_i$		A		$\chi^2$		var/mean	
	A	B	A	B	A	B	A	B	A	B
<i>P. edulis</i>										
Small	R	R	R	R*	R	R*	C	C	C	C
Medium	R	R	R	C	R	C	C	—	C	C
Medium and tall	R	U	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	R	R	—	R	R
<i>J. osteosperma</i>										
Small	R	C	R	R	R	R	—	C	C	C
Medium	U	R	R	R	R	R	—	—	R	C
Medium and tall	U	R	R	R	R	R	R	R	R	R
Tall	U	U	R	U	R	U	R	R	R	R
Species combined										
Small	C	C	R	R*	R	C	C	C	C	C
Medium	R	C	R	C	R	C	R	C	C	C
Medium and tall	R	R	R	R	R	R	R	R	C	R
Tall	R	U	R	R	R	U	R	R	R	R

1961, Yeaton and Cody 1976, and Yeaton, Travis, and Gilinsky 1977).

Plant cover (primarily of *Artemisia*) in stand C was approximately 20%, and about 96% of the *P. edulis* and about 71% of the *J. osteosperma* had become established under plant canopy. Plant cover in stand D was about 18%, and about 93% of the *P. edulis* and about 87% of the *J. osteosperma* had become established under plant canopy. The probability that establishment of *P. edulis* or *J. osteo-*

*sperma* is random with respect to plant cover is less than .001 in every case. The pattern statistic  $\alpha_i$  (Pielou 1960) showed no significant deviations from random dispersion among *P. edulis* or *J. osteosperma* in stands C and D.

#### DISCUSSION

Pielou (1959) and Goodall and West (1979) show that distance methods are more sensitive to uniformity and quadrat methods are

TABLE 4. Coefficients of log-log transformed regressions of Dirichlet domain area on canopy and basal areas. Significance is the probability of such data if the true slope and *r* equal zero.

Species	Stand	<i>n</i>	<i>r</i> <sup>2</sup>	Y-intercept	Slope	Significance
<i>P. edulis</i>						
Independent variable						
ln (canopy area)	A	98	0.056	10.12	0.13	0.019
ln (basal area)	A	98	0.052	11.05	0.11	0.024
ln (canopy area)	B	33	0.272	5.15	0.26	0.002
ln (basal area)	B	33	0.191	6.81	0.21	0.011
<i>J. osteosperma</i>						
ln (canopy area)	A	27	0.031	12.50	−0.06	0.377
ln (basal area)	A	27	0.020	12.04	−0.04	0.479
ln (canopy area)	B	31	0.367	5.41	0.23	0.000
ln (basal area)	B	31	0.352	6.84	0.18	0.000
Species combined						
ln (canopy area)	A	125	0.039	10.49	0.10	0.027
ln (basal area)	A	125	0.047	11.15	0.09	0.015
ln (canopy area)	B	64	0.333	5.27	0.25	0.000
ln (basal area)	B	64	0.268	6.88	0.18	0.000

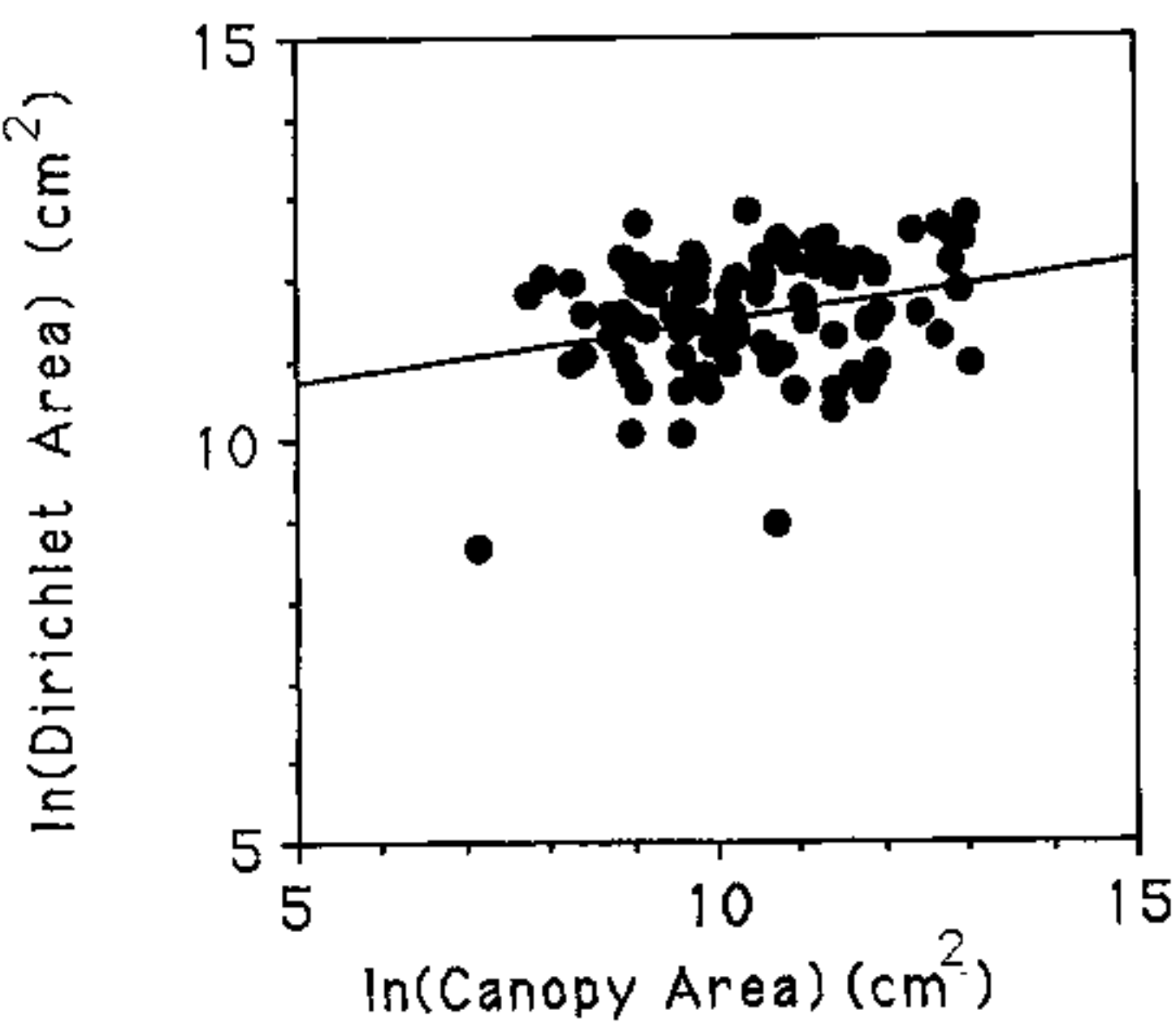


Fig. 2. Regression of Dirichlet domain area on canopy area of piñons in stand A. Both variates have been transformed to their natural logarithms.

more sensitive to clumping. This is borne out by Table 4, where it can be seen that the quadrat methods never detected uniform dispersion while the distance methods did. The distance methods, on the other hand, failed to detect clumping in several cases where it was detected by the quadrat methods.

The trees in the woodland stands (A and B) appear to be interfering (*sensu* Harper 1961, 1977) with one another, either by competition or by allelopathy. The trend from clumped to random to uniform dispersion with increasing plant size suggests density-dependent mortality. Density-independent mortality in a clumped population might con-

ceivably reduce sample sizes in successively larger size-classes until the clumping is no longer detectably different from a random dispersion, but it seems unlikely that it could produce a uniform dispersion (Phillips and MacMahon 1981).

The significant regressions of Dirichlet domain area on plant size indicate density-dependent mortality or density-dependent suppression of growth, or both. We envision two processes leading to this result. First, plants that become established farther from preexisting neighbors become larger because they have access to more unexploited (or unsequestered) resources. Second, established plants prevent the establishment of new neighbors nearby, or impede their growth, because they have exploited (or sequestered) most of the resources in their neighborhoods.

Mithen, Harper, and Weiner (1984) found significant positive relationships between Dirichlet domain area and plant dry weight in even-aged greenhouse populations of *Lapsana communis* L. Although the conditions of their experiments are different (particularly since their plants germinated synchronously), their interpretations of their results are similar to ours here.

Pielou's (1959, 1960) method did not detect any deviation from random spatial arrangement in stands C and D. However, both tree species are significantly associated with plant cover. We presume that these trees became established after long-distance dispersal (> 100 m) from nearby woodlands. The



significant interaction in these stands is evidently not interference between neighboring trees, but amelioration of abiotic stress under the canopies of preexisting plants. Fowells (1965) reports that *P. edulis* requires shade early in its development.

Our evidence for these interpretations is circumstantial. However, given the long lives and slow growth of these plants, and the varying physical environment of the study area, such evidence may be the most informative. These pattern methods integrate the effects of environment and biotic interactions over the life spans of the plants, a time scale not usually accessible to more mechanistic methods.

All our inferences of processes leading to the present pattern require further examination. Although *J. osteosperma* has been reported to produce allelochemicals (Jameson 1971), experiments should be done to determine whether allelopathic effects occur under the conditions and in the soils of the Piceance Basin, and more field studies are needed to determine whether establishment occurs more often near neighbors or far from them. The dynamic behavior of the various pattern indices and regressions should be explored under conditions of density-dependent and density-independent mortality.

#### LITERATURE CITED

- CLAPHAM, A. R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. *Journal of Ecology* 24: 232–251.
- FOWELLS, H. A., ED. 1965. Silvics of forest trees of the United States. Agriculture Handbook 271. 1965.
- FUENTES, E. R., AND J. R. GUTIERREZ. 1981. Intra- and interspecific competition between matorral shrubs. *Oecologia Plantarum* 16: 283–289.
- GOODALL, D. W., AND N. E. WEST. 1979. A comparison of techniques for assessing dispersion patterns. *Vegetatio* 40: 15–27.
- GOODRICH, S., AND E. NEESE. 1986. Uinta Basin flora. United States Department of Agriculture Forest Service—Intermountain Region. Ogden, Utah.
- GUTIERREZ, J. R., AND E. R. FUENTES. 1979. Evidence for intraspecific competition in the *Acacia caven* (Leguminosae) savanna of Chile. *Oecologia Plantarum* 14: 151–158.
- HARPER, J. L. 1961. Approaches to the study of plant competition. Pages 1–39 in *Mechanisms in biological competition*. Academic Press, New York.
- . 1977. *Population biology of plants*. Academic Press, New York.
- HONDA, H. 1978. Description of cellular patterns by Dirichlet domains: the two-dimensional case. *Journal of Theoretical Biology* 72: 523–543.
- HOPKINS, B. 1954. A new method for determining the type of distribution of plant individuals. *Annals of Botany (London)* 18: 213–227.
- JACK, W. H. 1967. Single tree sampling in even-aged plantations for survey and experimentation. *Proceedings, 14th I.U.F.R.O. Congress, Section 25, Munich*.
- JAMESON, D. A. 1971. Degradation and accumulation of inhibitory substances from *Juniperus osteosperma* (Torr.) Little. Pages 121–127 in *Biochemical interactions among plants*. National Academy of Science.
- MEAD, R. 1971. Models for interplant competition in irregularly distributed populations. Pages 13–32 in G. P. Patil, E. C. Pielou, and W. E. Waters, eds., *Statistical ecology, Vol. 2, Sampling and modeling biological populations and population dynamics*. Pennsylvania State University Press, University Park.
- MITHEN, R., J. L. HARPER, AND J. WEINER. 1984. Growth and mortality of individual plants as a function of "available area." *Oecologia* 62: 57–60.
- NOBEL, P. S. 1981. Spacing and transpiration of various sized clumps of a desert grass, *Hilaria rigida*. *Journal of Ecology* 69: 735–742.
- PHILLIPS, D. L., AND J. A. MCMAHON. 1981. Competition and spacing patterns in desert shrubs. *Journal of Ecology* 69: 97–115.
- PIELOU, E. C. 1959. The use of point-to-plant distances in the study of pattern in plant populations. *Journal of Ecology* 47: 607–613.
- . 1960. A single mechanism to account for regular, random and aggregated populations. *Journal of Ecology* 48: 575–584.
- . 1961. Segregation and symmetry in two-species populations as studied by nearest-neighbour relationships. *Journal of Ecology* 49: 255–269.
- TIEDEMAN, J. A., AND C. TERWILLIGER, JR. 1978. A phytosociological classification of the Piceance Basin. *Colorado State University Range Science Department Science Series* 31. 265 pp.
- WELDEN, C. W. 1984. Stress and competition among trees and shrubs of the Piceance Basin, Colorado. Unpublished dissertation, Colorado State University, Fort Collins.
- WELDEN, C. W., W. L. SLAUSON, AND R. T. WARD. 1988. Competition and abiotic stress among trees and shrubs in northwest Colorado. *Ecology* 69: 1566–1577.
- WYMORE, I. F. 1974. Estimated average annual water balance of Piceance and Yellow Creek watersheds. *Colorado State University Environmental Resources Center Technical Report Series* No. 2.
- YEATON, R. I., AND M. L. CODY. 1976. Competition and spacing in plant communities: the northern Mohave Desert. *Journal of Ecology* 64: 689–696.
- YEATON, R. I., J. TRAVIS, AND E. GILINSKY. 1977. Competition and spacing in plant communities: the Arizona upland association. *Journal of Ecology* 65: 587–595.

Received 20 May 1990

Revised 5 November 1990

Accepted 8 January 1991





## TRAMPLING DISTURBANCE AND RECOVERY OF CRYPTOGAMIC SOIL CRUSTS IN GRAND CANYON NATIONAL PARK

David N. Cole<sup>1</sup>

**ABSTRACT.**—Cryptogamic soil crusts in Grand Canyon National Park were trampled by hikers, under controlled conditions, to determine how rapidly they were pulverized and how rapidly they recovered. Only 15 trampling passes were required to destroy the structure of the crusts; visual evidence of bacteria and cryptogam cover was reduced to near zero after 50 passes. Soil crusts redeveloped in just one to three years, and after five years the extensive bacteria and cryptogam cover left little visual evidence of disturbance. Surface irregularity remained low after five years, however, suggesting that recovery was incomplete.

Cryptogamic soil crusts are common and functionally significant features of arid ecosystems. Bacteria, algae, fungi, lichens, and mosses bind surface soil particles together, creating a highly irregular surface crust of raised pedestals (typically black and several cm tall) and intervening cracks. Crusts provide favorable sites for the germination of vascular plants (St. Clair et al. 1984) and play important roles in water conservation (Brotherson and Rushforth 1983) and nitrogen fixation (Snyder and Wullstein 1973). These crusts are particularly significant in reducing soil erosion. Soil aggregation raises the wind and water velocities required to detach soil particles, while the irregular soil surface tends to reduce wind and soil velocities (Brotherson and Rushforth 1983). Increased water infiltration in crusted soils also reduces runoff and erosion. Increased soil stability is highly significant in arid environments where sparse vegetation and surface soil organic matter as well as sporadic torrential rainfall contribute to a high erosion hazard.

A number of recent studies have examined the response of cryptogamic soil crusts to disturbance by grazing and by fire (Anderson et al. 1982, Johansen et al. 1984, Johansen and St. Clair 1986, Marble and Harper 1989). The results of these studies suggest that crusts are unusually fragile and can be seriously disrupted by low levels of disturbance that have no noticeable effect on vascular plants (Kleiner and Harper 1972).

The fragility of crusts presents unique challenges to land managers attempting to avoid adverse impacts on desert lands. This is particularly true in the many national parks located in the arid lands of the southwestern United States. The popularity of these desert parks has made it increasingly difficult for managers to meet management objectives that stress the maintenance of natural conditions and processes. Many hikers now visit places that a decade or two ago had few visitors. These backcountry users can significantly impact cryptogamic soil crusts if they wander off the trail or set up camp in crusted areas.

The purpose of this study was to examine the effect of trampling disturbance on soil crusts to better understand how rapidly they are disturbed and how quickly they can recover. It was conducted in the backcountry of Grand Canyon National Park on a study site located close to the Bass Trail, at an elevation of about 1,650 m. The site is flat, and during the study the soil crusts exhibited well-developed pinnacles and were conspicuously blackened with lichens. The vegetation type is a *Coleogyne ramosissima*–*Pinus edulis*–*Juniperus osteosperma* woodland (Warren et al. 1982). Soils, derived from sandstones of the Supai Group, are shallow and highly sandy. The climate can be characterized as that of a cold desert; annual precipitation is about 25 cm with a bimodal occurrence in winter and summer.

<sup>1</sup>Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, Missoula, Montana 59807.



Fig. 1. The two trampling lanes immediately after 50 passes in tennis shoes (left) and 250 passes in lug-soled boots (right). Note horizontal bar for measuring vertical distances.

METHODS

Two lanes about 6 m long and 0.4 m wide were delineated with lengths of PVC pipe in an area of well-developed, undisturbed soil crust (Fig. 1). The lanes were separated by a path that was trampled during the period when the treatments were applied and then allowed to recover afterward. One lane was trampled by a 75-kg person in tennis shoes, the other by an 86-kg person in lug-soled boots. Measurements were taken prior to trampling and after 5, 15, 25, and 50 passes, a pass being one walk down the lane at a normal gait. The lane trampled with lug-soled boots was trampled another 200 times, for a total of 250 passes. Subsequent measurements were taken one, three, and five years after the treatments were administered. Treatments and measurements occurred in late spring—April or May 1984.

Each lane was sampled along five transects oriented perpendicular to the lane and lo-

TABLE 1. Changes in the cryptogam cover, vertical distance, and coefficient of variation of vertical distance in response to different levels of trampling.\*

Number of passes	Cryptogam cover (%)	Vertical distance (mm)	Coefficient of variation (%)
0	89 a	492 a	2.7 a
5	69 b	497 ab	1.9 b
15	45 c	505 bc	1.5 b
25	36 c	502 abc	1.4 b
50	9 d	511 c	1.4 b
250	0 d	511 c	1.4 b

\*Any two values in the same column followed by the same letter are not significantly different (Duncan's multiple range test,  $p = .05$ ).

cated 1 m apart. Each transect consisted of 10 measurement points 2 cm apart in the central part of the lane. At each point along the transect the vertical distance between a horizontal pipe, temporarily connecting the pipe at each end of the transect, and the ground surface was measured. Then the ground surface at that point was categorized as either bare soil or cryptogam.

These data provide three measures to evaluate disturbance. First, the vertical distances, a mean of 50 observations per lane, provide a measure of the degree to which crusts have been compressed by trampling. The variability of vertical distances across each transect provides an indication of surface roughness, which should decline with trampling. Roughness increases with crustal development and is important in reducing soil erosion. The measure used is the coefficient of variation of the vertical distances. Coefficients were calculated for each of the five transects across each lane and then averaged. The third measure is cryptogam cover, expressed as a percentage of the 50 ground surface observations for each lane. The significance of differences, between treatments and between years, was tested with analysis of variance and Duncan's multiple range test.

RESULTS

Cryptogamic crusts were immediately pulverized by trampling. Pedestals were flattened, and the black veneer of bacteria and cryptogams was obliterated. Changes in cryptogam cover, vertical distance, and the index of surface roughness were all statistically significant (Table 1). Differences between the effects of trampling with tennis shoes and boots were not significant, however.

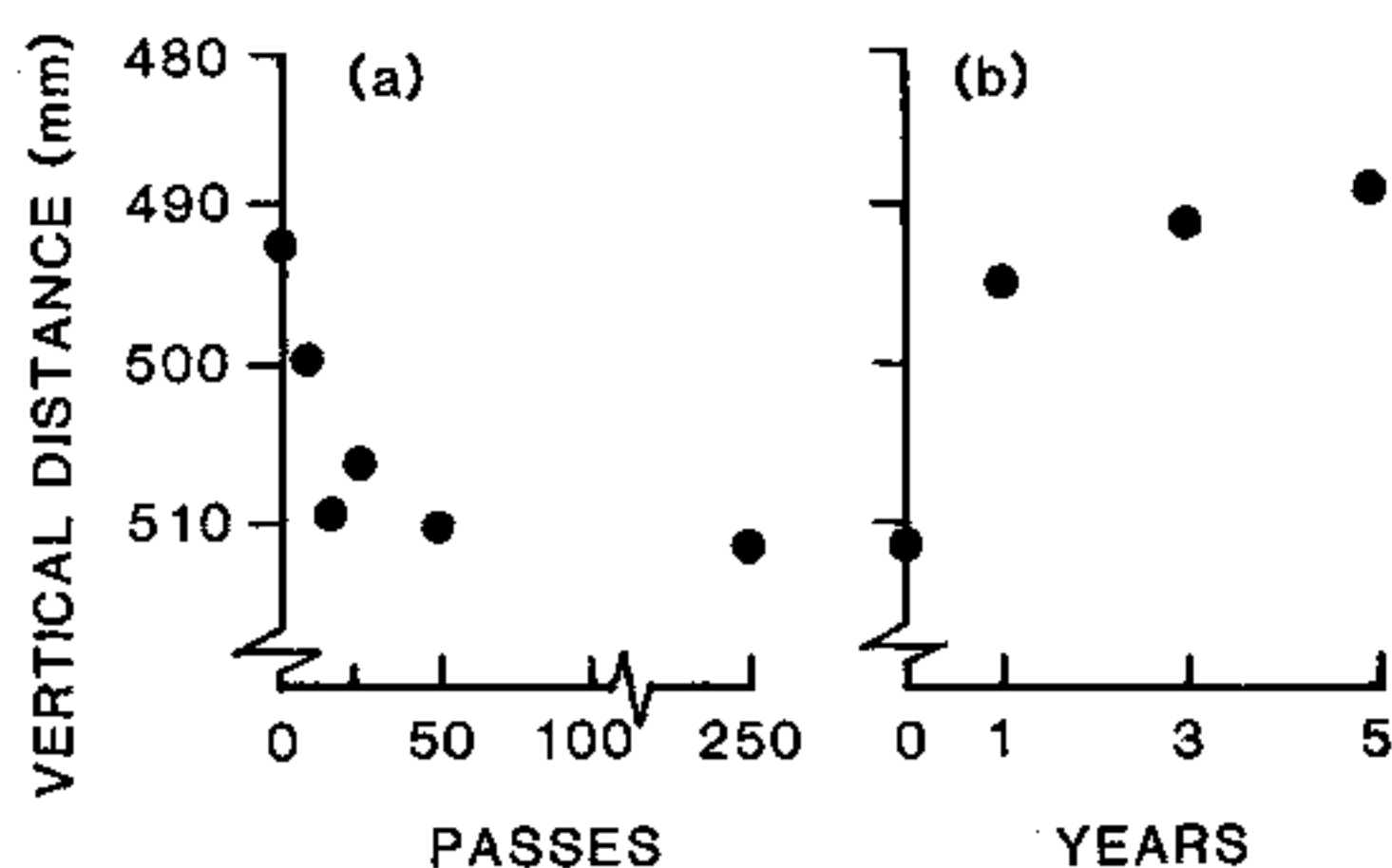


Fig. 2. Mean vertical distance from a horizontal transect to the ground surface (a) after different levels of trampling in lug-soled boots and (b) after one, three, and five years of recovery. Standards errors were all 2.2–2.8 mm.

TABLE 2. Cryptogam cover, vertical distance, and coefficient of variation of vertical distance 0, 1, 3, and 5 years following trampling.<sup>a</sup>

Years since trampling	Cryptogam cover (%)	Vertical distance (mm)	Coefficient of variation (%)
0	3 a	511 a	1.3 ab
1	20 b	499 b	1.0 a
3	71 c	491 c	1.9 b
5	85 d	490 c	1.9 b
Pre-trampling	89 d	492 c	2.7 c

<sup>a</sup>Any two values in the same column followed by the same letter are not significantly different (Duncan's multiple range test,  $p = .05$ ).

Cryptogam cover was reduced by 50% after 15 passes and was reduced to zero after 250 passes (Table 1). At this point the organisms were so widely dispersed that all visual evidence of their existence disappeared (Fig. 1). Destruction of pedestals also occurred rapidly (Fig. 2a). The vertical distance below the transect increased 13 mm following 15 passes. Additional trampling caused no significant further compression; the pedestals were already destroyed. Surface roughness, as measured by the mean coefficient of variation of the vertical distances, declined as the pedestals were pulverized (Table 1). All treatments were significantly different from the control, but not from each other. A blackened, irregular, aggregated soil surface was replaced after trampling by a flat surface of unconsolidated sands, which was much more vulnerable to erosion.

Substantial recovery occurred in the first



Fig. 3. The lane that received 250 passes in lug-soled boots after five years of recovery. View is from the end opposite that in Figure 1.

year after trampling ceased. After one year of recovery, cryptogam cover had increased significantly (Table 2), and vertical distance had decreased significantly (Fig. 2b); however, surface roughness had not increased (Table 2). The unconsolidated sands left by trampling had reaggregated into a smooth, raised crust, but neither pedestals nor the blackened veneer of organisms had reformed. After three years of recovery, vertical distances were similar to pre-trampling levels. Cryptogam cover had increased dramatically, as had surface roughness, although both were still below pre-trampling values (Table 2). After five years of recovery, cryptogam cover had returned to pre-trampling levels. At this point all visual evidence of damage was gone (Fig. 3). Surface roughness values remained depressed (Table 2), however, suggesting that pedestals had not redeveloped fully.

The typical pattern of structural destruction and recovery is illustrated in Figure 4, which



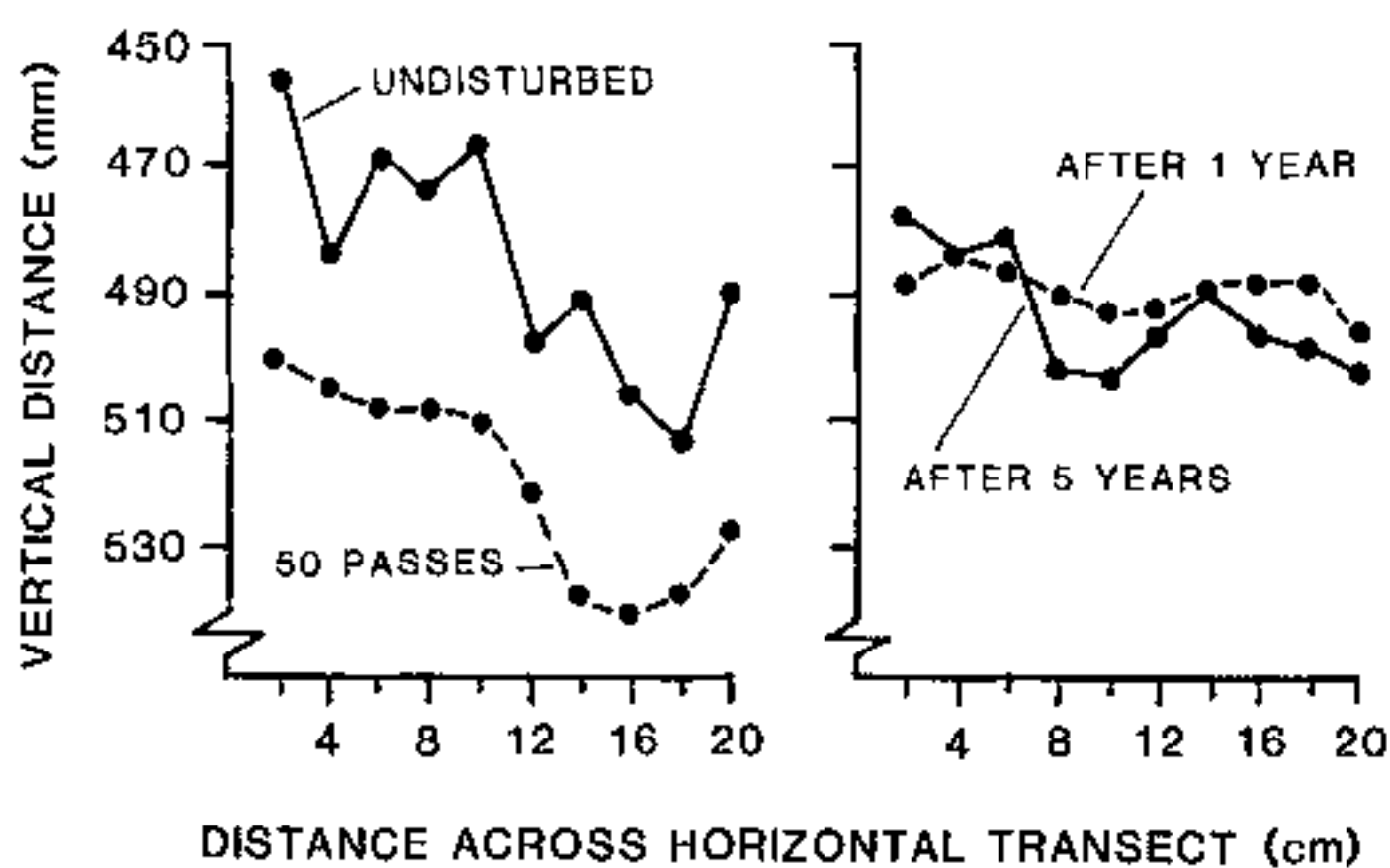


Fig. 4. Vertical distance from a horizontal transect to the ground surface (a) before trampling, (b) after 50 passes, (c) after one year of recovery, and (d) after five years of recovery. Data are for one of five transects across the lane trampled in tennis shoes.

shows the changes that occurred under one of the transects. Fifty passes with tennis shoes increased mean vertical distance and decreased variations between adjacent sample points. The redevelopment of a soil crust during the first year of recovery reduced vertical distance (i.e., the ground surface apparently rose), but surface irregularity remained low. After five years of recovery, the surface was more irregular than after trampling, but less irregular than before trampling.

DISCUSSION

These results illustrate the damage hikers can do to cryptogamic soil. The structure of these crusts was destroyed by only 15 passes, and cryptogam cover was negligible after only 50 passes. Compared with the response of vascular plants to similar levels of trampling disturbance, cryptogamic crusts are highly fragile but moderately resilient (Cole 1985, 1988). No other experimentally trampled vegetated surfaces have been denuded by such low levels of trampling.

Recovery was surprisingly rapid, however. This conclusion agrees with that of studies of recovery after grazing and fire (Johansen et al. 1984, Johansen and St. Clair 1986), which report more rapid and extensive recovery than anticipated. In this study recovery rates were probably increased by the close proximity of inoculum to the disturbed lanes and by the fact that disturbance occurred only once and was then removed. This study and previous ones rely primarily on visual criteria for

evaluating recovery. The depressed surface roughness values five years after trampling suggest that complete recovery will take longer than five years. On disturbed sites at Canyonlands National Park such parameters as chlorophyll content, species diversity, and the thickness of the subsurface gelatinous sheaths that bind soil particles remain low even after crusts appear to have recovered (Belnap 1990).

The finding that the crustal surface rose during the first few years following the cessation of trampling is intriguing. The process by which pinnacled crusts develop is not well understood, but this result suggests that they may develop through accretion rather than erosion. If they were erosional features, the undisturbed strips should have remained conspicuously higher than the treatment lanes. This was not the case.

Given the fragility of these crusts, random trampling by backcountry recreationists is capable of seriously impacting large areas. Very low levels of ongoing use will maintain high levels of disturbance. This shows up most commonly as webs of trails that surround trail junctions, camping areas, and points of interest. In arid parks of the southwestern United States it is important to educate visitors about the nature, importance, and fragility of cryptogamic crusts. With this knowledge, visitors are more likely to voluntarily minimize trampling of crusts and support management actions taken to protect areas of crust. Most visitors neither recognize cryptogams as fragile vegetation nor realize their importance to site stability. It is also important to locate trails, camping areas, and other activity sites away from places with well-developed crust and, where this is not possible, to try to confine traffic to one well-developed route.

The one positive management implication of this research lies in the finding of relatively fast visual recovery. Where it is possible to eliminate trampling, crusts can quickly reestablish themselves. In this experiment trampling left an apparently sterile surface of sand that, in reality, was heavily inoculated with crustal organisms. Managers can speed recovery of disturbed areas by inoculating them (St. Clair et al. 1986). Moreover, even though complete recovery may take much more than five years, the rapid elimination of

the visual evidence of damage is helpful. This makes it easier for managers to keep visitors off certain trails and campsites.

#### ACKNOWLEDGMENTS

Partial support for this research was provided by the Western Region, National Park Service, USDI. This paper profited from the comments, on an earlier draft, of Jayne Belnap, David Chapin, Jeff Johansen, and Jeff Marion.

#### LITERATURE CITED

- ANDERSON, D. C., K. T. HARPER, AND S. R. RUSHFORTH. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management* 35: 355-359.
- BELNAP, J. 1990. Microbiotic crusts: their role in past and present ecosystems. *Park Science* 10(3): 3-4.
- BROTHERSON, J. D., AND S. R. RUSHFORTH. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. *Great Basin Naturalist* 43: 73-78.
- COLE, D. N. 1985. Recreational trampling effects on six habitat types in western Montana. USDA Forest Service Research Paper INT-350. 43 pp.
- . 1988. Disturbance and recovery of trampled montane grassland and forests in Montana. USDA Forest Service Research Paper INT-389. 37 pp.
- JOHANSEN, J. R., AND L. L. ST. CLAIR. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. *Great Basin Naturalist* 46: 632-640.
- JOHANSEN, J. R., L. L. ST. CLAIR, B. L. WEBB, AND G. T. NEBEKER. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. *Bryologist* 87: 238-243.
- KLEINER, E. F., AND K. T. HARPER. 1972. Environment and community organization in grasslands of Canyonlands National Park. *Ecology* 53: 299-309.
- MARBLE, J. R., AND K. T. HARPER. 1989. Effect of timing of grazing on soil-surface cryptogamic communities in a Great Basin low-shrub desert: a preliminary report. *Great Basin Naturalist* 49: 104-107.
- SNYDER, J. M., AND L. H. WULLSTEIN. 1973. The role of desert cryptogams in nitrogen fixation. *American Naturalist* 90: 257-265.
- ST. CLAIR, L. L., J. R. JOHANSEN, AND B. L. WEBB. 1986. Rapid stabilization of fire-disturbed sites using a soil crust slurry: inoculation studies. *Reclamation and Revegetation Research* 4: 261-269.
- ST. CLAIR, L. L., B. L. WEBB, J. R. JOHANSEN, AND G. T. NEBEKER. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. *Reclamation and Revegetation Research* 3: 129-136.
- WARREN, P. L., K. L. REICHHARDT, D. A. MOUAT, B. T. BROWN, AND R. R. JOHNSON. 1982. Vegetation of Grand Canyon National Park. Technical Report 9, USDI National Park Service, University of Arizona, Tucson. 140 pp.

*Received 1 June 1990*

*Revised 2 November 1990*

*Accepted 8 January 1991*



## EIMERIA SP. (APICOMPLEXA: EIMERIIDAE) FROM WYOMING GROUND SQUIRRELS (*SPERMOPHILUS ELEGANS*) AND WHITE-TAILED PRAIRIE DOGS (*CYNOMYS LEUCURUS*) IN WYOMING

Larry M. Shults<sup>1,2</sup>, Robert S. Seville<sup>1</sup>, Nancy L. Stanton<sup>1</sup>, and George E. Menkens, Jr.<sup>1,3</sup>

**ABSTRACT.**—Six species of the coccidian genus *Eimeria* (*E. larimerensis* [prevalence = 17%], *E. bilamellata* [12%], *E. beecheyi* [34%], *E. morainensis* [43%], *E. callospermophili* [21%], and *E. spermophili* [5%]) were recovered from Wyoming ground squirrels (*Spermophilus elegans elegans*) collected during 1983, 1984, 1985, and 1986. Infected ground squirrels were found to harbor from one to five species simultaneously. The 1007 hosts examined were collected from two different habitats: (1) a xeric desert shrub-steppe and (2) an irrigated alfalfa-brome field. All species of *Eimeria* occurred at each study site during all years, although the prevalence of each species varied between years. This is the first report of these congeries of species infecting this host. In a second study of sympatric populations of Wyoming ground squirrels and white-tailed prairie dogs (*Cynomys leucurus*), we found three species of *Eimeria* present in both host populations (*E. beecheyi* [white-tailed prairie dog prevalence = 83%, Wyoming ground squirrel = 52%], *E. morainensis* [22%, 52%], and *E. bilamellata* [17%, 10%]). This is the first report of these three species infecting white-tailed prairie dogs. *Eimeria larimerensis* was found in Wyoming ground squirrels but not in prairie dogs.

Levine and Ivens (1990) recently reported 17 species of *Eimeria* from ground squirrels of the genus *Spermophilus*. In most cases these species of *Eimeria* were described from small samples of hosts collected from restricted geographic locations, and only 1 or 2 species were recovered from the limited sample population of squirrels. They listed no species from the Wyoming ground squirrel, *Spermophilus elegans* Kennicott, 1863.

Additionally, Duszynski (1986) has reported that the host specificity of the coccidian genus *Eimeria* may be rather broad. For example, *Eimeria bilamellata* Henry, 1932 has been reported in nine species of ground squirrels (*Spermophilus* spp.) (Levine and Ivens 1990); and *E. larimerensis* Vetterling, 1964 has been found in five ground squirrel species, white-tailed prairie dogs (*Cynomys leucurus* Merriam, 1890) (Todd and Hammond 1968a), and black-tailed prairie dogs (*C. ludovicianus* Ord, 1815) (Vetterling 1964). Cross-transmission experiments with oocysts from prairie dogs inoculated into ground squirrels have been successful (Todd and Hammond 1968a, 1968b, Todd et al. 1968).

The purpose of this paper is to report the prevalence of six eimerian species in two

populations of Wyoming ground squirrels occurring in two habitats and to report the eimerian parasites of sympatric populations of Wyoming ground squirrels and white-tailed prairie dogs.

### METHODS

As part of an ongoing study on the life history of the Wyoming ground squirrel, 1007 individuals were examined for the presence of coccidian parasites of the genus *Eimeria* over a four-year period. These hosts were collected from two habitats: (1) xeric cold desert shrub-steppe, 14 km north of Baggs, Wyoming (107°45'W, 41°17'N) and (2) an irrigated alfalfa-brome field, 10 km south of Laramie, Wyoming (105°33'W, 41°12'N).

In late June and early July of 1983 and 1986 ground squirrels were snap-trapped in both study areas using three 40 × 50 trapping grids (0.6 ha) with traps set every 5 m (240 total traps). In 1984 and 1985 squirrels were randomly shot within the study sites throughout their summer active season (April–August). All squirrels were weighed, sexed, and necropsied. Fecal material was obtained during necropsy from the lower large intestine.

<sup>1</sup>Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA 82071.

<sup>2</sup>Present address: Toxikon Environmental Sciences, 106 Coastal Way, Jupiter, Florida, USA 33477.

<sup>3</sup>Now deceased; Dr. Menkens' plane was lost at sea on 8 November 1990 while flying a polar bear survey for the USFWS.



The second study was initiated in conjunction with a white-tailed prairie dog study conducted by Menkens and Anderson (1989). The study area, located 11 km south of Laramie, Wyoming (105°40'W, 41°20'N), contained populations of both *C. leucurus* and *S. elegans* as well as a small population of 13-lined ground squirrels (*S. tridecemlineatus* Mitchell, 1821). A trapping grid of 11.3 ha containing 176 National live traps was established. Traps were baited with oats and opened before daylight each morning. After a four-hour trapping period the traps were closed for the remainder of the day. Trapped animals were weighed, sexed, and released; feces were collected from each trap following the animal's release. Trapping occurred over a five-day period, 3–7 July 1987.

All fecal samples collected in both studies were placed in 2% potassium dichromate solution at room temperature (25 C) for two to three weeks to allow oocyst sporulation for species identification. Sporulated oocysts were isolated by flotation in saturated sucrose flotation solution (specific gravity = 1.2) and identified at 100X objective with an Olympus (CH) compound microscope.

## RESULTS

In the first study 613 ground squirrels were collected from the irrigated site and 394 from the xeric site. Six species of *Eimeria* were found infecting both populations. For the entire sample, 26% of the squirrels harbored one eimerian species, 26% had two species, 13% had three species, 2% had four, and only two animals were infected with five species simultaneously.

During the four-year sampling period, 168 of 1007 (17%) *S. elegans* examined were infected with *E. larimerensis*. Significantly more hosts were infected in the irrigated study site (23%) than in the xeric site (6%) ( $\chi^2$ ,  $p \leq .01$ ) (Table 1).

*Eimeria bilamellata* was found infecting 11% of the squirrels examined. The prevalence of *E. bilamellata* varied among years and sites but there were never more than 21% of the hosts infected at any site during any year (Table 1). Overall, there was no significant difference in prevalence between the two sites over the four years ( $\chi^2$ ,  $p \leq .10$ ).

*Eimeria beecheyi* Henry, 1932 was the second most prevalent species found during the study (34%), and for the four-year period the prevalence was higher in the alfalfa field (38% vs. 27%), but the difference was not significant ( $\chi^2$ ,  $p \leq .10$ ) (Table 1).

*Eimeria morainensis* Torbett, Marquardt, and Carey, 1982 was the most prevalent species found during the study (43%). Significantly more hosts were infected with this species at the irrigated site (55% vs. 25%) during the four years ( $\chi^2$ ,  $p \leq .01$ ) (Table 1).

*Eimeria callospermophili* Henry, 1932 was found infecting 21% of the squirrels examined. It was present in both populations, but no difference in prevalence was found between the two study sites over the four years ( $\chi^2$ ,  $p \leq .10$ ) (Table 1).

*Eimeria spermophili* Hilton and Mahrt, 1971 was the least common species found during this study (5%). It occurred in only a few hosts from each study site, and no significant difference in prevalence occurred between the two sites ( $\chi^2$ ,  $p \leq .10$ ) (Table 1).

In the second study a total of 69 *S. elegans*, 18 *C. leucurus*, and one *S. tridecemlineatus* were trapped over the five-day period. Of these, 47 *S. elegans* (68%) and 17 *C. leucurus* (94%) were positive for the presence of *Eimeria* oocysts. Thirty-six *S. elegans* (52%) and 15 *C. leucurus* (83%) were infected with *E. beecheyi*. Similarly, 36 *S. elegans* (52%) and 4 *C. leucurus* (22%) harbored *E. morainensis*. Three *C. leucurus* (17%) and 7 *S. elegans* (10%) were infected with *E. bilamellata*. *Eimeria larimerensis* infected 3 *S. elegans* (4%) and none of the 18 *C. leucurus*. Up to three eimerian species were found co-occurring in individual hosts.

## DISCUSSION

*Eimeria larimerensis* was first described from *C. ludovicianus* from Larimer County, Colorado (Vetterling 1964). In 1968 this eimerian was reported by Todd and Hammond from an additional seven species of *Spermophilus*, including *S. armatus* Kennicott, 1863 from Utah and Montana; *S. variegatus* Erxleben, 1777 from Utah; *S. tridecemlineatus* from Wyoming; *S. lateralis* Say, 1823 from Utah; *S. beecheyi* Richardson, 1829 from California; *C. leucurus* Merriam, 1890 from Wyoming (Todd and Hammond 1968b); and

TABLE 1. Number and percentage of Wyoming ground squirrels (*Spermophilus elegans*) infected by *Eimeria* sp. by year. Samples ( $N = 1007$ ) were taken from two habitats in Wyoming. Animals may be infected simultaneously by more than one species of *Eimeria*.

Species of <i>Eimeria</i>	1983				1984				1985			
	Mesic ( $N = 314$ ) <sup>a</sup>		Xeric ( $N = 212$ )		Mesic ( $N = 34$ )		Xeric ( $N = 72$ )		Mesic ( $N = 86$ )		Xeric ( $N = 74$ )	
	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%
<i>larimerensis</i>	53	17	12	6	10	29	8	11	8	9	4	5
<i>bilamellata</i>	35	11	7	3	2	6	8	11	17	20	1	1
<i>beecheyi</i>	45	14	26	12	7	21	22	31	37	43	45	61
<i>morainensis</i>	128	41	34	16	13	38	28	39	52	60	25	34
<i>callospermophili</i>	83	26	33	16	16	47	30	42	18	21	17	23
<i>spermophili</i>	19	6	4	2	6	18	2	3	2	2	8	10

Species of <i>Eimeria</i>	1986				Total			
	Mesic ( $N = 179$ )		Xeric ( $N = 36$ )		Mesic ( $N = 613$ )		Xeric ( $N = 394$ )	
	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%	No. of squirrels infected	%
<i>larimerensis</i>	72	40	1	3	143	23	25 <sup>b</sup>	6
<i>bilamellata</i>	37	21	1	3	91	15	26	7
<i>beecheyi</i>	143	80	13	36	232	38	106	27
<i>morainensis</i>	143	80	12	33	336	55	99 <sup>b</sup>	25
<i>callospermophili</i>	16	9	0	0	133	22	80	20
<i>spermophili</i>	8	4	0	0	35	6	14	4

<sup>a</sup>Number of squirrels examined.

<sup>b</sup>Significant,  $p < .01$ .

*S. spilosoma* Bennett, 1833 from Colorado (Broda and Schmidt 1978). Experimentally, Todd and Hammond (1968b) inoculated what they called *S. richardsonii* Sabine, 1822 with *E. larimerensis*. Although all eight individuals developed "severe diarrhea" three to four days post-inoculation, no oocysts were recovered. *Spermophilus richardsonii* from Wyoming has since been elevated to specific status, *S. elegans*, by Zegers (1984).

*Eimeria bilamellata* was first described from *S. lateralis* in California (Henry 1932). It has been reported from *S. citellus* Linnaeus, 1766 in Hungary and Czechoslovakia (Pellerdy and Babos 1953), *S. franklinii* Sabine, 1822 from Iowa (Hall and Knipling 1935), *S. armatus* from Utah and Wyoming, *S. beecheyi* from California, and *S. variegatus* from Utah (Todd et al. 1968). Todd et al. (1968) were unable experimentally to infect *S. richardsonii* (syn. *S. elegans*) from Wyoming with sporulated oocysts from any of the above donor hosts.

*Eimeria beecheyi* was originally described from *S. beecheyi* collected in California

Henry 1932). Since its first report, it has been found only in *S. relictus* in the USSR (Abenov and Svanbaev (1982).

*Eimeria morainensis* was first described by Torbett et al. (1982) from *S. lateralis* collected in northern Colorado. This is only the second report of the occurrence of *E. morainensis*.

*Eimeria callospermophili* was first described from *S. lateralis* in California (Henry 1932). More recently it has been reported from that same host in northern Colorado (Torbett et al. 1982). This species is widespread both in its host and geographical distribution, having been reported from *S. fulvus* Lichtenstein, 1823 and *S. maximus* Pallas, 1778 in the Soviet Union (Levine and Ivens, 1990), *S. spilosoma* from Mexico (Levine et al. 1957), *S. beldingi* Merriam, 1888 from California (Veluvolu and Levine 1984), *S. columbianus* Ord, 1815, *S. franklinii*, and *S. richardsonii* in Alberta, Canada (Hilton and Mahrt 1971). In addition, Todd and Hammond (1968a) found this species in six species of *Spermophilus* and *C. leucurus* (*S. armatus*



from Utah and Montana, *S. richardsonii* from Montana and Wyoming [syn. *S. elegans*], *S. beecheyi* from California, *S. lateralis* and *S. variegatus* from Utah, and *S. tridecemlineatus* and *C. leucurus* from Wyoming).

*Eimeria spermophili* was first described by Hilton and Mahrt (1971) from *S. richardsonii* collected in Alberta, Canada. They also found this species in *S. franklinii* from the same area.

This is the first report of these six eimerian species infecting *S. elegans* and the first of *E. beecheyi*, *E. morainensis*, and *E. bilamellata* in *C. leucurus*.

In the first study, although the number of infected ground squirrels changed from year to year, the same species were present at both locations throughout the four-year period. The large sample collected from different habitats over a four-year period indicates that a single ground squirrel population can be infected with several species of *Eimeria*. With a few exceptions, the results of this study suggest that if intensive sampling were conducted with any of the other species of *Spermophilus*, more species of *Eimeria* would be found (Parker et al., in review).

Moreover, the known species of *Eimeria* may be considerably more widespread in their host distribution. As noted above, several reports of sharing of coccidian parasites between species within a genus and between different genera of sciurid hosts exist (Todd and Hammond 1968a, 1968b, Todd et al. 1968, Duszynski 1986). Veluvolu and Levine (1984) stated that an individual eimerian species may infect at least 11 host species. However, most previous coccidian surveys of host populations have reported a low species richness of the parasite community. Todd and Hammond (1968b) reported the presence of *E. larimerensis* in 5 species of *Spermophilus* and *C. leucurus*. They did not find this species in *S. elegans*, nor could they experimentally establish an infection in this species. This contrasts with the results of our first study in which we found 18% of the ground squirrels infected with this species. *Eimeria bilamellata* was also reported from a variety of ground squirrels by Todd et al. (1968), although they did not find this species in wild populations of *C. leucurus* or *S. richardsonii* (syn. *S. elegans*). These results also differ from ours in that we found 14% of 1007 *S. elegans* infected

with this species. However, Shults (1986) could not experimentally establish infections in this host even after immunosuppression with corticosteroids for seven days prior to inoculation.

*Eimeria morainensis* and *E. beecheyi* are two of the most common protozoan parasites infecting *S. elegans*, but neither species has been previously reported from *C. leucurus*.

It is interesting to note that of the species of *Eimeria* originally described from *C. ludoviciani* by Vetterling (1964) (*E. ludoviciani*, *E. cynomysis*, *E. larimerensis*), and which have also been identified from *C. leucurus* in northwestern Wyoming (Seville and Williams, 1989), none were found in *C. leucurus* from our site.

#### ACKNOWLEDGMENTS

The authors thank Dr. N. Kingston, Department of Veterinary Sciences, University of Wyoming, for critical review of the manuscript. This research was supported in part by NSF grant #BSR-8909887 and the Office of Research, University of Wyoming.

#### LITERATURE CITED

- ABENOV, D. B., AND S. K. SVANBAEV. 1982. Materialy po izucheniyu koktsidii reliktovogo suslika (*Citellus relictus*) v Kazakhstane. Pages 3-5 in Zayanchkauskas et al., eds., *Kishechnye Prosteiche Institute Zoology Parazitologica Litovsk SSR Akademii Nauk SSR Vil'nyus*.
- BRODA, R. J., AND G. D. SCHMIDT. 1978. Endoparasites of the spotted ground squirrel, *Spermophilus spilosoma* Bennett, 1833, from Colorado. *Journal of Helminthology* 52: 321-326.
- DUSZYNSKI, D. W. 1986. Host specificity in the coccidia of small mammals: fact or fiction? *Symposia Biologica Hungarica* 33: 325-337.
- HALL, P. R., AND E. F. KNIPLING. 1935. *Eimeria franklinii* and *Eimeria eubeckeri*, two new species of coccidia from Franklin ground squirrel, *Citellus franklinii*. *Journal of Parasitology* 21: 128-129.
- HENRY, D. P. 1932. Observations on the coccidia of small mammals in California with descriptions of seven new species. *University of California Publications in Zoology* 37: 279-290.
- HILTON, D. F. J., AND J. L. MAHRT. 1971. *Eimeria spermophili* n. sp. and other *Eimeria* spp. (Sporozoa, Eimeridae) from three species of Alberta *Spermophilus* (Rodentia, Sciuridae). *Canadian Journal of Zoology* 49: 699-701.
- LEVINE, N. D., V. IVENS, AND F. J. KRUIDENIER. 1957. New species of *Eimeria* from Arizona rodents. *Journal of Protozoology* 4: 80-88.

- . 1990. The coccidian parasites (Protozoa: Sporozoa) of rodents. CRC Press, Boca Raton, Florida. 228 pp.
- MENKENS, G. E., JR., AND S. H. ANDERSON. 1989. Temporal-spatial variation in the white-tailed prairie dog demography and life histories in Wyoming. *Canadian Journal of Zoology* 67: 343–349.
- PELLERDY, L., AND A. BABOS. 1953. Zur Kenntnis der Kokzidien aus *Citellus citellus*. *Acta Veterinaria Academiae Scientiarum Hungaricae* 3: 167–172.
- SEVILLE, R. S., AND E. S. WILLIAMS. 1989. Endoparasites of the white-tailed prairie dog, *Cynomys leucurus*, at Meeteetse, Park County, Wyoming. *Proceedings of the Helminthological Society of Washington* 56: 204–206.
- SHULTS, L. M. 1986. Coccidian parasites (Eimeriidae) of the Wyoming ground squirrel, *Spermophilus elegans*. Unpublished dissertation, University of Wyoming, Laramie. 101 pp.
- TODD, K. S., JR., AND D. M. HAMMOND. 1968a. Life cycle and host specificity of *Eimeria callospermophili* Henry, 1932 from the Uinta ground squirrel *Spermophilus armatus*. *Journal of Protozoology* 15: 1–8.
- . 1968b. Life cycle and host specificity of *Eimeria larimerensis* Vetterling, 1964, from the Uinta ground squirrel *Spermophilus armatus*. *Journal of Protozoology* 15: 268–275.
- TODD, K. S., JR., D. M. HAMMOND, AND L. C. ANDERSON. 1968. Observations on the life cycle of *Eimeria bilamellata* Henry, 1932, in the Uinta ground squirrel *Spermophilus armatus*. *Journal of Protozoology* 15: 732–740.
- TORBETT, B. E., W. C. MARQUARDT, AND A. C. CAREY. 1982. A new species of *Eimeria* from the golden-mantled ground squirrel, *Spermophilus lateralis*, in northern Colorado. *Journal of Protozoology* 29: 157–159.
- VELUVOLU, P., AND N. D. LEVINE. 1984. *Eimeria beldingii* n.sp. and other coccidia (Apicomplexa) of the ground squirrel *Spermophilus beldingii*. *Journal of Protozoology* 31: 357–358.
- VETTERLING, J. M. 1964. Coccidia (*Eimeria*) from the prairie dog, *Cynomys ludovicianus*, in northern Colorado. *Journal of Protozoology* 11: 89–91.
- ZEGERS, D. A. 1984. *Spermophilus elegans*. *Mammalian Species* No. 214: 1–7. American Society of Mammalogists.

Received 1 August 1990

Revised 8 January 1991

Accepted 24 January 1991





## EMERGENCE, ATTACK DENSITIES, AND HOST RELATIONSHIPS FOR THE DOUGLAS-FIR BEETLE (*DENDROCTONUS PSEUDOTSUGAE* HOPKINS) IN NORTHERN COLORADO

E. D. Lessard<sup>1</sup> and J. M. Schmid<sup>2</sup>

**ABSTRACT.**—Douglas-fir beetle-infested Douglas-fir trees were partially caged to determine the emergence period and beetle production. Beetles began emerging in April, but emergence peaked between 10 and 26 June. In 1987 and 1988 beetle emergence averaged 20 or more per sq. ft. of bark. Annual growth of the infested trees showed a decline prior to the beetle outbreak followed by an increase during the outbreak.

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is usually an insignificant pest of Douglas-fir (*Pseudotsugae menziesii* [Mirb.] Franco) in the Front Range of Colorado. The beetle's life cycle generally lasts one year, although a partial second generation has been noted in other parts of its range. The beetle prefers windthrown trees but will infest standing trees during droughts or high population levels (Wood 1963). Standing trees also become more susceptible to infestation by the Douglas-fir beetle after severe defoliation by insects (Wright et al. 1984).

In 1972 western spruce budworm (*Choristoneura occidentalis* Freeman) populations began to increase in Roosevelt National Forest west of Fort Collins. Defoliation was noticeable, moderate, and limited to 3500 acres (1378 ha) in 1974 (Minnemeyer 1974), but by 1976, 54,000 acres (21,260 ha) were moderately to severely defoliated. Parts of Poudre Canyon, the location in this study, were severely defoliated (Cresap 1976). In 1977, the area of severe defoliation more than doubled on the forest (115,840 acres [45,606 ha]). Defoliation continually increased from 1977 until 1983, reaching a maximum of 469,000 acres (184,646 ha) (see Raimo 1983). Defoliation in Poudre Canyon, while noted as early as 1976, was confined to particular portions and was not extensive throughout until 1980 (see Linnane 1977, 1981). Thereafter, it was extensive and moderate to severe on most north-facing slopes until 1983–84.

Although the acreage of moderately to severely defoliated stands progressively increased from 1977 to 1983, egg mass densities peaked in 1980, four years prior to the maximum acreage defoliation, and had declined substantially by 1984 (see Raimo 1983, 1984). By 1985 population levels became endemic, with only light defoliation visible.

As the budworm outbreak subsided, Douglas-fir beetle populations began to increase. Scattered groups of faded trees were observed in the mid-1970s. Subsequently, beetle-killed Douglas-fir have increased both in numbers and in geographic extent (J. M. Schmid, personal observation). Numerous stands of Douglas-fir on north-facing slopes suffered significant tree mortality.

Because tree mortality became significant and our knowledge of the life history and habits of the Douglas-fir beetle in Colorado was deficient, the current infestations provided an opportunity to learn more about the beetle's life history and habits in Douglas-fir stands in Colorado and expanded our knowledge of the geographic variation in these aspects of the beetle's biology.

### METHODS

To monitor beetle emergence, we attached 1 × 2-ft. (.3 × .6-m) wire screen emergence cages to infested trees in Poudre Canyon west of Fort Collins, Colorado, in late February 1987. Two cages were attached at breast height on each of five randomly selected

<sup>1</sup>Forest Pest Management, R-10, Anchorage, Alaska 99601.

<sup>2</sup>Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado 80526.

1986-infested trees at each of three locations: the Narrows, Pingree Park road turnoff, and near BM 6998 (east of Indian Meadows). On April 3 another five trees near Crystal Lakes (northwest of Red Feather Lakes) were caged in the same manner.

To monitor emergence in 1988, we attached cages, as described above, to five 1987-infested trees on each of four sites: near Crystal Lakes (northwest of Red Feather Lakes) and in Poudre Canyon in late September 1987, and also near Camman Springs (south of Poudre Canyon) and near Black Mountain (north of Red Feather Lakes) in late October.

Cages were attached at breast height for practical purposes. Furniss (1962) recommended sampling for attack and brood densities at the midpoint on the bole because attack densities were twice as great there as at breast height, attack success was greatest in the midpoint zone, and live brood was greater. Furniss worked on standing trees that averaged 20 inches in diameter at breast height and ranged in height from 79 to 162 ft.; the sampling point on the average tree was thus 40 ft. or more aboveground. In contrast, our trees averaged 15 inches in diameter at breast height with trees only at the Pingree Park road site averaging 20 inches; tree height ranged from 34 to 88 ft. Although Furniss recommended sampling at or near the midpoint of the bole, it should be noted that he felled his trees for sampling and did not extract his samples from standing trees. In addition, the zone of optimum sampling is lower on smaller trees in the southern portion of the trees' range, i.e., southern Utah, than in Idaho, where Furniss did his study. Because our trees were smaller and were not to be felled, the terrain was difficult at some sites, and there was no evidence to suggest that the beetle's emergence pattern varied with height, we attached cages at breast height.

During 1987 and 1988, cages were checked at one- to two-week intervals from 1 April to 1 July. After 1 July, cages were checked at irregular intervals through September. During each check period, the number of emerging adults was recorded for each cage, and observations were made on the discoloration of foliage on the infested trees.

The density of emerging beetles per sq. ft. (.09 m<sup>2</sup>) of bark surface was determined by dividing the total number of beetles emerging

in each cage by the surface area covered by each cage (ca. 2 sq. ft. [.18 m<sup>2</sup>]). Beetle numbers were subjected to one-way analysis of variance to determine if differences among locations were significant ( $\alpha = .05$ ). Beetle numbers at breast height were also tested against their respective tree diameters to determine if beetle production was related to tree diameter (DBH). For each year, tree diameters were grouped into three classes, and beetle numbers among diameter classes were tested for significant differences using analysis of variance ( $\alpha = .05$ ). For 1987 the diameter classes in inches (cm) were: 7.5–9.6 (19–24), 11.2–15.7 (31–61) and 16.2–24.3 (41–62). For 1988 diameter classes were: 9.3–12.5 (24–32), 12.6–13.3 (32–34), and 13.4–18.0 (34–46). Diameter classes differed between 1987 and 1988 because the diameters of the infested trees were different. A one-way ANOVA was used because all diameter classes were not equally present on all locations.

Population trend was evaluated by dividing the density of emerging beetles by twice the density of attacks (this assumes a pair of beetles creates each attack). When the ratio of emerging beetle density to attack density exceeds one, the beetle population is increasing. When the ratio is less than one, the population is decreasing.

The density of beetle attacks on standing trees was determined by removing 6 × 12-inch (15 × 30-cm) bark samples from or near breast height. Two samples were removed from each 1986-infested tree in late October 1987. Two samples from each 1987-infested tree were removed in late September 1987. The bark samples from 1987-infested trees were also used to determine brood density and stage of development.

To determine past growth rates of the 1986-infested trees, we extracted increment cores from the caged trees at breast height. Annual radial growth for each of the last 20 years was measured to .001 inch (.03 mm). Mean annual growth was determined for all trees from each of the four locations. Annual growth during the three preceding five-year periods (1972–76, 1977–81, 1982–86) was analyzed for significant differences in the periodic growth rate using one-way analysis of variance ( $\alpha = .05$ ). Separate one-way analysis of variance was used for each location because

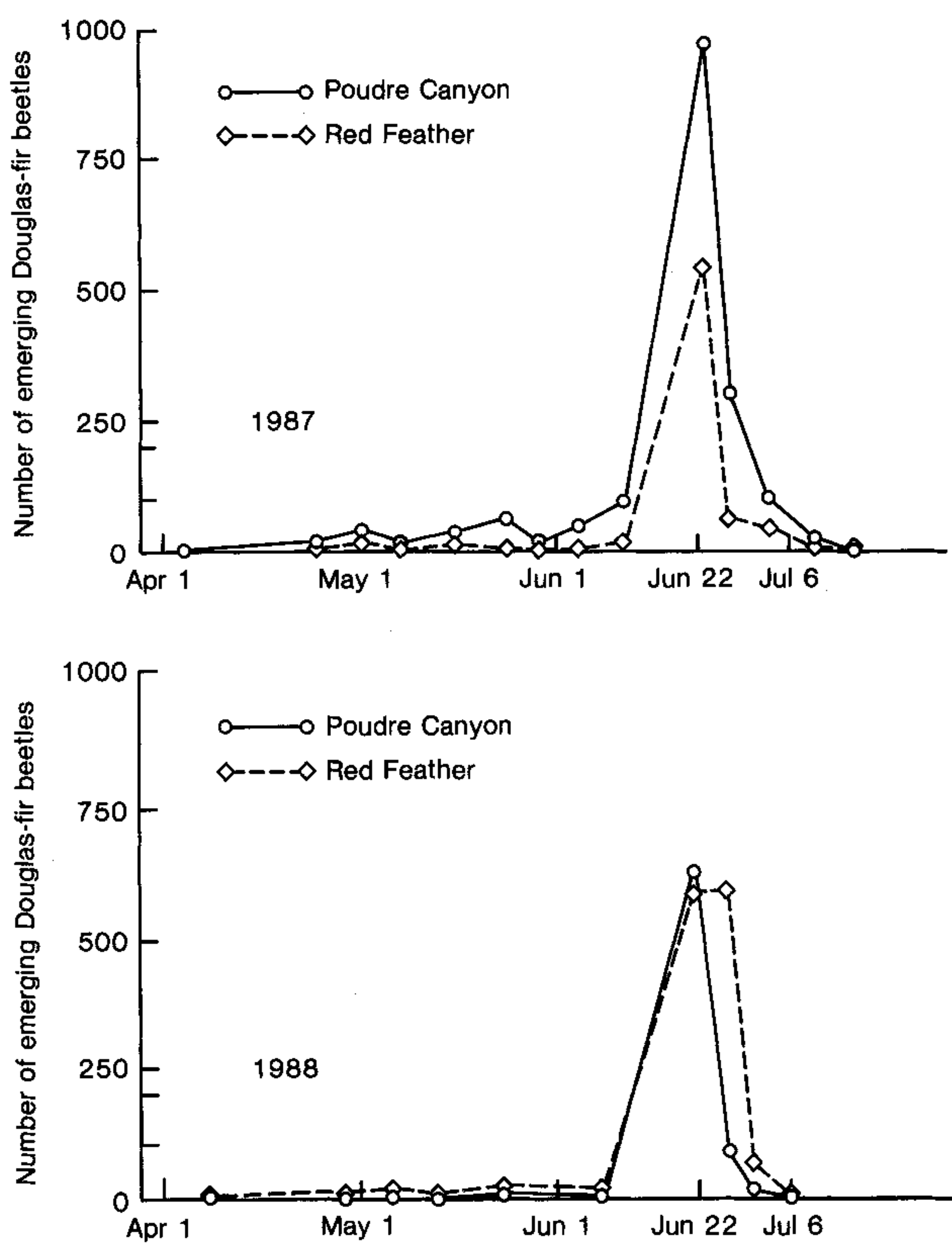


Fig. 1. Total number of Douglas-fir beetles emerging from five trees at four locations in the Arapaho-Roosevelt National Forest, Colorado, in 1987 and 1988.

the variability in site and stand conditions would not yield meaningful results in a more complex statistical design testing for differences among locations and their interactions. Periodic growth for the five-year periods was also used to compute Mahoney's PGR (Mahoney 1978), which is the ratio of the growth for one five-year period to the growth for the previous five years.

When analysis of variance indicated signifi-

cant differences among the means, Tukey's test was used to determine which means were different ( $\alpha = .05$ ) (Steel and Torrie 1960).

RESULTS AND DISCUSSION

EMERGENCE.—Adults began emerging in mid-April of both years (Fig. 1), continuing to emerge at low rates until early June. Emergence peaked between 10 and 26 June in both



TABLE 1. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m<sup>2</sup>) of bark for several locations in the Arapaho-Roosevelt National Forest. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Location	Number of trees		Cages per tree	Number of beetles ( $\bar{x} \pm S.D.$ )	
	1987	1988		1987	1988
Narrows	5	2	2	27 $\pm$ 14 a	
Pingree Park Road	5	2	2	40 $\pm$ 20 a	
BM 6998	5	5	2	21 $\pm$ 15 a	30 $\pm$ 28 ab
Crystal Lakes	5	5	2	39 $\pm$ 18 a	55 $\pm$ 33 a
Camman Spring		5	2		8 $\pm$ 10 b
Black Mountain		5	2		10 $\pm$ 11 b

years. Adults rarely emerged after 1 July. In terms of percentage of the emerging populations, 18% of the beetles had emerged by 10 June in 1987 and 4% in 1988; 77% and 92% emerged between 10 and 26 June in 1987 and 1988; 5% and 4% emerged after 26 June, respectively. After 1 July, 2% or less emerged in both years.

Wood (1963) noted two principal flight periods for the Douglas-fir beetle in California, Oregon, and Utah, depending on the overwintering life stage—one during May–June and another during July–August. In this study we found only one principal flight period. If a second flight period is occurring, we believe the beetles are reemerging adults, not new adults emerging later from the caged hosts.

DENSITY OF EMERGING ADULTS.—The number of adults emerging per sq. ft. (.09 m<sup>2</sup>) of bark surface ranged from 6 to 82 in 1987 and 0 to 88 in 1988. Mean numbers per sq. ft. (.09 m<sup>2</sup>) of bark showed significant variation among areas in 1987 and 1988, but Tukey’s test did not reveal significant pairwise comparisons in 1987 (Table 1).

Although the number of emerging beetles did not significantly correlate with DBH, areas where mean tree diameter was 8.5 inches (22 cm) or less produced the lowest number of beetles. In addition, numbers were influenced by the density of attacks and tree diameter. The population trend ratio was generally >1 when attack densities were  $\leq$ 12 per sq. ft. (.09 m<sup>2</sup>) and tree diameter was >10 inches (25 cm) DBH. When tree diameter was <10 inches (25 cm), the trend ratio was <1. Similarly, when the density of attacks was >14 per sq. ft. (.09 m<sup>2</sup>), the trend ratio was generally <1. Population trend thus appears to be influenced by competition (McMullen

TABLE 2. Mean number of Douglas-fir beetles emerging per sq. ft. (.09 m<sup>2</sup>) of bark by diameter class. Within the same year, means followed by the same letter are not significantly different (alpha = .05).

Diameter class (inches [cm])	Number of trees	Number of beetles ( $\bar{x} \pm S.D.$ )
	1987	
7.5 – 9.6 (19–24)	5	21 $\pm$ 15 a
11.2 – 15.7 (28–40)	7	36 $\pm$ 16 a
16.2 – 24.3 (41–62)	8	34 $\pm$ 21 a
	1988	
9.3 – 12.5 (24–32)	6	22 $\pm$ 25 a
12.6 – 13.3 (32–34)	7	20 $\pm$ 20 a
13.4 – 18.0 (34–46)	7	35 $\pm$ 38 a

and Atkins 1961) and quantity of food (tree size, not number of trees) as hypothesized by Wright et al. (1984). Larger trees provide adequate food to produce an increasing population until the attack density exceeds 12 per sq. ft. (.09 m<sup>2</sup>). At greater densities, competition causes beetle production to decrease. Smaller trees generally have production rates less than one, even when attack densities are 8–12 per sq. ft. (.09 m<sup>2</sup>), because smaller trees do not provide sufficient phloem for developing larvae.

Beetle densities in this study were about the same as or greater than those found by Fredericks and Jenkins (1988) in Logan Canyon, Utah. Beetle numbers of 21–22 per sq. ft. (.09 m<sup>2</sup>) in our diameter classes of 7–13 inches (18–33 cm) were comparable to the beetle numbers at 22–24 per sq. ft. (.09 m<sup>2</sup>) of Fredericks and Jenkins (1988). In trees of comparable diameters (i.e., 22 inches [56 cm]), beetle numbers of 34 per sq. ft. (.09 m<sup>2</sup>) (Table 2) in this study were slightly greater than the 22–24 per sq. ft. (.09 m<sup>2</sup>) of Fredericks and Jenkins (1988).

TABLE 3. Mean annual radial growth in .001 inch (.025 cm) for the periods 1972–76, 1977–81, and 1982–86 for the four 1987 locations. Within the same location, means followed by the same letter are not significantly different ( $\alpha = .05$ ).

Location	Mean annual growth (.001 inch) ( $\bar{x} \pm \text{S.E.}$ )		
	1972–76	1977–81	1982–86
Narrows	11 $\pm$ 1.0 a (28 $\pm$ 3)	12 $\pm$ 1.4 a (30 $\pm$ 4)	19 $\pm$ 1.3 b (48 $\pm$ 3)
Pingree Park Road	38 $\pm$ 2.3 a (97 $\pm$ 6)	30 $\pm$ 1.2 b (76 $\pm$ 3)	33 $\pm$ 1.2 ab (84 $\pm$ 3)
BM 6998	11 $\pm$ 0.9 a (28 $\pm$ 2)	7 $\pm$ 0.3 b (18 $\pm$ 1)	12 $\pm$ 1.8 a (30 $\pm$ 5)
Crystal Lakes	7 $\pm$ 0.6 ab (18 $\pm$ 2)	5 $\pm$ 0.3 b (13 $\pm$ 1)	8 $\pm$ 1.0 a (20 $\pm$ 3)

**ATTACK DENSITIES.**—The number of attacks per sq. ft. (.09 m<sup>2</sup>) of bark surface ranged from 8 to 20 in 1986 and 6 to 14 in 1987. Within each location, attack densities were not significantly different between aspects. Mean densities ranged from 9 to 15 in 1986 and 8 to 10 in 1987, comparable to the fifth-year attack densities in Oregon of Wright et al. (1984). Because the Colorado outbreak appeared to be in its fifth year, the pattern of attack densities during the outbreak may be the same as in the Oregon outbreak. In contrast, attack densities from our Colorado locations were 62–80% lower than those of the Utah outbreak. In the recent outbreak in Utah, attack densities were high and essentially the same throughout the first three years (Fredericks and Jenkins 1988). Apparently, the Utah outbreak exhibited a pattern of attacks different from either the Oregon or Colorado outbreaks.

**DISCOLORATION OF INFESTED TREES.**—In February following the attack, foliage of most infested trees was predominantly green, only the lower two or three whorls of branches having discolored to red-brown. By late April most trees had discolored, the color ranging from yellow-green to reddish. By mid-May most trees were reddish. Trees with extensive woodpecker debarking and foliage discoloration in February turned reddish first, usually by late April. Those without these characteristics discolored later but had turned by May. Foliage usually discolored at different rates in different crown levels, the lower crown fading first. When it was yellow-green, the rest of the crown was green. When the upper crown yellowed, the lower crown was already reddish. From August through October, the best external clues for Douglas-fir beetle infestation were cinnamon-colored boring dust and/or clear pitch “streamers.”

During winter the most notable external characteristic was the debarked bole caused by woodpecker activity. These boles are lighter in color and can be discerned from more than 100 feet away. After October, but before the foliage turned red, woodpecker activity was the best characteristic for locating currently infested trees.

**ANNUAL GROWTH.**—Annual radial growth varied significantly among and within locations. Significant variation in growth among locations was expected because of differing site conditions, stand densities, and tree ages. In three of four locations, mean annual growth declined significantly in the 1977–81 period, presumably a result of the budworm outbreak (Table 3). Mean annual radial growth in each location increased during 1982–86. Thus, the increase in Douglas-fir beetle populations coincided with increasing growth of the host.

Mean annual growth for the 1977–81 period ranged from .005 inch to .03 inch (.013 to .08 cm) and for 1982–86 from .008 to .033 inch (.02 to .08 cm) (Table 3). The growth rate was greatest on large trees situated in a ravine, a more favorable site.

The periodic growth ratio (PGR) exhibited changes similar to the changes in mean annual radial growth. In three of four locations, PGR became  $<1$  when 1977–81 was compared against 1972–76. PGR then became  $>1$  when 1982–86 was compared with 1977–81. Growth rates declined for 1977–81 because of the budworm defoliation; thus, the change in PGR for 1977–81 vs. 1972–76 was expected. However, the increase in Douglas-fir beetle populations with  $>1$  PGR for the 1982–86 period was unexpected. Most stands susceptible to the mountain pine beetle (*D. ponderosae* Hopkins) exhibit PGRs  $<1$ , and so a beetle outbreak coinciding with a period of increasing growth is unusual.

## LITERATURE CITED

- CRESAP, V. L. M. 1976. Western spruce budworm. USDA Forest Service, Rocky Mountain Region, Forest Insect and Disease Management, Lakewood, Colorado. Biological Evaluation R2-76-11.
- FREDERICKS, S. E., AND M. J. JENKINS. 1988. Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, Coleoptera: Scolytidae) brood production on Douglas-fir defoliated by western spruce budworm (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) in Logan Canyon, Utah. Great Basin Naturalist 48: 348-351.
- FURNISS, M. M. 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. Journal of Economic Entomology 55: 486-491.
- LINNANE, J. P. 1977. Western spruce budworm on national forest lands in Colorado. USDA Forest Service, Rocky Mountain Region, Forest Insect and Disease Management, Lakewood, Colorado. Biological Evaluation R2-77-15.
- . 1981. Western spruce budworm. Results of an egg mass survey on the Pike, and San Isabel and Arapahoe and Roosevelt National Forests in 1980. USDA Forest Service, Forest Pest Management, Rocky Mountain Region, Lakewood, Colorado. Biological Evaluation R2-81-2.
- MAHONEY, R. L. 1978. Lodgepole pine/mountain pine beetle risk classification methods and their application. Pages 106-113 in Theory and practice of mountain pine beetle management in lodgepole pine forests. Proceedings of a symposium at Washington State University, Pullman, Washington, 25-27 April 1978.
- MCMULLEN, L. H., AND M. D. ATKINS. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. Forest Science 7: 197-203.
- MINNEMEYER, C. D. 1974. Western spruce budworm. USDA Forest Service, State and Private Forestry, Region 2, Denver, Colorado. Biological Evaluation R2-74-9.
- RAIMO, B. J. 1983. Western spruce budworm in the Rocky Mountain Region 1983. USDA Forest Service, Timber, Forest Pest and Cooperative Forestry Management, Rocky Mountain Region, Lakewood, Colorado. Biological Evaluation R2-83-4.
- . 1984. Western spruce budworm in the Rocky Mountain Region. USDA Forest Service, Timber, Forest Pest and Cooperative Forestry Management, Rocky Mountain Region, Lakewood, Colorado. Biological Evaluation R2-84-5.
- STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Company Inc., New York. 481 pp.
- WOOD, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Great Basin Naturalist 23: 1-117.
- WRIGHT, L. C., A. A. BERRYMAN, AND B. E. WICKMAN. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. Canadian Entomologist 116: 293-305.

Accepted 3 October 1990



## ECOLOGICAL REVIEW OF BLACK-TAILED PRAIRIE DOGS AND ASSOCIATED SPECIES IN WESTERN SOUTH DAKOTA

Jon C. Sharps<sup>1</sup> and Daniel W. Uresk<sup>2</sup>

**ABSTRACT.**—Black-tailed prairie dogs (*Cynomys ludovicianus*) once occupied extensive areas throughout the Great Plains. In recent years massive control programs have been initiated to reduce prairie dog populations, primarily to benefit the livestock grazing industry. Currently in western South Dakota most prairie dogs are found on public lands. Control programs using toxicants for prairie dogs have been found to be economically unfeasible when not combined with reductions in livestock grazing. Control programs also have negatively impacted some nontarget species of birds and small mammals. Livestock grazing is directly related to prairie dog densities. Prairie dog and livestock grazing activities are responsible for keeping plant phenological development in a suppressed vegetative stage with higher nutritional qualities that attract greater herbivore use. Prairie dog colonies create and enhance habitat for many wildlife species; in western South Dakota 134 vertebrate wildlife species have been documented on prairie dog towns. Scientific evidence strongly suggests that prairie dogs are valuable components of the prairie ecosystem. They are responsible for maintaining, creating, and regulating habitat biodiversity through soil and vegetative manipulation for a host of vertebrate and invertebrate species dependent upon prairie dog activity for their survival.

Quantified information regarding vertebrate wildlife species living on or closely associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies is lacking or is only alluded to in scientific literature. To promote a better understanding of the complexity of prairie dogs and their habitat requirements and their importance to vertebrate species of wildlife, we conducted a review of scientific literature regarding prairie dog biology, ecology, and associated biopolitics pertaining to land management practices. Most of the studies and observations reported in this paper were conducted in western South Dakota. Where possible, corroborating studies and literature from other areas are presented and their importance discussed.

### HISTORICAL BACKGROUND

Historically, prairie dogs occupied extensive areas on the Great Plains, ranging from Texas to Saskatchewan (Hall 1981) (Fig. 1). Merriam (1902) noted that prairie dogs compete with livestock for forage and are systematically targeted for elimination by livestock producers. The largest areas of land in the United States currently occupied by prairie dogs are federally managed lands (Schenbeck

1982). In South Dakota most black-tailed prairie dogs are found on lands administered by USDA Forest Service, primarily the Buffalo Gap National Grasslands and Fort Pierre National Grasslands (Schenbeck 1982). Storch (1989) estimated that prairie dogs inhabited 3,000 acres on the South Dakota portion of the Nebraska National Forest in the 1960s. In the mid-1970s prairie dogs inhabited approximately 20,000 acres on the Conata Basin portion of the grasslands (Schenbeck 1982); Schenbeck's estimate represents an 87% increase over an eight-year period. The livestock grazing industry claimed estimated losses of up to \$10.29 per acre on pasture and rangeland and \$30.00 per acre for hayland on a statewide basis (Dobbs 1984) and objected to the increase in prairie dogs.

### ECONOMICS OF CONTROL AND LIVESTOCK GRAZING

The South Dakota livestock industry has recommended and instigated widespread wholesale reductions in prairie dog densities on public land, and in 1983 the state legislature listed the prairie dog as a pest and predator (Clarke 1988). Of the 707,000 acres in the Ft. Pierre and Buffalo Gap National Grasslands,

<sup>1</sup>Wildlife Systems, HC 82 Box 172B, Box Elder, South Dakota 57719.

<sup>2</sup>USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, 501 E. St. Joseph Street, Rapid City, South Dakota 57701.



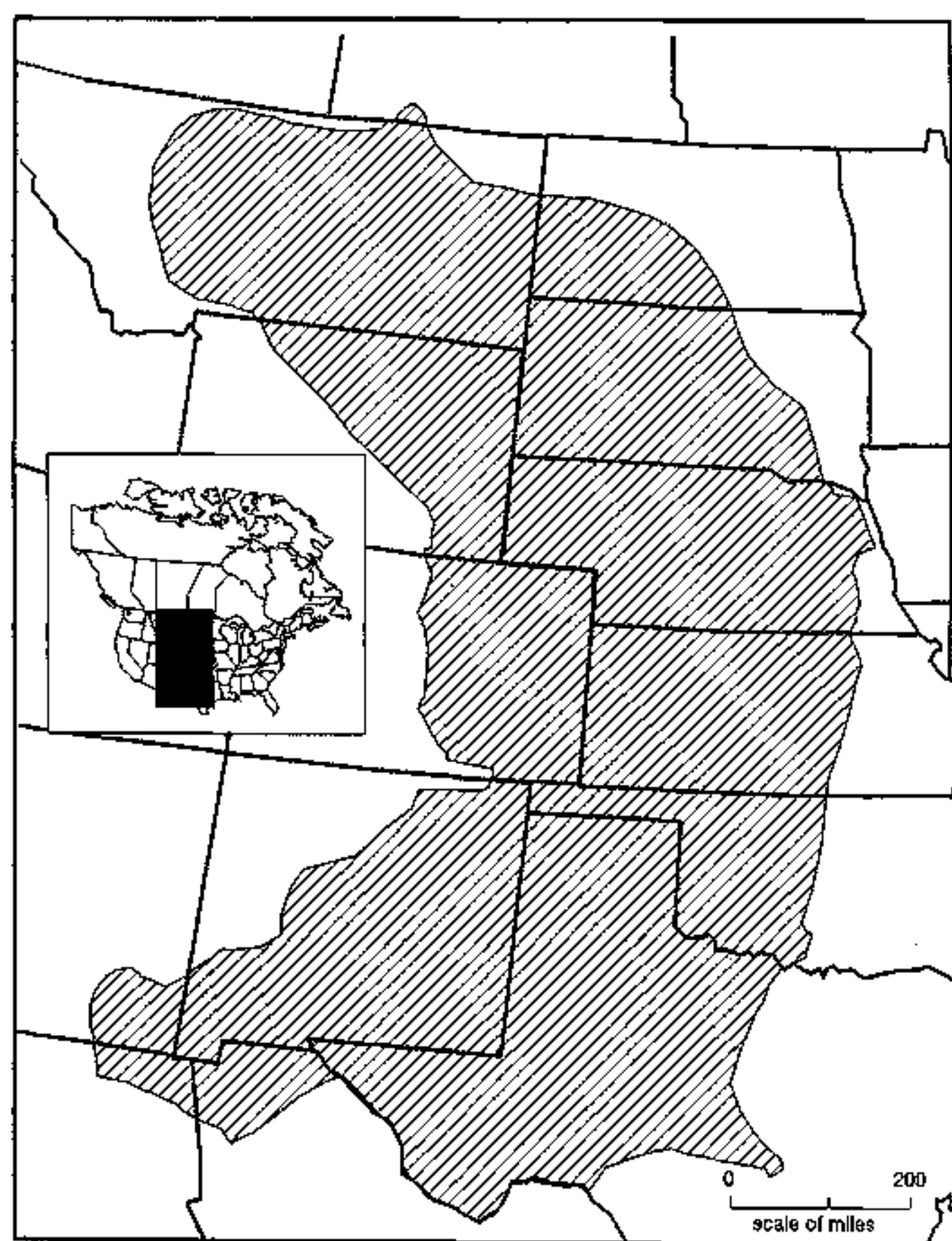


Fig. 1. Distribution of black-tailed prairie dog (*Cynomys ludovicianus*) on the Great Plains (adapted from Hall 1981).

approximately 10,000 acres are currently occupied by prairie dogs (Storch 1989). Control of prairie dogs has usually been initiated without consideration of the value of forage gained (Collins et al. 1984) or the effect on wildlife species associated with prairie dogs and their habitat (Sharps 1988).

An economic analysis of prairie dog control by Collins et al. (1984) found it was not economically feasible to poison prairie dogs in the Conata Basin using zinc phosphide because the annual control costs exceeded the value of forage gained. Also, based on burrow counts, prairie dog densities were significantly less on areas excluded to cattle than on areas grazed by cattle (Uresk et al. 1982). Herbicide applications to reduce forb production and thus reduce prairie dog densities were also found to be an inefficient control method because prairie dogs changed their diets from forbs to grasses (Fagerstone et al. 1977). It has long been known and extensively reported that cattle grazing will influence and is directly proportional to prairie dog densities (Koford 1958, Knowles 1982, Uresk et al. 1982, Cin-

cotta 1985, Snell 1985). Schenbeck (1986) reported that habitat suitability for prairie dogs can be reduced by combining rodenticide use with changes in livestock grazing practices.

The poison bait effects of zinc phosphide- and strychnine-treated oats on nontarget birds, small mammals, and other nontarget species were evaluated by Uresk et al. (1988). The effects on nontarget bird species showed varied losses to Horned Larks, depending upon the density of strychnine-treated oats used, with no losses to other avian seed-eaters. No measurable reductions in Horned Larks were found using zinc phosphide-treated oats, although there were indirect impacts on Horned Larks resulting from habitat changes. Prairie dog towns provide habitat for many seed-eating and insectivorous birds. Significantly, Apa (1985) reported that 50 species of birds were observed using prairie dog towns during the course of his study.

While zinc phosphide may not be detrimental to Horned Larks and the smaller seed-eating birds, it has been reported to be relatively toxic to gallinaceous birds (Record and Swick 1983).

Studies by Koford (1958), Smith (1958), Snell and Hlavacek (1980), and Uresk et al. (1982) indicated that excluding or decreasing cattle grazing increases cool-season grass density (wheatgrass and needlegrass) and reduces prairie dog colony size on mid- and short-grass rangeland. This method of prairie dog control has historically been opposed or rejected by the livestock grazing community. Although heavily grazed rangelands give rise to very slow forage improvement, prairie dogs alone are generally not responsible for range deterioration (Uresk 1987). Prairie dog expansion is related to livestock grazing (Uresk et al. 1982, Uresk and Bjugstad 1983). Black-tailed prairie dogs usually disperse during May and June and have been reported to move and become established an average of three miles from their original towns (Garrett and Franklin 1981, Cincotta et al. 1987). They will repopulate their towns to initial population numbers in three years (Schenbeck 1982, Cincotta et al. 1987). Economically, control of prairie dogs is not feasible except at very low maintenance levels—below 5%—based on an increase of forage for livestock of only 50 pounds per acre, a 4.4% increase (Uresk et al. 1982, Collins et al. 1984, Uresk 1985, 1986).

## ASSOCIATED VERTEBRATE SPECIES

Prairie dogs create a biological niche or habitat for many species of wildlife (King 1955, Reading et al. 1989). Agnew et al. (1986) found that bird species diversity and rodent abundance were higher on prairie dog towns than on mixed-grass prairie sites. The high diversity of bird species was attributed to heterogeneous plant cover and species composition (Agnew et al. 1986, Cincotta et al. 1987). In a survey of prairie dog towns extending through portions of Utah, Colorado, and New Mexico, Clark et al. (1982) recorded 107 vertebrate species and subspecies of wildlife; more species were associated with larger prairie dog towns than with smaller towns. Sixty-four vertebrate wildlife species were recorded by Campbell and Clark (1981) on 25 white-tailed and 21 black-tailed prairie dog colonies in Wyoming. Reading et al. (1989) listed 163 vertebrate species sighted on black-tailed prairie dog colonies. They suggest that "richness of associated vertebrate species on black-tailed prairie dog colonies increases with colony size and regional colony density."

Data pertaining to vertebrate wildlife species associated with black-tailed prairie dog colonies were obtained from an extensive literature review, personal field notes (J. C. Sharps, unpublished), observations while conducting endangered species surveys, or observations incidental to other research on prairie dog colonies. In South Dakota, 600 vertebrate wildlife taxa were found statewide. There are 332 species located west of the Missouri River (excluding fish) (Sharps and Benzon 1984). Of western wildlife species, 40% were found to be associated with prairie dog colonies. This 40% represents 134 vertebrate wildlife species (Table 1) associated with prairie dog colonies in western South Dakota: 88 birds, 36 mammals, 6 reptiles, and 4 amphibians (Agnew 1983, Apa 1985, MacCracken et al. 1985, Agnew et al. 1986, Uresk et al. 1986, Deisch et al. 1989). Whitney et al. (1978) reported that approximately 33 bird species, or 39% of the birds found in South Dakota, are conspicuous on the grasslands. Of those 33 species only 5, or approximately 15%, were not observed or reported on prairie dog colonies.

## PLANT-SOIL-ANIMAL INTERACTIONS

Agnew et al. (1986) and Deisch et al. (1989) found five classes of invertebrates on prairie

dog colonies located on the Badlands National Park and Buffalo Gap National Grasslands, respectively. The five classes consisted of Insecta (6 orders, 26 families), Arachnida (4 orders, 10 families), Chilopoda, Diplopoda, and Crustacea. Agnew et al. (1988) found that insectivorous rodent species favor prairie dog colonies; these mammals, by consuming arthropods, may reduce localized arthropod outbreaks.

Prairie dog colonies provide habitat diversity in the prairie ecosystem by mixing soils and regulating vegetative species diversity (Koford 1958, Bonham and Lerwick 1976, Agnew et al. 1986, Detling and Whicker 1988, Sieg 1988). This in turn creates interactions and numerous niches, thereby contributing to the food chain for a host of invertebrate and vertebrate wildlife species. Prairie dogs alter soil structure and chemical composition by their burrowing activities, excrement, and addition of plant material, which contribute to vegetation diversity (Gold 1976, Hansen and Gold 1977, O'Meilia et al. 1982, Cincotta 1985, Agnew et al. 1986). Prairie dog activity results in the aeration, pulverization, granulation, and transfer of considerable quantities of soil (Buckman and Brady 1971, Sieg 1988). Soils in prairie dog colonies are richer in nitrogen, phosphorus, and organic matter than soils in adjacent grasslands. Sheets et al. (1971) found prairie dog and cattle feces, grass seeds, stolons, roots, and remains of prairie dogs and mice while excavating 18 prairie dog burrows to retrieve black-footed ferret scats in south central South Dakota. Soil-enrichment activity of the prairie dog is beneficial to the macroarthropods living in the soil. Forbs and grasses in prairie dog colonies are constantly clipped by prairie dogs and remain in a state of regrowth (O'Meilia et al. 1982, Cincotta 1985). Ingham and Detling (1984) reported that prairie dog colonies support higher populations of nematodes than adjacent areas away from the colonies. They also stated that prairie dog activities suppress plant phenological development, thus maintaining the plants in a vegetative state. Young vegetation, which is higher in nutritional qualities than mature plants, attracts cattle, bison, and pronghorn to prairie dog colonies (Uresk and Bjugstad 1983, Coppock et al. 1983, Knowles 1986, Krueger 1986, Detling and Whicker 1988).

TABLE 1. Vertebrate wildlife species associated with black-tailed prairie dog colonies in western South Dakota.

Eastern tiger salamander	<i>Ambystoma tigrinum tigrinum</i>	Black-billed Magpie <sup>b</sup>	<i>Pica pica</i>
Great plains toad	<i>Bufo cognatus</i>	Common Raven <sup>b</sup>	<i>Corvus corax</i>
Western chorus frog	<i>Pseudacris triserata</i>	American Crow <sup>b</sup>	<i>C. brachyrhynchos</i>
Bullfrog	<i>Rana catesbeiana</i>	Northern Mockingbird <sup>c</sup>	<i>Mimus polyglottos</i>
Turtles	Emydidae unk spp.	Gray Catbird <sup>b</sup>	<i>Dumetella carolinensis</i>
Lizards	Iguanidae unk spp.	American Robin <sup>b</sup>	<i>Turdus migratorius</i>
Plains garter snake	<i>Thamnophis radix</i>	Eastern Bluebird <sup>c</sup>	<i>Sialia sialis</i>
Smooth green snake	<i>Opheodrys vernalis</i>	Mountain Bluebird <sup>b</sup>	<i>S. currucoides</i>
Bullsnake	<i>Pituophis melanoleucus sayi</i>	Water Pipit <sup>c</sup>	<i>Anthus spinoletta</i>
Prairie rattlesnake	<i>Crotalus viridis viridis</i>	Northern Shrike <sup>d</sup>	<i>Lanius excubitor</i>
Great Blue Heron <sup>a</sup>	<i>Ardea herodias</i>	Loggerhead Shrike <sup>b</sup>	<i>L. ludovicianus</i>
Trumpeter Swan <sup>a</sup>	<i>Cygnus buccinator</i>	European Starling <sup>b</sup>	<i>Sturnus vulgaris</i>
Canada Goose <sup>a</sup>	<i>Branta canadensis</i>	Yellow Warbler <sup>b</sup>	<i>Dendroica petechia</i>
Mallard <sup>a</sup>	<i>Anas platyrhynchos</i>	Common Yellowthroat <sup>b</sup>	<i>Geothlypis trichas</i>
Gadwall <sup>a</sup>	<i>A. strepera</i>	Yellow-breasted Chat <sup>b</sup>	<i>Icteria virens</i>
Northern Pintail <sup>a</sup>	<i>A. acuta</i>	House Sparrow <sup>b</sup>	<i>Passer domesticus</i>
Blue-winged Teal <sup>a</sup>	<i>A. discors</i>	Bobolink <sup>b</sup>	<i>Dolichonyx oryzivorus</i>
Northern Shoveler <sup>a</sup>	<i>A. clypeata</i>	Western Meadowlark <sup>b</sup>	<i>Sturnella neglecta</i>
Canvasback <sup>a</sup>	<i>Aythya valisineria</i>	Yellow-headed Blackbird <sup>c</sup>	<i>Xanthocephalus xanthocephalus</i>
Turkey Vulture <sup>b</sup>	<i>Cathartes aura</i>	Red-winged Blackbird <sup>b</sup>	<i>Agelaius phoeniceus</i>
Red-tailed Hawk <sup>b</sup>	<i>Buteo jamaicensis</i>	Brewer's Blackbird <sup>b</sup>	<i>Euphagus cyanocephalus</i>
Swainson's Hawk <sup>b</sup>	<i>B. swainsoni</i>	Common Grackle <sup>b</sup>	<i>Quiscalus quiscula</i>
Rough-legged Hawk <sup>c</sup>	<i>B. lagopus</i>	Brown-headed Cowbird <sup>b</sup>	<i>Molothrus ater</i>
Ferruginous Hawk <sup>b</sup>	<i>B. regalis</i>	Western Tanager <sup>b</sup>	<i>Piranga ludoviciana</i>
Golden Eagle <sup>b</sup>	<i>Aquila chrysaetos</i>	Dickcissel <sup>b</sup>	<i>Spiza americana</i>
Bald Eagle <sup>d</sup>	<i>Haliaeetus leucocephalus</i>	Common Redpoll <sup>d</sup>	<i>Carduelis flammea</i>
Northern Harrier <sup>b</sup>	<i>Circus cyaneus</i>	Pine Siskin <sup>b</sup>	<i>C. pinus</i>
Prairie Falcon <sup>b</sup>	<i>Falco mexicanus</i>	American Goldfinch <sup>b</sup>	<i>C. tristis</i>
Merlin <sup>c</sup>	<i>F. columbarius</i>	Rufous-sided Towhee <sup>b</sup>	<i>Pipilo erythrophthalmus</i>
American Kestrel <sup>b</sup>	<i>F. sparverius</i>	Lark Bunting <sup>b</sup>	<i>Calamospiza melanocorys</i>
Sharp-tailed Grouse <sup>b</sup>	<i>Tympanuchus phasianellus</i>	Grasshopper Sparrow <sup>b</sup>	<i>Ammodramus savannarum</i>
Ring-necked Pheasant <sup>c</sup>	<i>Phasianus colchicus</i>	Vesper Sparrow <sup>b</sup>	<i>Poocetes gramineus</i>
Sora <sup>a</sup>	<i>Porzana carolina</i>	Lark Sparrow <sup>b</sup>	<i>Chondestes grammacus</i>
Killdeer <sup>b</sup>	<i>Charadrius vociferus</i>	Slate-colored Junco <sup>d</sup>	<i>Junco hyemalis</i>
Long-billed Curlew <sup>b</sup>	<i>Numenius americanus</i>	Oregon Junco <sup>c</sup>	<i>J. oreganus</i>
Upland Sandpiper <sup>b</sup>	<i>Bartramia longicauda</i>	Chipping Sparrow <sup>b</sup>	<i>Spizella passerina</i>
Long-billed Dowitcher <sup>a</sup>	<i>Limnodromus scolopaceus</i>	White-crowned Sparrow <sup>c</sup>	<i>Zonotrichia leucophrys</i>
Wilson's Phalarope <sup>a</sup>	<i>Phalaropus tricolor</i>	McCown's Longspur <sup>c</sup>	<i>Calcarius mccownii</i>
Ring-billed Gull <sup>c</sup>	<i>Larus delawarensis</i>	Chestnut-collared Longspur <sup>b</sup>	<i>C. ornatus</i>
Rock Dove <sup>b</sup>	<i>Columba livia</i>	Shrews	Soricidae unk. spp.
Mourning Dove <sup>b</sup>	<i>Zenaida macroura</i>	Bats	Vespertilionidae unk. spp.
Great-horned Owl <sup>b</sup>	<i>Bubo virginianus</i>	Eastern cottontail	<i>Sylvilagus floridanus</i>
Snowy Owl <sup>d</sup>	<i>Nyctea scandiaca</i>	Desert cottontail	<i>S. auduboni</i>
Burrowing Owl <sup>b</sup>	<i>Athene cunicularia</i>	White-tailed jackrabbit	<i>Lepus townsendii</i>
Short-eared Owl <sup>b</sup>	<i>Asio flammeus</i>	Black-tailed jackrabbit	<i>L. californicus</i>
Common Nighthawk <sup>b</sup>	<i>Chordeiles minor</i>	Thirteen-lined ground squirrel	<i>Spermophilus tridecemlineatus</i>
Belted Kingfisher <sup>c</sup>	<i>Ceryle alcyon</i>	Black-tailed prairie dog	<i>Cynomys ludovicianus</i>
Northern Flicker <sup>b</sup>	<i>Colaptes auratus</i>	Northern pocket gopher	<i>Thomomys talpoides</i>
Red-headed Woodpecker <sup>b,e</sup>	<i>Melanerpes erythrocephalus</i>	Plains pocket gopher	<i>Geomys bursarius</i>
Downy Woodpecker <sup>c</sup>	<i>Picoides pubescens</i>	Olive-backed pocket mouse	<i>Perognathus fasciatus</i>
Eastern Kingbird <sup>b</sup>	<i>Tyrannus tyrannus</i>	Hispid pocket mouse	<i>P. hispidus</i>
Western Kingbird <sup>b</sup>	<i>T. verticalis</i>	Ord's kangaroo rat	<i>Dipodomys ordii</i>
Say's Phoebe <sup>b</sup>	<i>Sayornis saya</i>	Plains harvest mouse	<i>Reithrodontomys montanus</i>
Horned Lark <sup>b,d</sup>	<i>Eremophila alpestris</i>	Western harvest mouse	<i>R. megalotis</i>
Violet-green Swallow <sup>b</sup>	<i>Tachycineta thalassina</i>	Deer mouse	<i>Peromyscus maniculatus</i>
Northern rough-winged Swallow <sup>b</sup>	<i>Stelgidopteryx serripennis</i>	Northern grasshopper mouse	<i>Onychomys leucogaster</i>
Barn Swallow <sup>b</sup>	<i>Hirundo rustica</i>		
Cliff Swallow <sup>b</sup>	<i>H. pyrrhonota</i>		
Blue Jay <sup>c</sup>	<i>Cyanocitta cristata</i>		



TABLE 1 continued.

Prairie vole	<i>Microtus ochrogaster</i>
Norway rat	<i>Rattus norvegicus</i>
House mouse	<i>Mus musculus</i>
Porcupine	<i>Erethizon dorsatum</i>
Raccoon	<i>Procyon lotor</i>
Long-tailed weasel	<i>Mustela frenata</i>
Black-footed ferret	<i>M. nigripes</i>
Mink	<i>M. vison</i>
Badger	<i>Taxidea taxus</i>
Spotted skunk	<i>Spilogale Putorius</i>
Striped skunk	<i>Mephitis mephitis</i>
Coyote	<i>Canis latrans</i>
Red fox	<i>Vulpes vulpes</i>
Northern swift fox	<i>Vulpes velox hebes</i>
Bobcat	<i>Lynx rufus</i>
Mule deer	<i>Odocoileus hemionus</i>
White-tailed deer	<i>O. virginianus</i>
Pronghorn	<i>Antilocapra americana</i>
Bison	<i>Bison bison</i>

<sup>a</sup>Birds associated with wet years.  
<sup>b</sup>Breeding birds.  
<sup>c</sup>Transient birds.  
<sup>d</sup>Wintering birds.  
<sup>e</sup>Birds in riparian habitat adjacent to prairie dog colonies.

IMPORTANCE OF PRAIRIE DOG COLONIES  
TO ASSOCIATED WILDLIFE

Prairie dog colonies attract many insectivorous and carnivorous birds and mammals because of the concentration of numerous prey species (Clark et al. 1982, Agnew et al. 1986, Agnew et al. 1988). Hillman (1968) reported that prairie dogs are the principal food source of black-footed ferrets. Ferret decline has been attributed to prairie dog control practices and agricultural land use changes (Hillman and Clark 1980). Swift fox were found to have their dens on or within 0.8 km of prairie dog colonies (Hillman and Sharps 1978). The major portion of the swift fox diet is prairie dogs, 49%, and insects, 27% (Uresk and Sharps 1986). Raptors are particularly attracted to South Dakota prairie dog colonies. Juvenile Snowy Owls and Bald Eagles have been observed utilizing prairie dog colonies during the winter months; Golden Eagles can be found near prairie dog colonies all year; Ferruginous Hawks, Red-tailed Hawks, Kestrels, Prairie Falcons, Harriers, Rough-legged Hawks, Short-eared Owls, and Burrowing Owls use prairie dog colonies in the spring, summer, and fall months. Great-horned Owls have been observed hunting for cottontails and jackrabbits on prairie dog colonies at night. The principal mammalian

predator species observed on prairie dog colonies are coyote, badger, and bobcat (Hillman and Sharps 1978).

Scientific evidence strongly suggests that prairie dogs are valuable components of the prairie ecosystem. Their burrowing activities and feeding habits are directly responsible for creating habitat diversity and thus providing a niche for 134 vertebrate wildlife species and over 36 families of invertebrate fauna (Agnew 1983, Deisch et al. 1989). Clark (1968) stated:

prairie dogs have been in the grassland community for at least 1,000,000 years, probably occurring in great numbers; it would seem that if prairie dogs were detrimental they would have long ago destroyed the community of which they are a part.

SUMMARY

Prairie dogs were once significantly more numerous on public lands in South Dakota than they are today. Massive control programs have been initiated with little or no thought to the biological importance and ecological role of the prairie dog in the prairie ecosystem. Studies of prairie dog biology and ecology have shown that prairie dogs are not as detrimental as once believed to the livestock grazing industry. Studies have also shown that prairie dogs are extremely important to the ecosystem because they provide habitat and vegetation diversity in the prairie biome. Field observations and studies found 134 species and subspecies of vertebrate wildlife associated with prairie dog colonies in western South Dakota.

LITERATURE CITED

AGNEW, W. D. 1983. Flora and fauna associated with prairie dog ecosystems. Unpublished thesis, Colorado State University, Fort Collins. 47 pp.  
AGNEW, W., D. W. URESK, AND R. M. HANSEN. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* 39: 135-139.  
———. 1988. Arthropod consumption by small mammals on prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. Pages 81-87 in *Eighth Great Plains wildlife damage control workshop proceedings*. USDA Forest Service General Technical Report RM-154. 231 pp.  
APA, A. D. 1985. Efficiency of two black-tailed prairie dog rodenticides and their impacts on non-target bird species. Unpublished thesis, South Dakota State University, Brookings. 71 pp.



- BONHAM, C. D., AND A. LERWICK. 1976. Vegetation changes induced by prairie dogs on shortgrass range. *Journal of Range Management* 29: 221-225.
- BUCKMAN, H. O., AND N. C. BRADY. 1971. The nature and property of soils. The Macmillan Co., New York.
- CAMPBELL, T. M., III, AND T. W. CLARK. 1981. Colony characteristics and vertebrate associations of white-tailed and black-tailed prairie dogs in Wyoming. *American Midland Naturalist* 105: 269-276.
- CINCOTTA, R. P. 1985. Habitat and dispersal of black-tailed prairie dogs in Badlands National Park. Unpublished dissertation, Colorado State University, Fort Collins. 52 pp.
- CINCOTTA, R. P., D. W. URESK, AND R. M. HANSEN. 1987. Demography of black-tailed prairie dog populations reoccupying sites treated with rodenticide. *Great Basin Naturalist* 47: 339-343.
- CLARK, T. W. 1968. Ecological roles of prairie dogs. *Wyoming Range Management* 261: 102-104.
- CLARK, T. W., T. M. CAMPBELL III, D. C. SOCHA, AND D. E. CASEY. 1982. Prairie dog colony attributes and associated vertebrate species. *Great Basin Naturalist* 42: 577-582.
- CLARKE, D. C. 1988. Prairie dog control—a regulatory viewpoint. Pages 115-116 in Eighth Great Plains wildlife damage control workshop proceedings. USDA Forest Service General Technical Report RM-154. 231 pp.
- COLLINS, A. R., J. P. WORKMAN, AND D. W. URESK. 1984. An economic analysis of black-tailed prairie dog (*Cynomys ludovicianus*) control. *Journal of Range Management* 37: 358-361.
- COPPOCK, D. L., J. K. DETLING, J. E. ELLIS, AND M. I. DYER. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intra-seasonal above ground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56: 1-9.
- DEISCH, M. S., D. W. URESK, AND R. L. LINDER. 1989. Effects of two prairie dog rodenticides on ground-dwelling invertebrates in western South Dakota. Pages 166-170 in Ninth Great Plains wildlife damage control workshop proceedings. USDA Forest Service General Technical Report RM-171. 181 pp.
- DETLING, J. K., AND A. D. WHICKER. 1988. Control of ecosystem processes by prairie dogs and other grassland herbivores. Pages 23-29 in Eighth Great Plains wildlife damage control workshop proceedings. USDA Forest Service General Technical Report RM-154. 231 pp.
- DOBBS, T. L. 1984. Economic losses due to prairie dogs in South Dakota. South Dakota Department of Agriculture, Division of Agriculture Regulations and Inspection, Pierre. 15 pp.
- FAGERSTONE, K. A., H. P. TIETJEN, AND G. K. LAVOIE. 1977. Effects of range treatment with 2,4-D on prairie dog diet. *Journal of Range Management* 30: 57-60.
- GARRETT, M. G., AND W. L. FRANKLIN. 1981. Prairie dog dispersal in Wind Cave National Park: possibilities for control. Pages 185-198 in R. M. Timm and R. J. Johnson, eds., Fifth Great Plains wildlife damage control workshop proceedings, 13-15 October 1981. University of Nebraska, Lincoln.
- GOLD, I. K. 1976. Effects of black-tailed prairie dog mounds on shortgrass vegetation. Unpublished thesis, Colorado State University, Fort Collins. 41 pp.
- HALL, E. R. 1981. The mammals of North America. Vol. 1. 2d ed. John Wiley and Sons, New York. 690 pp.
- HANSEN, R. M., AND I. K. GOLD. 1977. Black-tailed prairie dogs, desert cottontails and cattle trophic relations on shortgrass range. *Journal of Range Management* 30: 210-213.
- HILLMAN, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Pages 434-443 in 33rd North American Wildlife Conference. Wildlife Natural Resource Conference.
- HILLMAN, C. N., AND J. C. SHARPS. 1978. Return of swift fox to northern Great Plains. *Proceedings of South Dakota Academy of Science* 57: 154-162.
- HILLMAN, C. N., AND T. W. CLARK. 1980. *Mustela nigripes* Mammalian species. American Society of Mammalogists No. 126. 3 pp.
- INGHAM, R. E., AND J. K. DETLING. 1984. Plant-herbivore interactions in a North American mixed-grass prairie: III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent colonies and adjacent uncolonized areas. *Oecologia (Berlin)* 63: 307-313.
- KING, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contributions from the Lab of Vertebrate Biology, No. 67. University of Michigan, Ann Arbor. 127 pp.
- KNOWLES, C. J. 1982. Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge. Unpublished dissertation, University of Montana, Missoula. 171 pp.
- KNOWLES, C. J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Great Basin Naturalist* 46: 198-203.
- KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* No. 3. 78 pp.
- KRUEGER, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology* 67: 760-770.
- MACCRACKEN, J. G., D. W. URESK, AND R. M. HANSEN. 1985. Burrowing owl foods in Conata Basin, South Dakota. *Great Basin Naturalist* 45: 287-290.
- MERRIAM, C. J. 1902. The prairie dog of the Great Plains. Pages 257-270 in USDA yearbook 1901. U.S. Department of Agriculture, Washington, D.C.
- O'MEILIA, M. E., F. L. KNOPF, AND J. C. LEWIS. 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35: 580-585.
- READING, R. P., S. R. BEISSINGER, J. J. GRENSTEN, AND T. W. CLARK. 1989. Attributes of black-tailed prairie dog colonies in northcentral Montana, with management recommendations for the conservation of biodiversity. Pages 13-27 in T. W. Clark, ed., The prairie dog ecosystem: managing for biological diversity. Montana BLM Wildlife Technical Bulletin No. 2. 55 pp.
- RECORD, R., AND C. SWICK. 1983. A comparison of zinc phosphide, compound 1080 and strychnine baits for black-tailed prairie dog control in South

- Dakota. A report for South Dakota Department of Agriculture, Pierre. 20 pp.
- SCHENBECK, C. L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207–217 in R. M. Timm and R. J. Johnson, eds., Fifth Great Plains wildlife damage control workshop proceedings, 13–15 October 1981. University of Nebraska, Lincoln.
- . 1986. Black-tailed prairie dog management on the northern Great Plains. Pages 28–33 in D. B. Fagre, ed., Proceedings, Seventh Great Plains wildlife damage control workshop, 3–5 December 1985, Texas A&M University, College Station.
- SHARPS, J. C. 1988. Politics, prairie dogs and the sportsman. Pages 117–118 in Eighth Great Plains wildlife damage control workshop proceedings, Rapid City, South Dakota, 28–30 April 1987. USDA Forest Service General Technical Report RM-154. 231 pp.
- SHARPS, J. C., AND T. A. BENZON. 1984. A compiled list of South Dakota wildlife. South Dakota Department of Game, Fish and Parks, Rapid City. 27 pp.
- SHEETS, R. G., R. L. LINDER, AND R. B. DAHLGREN. 1971. Burrow systems of prairie dogs in South Dakota. *Journal of Mammalogy* 52: 451–453.
- SIEG, C. H. 1988. Small mammals: pests or vital components of the ecosystem. Pages 88–92 in Eighth Great Plains wildlife damage control workshop proceedings. USDA Forest Service General Technical Report RM-154. 231 pp.
- SMITH, R. E. 1958. Natural history of the prairie dog in Kansas. University of Kansas, Museum of Natural History and State Biological Survey Miscellaneous Publication No. 16. 36 pp.
- SNELL, G. P. 1985. Results of control of prairie dogs. *Rangelands* 7: 30.
- SNELL, G. P., AND B. D. HLAVACHEK. 1980. Control of prairie dogs—the easy way. *Rangelands* 2: 239–240.
- STORCH, R. L. 1989. Black-tailed prairie dog management on the Nebraska National Forest, Samuel R. McKelvie National Forest and Ogalala, Buffalo Gap, and Fort Pierre National Grasslands. Decision notice. Nebraska National Forest, Chadron. 32 pp.
- URESK, D. W. 1985. Effects of controlling black-tailed prairie dogs on plant production. *Journal of Range Management* 38: 466–468.
- . 1986. Food habits of cattle on mixed-grass prairie on the northern Great Plains. *Prairie Naturalist* 18: 211–218.
- . 1987. Relation of black-tailed prairie dogs and control programs to vegetation, livestock, and wildlife. Pages 312–323 in J. L. Capinera, ed., Integrated pest management on rangeland: a shortgrass prairie perspective. Westview Press, Boulder, Colorado. 426 pp.
- URESK, D. W., AND A. J. BJUGSTAD. 1983. Prairie dogs as ecosystem regulators on the northern High Plains. Pages 91–94 in Seventh North American prairie conference proceedings, 4–6 August 1980. Southwest Missouri State University, Springfield.
- URESK, D. W., R. M. KING, A. D. APA, M. S. DEISCH, AND R. L. LINDER. 1986. Efficacy of zinc phosphide and strychnine for black-tailed prairie dog control. *Journal of Range Management* 39: 298–299.
- . 1988. Rodenticidal effects of zinc phosphide and strychnine on nontarget species. Pages 57–63 in Eighth Great Plains wildlife damage control workshop proceedings, Rapid City, South Dakota, 28–30 April 1987. USDA Forest Service General Technical Report RM-154. 231 pp.
- URESK, D. W., J. G. MACCRACKEN, AND A. J. BJUGSTAD. 1982. Prairie dog density and cattle grazing relationships. Pages 199–201 in Fifth Great Plains wildlife damage control workshop proceedings, 13–15 October 1982, University of Nebraska, Lincoln.
- URESK, D. W., AND J. C. SHARPS. 1986. Denning habitat and diet of the swift fox in western South Dakota. *Great Basin Naturalist* 46: 249–253.
- WHITNEY, N. R., B. E. HARRELL, B. K. HARRIS, N. HOLDEN, J. W. JOHNSON, B. J. ROSE, AND P. F. SPRINGER. 1978. The birds of South Dakota. South Dakota Ornithologists Union, Vermillion. 311 pp.

*Received 5 December 1990*

*Accepted 28 January 1991*





## EFFECTS OF PRAIRIE DOG RODENTICIDES ON DEER MICE IN WESTERN SOUTH DAKOTA

Michele S. Deisch<sup>1</sup>, Daniel W. Uresk<sup>2</sup>, and Raymond L. Linder<sup>3</sup>

**ABSTRACT.**—Mortality of nontarget small mammals was determined after application of three black-tailed prairie dog (*Cynomys ludovicianus*) rodenticide treatments (prebaited zinc phosphide, prebaited strychnine, and strychnine alone) in western South Dakota. Immediate (September 1983) and long-term (September 1983 through August 1984) impacts on deer mouse (*Peromyscus maniculatus*) relative densities were evaluated, and the three rodenticide treatments were compared for efficacy. The three treatments had no significant ( $\alpha < .10$ ) immediate impacts on deer mouse relative densities, although zinc phosphide did lower them; that impact was not, however, long term. Long-term impacts of the two strychnine treatments were variable, with an increase in deer mouse densities with the strychnine only treatment. Overall, comparisons among the three treatments indicated that zinc phosphide was more effective than either strychnine treatment in reducing deer mouse densities.

Considerable time and money have been spent on control of prairie dogs to reduce the agricultural damage they cause (Collins et al. 1984). However, efforts to evaluate the impact of prairie dog control methods on the total biotic communities of prairie dog towns have been limited. For example, immediate and long-term rodenticidal effects on nontarget wildlife such as deer mice (*Peromyscus maniculatus*) have not been fully evaluated. Applicators, when selecting toxic baits, often overlook information on the margin of safety to nontarget wildlife.

Small mammals are important components of prairie dog towns. Their fossorial activities mix and enrich soils; their food habits may affect vegetation, seed, and invertebrate distribution and abundance; and they provide a food base for predators. When small mammals ingest rodenticides used to control prairie dogs, incidental loss may change the ecological balance on prairie dog towns.

Rodenticides, in addition to causing direct mortality to nontarget wildlife, may impact them indirectly by removing or reducing prairie dog populations. Prairie dogs create niches for small mammals in rangeland ecosystems (Koford 1958, Allen 1967, O'Meilie et al. 1982, MacCracken et al. 1985, Agnew et al. 1986). For example, prairie dogs act as ecosystem regulators by maintaining habitat

suitable for some small mammals, such as deer mice, that are associated with sparse, heterogeneous vegetative cover. Prairie dog burrows provide security cover and nesting habitat for small mammals. When prairie dog activity ceases, burrows are no longer maintained, soil erodes into the holes, and vegetation recaptures the mounds (Klatt 1971, Potter 1980).

Rodenticides used for prairie dog control include zinc phosphide and strychnine. Zinc phosphide is an acute rodenticide that appears to have limited environmental impact (Hilton et al. 1972). Its increased use in recent years (Schenbeck 1982) has resulted in improved formulations and application rates (Tietjen 1976). Secondary poisoning from zinc phosphide poses minimal threat to predators and scavengers that feed on poisoned rodent carcasses (Bell and Dimmick 1975, Schitoskey 1975, Hegdal et al. 1981).

Nontarget wildlife that consume strychnine bait or strychnine-poisoned carcasses are at risk (Rudd and Genelly 1956, Schitoskey 1975, Hegdal and Gatz 1977, Deisch et al. 1989). Apa (1985), in a companion study, found that strychnine used for prairie dog control reduced Horned Lark (*Eremophila alpestris*) densities.

Little information is available on repopulation of small mammals following rodenticide

<sup>1</sup>Institute for Wildlife Studies, Box 2500, Avalon, California 90704.

<sup>2</sup>USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Rapid City, South Dakota 57701.

<sup>3</sup>Retired, Cooperative Fish and Wildlife Research Unit, South Dakota State University, Brookings, South Dakota 57006.



treatment (Wood 1965). Such information is needed to formulate guidelines for federal, state, and private landowners for minimizing nontarget wildlife losses caused by prairie dog rodenticides. A program to control black-tailed prairie dogs (*Cynomys ludovicianus*) in western South Dakota provided us the opportunity to assess and compare immediate (direct) and long-term (indirect) impacts on deer mouse densities of three prairie dog control treatments: prebaited zinc phosphide, prebaited strychnine, and strychnine alone.

#### STUDY AREA

This study was conducted on the Buffalo Gap National Grasslands and in the Badlands National Park of western South Dakota at elevations of 820–900 m. Geological formations consisted of sharp pinnacles, towers, steep gorges, and faults. Vegetated tabletop buttes and gently rolling mixed grasslands scattered throughout the area supported prairie dog towns.

The National Grasslands, located in Conata Basin, is grazed by cattle from mid-May to late October each year. Native herbivores include black-tailed (*Lepus californicus*) and white-tailed jackrabbit (*L. townsendii*), eastern cottontail (*Sylvilagus floridanus*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and various small mammals. The Badlands National Park excludes cattle, but American bison (*Bison bison*) are present.

Dominant grasses are western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), and needleleaf sedge (*Carex eleocharis*). Prairie dogweed (*Dysodia papposa*), Patagonia Indianwheat (*Plantago patagonica*), buckhorn (*Plantago spinulosa*), scarlet globemallow (*Sphaeralcea coccinea*), and prostrate bigbract verbena (*Verbena bracteata*) are dominant forbs.

Climate is semiarid-continental with extremely cold winters and hot, fluctuating summer temperatures. Average annual precipitation is 39.7 cm, most of which falls as high-intensity thundershowers from April through September.

#### METHODS AND MATERIALS

Small mammals were sampled from May through October 1983 (pretreatment) and

May through August 1984 (posttreatment). Eighteen permanent 100 × 100-m (1.0-ha) sampling sites were established on 15 prairie dog towns. Rodenticide treatments were clustered into three separate groups to prevent cross-contamination with respect to wide-ranging nontarget species (6 sites per rodenticide treatment) 13 and 16 km apart. Each rodenticide treatment had 3 control and 3 treated sites. Only zinc phosphide treatments were applied to the park sites because strychnine use is forbidden. Prebaited strychnine and strychnine alone were applied to the grasslands sites.

Relative densities of small mammals (unique mammals/trap session) were determined for each of the 18 sites. A trapping grid included 64 Sherman live traps 10 m apart and a 10-m buffer border. Trapping began in May of each year and continued at four-week intervals. Each trap session consisted of one night of prebaiting followed by four consecutive nights of trapping (256 trap nights/session). Traps were baited with a peanut butter-rolled oats mixture. Captured rodents were identified to species, assigned a unique number by toe amputation (Taber and Cowan 1969), then released. Density was measured as the number of unique captures.

#### Rodenticides and Bait Application

Steam-rolled oats used for prebait and poisoned baits were formulated at the U.S. Fish and Wildlife Service Pocatello Supply Depot. Zinc phosphide was applied to steam-rolled oats at a concentration of 2.0% by weight active ingredients. (Alcolec S, used as an adhesive, was made by American Lecithin Co., Inc.) Strychnine alkaloid was applied to oats at 0.5% by weight. Nontreated steam-rolled oats (4 g) were applied as prebait for zinc phosphide and for one strychnine treatment during 20–21 September 1983. Prebaited areas were visited prior to baiting to assure that most of the prebait had been consumed. Active rodenticides on oats (4 g) were applied three days after prebaiting (22–24 September 1983) in accordance with federal instructions. Both prebait and rodenticides were applied from bait dispensers affixed to Honda 3-wheel ATV's (Schenbeck 1982).

#### Statistical Aspects

Small mammals, including nontarget deer mice, were sampled on each of 18 sites one

TABLE 1. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on zinc phosphide treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ( $\bar{x} \pm SE$ )			Treatment effect	Significance level (control versus treated) <sup>a</sup>
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	8.3 $\pm$ 2.6	1.3 $\pm$ 0.7	-7.0 $\pm$ 2.6		
Control	4.3 $\pm$ 1.9	2.7 $\pm$ 0.9	-1.7 $\pm$ 1.2	-5.3 $\pm$ 2.6 <sup>b</sup>	—
POSTTREATMENT IMPACTS					
May					
Treated	8.0 $\pm$ 1.5	8.7 $\pm$ 0.3	0.7 $\pm$ 1.2		
Control	11.0 $\pm$ 3.0	12.3 $\pm$ 3.3	1.3 $\pm$ 3.8	-0.7 $\pm$ 2.1	0.878
June					
Treated	7.0 $\pm$ 2.1	7.6 $\pm$ 0.3	0.7 $\pm$ 2.4		
Control	3.7 $\pm$ 1.9	10.7 $\pm$ 2.6	7.0 $\pm$ 4.2	-6.3 $\pm$ 1.6	0.253
July					
Treated	3.0 $\pm$ 1.2	8.3 $\pm$ 2.3	5.3 $\pm$ 1.9		
Control	2.0 $\pm$ 1.0	10.7 $\pm$ 1.7	8.7 $\pm$ 1.5	-3.3 $\pm$ 1.6	0.223
August					
Treated	8.3 $\pm$ 2.6	4.3 $\pm$ 0.3	-4.0 $\pm$ 2.6		
Control	4.3 $\pm$ 1.9	4.7 $\pm$ 1.9	0.3 $\pm$ 1.9	-4.3 $\pm$ 1.0	0.254

<sup>a</sup>Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at  $\alpha < .10$ .

<sup>b</sup>Treatment effects were not significant ( $P = .295$ ); therefore, statistical significance of contrasts was not determined for September.

week prior to rodenticide application in September 1983 (pretreatment). The fourth day after rodenticides were applied, posttreatment counts were taken on all sites to assess immediate impacts. We evaluated long-term (September 1983 through August 1984) impacts by comparing small mammal data collected during September 1983 with all 1984 trap sessions. Rodenticides were not applied in 1984.

Each rodenticide was evaluated for impacts on nontarget small mammals by comparing the change of mean relative density on each cluster of treated sites with the change observed on respective control sites (Uresk et al. 1988) (Tables 1–3). Five comparisons through time included one for immediate impacts (September 1983), measured between pretreatment and posttreatment (1983) poisoning, and four comparisons that measured differences between pretreatment (1983) and posttreatment (1984) densities. When a significant correlation existed between pretreatment and posttreatment observations, analysis of covariance was used to estimate treatment effect (Deisch 1986, Uresk et al. 1988). Subtraction (Green 1979) was used if the correlation was nonsignificant.

Comparisons between and among rodenticides for impact were produced by forming pairwise contrasts between individual rodenticide treatment effects. Randomization procedures were used to estimate statistical significance of the various contrasts (Edgington 1980, Romesburg 1981, Uresk et al. 1986, Uresk et al. 1988). Rejection of any rodenticide impact (type II error) to nontarget small mammals was considered more serious than potential incorrect acceptance of a significant treatment effect (type I error) (Tacha et al. 1982). After significant ( $P = .10$ ) treatment effects were detected, type II error protection was produced by testing each contrast individually. Type I error protection was afforded by testing for treatment effects with analysis of variance or covariance (Carmer and Swanson 1973).

Individual contrasts were considered biologically significant at  $P = .20$ . Although an alpha of .20 is not a standard level of significance, it is becoming more accepted for ecological field studies (Hayne 1976) and is used here to protect against missing effects on nontarget species. The number of sites available in this study produced a power of .80. This was an acceptable combination of type I



TABLE 2. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on strychnine only treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ( $\bar{x} \pm SE$ )			Treatment effect	Significance level (control versus treated) <sup>a</sup>
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	0.7 $\pm$ 0.7	1.7 $\pm$ 1.7	1.0 $\pm$ 2.1		
Control	9.0 $\pm$ 3.2	6.0 $\pm$ 4.0	-3.0 $\pm$ 2.0	4.0 $\pm$ 2.8 <sup>b</sup>	—
POSTTREATMENT IMPACTS					
May					
Treated	5.7 $\pm$ 3.0	1.7 $\pm$ 1.7	-4.0 $\pm$ 2.1		
Control	11.7 $\pm$ 1.8	3.0 $\pm$ 1.5	-8.7 $\pm$ 3.3	4.7 $\pm$ 2.1	0.314
June					
Treated	2.7 $\pm$ 1.5	0.3 $\pm$ 0.3	-2.3 $\pm$ 1.5		
Control	13.0 $\pm$ 1.2	2.3 $\pm$ 1.9	-10.7 $\pm$ 2.3	8.3 $\pm$ 1.8	0.043
July					
Treated	3.7 $\pm$ 2.7	0.3 $\pm$ 0.3	-3.3 $\pm$ 2.8		
Control	4.3 $\pm$ 2.3	1.0 $\pm$ 1.0	-3.3 $\pm$ 1.7	-0.1 $\pm$ 1.6	0.999
August					
Treated	0.7 $\pm$ 0.7	0.0 $\pm$ 0.0	-0.7 $\pm$ 0.7		
Control	9.0 $\pm$ 3.2	1.3 $\pm$ 1.3	-7.7 $\pm$ 2.0	7.0 $\pm$ 1.1	0.034

<sup>a</sup>Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at  $\alpha < .10$ .  
<sup>b</sup>Treatment effects were not significant ( $P = .295$ ); therefore, statistical significance of contrasts was not determined for September.

and II error protection (Carmer 1976) and allowed for reasonable biological inferences to be drawn from the data.

RESULTS

Effects of Rodenticides

Eleven small mammal species captured on 18 sites included deer mouse (*Peromyscus maniculatus*), northern grasshopper mouse (*Onychomys leucogaster*), Ord's kangaroo rat (*Dipodomys ordii*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), western harvest mouse (*Reithrodontomys megalotis*), hispid pocket mouse (*Perognathus hispidus*), plains pocket gopher (*Geomys bursarius*), prairie vole (*Microtus ochrogaster*), house mouse (*Mus musculus*), olive-backed pocket mouse (*Perognathus fasciatus*), and Norway rat (*Rattus norvegicus*). Deer mouse was the only species captured in sufficient numbers to statistically evaluate for rodenticide effects.

There were no immediate impacts of any of the three rodenticide treatments ( $P = .295$ ) on deer mouse relative densities in September 1983 (Tables 1–3). However, relative densities of deer mice changed 79% from 5.8 to 1.2

unique animals immediately after application of zinc phosphide (Uresk et al. 1988). Long-term impacts of the three rodenticides were detected.

On zinc phosphide sites, deer mouse densities were not significantly different between control and treated sites, but densities on treated sites were consistently lower compared with control sites (Table 1). On strychnine sites, relative densities of deer mice were significantly higher on treated sites in June ( $P = .043$ ) and August ( $P = .034$ ) (Table 2). Sites with prebaited strychnine showed higher densities on treated sites in August 1984 ( $P = .063$ ) (Table 3).

Comparisons of Three Rodenticides for Impacts

Comparisons of the impacts of the three rodenticides immediately after application showed no differences ( $P = .10$ ) for deer mouse densities in September 1983. Zinc phosphide lowered densities of deer mice more than did strychnine alone in June 1984 ( $P = .030$ ) and August ( $P = .018$ ); in May and July no differences in reduction rates were measured. There were no differences among treatment effects of zinc phosphide compared

TABLE 3. Pretreatment and posttreatment relative densities (unique mammals/trap night) of deer mice (*Peromyscus maniculatus*) on prebaited strychnine treated and control sites. Adjusted means were estimated as posttreatment minus pretreatment.

Treatment	Relative density ( $\bar{x} \pm SE$ )			Treatment effect	Significance level (control versus treated) <sup>a</sup>
	Pretreatment (1983)	Posttreatment (1984)	Adjusted means		
IMMEDIATE IMPACTS					
September					
Treated	9.3 $\pm$ 0.9	4.0 $\pm$ 1.2	-5.3 $\pm$ 1.9		
Control	16.3 $\pm$ 2.7	13.0 $\pm$ 5.5	-3.3 $\pm$ 3.7	-2.0 $\pm$ 2.7 <sup>b</sup>	—
POSTTREATMENT IMPACTS					
May					
Treated	17.0 $\pm$ 3.1	5.3 $\pm$ 0.9	-11.7 $\pm$ 2.3		
Control	20.3 $\pm$ 3.0	7.7 $\pm$ 1.5	-12.7 $\pm$ 4.7	1.0 $\pm$ 2.1	0.864
June					
Treated	20.7 $\pm$ 4.3	0.3 $\pm$ 0.3	-20.3 $\pm$ 4.5		
Control	21.3 $\pm$ 2.2	2.7 $\pm$ 2.2	-18.7 $\pm$ 4.3	-1.7 $\pm$ 1.6	0.795
July					
Treated	10.3 $\pm$ 3.0	0.0 $\pm$ 0.0	-10.3 $\pm$ 3.0		
Control	11.0 $\pm$ 3.8	3.0 $\pm$ 2.1	-8.0 $\pm$ 5.9	-2.3 $\pm$ 1.6	0.726
August					
Treated	9.3 $\pm$ 0.9	0.7 $\pm$ 0.7	-8.7 $\pm$ 0.3		
Control	16.3 $\pm$ 2.7	0.3 $\pm$ 0.3	-16.0 $\pm$ 3.0	7.3 $\pm$ 1.1	0.063

<sup>a</sup>Randomization test used to detect differences between pairs of adjusted means, after significant F-protection at  $\alpha < .10$ .

<sup>b</sup>Treatment effects were not significant ( $P = .295$ ); therefore, statistical significance of contrasts was not determined for September.

with prebaited strychnine on deer mice from May through July. Impact of zinc phosphide in August ( $P = .027$ ) was greater than that of prebaited strychnine. Comparison of treatment effects between the two strychnine rodenticides indicated that strychnine alone was more effective than prebaited strychnine for lowering densities of deer mice in June ( $P = .174$ ).

#### DISCUSSION

Of the three rodenticide applications used for prairie dog control, only zinc phosphide consistently lowered deer mouse densities. On these sites zinc phosphide was also most effective in reducing prairie dog burrow activity (Apa 1985). Deer mice consume seeds (Baker 1968, Flake 1973, Sieg et al. 1986) and are susceptible to granular rodenticides. After initial rodenticide treatments, long-term changes in deer mouse populations are associated with habitat changes such as increased density of vegetation (Uresk 1985) because of lack of clipping by prairie dogs. Deer mice are adapted to live in more open habitat (Baker 1968, Jones et al. 1983, MacCracken et al. 1985, Agnew et al. 1986), and

their numbers decrease with increased vegetation height and canopy cover. Prairie dog burrows were initially devoid of vegetation before rodenticide application; increased plant canopy cover and aboveground biomass occurred with absence of prairie dogs (Klatt 1971, Potter 1980) and contributed to a decrease in deer mouse densities.

Deer mouse densities were variable over the long-term period with the two strychnine treatments, especially when prebaiting was applied. Deer mouse populations generally increased after treatment with the strychnine only. This increase can be attributed to limited control of the black-tailed prairie dogs (Uresk et al. 1986), which provided and maintained suitable habitat for deer mice (Agnew et al. 1986). Changes in densities of deer mice may also be attributed to seasonal movements of these animals from other areas (Terman 1968) and possible lower predation. An influx of rodents usually occurred in the spring when yearling deer mice established home ranges (MacCracken et al. 1985), and lower densities in August were due to dispersal of young-of-the-year (Falls 1968, Metzgar 1980).

Crabtree (1962) and Marsh et al. (1970) found that zinc phosphide produced a



response-stimulating odor that proved attractive to small mammals, but strychnine did not have an attractive effect on rodents. Based on these findings, discontinuation of zinc phosphide for prairie dog control is not recommended or required, but land management plans should include considerations for possible nontarget deer mouse losses. We found that use of strychnine alone or prebaited strychnine generally showed a long-term increase in deer mouse densities. Use of these two strychnine treatments for prairie dog control appears to impose the least threat to nontarget deer mice.

While this study addressed direct effects of rodenticides (zinc phosphide, prebaited strychnine, and strychnine alone) on deer mouse densities, impacts on other nontarget small mammals could not be evaluated because of the small populations observed. We suspect that granivores, such as *Perognathus* spp. and *Dipodomys* spp., found on prairie dog towns in western South Dakota, may also be affected by rodenticides. Further investigations are needed to assess nontarget losses of small mammals other than deer mice.

#### ACKNOWLEDGMENTS

This study was funded under cooperative agreement IAG-57 with the USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Nebraska National Forest, USDI Fish and Wildlife Service, the South Dakota Cooperative Fish and Wildlife Research Unit, and the National Pesticide Impact Assessment Program (NAPIAP). Thanks are extended to Nebraska National Forest and Badlands National Park for providing study areas.

#### LITERATURE CITED

- AGNEW, W., D. W. URESK, AND R. M. HANSEN. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* 39: 135–139.
- ALLEN, D. L. 1967. *The life of prairies and plains*. McGraw-Hill, Inc., New York. 232 pp.
- APA, A. D. 1985. Efficiency of two black-tailed prairie dog rodenticides and their impacts on non-target bird species. Unpublished thesis, South Dakota State University, Brookings. 71 pp.
- BAKER, R. H. 1968. Habitats and distribution. Pages 98–122 in J. A. King, ed., *Biology of Peromyscus* (Rodentia). The American Society of Mammalogists. Special Publication No. 2.
- BELL, H. B., AND R. W. DIMMICK. 1975. Hazards to predators feeding on prairie voles killed with zinc phosphide. *Journal of Wildlife Management* 9: 816–819.
- CARMER, S. G. 1976. Optimal significance levels for application of the least significant difference in crop performance trials. *Crop Science* 16: 95–99.
- CARMER, S. G., AND M. R. SWANSON. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *Journal of American Statistical Association* 68: 66–74.
- COLLINS, A. R., J. P. WORKMAN, AND D. W. URESK. 1984. An economic analysis of black-tailed prairie dog (*Cynomys ludovicianus*) control. *Journal of Range Management* 37: 358–361.
- CRABTREE, D. G. 1962. Review of current vertebrate pesticides. Pages 327–362 in *Proceedings, Vertebrate pest control conference, California Vertebrate Pest Control Tech*, Sacramento.
- DEISCH, M. S. 1986. The effects of three rodenticides on nontarget small mammals and invertebrates. Unpublished thesis, South Dakota State University, Brookings. 149 pp.
- DEISCH, M. S., D. W. URESK, AND R. L. LINDER. 1989. Effects of two prairie dog rodenticides on ground-dwelling invertebrates in western South Dakota. Pages 166–170 in A. J. Bjugstad, D. W. Uresk, and R. H. Hamre, eds., *Ninth Great Plains wildlife damage control workshop proceedings*. USDA Forest Service General Technical Report RM-171. Fort Collins, Colorado. 181 pp.
- EDGINGTON, E. S. 1980. *Randomization tests*. Marcel Dekker, Inc., New York.
- FALLS, J. B. 1968. Activity. Pages 543–567 in J. A. King, ed., *Biology of Peromyscus* (Rodentia). The American Society of Mammalogists. Special Publication No. 2.
- FLAKE, L. D. 1973. Food habits of four species of rodents on a short-grass prairie in Colorado. *Journal of Mammalogy* 54: 636–647.
- GREEN, R. H. 1979. *Sampling design and statistical methods for environmental biologists*. John Wiley and Sons, New York. 257 pp.
- HAYNE, D. W. 1976. Experimental designs and statistical analyses in small mammal population studies. Pages 3–13 in *Populations of small mammals under natural conditions*. Pymatuning Laboratory of Ecology. Special Publication Series Volume 5. University of Pittsburgh.
- HEGDAL, P. L., AND T. A. GATZ. 1977. Hazards to seed eating birds and other wildlife associated with surface strychnine baiting for Richardson's ground squirrels. EPA report under Interagency Agreement EPA-IAG-D4-0449.
- HEGDAL, P. L., T. A. GATZ, AND E. C. FITE. 1981. Secondary effects of rodenticides on mammalian predators. Pages 1781–1793 in J. A. Chapman and D. Pursley, eds., *The world furbearer conference proceedings*.
- HILTON, H. W., W. II. ROBISON, AND A. H. TESHIMA. 1972. Zinc phosphide as a rodenticide for rats in Hawaiian sugarcane. *Entomology* 1972: 561–571.
- JONES, J. K., JR., D. M. ARMSTRONG, R. S. HOFFMANN, AND C. JONES. 1983. *Mammals of the northern Great Plains*. University of Nebraska Press, Lincoln.

- KLATT, L. E. 1971. A comparison of the ecology of active and abandoned black-tailed prairie dog (*Cynomys ludovicianus*) towns. Unpublished thesis, Colorado State University, Fort Collins.
- KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama. *Wildlife Monographs* 3: 78 pp.
- MACCRACKEN, J. G., D. W. URESK, AND R. A. HANSEN. 1985. Rodent-vegetation relationships in southeastern Montana. *Northwest Science* 4: 272-278.
- MARSH, R. E., W. E. HOWARD, AND S. D. PALMATEER. 1970. Effects of odors of rodenticides and adherents on attractiveness of oats to ground squirrels. *Journal of Wildlife Management* 34: 821-825.
- METZGAR, L. H. 1980. Dispersion and numbers in *Peromyscus* populations. *American Midland Naturalist* 103: 26-31.
- O'MEILIA, M. E., F. L. KNOFF, AND J. C. LEWIS. 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35: 580-585.
- POTTER, R. L. 1980. Secondary successional patterns following prairie dog removal on shortgrass range. Unpublished thesis, Colorado State University, Fort Collins.
- ROMESBURG, C. 1981. Randomization tests. *Resource Evaluation Newsletter*. Pages 1-3 in Technical Article 1. USDI Bureau of Land Management, Denver Federal Center, Denver.
- RUDD, R. L., AND R. E. GENELLY. 1956. Pesticides: their use and toxicity in relation to wildlife. *California Fish and Game Bulletin* No. 7. 208 pp.
- SCHENBECK, G. L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207-217 in R. M. Timm and R. J. Johnson, eds., *Fifth Great Plains wildlife damage control workshop proceedings*, University of Nebraska, Lincoln.
- SCHITOSKEY, F., JR. 1975. Primary and secondary hazards of three rodenticides to kit fox. *Journal of Wildlife Management* 39: 416-418.
- SIEG, C. H., D. W. URESK, AND R. M. HANSEN. 1986. Seasonal diets of deer mice on bentonite mine spoils and sagebrush grasslands in southeastern Montana. *Northwest Science* 60: 81-89.
- TABER, R. D., AND I. MCT. COWAN. 1969. Capturing and marking wild animals. Pages 277-317 in R. H. Giles, ed., *Wildlife management techniques*. 3rd ed. The Wildlife Society, Washington, D.C.
- TACHA, T. C., W. D. WARDE, AND K. P. BURNHAM. 1982. Use and interpretation of statistics in wildlife journals. *Wildlife Society Bulletin* 10: 355-362.
- TERMAN, C. R. 1968. Populations dynamics. Pages 412-445 in J. A. King, ed., *Biology of Peromyscus (Rodentia)*. The American Society of Mammalogists. Special Publication No. 2.
- TIETJEN, H. P. 1976. Zinc phosphide: its development as a control agent for black-tailed prairie dogs. U.S. Department of International Fish and Wildlife Service. Special Science Report Wildlife No. 195. 14 pp.
- URESK, D. W. 1985. Effects of controlling black-tailed prairie dogs on plant production. *Journal of Range Management* 38: 466-468.
- URESK, D. W., R. M. KING, A. D. APA, M. S. DEISCH, AND R. L. LINDER. 1988. Rodenticidal effects of zinc phosphide and strychnine on nontarget species. Pages 57-63 in D. W. Uresk, G. L. Schenbeck, and R. Cefkin, eds., *Eighth Great Plains wildlife damage control workshop proceedings*. USDA Forest Service General Technical Report RM-154.
- URESK, D. W., R. M. KING, A. D. APA, AND R. L. LINDER. 1986. Efficacy of zinc phosphide and strychnine for black-tailed prairie dog control. *Journal of Range Management* 39: 298-299.
- WOOD, J. E. 1965. Response of rodent populations to controls. *Journal of Wildlife Management* 29: 425-438.

Received 20 December 1990

Accepted 28 January 1991





## ON THE TYPIFICATION OF *OXYTROPIS BOREALIS* DC.

Stanley L. Welsh<sup>1</sup>

**ABSTRACT.**—The status of the name *Oxytropis borealis* DC. is reviewed as it applies to North American plants. A summary of the infraspecific taxa is presented, and several nomenclatural combinations are proposed: *Oxytropis borealis* DC. var. *hudsonica* (Greene) Welsh; *O. borealis* var. *sulphurea* (Pors.) Welsh; *O. borealis* DC. var. *viscida* (Nutt.) Welsh. One new taxon, *Oxytropis borealis* DC. var. *australis* Welsh, is described from Utah and Nevada, USA.

Preparation of a revisionary summary of the genus *Oxytropis* DC. for the Flora North America Project necessitates that nomenclatural changes and new taxa be presented prior to publication in that project. The principal reason for this paper involves the nomenclature of *O. borealis*, a name that has figured in various taxonomic treatments of the genus in North America and elsewhere for more than a century (Barneby 1952, Bunge 1874, Gray 1884, Jurtsev 1986, Torrey and Gray 1838, Vasil'chenko, Fedchenko, and Shishkin 1948). The American phases of *Oxytropis* section *Gleocephala* have passed under a series of names centering on *Oxytropis viscida* Nutt. ex Torr. & Gray (1838). Since the section *Gleocephala* has circumboreal or at least amphiberingian representation, American workers were almost certain that there was an older name in the Old World literature. Indeed, Barneby (1952) in his revision of the North American species of *Oxytropis* cited two specific epithets older than that of *O. viscida*. And Boivin (1967), in his attempt at summarizing the Canadian portion of the section, transferred the infraspecific taxa to *O. leucantha* (Pallas) Pers. An examination of the type of that species demonstrated that it lacked glands typical of members of the section *Gleocephala*; it was indeed a portion of the *O. campestris* (L.) DC. sensu lato (Welsh 1972). The transfers to that entity, thus, are incorrect and are merely nomenclatural baggage that accompanies the genus in perpetuity.

Welsh (1967, 1974) and Welsh et al. (1987) essentially followed the lead of Barneby

(1952), who chose a wait-and-see attitude with regard to the earliest name for the North American complex. Examination of the types was necessary prior to a final determination of the question of an earlier name for the North American materials.

Bunge (1874) treated two main sections of glandular oxytropes, *Gleocephala* and *Polyadenia*. The main diagnostic feature used in segregation of members of these sections is the arrangement of the leaflets—*Gleocephala* having opposite, subopposite, or scattered leaflets and *Polyadenia* having pseudofaciculate leaflets. Since North American viscid oxytropes have both leaflet arrangements, but mainly opposite, subopposite, or scattered, it is necessary to review the names of Old World representatives of both *Gleocephala* and *Polyadenia*. The names *O. muricata* (Pallas) DC. (*Phaca muricata* Pallas, Reise 3: 318. 1776) and *O. microphylla* (Pallas) DC. (*Phaca microphylla* Pallas, Reise 3: 744. 1776) were both published prior to the next available name in *Gleocephala*, i.e., *O. borealis* DC. Authentic (probable type) specimens of these and others of the *Polyadenia* were obtained on loan from the herbarium of the Komarov Botanical Institute herbarium (LE). Neither *O. muricata* nor *O. microphylla* seems to be within the concept of the glandular phases of *O. borealis* with pseudofaciculate leaflets as they occur in North America.

Thus, the earliest name available in section *Gleocephala* in North America is *O. borealis* DC., which is based on a specimen (Fig. 1) deposited in the Prodromus herbarium at

<sup>1</sup>Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.



Fig. 1. Holotype of *Oxytropis borealis* DC. The specimen is at G-DC.

Geneva. The specimen is in poor, but not terrible, condition, essentially what is expected for many historical types. The specimen appears never to have been in good condition after its collection. The flowers are crumpled as though they had been wet following collection, or even following mounting. The question of glandularity was left unanswered in the description by de Candolle in *Prodromus* (see below). The need to examine portions of the material was critical as to its nomenclatural importance in North American taxonomy.

Detailed photos and fragments of the specimen were sent for examination through the generosity of Dr. A. Charpin, conservateur at Geneve (G-DC.). Of particular importance among the fragments loaned is a black, hairy bud with calyx teeth still connivent. The teeth are clearly glandular verrucose. Other fragments include a portion of a flower and part of a floral bract. The bract, a very long structure not unlike those of many Alaskan specimens, is definitely dorsally glandular also. The plant size and nature of other features, though shattered, are well within the morphological limits of the group as it occurs in North America. Clearly this material belongs to that portion of the *Gloecephala* complex treated by Barneby in 1952 as *O. viscida* var. *subsucculenta*. Having priority, the name *O. borealis* must replace *O. viscida* for North American portions of the complex. The author hopes the transfers proposed below are not additional nomenclatural baggage.

*Oxytropis borealis* DC., Prodr. 2: 275. 1825.

*O. borealis*, subacaulis, pilis scaporum stipularumque setosis patulis, petiolorum paucis, foliolis elliptico-lanceolatis subtus glabris superne pilosis scapi folii longitudine, floribus capitatis, bracteis calycis nigro-hispidissimi longitudine. In terra Tschuktschorum ad Sinum Sancti-Laurentii. Stipulae pallidae. (v.s. Comm. a cl. Fisch.) (l.c.).

TYPE LOCALITY.—“In terra Tschuktschorum ad sinum Sancti-Laurentii,” collector not stated.

TYPE.—“e sinu S. Laurentii in terra Tschuktschorum (pays des Tchouktchi) septentrionem versus a fretu Beringii. Legumina diversa a leg. ox. montana. m. [Messien] Fischer 1825” G-DC.!. The specimen cited above is the only one bearing the name *O. borealis* in the *Prodromus* herbarium, and it is regarded as the holotype (Fig. 1).

The species, as it occurs in North America, consists of a series of mainly intergrading varieties as indicated below. They differ in compactness of inflorescence, size of flowers, length of floral bracts, and other features that tend to grade individually and collectively into each other. As intergradation occurs, the taxa within the *boreale* complex match those of infraspecific taxa in other specific complexes in this genus.

Presented below is a summary of the infraspecific taxa as they occur in North America. The writer has examined herbarium materials from all regions of distribution in the continent. Additionally, he has examined the species in the field from the arctic regions of Alaska, Yukon, and Northwest Territories south to its southern limits in Utah and Nevada. Variation is huge in the species as a whole and in the infraspecific taxa. The group has received several interpretations in the past and will undoubtedly be interpreted differently in the future.

#### *Oxytropis borealis* DC. var. *borealis*

Distribution: N.W.T. and Alaska; Chukotsk.

*Oxytropis uralensis*  $\beta$  *subsucculenta* Hook., Fl. Bor.-Amer. 1: 146. 1831. *Oxytropis viscida* var. *subsucculenta* (Hook.) Barneby, Proc. Calif. Acad. IV, 27: 246. 1952. Type: “Arctic seashore, to the east of the Mackenzie River,” Dr. Richardson s.n.; holotype K.

*Oxytropis borealis*  $\beta$  Hook. & Arnott, Bot. Beechey Bot. 122. 1832.

*Oxytropis campestris* var. *verrucosa* Ledebour, Fl. Ross. 1: 591. 1842. Type: “in terra Tschuktschorum ad sinum Sancti-Laurentii,” the collector not stated.

The relatively few leaflets, ample flowers, and condensed, copiously hirsute inflorescence in combination allow this entity to be rather readily identified. It consists, at least in part, of what has passed under the name of *O. glutinosa* Pors., who excluded the type of “*subsucculenta*” from consideration in treatment of the genus in “Vascular Plants of Continental Northwest Territories, Canada” (Porsild and Cody 1980). Included within the concept of var. *borealis* is the *O. uralensis*  $\beta$  *subsucculenta* Hook., the basis of *O. viscida* var. *subsucculenta* (Hook.) Barneby.

#### *Oxytropis borealis* var. *hudsonica* (Greene) Welsh, comb. nov.

*Aragallus hudsonicus* Greene, Proc. Biol. Soc. Wash. 18: 17. 1905. *Oxytropis viscida* var. *hudsonica* (Greene) Barneby, Proc. Calif. Acad. IV, 27: 245.



1952. *O. viscida* ssp. *hudsonica* (Greene) Love & Love, *Taxon* 31: 347. 1982. *O. leucantha* var. *hudsonica* (Greene) Boivin, *Naturaliste Canad.* 94: 76. 1967. Type: Whale River, Hudson Bay; A. P. Low 14272, 24 June 1896; holotype NDG!

*Oxytropis leucantha* var. *hudsonica* f. *galactantha* Boivin, *Naturaliste Canad.* 94: 76. 1967. Type: Canada: Franklin District, Melville Peninsula, Repulse Bay, along Nauja River, 27 July 1950, P. F. Bruggeman 52; holotype DAO!

*Oxytropis leucantha* var. *leuchippiana* Boivin, *Naturaliste Canad.* 94: 76. 1967. Type: Yukon: Whitehorse, airport area, steep slope, flowers varying in color from yellow to purple, abundant, Gillette & Calder 3181; lectotype here selected DAO!

This is the phase of the species that occurs in North America mainly east of the Yukon, but with some representation in that province, where it is transitional with both var. *viscida* and var. *sulphurea*. The main diagnostic feature involves the short calyx teeth.

*Oxytropis borealis* var. *sulphurea*  
(Pors.) Welsh, comb. nov.

*O. viscidula* ssp. *sulphurea* Pors., *Bull. Nat. Mus. Canad.* 121: 247. 1951. Type: Yukon, Rose-Lapie Pass, shaly cliffs by waterfall E of Lapie Lake, mile 105 [Canol Road], Pors. & Breitung 10198, 19 July 1944; holotype CAN; isotypes ISC!, S!

*Oxytropis sheldonensis* Pors., *Bull. Nat. Mus. Canad.* 121: 246. 1951. Type: Mount Sheldon, on rocky granite ledges at or near the summit, opposite mile 122 [Canol Road], Pors. & Breitung 11750, 11 August 1944; holotype CAN!; isotypes ISC!, US!

*Oxytropis verruculosa* Pors., *Bull. Nat. Mus. Canad.* 121: 246. 1951. Type: Yukon: Rose-Lapie Pass, rocky ledges on dry slope W of mile 116 [Canol Road], Pors. 10072, 1944; holotype CAN!; isotype S!

These are the pallid-flowered plants of the Yukon and Alaska. In their most typical condition the racemes are compactly and uniformly small flowered. They vary from that norm to elongate racemes with small to large flowers. The bracts are mainly small, but in some they are very long and conspicuous in the inflorescence. On the one side the plants seem to grade with var. *hudsonica* and on the other with both var. *viscida* and var. *borealis*.

*Oxytropis borealis* var. *viscida*  
(Nutt.) Welsh, comb. nov.

*Oxytropis viscida* Nutt., ex Torr. & Gray, *Flora N. Amer.* 1: 341. 1838. *Aragallus viscidus* (Nutt.) Greene, *Pittonia* 3: 211. 1897. *Astragalus viscidus* (Nutt.) Tidestrom, *Proc. Biol. Soc. Wash.* 50: 19. 1937. *O. campestris* var. *viscida* (Nutt.) S. Watson, *U.S. Geol. Expl. 40th Parallel, Bot.* 5: 55. 1871. *Spiesia viscida* (Nutt.) Kuntze, *Rev. Gen.* 206. 1891. *O. leucantha* var. *viscida* (Nutt.) Boivin, *Naturaliste*

*Canad.* 94: 77. 1967. Type: Rocky Mountains, near the sources of the Oregon [SW Wyoming], Nuttall s.n. 1834; syntypes NY!, PH.

*Aragallus viscidulus* Rydb., *Mem. N.Y. Bot. Gard.* 1: 253. 1900. *O. viscidula* (Rydb.) Tidestrom, *Contr. U.S. Nat. Herb.* 25: 332. 1925. Type: Montana, Melrose, Silver Bow County, Rydberg 2716; holotype NY! (type specified by Barneby 1952).

*Aragallus viscidula* var. *depressus* Rydb., *Mem. N.Y. Bot. Gard.* 1: 523. 1900. *Oxytropis leucantha* var. *depressa* (Rydb.) Boivin, *Naturaliste Canad.* 94: 77. 1967. Type: Haystack Mt., Stillwater County, Montana, Tweedy 120; holotype NY!

*Oxytropis gaspensis* Fern. & Kelsey, *Rhodora* 30: 123. 1928. *Astragalus gaspensis* (Fern. & Kelsey) Tidestrom, *Proc. Biol. Soc. Wash.* 50: 19. 1937. *O. leucantha* var. *gaspensis* (Fern. & Kelsey) Boivin, *Naturaliste Canad.* 94: 76. 1967. Type: Quebec, Mont St. Pierre, Gaspé County, Fernald & Smith 25874, 14 August 1933; holotype GH; isotypes CAS!, NY!

*Oxytropis ixodes* Butters & Abbe, *Rhodora* 45: 2, tab. 745, figs. 1–6. 1943. *O. leucantha* var. *ixodes* (Butters & Abbe) Boivin, *Naturaliste Canad.* 94: 76. 1967. Type: Minnesota, South Fowl Lake, Cook County, Butters, Abbe, & Burns 611, 27 June 1940; holotype MINN; isotypes GH, NY!, PH!, US!

*Oxytropis leucantha* var. *magnifica* Boivin, *Naturaliste Canad.* 94: 77. 1967. Type: Alberta, Macloed, High River, 27 June 1902, J. Fletcher s. n.; holotype DAO!

*Oxytropis ixodes* var. *ecaadata* Butters & Abbe, *Rhodora* 45: 4. 1943. Type: Ontario, Thunder Bay District, Butters, Abbe, & Burns 682; holotype MINN.

DISTRIBUTION.—Alaska, Yukon, N.W.T., Quebec, British Columbia, Alberta, Minnesota, Oregon, Idaho, Wyoming, Nevada, Utah, Colorado, and California.

This variety includes almost as much diversity as the species as a whole. The numerous subunits are held together by tenuous characteristics that are difficult to define or place in a key. Variation is often great in subpopulations from adjacent hillsides or even on a single gravel bar, especially in the arctic. One is reminded of the conditions of morphological variation occurring in the boreal *O. nigrescens* var. *nigrescens*, as regarded by this author. Unless one is willing to support a taxonomy wherein the purported taxa are largely sympatric and consist of morphological subunits whose genetic continuity is questionable, made up of a series of similar plants held together by that similarity and not by genetic linkage, there seems to be no reasonable way to segregate the morphological variants as taxa. The rather large number of synonyms, often at specific or varietal levels, reflects the attempts at segregation.

*Oxytropis borealis* var. *australis*  
Welsh, var. nov.

Similis *O. boreali* var. *viscida* (Nutt.)  
Welsh sed in floribus pallidis et inflorescentia  
vulgo foliis saepe subaequalis distinguitur.

Caespitose, acaulescent, 6–19 cm tall; pubescence basifixed; stipules glabrous to glandular or sparingly so; leaves 4–15.5 cm long; leaflets 15–33, 1.5–20 mm long, 1–5 mm wide, oblong to lanceolate or elliptic, sparingly pilose to glabrate or glabrous on both sides, sometimes also glandular; scapes 2–16.5 cm long, spreading-hairy; racemes 2- to 11-flowered, the flowers spreading-ascending, the axis 1–3 cm long in fruit; bracts glabrous dorsally, glandular; flowers 11–19 mm long, whitish or rarely suffused with pink; calyx 5–11 mm long, the shortly cylindric tube 4–7 mm long, the teeth 1.5–3.5 mm long, triangular-subulate, commonly glandular; pods erect, sessile, ovoid to subcylindric, 8–16 mm long, 4–6 mm thick, glandular.

DISTRIBUTION.—Utah and Nevada, USA.

TYPE.—Utah: Sevier Co., open hillside, E of Hogan Pass, along Utah Hwy 72, at 8300 ft. elevation. Flowers white. T25S, R4E, 23 July 1967, S. L. Welsh, D. Isely, & G. Moore 6452; holotype BRY!, isotype ISC!, NY! (a total of 17 duplicates distributed earlier as *O. viscida* Nutt.). Other collections: Utah: Emery Co., 10 km due W of Ferron, 2 June 1977, E. Neese & S. White 3022; do, E end of Bald Ridge, T16S, R8E, S10, 11 July 1979, R. Foster. Sanpete Co., 20 km up Ferron Canyon, T19S, R5E, S36, 9 June 1977, S. Clark & K. Taylor 2473; do, Ferron Mt., T20S, R5E, S33, 11 July 1989, M. A. Franklin 6794. Sevier Co., Aspen Spring, Salina Canyon, 18 June 1943, W. P. Cottam 9191; do, 1 km SE of Mt. Hilgard, 25 August 1965, R. Stevens 110; do, Desert View, ca 1.5 km S of Hogan Pass, ca 23 km N of Fremont, T25S, R4W, 10 May 1969, S. L. Welsh, D. Atwood, L. Higgins 8971; do, 21 km due SSW of Fremont Jct., T26S, R4E, S4, 8 July 1977, S. L. Welsh 15359; do, head of Clear Creek below Hilgard Mt., T24S, R4E, S26, 30 June 1977, S. Clark 2662; do, Clear Creek ca 3 km SE of Clear Creek Guard Station, T24S, R4E, 10 June 1981, D. Atwood 7947; do, milepost 18 on Utah Hwy 72, T25S, R4E, S22, 31 May 1986, R. Kass, E. Neese, B. Neely 2345; do, milepost 18 on Utah Hwy 72, T26S, R4E, S4,

31 May 1986, E. Neese, B. Neely, R. Kass 17521; do, ca 13 km N of Fish Lake, T24S, R3E, S33, 25 July 1987, B. Franklin & J. & J. Chandler 4999. Wayne Co., Elk Horn Guard Station, T27S, R4E, S15, 17 June 1977, S. Welsh 14982; do, Paradise Valley, T25S, R4E, 24 July 1978, D. Atwood 6922; do, Elkhorn Campground, T24S, R4E, S15, 16 June 1986, J. M. Porter 3918; do, on the slopes overlooking Deep Creek, T27N, R4E, S25, 17 June 1986, J. M. Porter 3863. Nevada: Elko Co., Ruby Mountains, S of Harrison Pass, T28N, R57E, ca S25, 7 August 1967, J. L. Gentry & G. Davidse 1823. Nye Co., Toquima Range, Pine Creek drainage, T11N, R45E, 24 July 1964, J. L. Reveal 657; do, Toquima Mts. ca 110 km S of Austin, T11N, R45E, ca S28, 15 July 1973, A. Cronquist 11048; do, Toquima Range, Mt. Jefferson, head of South Fork Pine Creek, T11N, R45E, S29 & S32, 18 July 1978, K. R. Genz 8246; do, north side of Timber Mountain, Grant Range, T6N, R57E, 27 June 1979, M. J. Williams & A. Tiehm 79-109-4.

This southern phase of *O. borealis*, though mainly montane in distribution, occurs mostly on xeric sites in sagebrush, black sagebrush, grass, ponderosa pine, and aspen parkland communities, often on exposed ridges or outcrops. Main substrate types are of igneous origin, either granitic- or basaltic-derived soils, but limestone also serves as a substrate. Elevational range varies from 2135 to 3355 m.

The differences cited in the diagnosis are not absolute, as is usual for infraspecific and even specific taxa in this genus. Flower color is typically white or ochroleucous, but some are occasionally tinged with pink; and some that appear to be white when fresh fade slightly lavender on drying. Inflorescences tend to be only slightly longer than the leaves, or even slightly shorter, but some have inflorescences much surpassing what appear to be juvenile leaves with tiny leaflets. The herbage is often conspicuously glandular, with sand grains and plant fragments adhering. The stipules are occasionally quite glandless, however. In spite of the variation in morphology, these plants appear to represent a xeric southern phase related to the typically more mesic var. *viscida*. That variety, shorn of var. *australis*, is not much less polymorphic. There are individual plants, and possibly even subpopulations, within var. *viscida* that simulate

var. *australis*. Plants from the Wallowa Mountains of northeastern Oregon are almost as variable as var. *viscida* as a whole.

#### LITERATURE CITED

- BARNEBY, R. C. 1952. A revision of the North American species of *Oxytropis* DC. Proceedings of the California Academy of Science IV, 27: 177–312.
- BOIVIN, B. 1967. Etudes sur les *Oxytropis* DC. II. Naturaliste Canadienne 94: 73–78.
- BUNGE, A. 1874. Species Generis *Oxytropis*, DC. Memoirs of the Academy of Science, St. Petersburg VII, 22: 1–166.
- GRAY, A. 1884. A revision of the North American species of *Oxytropis* DC. Proceedings of the American Academy of Science 20: 1–7.
- JURTSEV, B. A. 1986. *Oxytropis* DC. Arctic flora S.S.S.R. 9: 61–146, 178–182.
- PORSILD, A. E., AND W. J. CODY. 1980. *Oxytropis* DC. Pages 438–442 in Vascular plants of the continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada. 667 pp.
- TORREY, J., AND A. GRAY. 1838. Flora of North America. Vol. 1. G. C. Carvill & Co., New York.
- VASIL'CHENKO, I. T., B. A. FEDCHENKO, AND B. K. SHISHKIN. 1948. *Oxytropis* DC. In Flora U.S.S.R. 13: 1–229.
- WELSH, S. L. 1967. Legumes of Alaska II: *Oxytropis* DC. Iowa State Journal of Science 41: 277–303.
- . 1972. On the typification of *Oxytropis leucantha* (Pallas) Pers. Taxon 21: 155–157.
- . 1974. *Oxytropis*, DC. Pages 275–282 in Anderson's flora of Alaska and adjacent parts of Canada. Brigham Young University Press, Provo, Utah. 724 pp.
- . 1987. *Oxytropis* DC. Pages 396–398 in S. L. Welsh, N. D. Atwood, S. Goodrich, and L. C. Higgins, A Utah flora. Great Basin Naturalist Memoir 9: 1–984.

Received 5 February 1991  
Accepted 25 February 1991



## REPRODUCTION OF THREE SPECIES OF POCKET MICE (*PEROGNATHUS*) IN THE BONNEVILLE BASIN, UTAH

Kenneth L. Cramer<sup>1,2</sup> and Joseph A. Chapman<sup>1</sup>

**ABSTRACT.**—Data on reproduction of three species of pocket mice (*Perognathus*) occurring in northern Utah are summarized. *Perognathus parvus* and *P. formosus* bred in spring but not the remainder of the year. This occurred despite mild fall and winter temperatures and shallow snowcover. Litter sizes for *P. parvus* and *P. formosus* were similar to those reported by previous investigators. A small sample of *P. longimembris* indicated they may have much larger litters (averaging 5.78 young) than previously reported for laboratory populations. Adult body mass was positively correlated with testis mass in all species, and with litter size in *P. parvus*.

Pocket mice (genus *Perognathus*) are widespread and ubiquitous components of rodent communities in western North America. Despite a growing body of knowledge concerning their ecology, such as competitive interactions (e.g., Brown and Lieberman 1973), seed-caching (e.g., Kenagy 1973, Reichman 1975), and physiological adaptations to arid environments (MacMillen 1972), studies of pocket mouse reproduction are primarily anecdotal or based on laboratory colonies (Jones 1985).

Here we report on reproduction in field populations of the long-tailed pocket mouse (*Perognathus formosus*), Great Basin pocket mouse (*P. parvus*), and little pocket mouse (*P. longimembris*) in the Bonneville Basin of northwestern Utah. Specifically, we examine seasonal variation in reproductive activity, litter size, and allometric relationships between body mass and reproductive variables.

### STUDY AREAS

Most *P. formosus* were trapped on the north end of the Newfoundland Mountains ( $N = 161$ ), with a few specimens from the Grassy Mountains ( $N = 24$ ) and Floating Island ( $N = 12$ ). *P. parvus* were collected primarily from the Grassy Mountains ( $N = 21$ ), Hogup Mountains ( $N = 36$ ), and Stansbury Island ( $N = 32$ ). *P. longimembris* in this study were sampled from Floating Island ( $N = 16$ ), located 30 miles NE of Wendover

(Tooele County), Utah, in the Bonneville Salt Flats. Collection sites are between 1300 and 1420 m in elevation on the Floating Island, Newfoundland Mountain, and Stansbury Island sites; and 1650 m in the Hogup Mountain and Grassy Mountain sites (Fig. 1).

All collection sites are dominated by northern cold-desert vegetation, including sagebrush (*Artemisia* spp.), saltbush (*Atriplex* spp.), rabbitbrush (*Chrysothamnus* spp.), horsebrush (*Tetradymia* spp.), greasewood (*Sarcobatus* spp.), and juniper (*Juniperus osteosperma*). The dominant shrubs vary according to elevational, moisture, and soil salinity gradients. All sites show a high degree of similarity in plant genera (39–52% overlap, using Jaccard's index of similarity) with the exception of Stansbury Island, which ranges between 22% and 29% similarity when paired with other sites. This is probably due to the increased diversity found in dunes sampled on the north shore of this island.

### METHODS

Specimens were live-trapped or snap-trapped on a monthly basis in 1986 on the Newfoundland and Grassy mountains for approximately 500 trap nights per month. Pocket mice from Stansbury Island and Floating Island were sampled between April and September.

Mice were euthanized and frozen on dry ice in the field. In the laboratory, mice were

<sup>1</sup>Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322-5210.

<sup>2</sup>Present address: Biology Department, Central Missouri State University, Warrensburg, Missouri 64093.

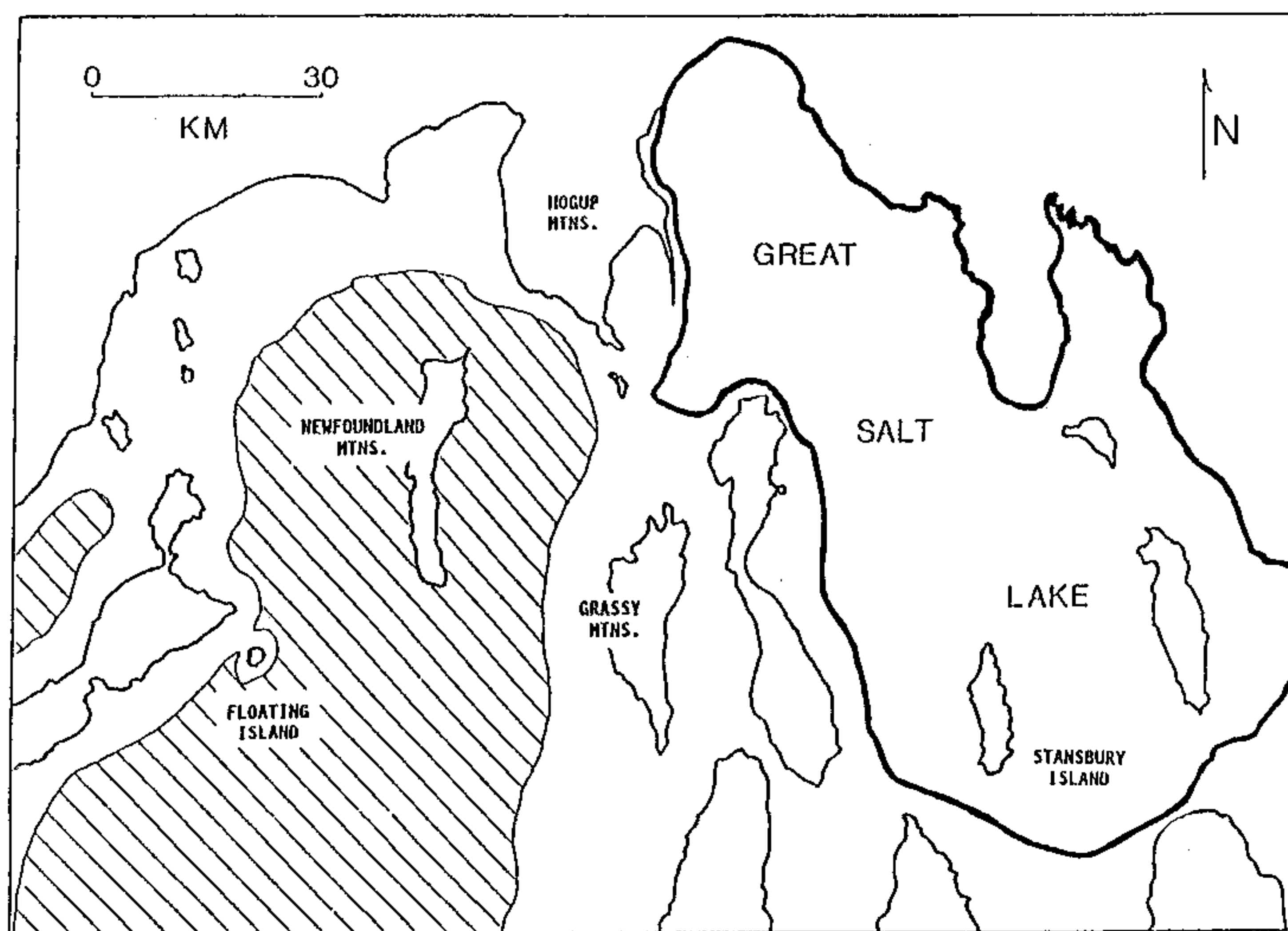


Fig. 1. Study areas in northwestern Utah sampled for three species of *Perognathus*. Area in hatchmarks indicates the extent of barren salt flats. Contour lines are drawn at approximately 1300 m.

weighed to the nearest 0.5 g and measured (total length, tail, hind foot, ear) to the nearest millimeter. Reproductive tracts were removed and placed in alcohol/formalin/acetic acid (AFA) mixture (90 parts 70% ethanol, 5 parts each formalin and glacial acetic acid). Histological procedures followed those of Brown (1964) and Duke (1957).

Testes were stripped of the epididymides and measured lengthwise to the nearest 0.1 mm using an ocular micrometer. Testes were then dried at 80 C for 48 h and weighed to the nearest 0.1 mg on a Mettler AE160 electronic analytical balance.

Uteri and ovaries were cleared through an alcohol-xylene series using Hemo-De, a xylene substitute. Placental scars were counted at this stage and ovaries infiltrated and embedded in paraffin for sectioning. Serial sections 10 microns thick of the entire ovary were stained in Gill's hematoxylin and mounted with Permount mounting medium. Corpora lutea were counted on a dissecting

microscope at 25X magnification. Embryos present were counted and measured to the nearest 1 mm.

## RESULTS

Results are based on data from 104 female and 93 male *P. formosus*, 25 female and 64 male *P. parvus*, and 9 female and 7 male *P. longimembris*. All data were taken from individuals in adult pelage. The 1986 field season was divided into three seasons as follows: emergence to late June, July through mid-September, and mid-September through early December. This was done to divide the aboveground activity of the heteromyids into three time lengths of equal sampling intensity.

**LONG-TAILED POCKET MICE.**—Males were first captured in early March, females in mid-April, and neither showed evidence of breeding at that time. Twenty-nine percent of the females sampled ( $N = 17$ ) through the end of

TABLE 1. Seasonal variation of testis mass (dry weight, mg) and seminal vesicle length (mm) of *Perognathus formosus*.

Season	April-June	July-mid-Sept.	Sept.-Dec.
Testis	158.68 ( $\pm 5.73$ ) N = 22	25.25 ( $\pm 2.41$ ) N = 57	27.28 ( $\pm 1.81$ ) N = 11
Seminal vesicle	8.80 ( $\pm 0.40$ ) N = 20	4.76 ( $\pm 0.20$ ) N = 17	No data*

\*No animals with seminal vesicles developed.

TABLE 2. Correlations of body mass with male reproductive variables in three species of *Perognathus*.

Species		<i>formosus</i>	<i>parvus</i>	<i>longimembris</i>
Testis mass	rho (N)	.502 (90)	.702 (64)	.618 (7)
	P	<.001	<.001	.139
Seminal vesicle length	rho (N)	-.167 (37)	.672 (49)	.314 (6)
	P	.324	<.001	.545

June had corpora lutea. This dropped to only 6.3% ( $N = 63$ ) for July-September (Fisher's Exact test,  $X^2 = 7.04$ ,  $P = .018$ ), and none captured after mid-September showed any signs of reproductive activity. Ten percent of the females ( $N = 19$ ) carried embryos early in the season through June, whereas only 1.3% ( $N = 79$ ) carried embryos in the summer (Fisher's Exact test,  $X^2 = 4.38$ ,  $P = .095$ ).

Male reproductive activity paralleled the observations for females. Testis mass and seminal vesicle lengths were smaller as the season progressed (Table 1), reflecting a spring (April-June) breeding peak followed by breeding inactivity the remainder of the year. Mean testis mass was more than five times greater in the spring than in either summer or fall (Kruskal-Wallis,  $X^2 = 50.9$ ,  $P < .001$ ). Seminal vesicles were nearly twice as long in spring (8.8 mm) as in fall (4.8 mm), reflecting a similar pattern (Mann-Whitney  $U = 2.5$ ,  $P < .001$ ). Adult male body mass was significantly correlated with testis mass (Spearman's rho = 0.502,  $P < .001$ ,  $N = 90$ , Table 2).

The mean litter size estimated from 35 females with one set of placental scars was 5.89 ( $\pm 0.30$ ). Nine sets of corpora lutea from separate individuals revealed a smaller estimate of 4.78 ( $\pm 0.74$ ). Our small sample sizes for these data may reflect the fact that corpora lutea in *Perognathus* regress rapidly (Duke 1957) compared with other species where they may persist for months (Brown and Conaway 1964). Three females with embryos had litters of six, six, and five. Thirty-four

percent of the females with placental scars had given birth to more than one litter. No evidence of resorbing embryos or polyovuly was observed.

GREAT BASIN POCKET MICE.—This species also apparently has only one peak breeding effort in the spring, although sample sizes are too small to permit meaningful statistical tests. Males were first captured in mid-April, females about two weeks later. Females were reproductively active (corpora lutea or embryos present) when first captured. Forty-five percent (9 of 20) of females captured had corpora lutea, and 28% (7 of 25) were carrying embryos.

Males caught between April and June had significantly larger testes and seminal vesicles (Table 3) than individuals from the remainder of the season (Mann-Whitney  $U = 28.0$ ,  $P < .001$  for testes mass;  $U = 46.5$ ,  $P < .001$  for seminal vesicle lengths). Adult male body mass was significantly correlated with testis mass (Spearman's rho = 0.702,  $P < .001$ ,  $N = 64$ ) and seminal vesicle length (Spearman's rho = 0.672,  $P < .001$ ,  $N = 49$ ) (Table 2).

Litter size in this species was approximately five, although this was from a sample of only nine females. One set of placental scars numbered five, seven pregnant females averaged 5.17 ( $\pm 0.46$ ) embryos, and nine sets of corpora lutea averaged 5.33 ( $\pm 0.37$ ). No evidence of polyovuly or resorption of embryos was observed. Size of the mother was correlated with the number of corpora lutea (Spearman's rho = 0.738,  $P = .023$ ,  $N = 9$ ) and



TABLE 3. Seasonal variation of testis mass (dry weight, mg) and seminal vesicle length (mm) of *Perognathus parvus*.

Season	April-June	July-Dec.
Testis	153.09 ( $\pm 6.54$ ) N = 22	61.33 ( $\pm 5.63$ ) N = 42
Seminal vesicle	10.50 ( $\pm 0.36$ ) N = 22	6.77 ( $\pm 0.39$ ) N = 27

embryos (Spearman's  $\rho = 0.611$ ,  $P = .145$ ,  $N = 7$ ). Although based on an extremely small sample, this agrees with correlations found in *Peromyscus maniculatus* (Myers and Master 1983, Cramer 1988).

**LITTLE POCKET MICE.**—Litter size averaged  $5.78 (\pm 0.22)$  embryos per litter ( $N = 9$ ). The modal size was six, but most of these were in very early stages of development where uterine swellings were less than 3 mm. One female captured later in pregnancy (crown-rump length of embryos 10 mm) had resorbed one embryo, leaving a potential litter of five. Some preimplantation loss was also noted. Two of the litters of six resulted from seven ova as inferred from corpora lutea counts.

## DISCUSSION

**LONG-TAILED POCKET MICE.**—Previous published reports on reproduction in *P. formosus* are few but generally support our findings. For a population in southeastern Washington, French et al. (1974) reported an average litter size of 5.6 (77 litters) and a mean corpora lutea count of 6.0 ( $N = 51$ ), both comparable to the present results. The high proportion of long-tailed pocket mice with placental scars from multiple litters may simply reflect the longevity of this species, which has been estimated as up to four years in mark-recapture studies (French et al. 1974).

The only information on the length of the breeding season for this species was offered by Hall (1946), who found embryos in only 2 of 91 females captured in July in Nevada. Our data on male and female reproductive activity indicating a spring peak and cessation of breeding activity by early July support those observations. Even given a combination of apparently favorable weather conditions in fall and winter, no breeding occurred during this period in long-tailed pocket mice. September and

October had above average rainfall (196% and 155% above normal, respectively) but cooler than average temperatures (2.6 and 1.1 C below normal). November and December had below average precipitation (snowcover) (39% and 15% of normal, respectively), and November was 0.9 C warmer than normal (NOAA Climatological Data Annual Summary, Utah 1986). *Peromyscus maniculatus* in the same area continued to breed into December (Cramer 1988). These data suggest that reproductive activity in the fall in these species of pocket mice may be more closely tied to photoperiod than to climatic factors. Reichman and Van De Graaff (1975) showed the onset of reproduction in *Dipodomys merriami* to be dependent on winter rainfall and subsequent spring production of annual seeds and green vegetation. Kenagy and Bartholomew (1981) reported a similar effect of green vegetation on male reproductive development in *Perognathus formosus*. It is possible, then, that habitat productivity cues are important for the onset of breeding in the spring, but cessation of breeding in the fall is dependent on photoperiod.

**GREAT BASIN POCKET MICE.**—In a Washington population of Great Basin pocket mice, Scheffer (1938) found an average litter size of 5.16 ( $N = 77$ ) from embryo counts and estimated that few individuals produced more than one litter per year. Iverson (1967) reported a mean litter size of 4.85 ( $N = 39$ ) for a population of *P. parvus* in south central British Columbia. He also found that females bred from April to August and that males were reproductively inactive by mid-August. O'Farrell et al. (1975) also suggested that an average of 1.1 litters per year was produced by this species in south central Washington. Our data support previous estimates of litter size in this species and confirm indirectly the supposition that only one litter per year is produced on average, since we found only a short spring breeding peak. Reproductive activity in both males and females supports the hypothesis of a single spring breeding peak with young-of-the-year deferring reproduction until the following spring.

**LITTLE POCKET MICE.**—This species produced an average of four young ( $N = 52$ ) in the laboratory, with a range of one to six (Hayden et al. 1966). Other than Hayden's study, data for this species are scarce. Duke's (1957) study

does not specify litter sizes for the three species he studied (same three as in this study), but he cited an average litter size for all three species of 5.38. In our samples, the modal litter size for *P. longimembris* is six, much higher than the average of four reported in the laboratory (Hayden et al. 1966).

Our results suggest that pocket mice in northern Utah generally breed only in the spring although they may produce more than one litter per year. Long-tailed pocket mice and little pocket mice usually have six young per litter, while Great Basin pocket mice usually produce about five young per litter. These data are consistent with previous literature with the exception of our litter estimates for little pocket mice. Even given our relatively small sample sizes, the large discrepancy (two young per litter) between our field data and previous lab estimates (Hayden et al. 1966) suggests that caution be exercised in extrapolating from the lab to the field. This could be particularly misleading when drawing inferences from large literature reviews of diverse data sets (e.g., Jones 1985).

#### ACKNOWLEDGMENTS

This study was funded in part by U.S. Air Force Department of Defense Contract No. F42650-84-C3559 through the Utah State University Foundation. The Department of Fisheries and Wildlife and the Ecology Center of Utah State University provided vehicles and other logistical and technical support. The Utah Department of Wildlife Resources granted the necessary collection permits. This paper is part of a dissertation completed by the first author in partial fulfillment of the requirements for a doctoral degree in Wildlife Ecology at Utah State University.

#### LITERATURE CITED

- BROWN, J. H., AND G. A. LIEBERMAN. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* 54: 788-797.
- BROWN, L. N. 1964. Reproduction of the brush mouse and white-footed mouse in the central United States. *American Midland Naturalist* 72: 226-240.
- BROWN, L. N., AND C. H. CONAWAY. 1964. Persistence of corpora lutea at the end of the breeding season in *Peromyscus*. *Journal of Mammalogy* 45: 260-265.
- CRAMER, K. L. 1988. Reproduction and life history patterns of *Peromyscus maniculatus* and *Perognathus* spp. in the northern Bonneville Basin, Utah. Doctoral dissertation, Utah State University, Logan, Utah. 101 pp.
- DUKE, K. L. 1957. Reproduction in *Perognathus*. *Journal of Mammalogy* 38: 207-210.
- FRENCH, N. R., B. G. MAZA, AND A. P. ASCHWANDEN. 1974. A population study of irradiated desert rodents. *Ecological Monographs* 44: 45-72.
- HALL, E. R. 1946. The mammals of Nevada. University of California Press, Berkeley.
- HAYDEN, P., J. J. GAMBINO, AND R. G. LINDBERG. 1966. Laboratory breeding of the little pocket mouse, *Perognathus longimembris*. *Journal of Mammalogy* 47: 412-423.
- IVERSON, S. L. 1967. Adaptations to arid environments in *Perognathus parvus* (Peale). Doctoral dissertation, University of British Columbia, Vancouver. 130 pp.
- JONES, W. T. 1985. Body size and life-history variables in heteromyids. *Journal of Mammalogy* 66: 128-132.
- KENAGY, G. J. 1973. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* 54: 1201-1219.
- KENAGY, G. J., AND G. A. BARTHOLOMEW. 1981. Effects of day length, temperature, and green food on testicular development in a desert pocket mouse, *Perognathus formosus*. *Physiological Zoology* 54: 62-73.
- MACMILLEN, R. E. 1972. Water economy of nocturnal desert rodents. Pages 147-174 in G. M. O. Maloiy, ed., *Comparative physiology of desert animals*. Academic Press, New York.
- MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
- MYERS, P., AND L. L. MASTER. 1983. Reproduction by *Peromyscus maniculatus*: size and compromise. *Journal of Mammalogy* 64: 1-18.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1986. Climatological Data Annual Summary, Utah, 1986. Vol. 88, No. 13.
- O'FARRELL, T. P., R. J. OLSON, R. O. GILBERT, AND J. D. HEDLUND. 1975. A population of Great Basin pocket mice, *Perognathus parvus*, in the shrub-steppe of southcentral Washington. *Ecological Monographs* 45: 1-28.
- REICHMAN, O. J. 1975. Relation of desert rodent diets to available resources. *Journal of Mammalogy* 56: 731-751.
- REICHMAN, O. J., AND K. M. VAN DE GRAAFF. 1975. Association between ingestion of green vegetation and desert rodent reproduction. *Journal of Mammalogy* 56: 503-506.
- SCHEFFER, T. H. 1938. Determining the rate of replacement in a species. *Journal of Mammalogy* 11: 466-469.
- SMITH, H. D., AND C. D. JORGENSEN. 1975. Reproductive biology of North American desert rodents. Pages 305-330 in I. Prakash and P. K. Ghosh, eds., *Rodents in desert environments*. Dr. W. Junk Publishers, The Hague.

Received 1 September 1989

Revised 8 October 1990

Accepted 15 December 1990





ECTOMYCORRHIZAL FORMATION BY *PISOLITHUS TINCTORIUS*  
ON *QUERCUS GAMBELII* × *QUERCUS TURBINELLA* HYBRID  
IN AN ACIDIC SIERRA NEVADA MINESOIL

R. F. Walker<sup>1</sup>

Recent reports (Walker 1989, 1990) disclosed *Pisolithus tinctorius* (Pers.) Coker & Couch occurring in ectomycorrhizal association with Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), Sierra lodgepole pine (*P. contorta* var. *murrayana* [Grev. & Balf.] Engelm.), and California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.) on spoils of the Leviathan Mine in Alpine County, California. This Gasteromycete, which has a near worldwide distribution in temperate, subtropical, and tropical latitudes, is a mycobiont of numerous conifer and hardwood hosts (Marx 1977). In the United States it has been most often observed in association with various pine species on harsh sites in the East, South, and Midwest (Lampky and Peterson 1963, Schramm 1966, Hile and Hennen 1969, Lampky and Lampky 1973, Marx 1975, Medve et al. 1977). Subsequently, *P. tinctorius* has been the focus of concerted efforts to develop pure culture inoculation techniques for nursery-grown pine seedlings (Marx et al. 1976, 1984, 1989a, 1989b). Outplanting trials on southern Appalachian surface mines have demonstrated the potential benefits of planting inoculated seedlings on marginal sites, which include improved survival and growth attributable to enhanced uptake of nutrients (Marx and Artman 1979) and water (Walker et al. 1989). Currently, research is concentrated on identification of potential new host species and sources of locally adapted *P. tinctorius* isolates, as well as improvement of inoculation methods. The findings reported here result from efforts to ascertain the host range of this fungus in the Sierra Nevada and Great Basin.

Leviathan Mine, an inactive, open-pit sul-

fur mine of approximately 100 ha, is located on the eastern slope of the central Sierra Nevada (38°42'30"N, 119°39'15"W) at an elevation of 2,200 m and receives an average annual precipitation of 50 cm, primarily as snowfall. A comprehensive evaluation of the chemical properties of the minesoil (Butterfield and Tueller 1980) revealed a pH of 4.0–4.5, a deficiency of plant-available N, and a potentially phytotoxic Al concentration. Efforts to revegetate the mine since its closure in 1962 have met with limited success, although more recent attempts using a variety of native and nonnative woody species have been somewhat encouraging. Additionally, the periphery of the mine has been recolonized by several species from the adjoining undisturbed forest, primarily Jeffrey and Sierra lodgepole pine and California white fir. Overall, however, much of the site is either sparsely vegetated or barren.

Further examination of Leviathan Mine spoils in September of 1989 and 1990 revealed *P. tinctorius* in ectomycorrhizal association with seedlings of the hybrid Gambel oak (*Quercus gambelii* Nutt.) × turbinella oak (*Q. turbinella* Greene). These seedlings were planted in 1987 as containerized stock grown from acorns collected in southern Nevada, the only location in the state where this hybrid occurs naturally (Tucker et al. 1961). One to three *P. tinctorius* basidiocarps, dark yellow to brown in color and matching the description of Coker and Couch (1928), were observed near solitary seedlings (Fig. 1A), while numerous basidiocarps were often interspersed among clusters of seedlings. Stipitate, substipitate, and sessile forms were encountered, varying in size from 3 to 6 cm in

<sup>1</sup>University of Nevada, Reno, Department of Range, Wildlife and Forestry, 1000 Valley Road, Reno, Nevada 89512.



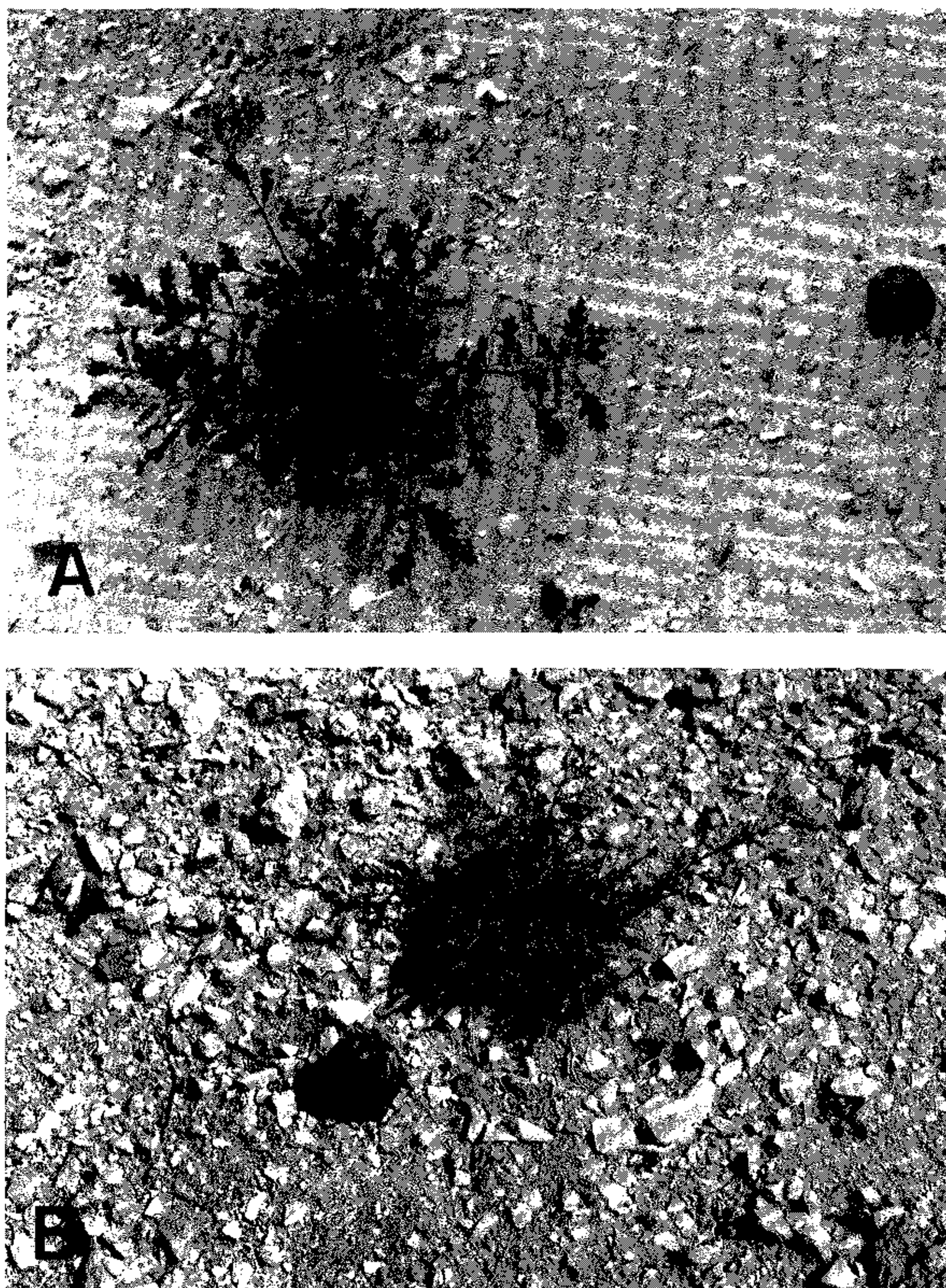


Fig. 1. *Pisolithus tinctorius* basidiocarps on spoils of the Leviathan Mine in Alpine County, California, associated with: A, Gambel oak  $\times$  turbinella oak hybrid; B, Rocky Mountain juniper.

diameter and from 8 to 15 cm in length; the basidiocarps were rarely more than one meter from the host. Mycelial strands with the characteristic gold-yellow pigmentation of *P. tinctorius* (Schramm 1966) were traced through the minesoil from basidiocarps to seedling root systems, which exhibited the similarly pigmented monopodial, bifurcate, and coral-loid ectomycorrhizae formed by this mycobiont (Marx and Bryan 1975a). Excavation of

a single representative oak root system revealed that approximately 20% of the lateral roots bore *P. tinctorius* mycorrhizae or an obvious fungal mantle.

Additional *P. tinctorius* basidiocarps were observed in the immediate vicinity of seedlings of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Woods rose (*Rosa woodsii* Lindl. var. *ultramontana* [Wats.] Jeps.), and Siberian peashrub (*Caragana arborescens*



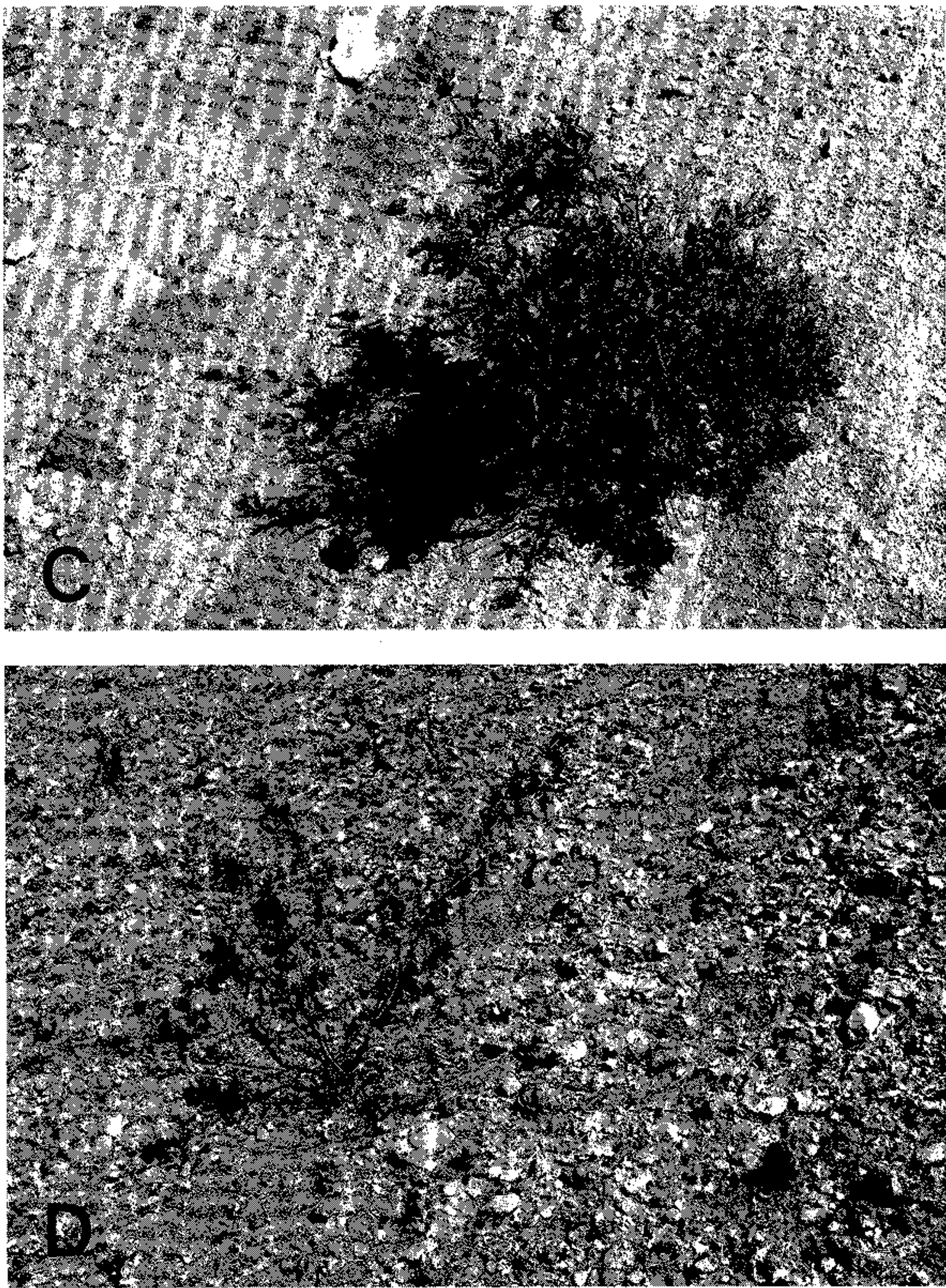


Fig. 1 continued. *Pisolithus tinctorius* basidiocarps on spoils of the Leviathan Mine in Alpine County, California, associated with: C, Woods rose; and D, Siberian peashrub.

Lam.). These three species were also planted as containerized stock with the plantings of Rocky Mountain juniper in 1984 and Woods rose and Siberian peashrub in 1986. Typically, one or two basidiocarps, similar in appearance and size to those found with the hybrid oaks, were again observed within one meter of isolated seedlings of the three species (Figs. 1B-D), and *P. tinctorius* mycelial strands were also traced through the minesoil

from the basidiocarps to the root systems. However, no ectomycorrhizae were found on any of these three species following excavation of complete root systems, although species within the genera *Juniperus* and *Rosa* are known to form ectomycorrhizal relationships (Harley and Smith 1983). Rather, on the juniper, rose, and peashrub observed here, only a loose fungal mantle of the characteristic gold-yellow *P. tinctorius* hyphae was



apparent on the fine roots. Given that excavated seedling specimens and the associated basidiocarps were  $\geq 10$  m from any other vegetation, it is likely the fungus derived its requisite carbohydrates solely from these seedlings, as most ectomycorrhizal fungi are assumed to rely on the carbohydrates obtained through the infection of an autotrophic host for completion of their life cycles and subsequent fruiting body production (Marx and Bryan 1975b). Thus, the apparent lack of ectomycorrhizal formation on the juniper, rose, and peashrub may indicate the development of a parasitic, or perhaps ectendomycorrhizal, relationship between *P. tinctorius* and these hosts in the Leviathan Mine, although there are no reports of this fungus forming either of these relationships with any of its previously identified host species.

#### ACKNOWLEDGMENTS

This paper contains results of the Nevada Agricultural Experiment Station Research Project 612 funded by the McIntire-Stennis Cooperative Forestry Research Program. The author is indebted to P. M. Murphy of the Division of Forestry, Nevada Department of Conservation and Natural Resources; A. T. Leiser of the Department of Environmental Horticulture, University of California, Davis; and D. C. Prusso of the Department of Biology, University of Nevada, Reno, for their invaluable assistance.

#### LITERATURE CITED

- BUTTERFIELD, R. L., AND P. T. TUELLER. 1980. Revegetation potential of acid mine wastes in northeastern California. *Reclamation Review* 3: 21–31.
- COKER, W. C., AND J. N. COUCH. 1928. The Gastromycetes of the eastern United States and Canada. University of North Carolina Press, Chapel Hill. 201 pp.
- HARLEY, J. L., AND S. E. SMITH. 1983. Mycorrhizal symbiosis. Academic Press, New York. 483 pp.
- HILE, N., AND J. F. HENNEN. 1969. In vitro culture of *Pisolithus tinctorius* mycelium. *Mycologia* 61: 195–198.
- LAMPKY, J. R., AND J. H. PETERSON. 1963. *Pisolithus tinctorius* associated with pines in Missouri. *Mycologia* 55: 675–678.
- LAMPKY, S. A., AND J. R. LAMPKY. 1973. *Pisolithus* in central Florida. *Mycologia* 65: 1210–1212.
- MARX, D. H. 1975. Mycorrhizae and establishment of trees on strip-mined land. *Ohio Journal of Science* 75: 288–297.
- . 1977. Tree host range and world distribution of the ectomycorrhizal fungus *Pisolithus tinctorius*. *Canadian Journal of Microbiology* 23: 217–223.
- MARX, D. H., AND J. D. ARTMAN. 1979. *Pisolithus tinctorius* ectomycorrhizae improve survival and growth of pine seedlings on acid coal spoils in Kentucky and Virginia. *Reclamation Review* 2: 23–31.
- MARX, D. H., AND W. C. BRYAN. 1975a. Growth and ectomycorrhizal development of loblolly pine seedlings in fumigated soil infested with the fungal symbiont *Pisolithus tinctorius*. *Forest Science* 21: 245–254.
- . 1975b. The significance of mycorrhizae to forest trees. Pages 107–117 in B. Bernier and C. H. Winget, eds., *Proceedings of the fourth North American forest soils conference*, August 1973, Laval University, Quebec. International Scholarly Books Services, Portland, Oregon. 675 pp.
- MARX, D. H., W. C. BRYAN, AND C. E. CORDELL. 1976. Growth and ectomycorrhizal development of pine seedlings in nursery soils infested with the fungal symbiont *Pisolithus tinctorius*. *Forest Science* 22: 91–100.
- MARX, D. H., C. E. CORDELL, D. S. KENNEY, J. G. MEXAL, J. D. ARTMAN, J. W. RIFFLE, AND R. J. MOLINA. 1984. Commercial vegetative inoculum of *Pisolithus tinctorius* and inoculation techniques for development of ectomycorrhizae on bare-root tree seedlings. *Forest Science Monograph* 25. 101 pp.
- MARX, D. H., C. E. CORDELL, S. B. MAUL, AND J. L. RUEHLE. 1989a. Ectomycorrhizal development on pine by *Pisolithus tinctorius* in bare-root and container seedling nurseries. I. Efficacy of various vegetative inoculum formulations. *New Forests* 3: 45–56.
- . 1989b. Ectomycorrhizal development on pine by *Pisolithus tinctorius* in bare-root and container seedling nurseries. II. Efficacy of various vegetative and spore inocula. *New Forests* 3: 57–66.
- MEDVE, R. J., F. M. HOFFMAN, AND T. W. GAITHER. 1977. The effects of mycorrhizal-forming amendments on the revegetation of bituminous stripmine spoils. *Bulletin of the Torrey Botanical Club* 104: 218–225.
- SCHRAMM, J. R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. *Transactions of the American Philosophical Society* 56: 1–194.
- TUCKER, J. M., W. P. COTTAM, AND R. DROBNICK. 1961. Studies in the *Quercus undulata* complex. II. The contribution of *Quercus turbinella*. *American Journal of Botany* 48: 329–339.
- WALKER, R. F. 1989. *Pisolithus tinctorius*, a Gastromycete, associated with Jeffrey and Sierra lodgepole pine on acid mine spoils in the Sierra Nevada. *Great Basin Naturalist* 49: 111–112.
- . 1990. Formation of *Pisolithus tinctorius* ectomycorrhizae on California white fir in an eastern Sierra Nevada minesoil. *Great Basin Naturalist* 50: 85–87.
- WALKER, R. F., D. C. WEST, S. B. McLAUGHLIN, AND C. C. AMUNDSEN. 1989. Growth, xylem pressure potential, and nutrient absorption of loblolly pine on a reclaimed surface mine as affected by an induced *Pisolithus tinctorius* infection. *Forest Science* 35: 569–581.

Received 10 November 1990

Accepted 28 January 1991

NATURAL HYBRID BETWEEN THE GREAT PLAINS TOAD  
(*BUFO COGNATUS*) AND THE RED-SPOTTED TOAD (*BUFO PUNCTATUS*)  
FROM CENTRAL ARIZONA

Brian K. Sullivan<sup>1</sup>

Hybridization among toads of the genus *Bufo* is well known (Sullivan 1986). In the southwestern United States hybridization has been documented within both the *americanus* and *punctatus* species groups (Ferguson and Lowe 1969, Sullivan 1986). However, natural hybridization between members of more distantly related species groups is relatively rare. Natural hybrids between *Bufo punctatus* and both *B. boreas* (Feder 1978) and *B. woodhousii* (McCoy et al. 1967) have been described. Documentation of hybridization is important because it provides information about the genetic relatedness of taxa, as well as potential insights into proximate aspects of species recognition and reproductive behavior. Herein I report on a natural hybrid between *B. cognatus* (Great Plains toad) and *B. punctatus* (red-spotted toad), members of separate species groups within the “thin-skulled” lineage of North American toads.

The hybrid male was collected in a rain-formed pool on the evening of 13 August 1990 at the Cave Buttes Recreation Area along Cave Creek, 12 km southwest of Cave Creek, Maricopa County, Arizona. Approximately 50 mm of rain fell from 11 to 13 August; on each evening, a number of anurans called along a narrow (3-m wide), flowing stream and a large, shallow pool (40-m diameter) created by an earthen dike across the stream channel. Male *B. alvarius*, *B. cognatus*, and *Scaphiopus couchii* called from the pool, while male *B. punctatus* were restricted to the channel.

The hybrid was calling among the male *B. cognatus* at the large pool. I recorded a series of its advertisement calls using a Marantz PMD 430 cassette recorder and Sennheiser ME-80 microphone, and I mea-

sured its cloacal temperature with a Weber Quick Recorder thermometer. Five calls were analyzed with a DATA Precision 6000 Waveform Analyzer (see Sullivan 1989 for details), and mean values were calculated for each call variable. Data are reported as the mean  $\pm$  standard deviation.

The mean pulse rate of the advertisement call of the hybrid was 45 p/s, and the mean duration was 7.8 s, at a cloacal temperature of 24 C. The corresponding values for 13 *B. punctatus* recorded on the same night were  $55 \pm 2.60$  p/s and  $6.4 \pm 1.23$  s (cloacal temperatures =  $25 \pm .34$  C); the values for 8 *B. cognatus* were  $24 \pm 1.66$  p/s and  $18 \pm 7.58$  s (cloacal temperatures =  $25 \pm .82$  C). The dominant frequency of the hybrid's advertisement call was 2.109 kHz, lower than both *B. punctatus* ( $2.538 \pm .111$  kHz) and *B. cognatus* ( $2.700 \pm .207$  kHz). Hence, the advertisement call of the hybrid, although more similar to that of *B. punctatus*, was intermediate in pulse rate and duration and dramatically lower than either parental species in dominant frequency. However, the vocal sac was darkly pigmented and sausage-shaped when inflated (Fig. 1), the condition typical of *B. cognatus*.

The hybrid was intermediate in size (63 mm snout-vent length) relative to *B. punctatus* ( $54 \pm 2.59$  mm) and *B. cognatus* ( $75 \pm 4.83$  mm). The oval parotoid glands, enlarged cranial crests, and boss of the hybrid were also intermediate to *B. cognatus* and *B. punctatus*. Following the methodology of Ferguson and Lowe (1969), I determined four ratios (parotoid length/parotoid width, svl/parotoid width, parotoid length/eyelid length, tibia/parotoid length) for the two parental species

<sup>1</sup>Life Sciences Program, Box 37100, Arizona State University West, Phoenix, Arizona 85069-7100.





Fig. 1. (a) *Bufo cognatus*, (b) hybrid, and (c) *Bufo punctatus* from Cave Buttes Recreation Area, Maricopa, County, Arizona.

and the hybrid. All of the ratios calculated for the hybrid were between the mean values and exclusive of the 95% confidence intervals for the two parental species.

Unfortunately, the hybrid escaped after these observations were completed. Documentation of a natural hybrid between members of these two distinct species groups is noteworthy. Although *B. cognatus* and *B. punctatus* typically breed in dissimilar habitats, the present observations reveal that they may interact if they breed sympatrically, and that they can produce hybrid offspring. Additional work will be required to determine the evolutionary importance, if any, of such interactions.

#### ACKNOWLEDGMENTS

I thank Ken Johnson of the Maricopa County Flood Control office for providing assistance in the early stages of my work. This investigation was supported by a Faculty Grant in Aid award and a Summer Research Grant from Arizona State University.

#### LITERATURE CITED

- FEDER, J. H. 1979. Natural hybridization and genetic divergence between the toads *Bufo boreas* and *Bufo punctatus*. *Evolution* 33: 1089–1097.
- FERGUSON, J. H., AND C. H. LOWE. 1969. Evolutionary relationships in the *Bufo punctatus* group. *American Midland Naturalist* 81: 435–466.
- MCCOY, C. J., H. M. SMITH, AND J. A. TIHEN. 1967. Natural hybrid toads, *Bufo punctatus* × *Bufo woodhousei*, from Colorado. *Southwestern Naturalist* 12: 45–54.
- SULLIVAN, B. K. 1986. Hybridization between the toads *Bufo microscaphus* and *Bufo woodhousei* in Arizona: morphological variation. *Journal of Herpetology* 20: 11–21.
- . 1989. Interpopulational variation in vocalizations of *Bufo woodhousei*. *Journal of Herpetology* 23: 368–373.

Received 18 December 1990

Accepted 28 January 1991



NEW VARIETY OF *OXYTROPIS CAMPESTRIS* (FABACEAE)  
FROM THE COLUMBIA BASIN, WASHINGTON

Elaine Joyal<sup>1</sup>

In 1984 I found an *Oxytropis* in central Washington that I was unable to identify. Collection was made and sent for determination to Rupert Barneby, who puzzled over it for some time before concluding that it lacked a published name. What follows is a description of that taxon. This is a rare taxon, presently known from a single population on an isolated mountain. Habitat and ecological notes are included, therefore, to facilitate understanding of the taxon's conservation status.

*Oxytropis campestris* (L.) DC.  
var. *wanapum* Joyal, var. nov.

Fig. 1

*O. campestris* (L.) DC. var. *gracili* (A. Nels.) Barneby affinis, plantis dense sericeo pilosis, robustis, foliolis 20–25, corollis lavandulis, carinis maculatis, differt.

Caespitose perennial, acaulescent, 17–30 cm tall; herbage silvery, densely silky-pilose to villous; stipules membranous, pilose to densely pilose, the blades free for half their length, (5) 6.5–9 (16) mm long, margins ciliate to densely ciliate; leaves (11) 14–18 (22) cm long, with (13) 19–26 (32) linear to narrowly oblong leaflets, (8) 15–25 (33) mm long, scattered, sub-opposite; scapes erect to spreading, (10) 17–21 (30) dm long, pubescence spreading-appressed; racemes in part exceeding the leaves, (5) 6–12 (17) flowered, congested in flower, (4) 6–8 (12) cm long in fruit; calyx sericeous-pilose, 7–9 mm long, greater than half the length of the corolla, with a few dark hairs, the tube 5–7 mm long, the teeth (1) 2–3 mm long, linear-lanceolate; corolla pale lavender with darker penciling, keel maculate, drying blue; banner obovate, 14–16 (23) mm long; wings 13–15 (19) mm long; keel (10) 11–14 (17) mm long; pod sessile

to short-stipitate, erect, 1-celled with the suture not or only slightly intruded, the wall membranous-leathery, 10–20 mm long, beak about 6 mm long.

TYPE: UNITED STATES: Washington, Grant County, Saddle Mountain, above Lower Crab Creek and E of Beverly, T15N, R24E, S2, N1/2, elev. ca 550 m, NNE aspect at crest of ridge, in sandy (volcanic ash) soils above steep basalt talus, 25 May 1987 (flower and early fruit), Joyal 1264 (Holotype: US; Isotypes: BRY, CAN, CAS, ISC, K, MO, MONTU, NY, OSC, S, UBC, WS, WTU).

PARATYPE: UNITED STATES: Washington, Grant County, Saddle Mountain, above Lower Crab Creek, T15N, R24E, S2, elev. ca 550 m, NNE aspect at crest of ridge, in sandy soil, 15 May 1984 (flower), Joyal 467 (BLM—Spokane, NY, OSC).

There are currently at least 10 varieties of *O. campestris* recognized in North America (Barneby 1952, Elisens and Packer 1980, Welsh, personal communication). Characters used to distinguish the infraspecific taxa are: length of leaves and of scapes, number of leaflets, numbers of flowers per raceme, length and density of flowers in raceme, color of corolla, habitat, and distribution. There are notable differences in these characters in variety *wanapum* when compared with other varieties of *O. campestris*. The three varieties that occur in eastern Washington with var. *wanapum* are compared below; a key also is provided to separate these four varieties (see Barneby 1952, Elisens and Packer 1980, Welsh, personal communication, for comparison with other *O. campestris* varieties). On the average, plants of var. *wanapum* are more robust and have a greater number of leaflets. The length of the leaves (16 cm) averages

<sup>1</sup>Department of Botany, Arizona State University, Tempe, Arizona 85287.



Fig. 1. *Oxytropis campestris* var. *wanapum*. Habit. Flower (bar = 1 cm). Composite drawing from Joyal 467, 1264, and photos of the Saddle Mountain population.

greater than those of var. *columbiana* (St. John) Barneby, *cusickii* (Greenm.) Barneby, and *gracilis* (A. Nels.) Barneby (11, 6, and 11 cm, respectively); leaflet length (20 mm) likewise averages greater than those of the other three varieties, (14, 8, and 12 mm); scape length (20 cm) is also greater than the other three (17, 7, and 16 cm); the mean number of leaflets (22) is greater than the first two varieties (each = 15) and within the range of the third variety (17); the average number of flowers per raceme (8.5) is within the range of three related taxa (8–12), with *columbiana* and *gracilis* occasionally having as many as 30 flowers/raceme; keel length (12 mm) is similar for all four taxa, with *gracilis* showing slightly larger dimensions; the pale lavender flower color, while not unique in the group, is unknown among northwest members of *O. campestris*. Some of these differences might be explained as a phenotypic response of a primarily montane taxon to a desert environment. Its desert habitat sets this taxon apart from its close relatives in nearby mountains; precipitation is about half that of the mountains (20 cm vs 40 cm/yr), the climate is warmer, the vegetation is shrub-steppe rather than forested, the geologic substrate is sedimentary and volcanic rather than intrusive with some volcanic rocks, and it lies south of the glaciated portions of the Okanogan Highlands and Cascade Range.

Key to closely related varieties of  
*Oxytropis campestris* in the Pacific Northwest  
(after Hitchcock and Cronquist 1973)

- 1 Corolla white with maculate keel; leaflets 12–17 (23); in wet gravel along the Columbia River in Washington (historically) and near Flathead Lake, Montana ..... var. *columbiana*
- 1' Corolla other than white with maculate keel; leaflets often more than 17
- 2 Stipules glabrous or glabrate; scapes rarely greater than 15 cm; leaflets seldom greater than 17; range of var. *gracilis*, but not above 2000 m elevation and not west of the Cascades ..... var. *cusickii*
- 2' Stipules very hairy; scapes mostly greater than 15 cm; leaflets generally greater than 17
- 3 Corolla ochroleucous or white, keel rarely maculate; leaflets 15–20; plants averaging smaller than the next, scapes averaging 16 cm; usually montane plants (in prairies east of the Rocky Mountains); western Washington to Alberta and South Dakota, south in Rocky Mountains to Colorado ..... var. *gracilis*

- 3' Corolla pale lavender with darker penciling, maculate keel, drying blue; leaflets 20–25; plants larger than the preceding, scapes averaging 20 cm; desert plants; at low elevation in the Columbia Basin of central Washington ..... var. *wanapum*

Elisens and Packer (1980) most recently treated the *O. campestris* complex in northwestern North America. They introduced new cytological information for several of the taxa in this difficult complex; on the basis of these data they reelevated several taxa, including the eastern Washington var. *columbiana*, to full species status. While accepting their findings, I do not see that it necessarily follows that taxa such as *O. campestris* var. “*columbiana*” should be given specific status based on Elisens and Packer’s new data. More importantly, Barneby (personal communication) and I agree that it is preferable to treat the undescribed taxon in a conservative fashion and place it at what we consider the appropriate rank as a variety of *O. campestris*, near var. *gracilis*. It may well be that future studies (Welsh, personal communication) in the *O. campestris* complex will result in this entity being raised to a higher rank. However, until that work is completed, varietal status under *O. campestris* seems more appropriate.

*Oxytropis campestris* var. *wanapum* is presently known only from Saddle Mountain in the Columbia Basin of central Washington (Fig. 2). Saddle Mountain is an isolated east-west trending ridge formed from a partly faulted anticline that stretches approximately 50 km, being cut by the Columbia River at Beverly. Several ranges to the southwest conceivably may contain habitat suitable for var. *wanapum*. Whereas the north slope is steep basalt talus, the south slope is gentle and sandy and dominated by *Artemisia tridentata*. The *Oxytropis* grows in a narrow band of deep sand, derived from volcanic ash, slightly below the crest of the north-facing ridge. The community is very open, as is typical of many sandy habitats. It is dominated by *Chrysothamnus nauseosus*, *Salvia dorrii*, *Monardella odoratissima*, *Agropyron spicatum*, and *Bromus tectorum*. Other species present include *Achillea millefolium*, *Arenaria franklinii*, *Astragalus caricinus*, *A. purshii*, *Castilleja* cf. *thompsonii*, *Chaenactis douglasii*, *Comandra umbellata*, *Crepis modocensis*, *Cryptantha pterocarya*, *Erigeron linearis*,



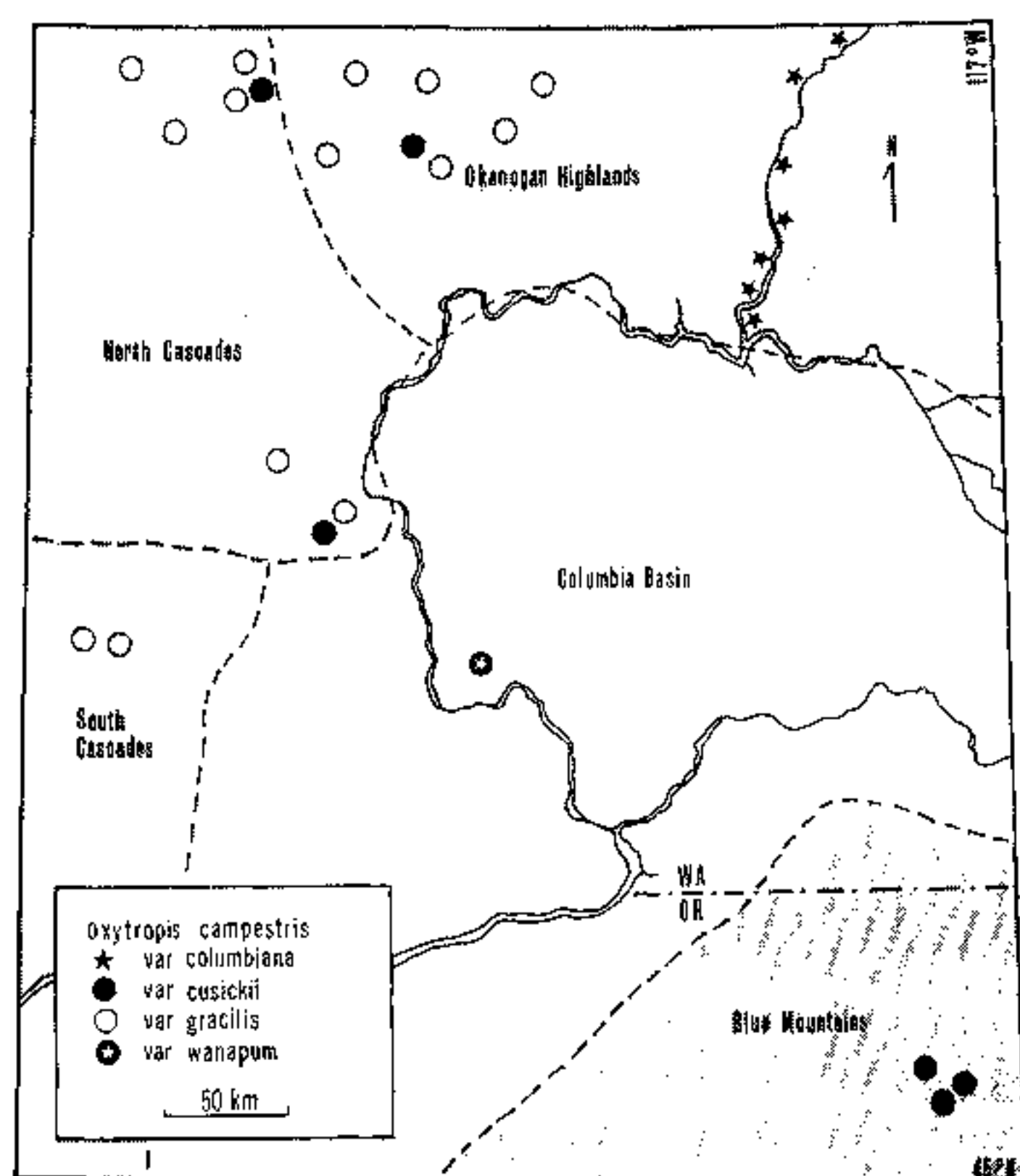


Fig. 2. Distribution of *Oxytropis campestris* varieties in eastern Washington and adjacent Oregon. Data points are of representative specimens from MO, OSC, US and WTU. Elevations in the Columbia Basin physiographic province average less than 500 m (unshaded); those in the Blue Mountain, North and South Cascade, and Okanogan Highland physiographic provinces average greater than 500 m (shaded).

*Eriogonum microthecum*, *E. ovalifolium*, *Eriophyllum lanatum*, *Galium multiflorum*, *Gilia sinuata*, *Hackelia arida*, *Lupinus* sp., *Penstemon richardsonii*, and *Poa* sp. (taxonomy follows Hitchcock and Cronquist 1973). No other *Oxytropis* spp. were noted in the immediate vicinity.

Plants of this taxon are frequent (several hundred individuals) in this restricted area, and there is a good size-class distribution of individuals. I observed seedlings, which I presumed to be from the previous year, small vegetative individuals, and flowering plants. The largest plants had many flowering stems (as many as 48 stems per plant observed) and covered areas up to 0.5 meter across. This *Oxytropis* flowers profusely. My first collection of the taxon was made at peak flowering, in the middle of May 1984, an average season with respect to temperature and precipitation. During my second visit in late May 1987, an early and dry spring, I found the plants mostly past flower and well into fruit. The flowers of this *Oxytropis* are held at

a 45-degree angle from the rachis, or higher, becoming erect in fruit. The only floral visitors I observed were several iridescent blue-green metallic-leafcutter bees (*Osmia integra* Cresson, Hymenoptera: Megachilidae), working *Oxytropis* flowers on the upper slope. The pods have a short pubescence and redden as they mature. Seed set appeared to be good, but predation of seed pods was high. Some pods had their sides chewed out in a pattern typical of departing larvae with not a single seed remaining within; more often the upper one-half or one-third of the pod had been eaten away entirely, along with all developing seeds. No larvae were observed, but several small weevils collected from the pods were identified as species of *Tychius* (Coleoptera: Tychiinae).

*Oxytropis campestris* var. *wanapum* occurs on land that is a "checkerboard" of Bureau of Land Management (BLM) and private lands. The primary land use is grazing; some recreational vehicle use occurs on the mountain as does natural gas exploration. The area in which the *Oxytropis* grows is isolated by low rimrock from the bulk of the grazing activity to the south. The BLM's Spokane District is treating the taxon as a "sensitive" species.

The varietal epithet honors the Wanapum tribe, who originally called Saddle Mountain and the desert surrounding it home. The Wanapum, except for one small community on the south side of the mountain, have mostly disappeared from the landscape.

#### ACKNOWLEDGMENTS

The original discovery of this taxon was made while I was employed by the Spokane District Office of the Bureau of Land Management, U.S. Department of Interior. Gary Parsons identified insects; Richard Rust provided the specific epithet for *Osmia*; Kay Thorne did the illustration; Kenton Chambers of Oregon State University provided work space and herbarium support on a regular basis during my western tenure; the Smithsonian Institution staff has generously allowed me use of their herbarium; and Rupert Barneby and Stan Welsh provided valuable comments on the manuscript. I am especially indebted to Rupert Barneby, for whom I first thought of collecting this taxon. It was he who later confirmed why I was unable to put a name on it, and who encouraged me to write this paper.

## LITERATURE CITED

- BARNEBY R. C. 1952. A revision of the North American species of *Oxytropis* DC. Proceedings of the California Academy of Science IV, 27: 177–312.
- ELISENS, W. J., AND J. G. PACKER. 1980. A contribution to the taxonomy of the *Oxytropis campestris* complex in northwestern North America. Canadian Journal of Botany 58: 1820–1831.
- HITCHCOCK, C. L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

*Received 9 January 1991*  
*Accepted 28 January 1991*





## EFFECT OF BACKPACK RADIO TRANSMITTER ATTACHMENT ON CHUKAR MATING

Bartel T. Slauch<sup>1,3</sup>, Jerran T. Flinders<sup>1</sup>, Jay A. Roberson<sup>2</sup>, and N. Paul Johnston<sup>3</sup>

Results of a previous study (Slauch et al. 1989) indicate that backpack radio transmitter attachment is more compatible with Chukars (*Alectoris chukar*) than is a poncho apparatus. It appears, though, that backpacks, especially the antenna angle, could inhibit Chukar mating. The objective of this study was to determine the effects, if any, of backpacks and antenna position on mating and fertility.

### MATERIALS AND METHODS

Chukars were housed (as pairs or trios) in 45-cm-high × 75-cm-wide × 90-cm-long wire cages. Six pairs had no radio transmitters attached (group I). In group II each of six cages contained one male and one female without radios plus one female with a simulated backpack radio with the antenna angled downward along the tail (Fig. 1). In group III each of six cages contained one male and one female without radios plus one female with a simulated backpack radio with the antenna angled upward (Fig. 1). The purpose was to determine if the males would prefer to mate with the females without radios and exclude the females with radios. Eggs were collected from females for one week prior to exposure to males to ascertain fertility status. Females were exposed to males for four days and then separated and caged individually to facilitate individual fertility observations. Eggs were collected for one week, incubated for one week, and then opened to determine fertility.

### RESULTS AND DISCUSSION

Females in all groups produced fertile eggs, indicating that males did not exclude radio-

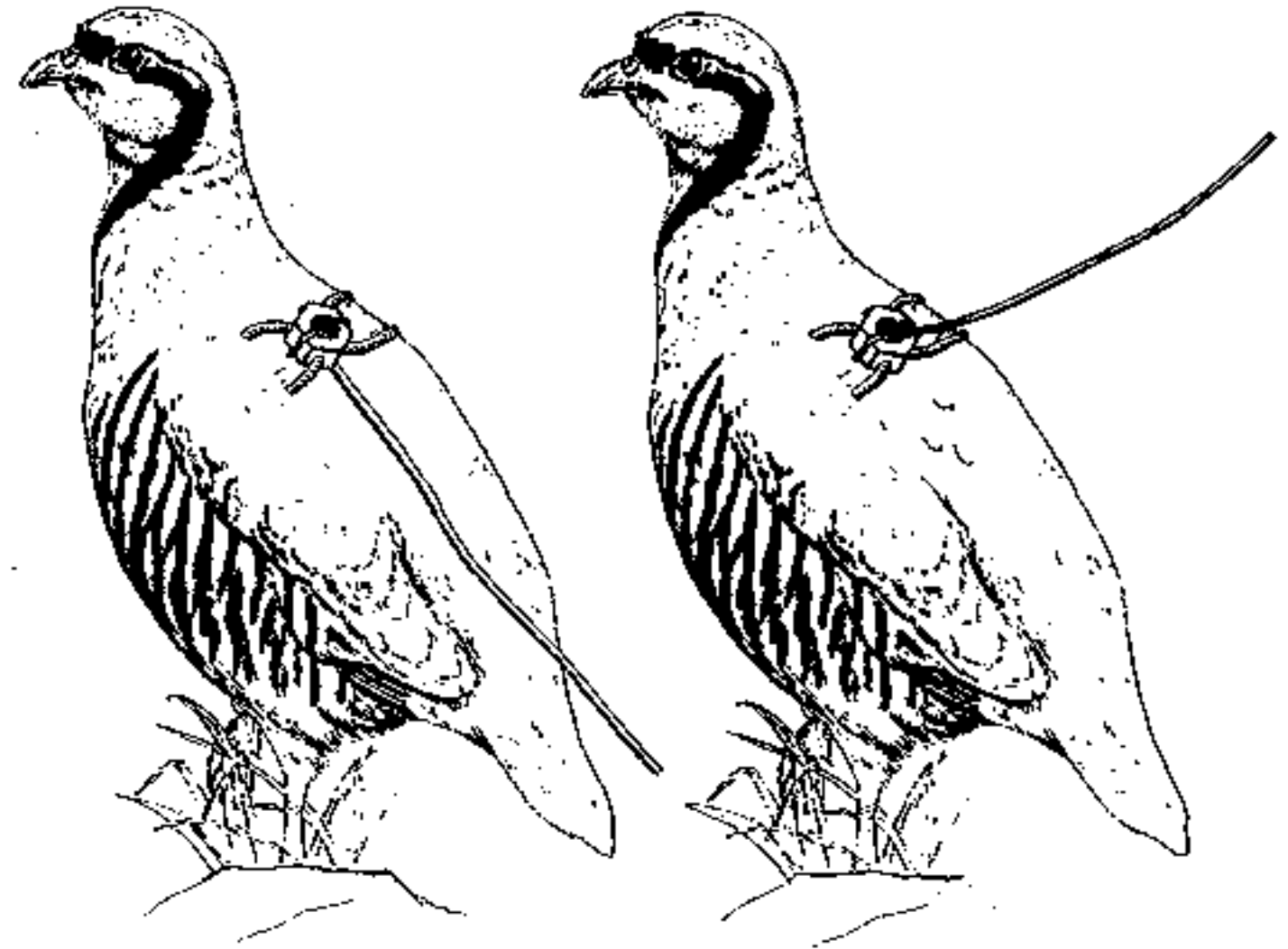


Fig. 1. Backpack attachment of simulated radio transmitters with antenna angled downward (left) and upward (right).

attached females from their mating. The radios and antennae did not impair mating even when antennae were angled upward. Males were observed to either straddle the antenna or grasp it with a foot and bend it downward while mating. These results indicate no mating problems with captive Chukars fitted with radio transmitters. Their behavior, however, could possibly differ in the wild.

This study did not include any field observations of mating or fertility. The only problem observed with released Chukars carrying backpacks was that, with the antenna angled upward, some birds experienced difficulty in flying as a result of a wing coming in contact with the antenna. Attachment one week prior to release (to allow time to become accustomed to radios) did not affect flight ability or survival.

<sup>1</sup>Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

<sup>2</sup>Utah Division of Wildlife Resources, 1596 West North Temple, Salt Lake City, Utah 84116.

<sup>3</sup>Department of Animal Science, Brigham Young University, Provo, Utah 84602.

ACKNOWLEDGMENTS

This research was funded by the Utah Division of Wildlife Resources.

LITERATURE CITED

SLAUGH, B. T., J. T. FLINDERS, J. A. ROBERSON, M. R. OLSON, AND N. P. JOHNSTON. 1989. Radio transmitter attachment for Chukars. Great Basin Naturalist 49: 632-636.

*Received 15 July 1990*  
*Accepted 15 January 1991*

## FOOD CACHING AND HANDLING BY MARTEN

Stephen E. Henry<sup>1</sup>, Martin G. Raphael<sup>2</sup>, and Leonard F. Ruggiero<sup>1</sup>

Various studies provide evidence of food caching by marten (*Martes americana*). Marten have been seen uncovering or retrieving food items (Murie 1961, Simon 1980, Buskirk 1983), but whether these items were initially cached by marten was unknown. Hawbecker (1945) and Thompson (1986) documented food concealment by marten, but neither reported subsequent recovery of prey. Due to lack of evidence, Stordeur (1986) concluded that caching of food is uncommon in marten. Prey caching has important implications for foraging frequency and energetics of marten.

### STUDY AREA AND METHODS

The primary objective of our research was to quantify changes in marten home range characteristics and habitat use following the fragmentation of a subalpine coniferous forest. An ancillary research objective was to describe the characteristics of marten resting sites. Our study area was in the Medicine Bow National Forest, 18 km south of Encampment, Wyoming. The area was characterized by stands of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Small meadows and rock outcrops were interspersed throughout the area. Elevations at the observation sites ranged from 2935 to 3387 m.

Most observations were made during field efforts to locate resting sites of radio-collared marten. Resting sites were defined as locations in which a marten remained stationary and inactive for at least 0.5 h. The radio-signal strength was monitored for 0.4–1.5 h from a distance of at least 70 m. After the signal indicated inactivity, the potential resting site was quietly approached on foot to avoid alert-

ing the marten or causing it to flee. Precautions were made to minimize the observer's influence in order to maximize observations of natural behavior. These precautions included reduction of receiver volume, concealment of the observer, and removal of shoes if necessary.

### OBSERVATIONS

CASE 1.—9 June 1987, 1445 h. Adult male marten M3 was seen carrying the hind half of a snowshoe hare (*Lepus americanus*) for about 20 m near a known resting site. He cached the hare under a leaning stump and then foraged within 400 m for about 0.5 h before returning to the hare and carrying it away.

CASE 2.—8 July 1987, 1015 h. M3 was seen foraging in and around a rock outcrop. After 5 min the marten emerged from the rocks, grasping a juvenile yellow-bellied marmot (*Marmota flaviventris*) by the neck. He immediately carried the prey approximately 550 m, deposited it in a rock crevice in a road fill, and then left the site. There were six marten scats at the entrance of this den, indicating prior use by this or other marten.

CASE 3.—1 September 1987, 1900 h. M3 was found resting in a bushy-tailed wood rat (*Neotoma cinerea*) nest in a rock outcrop. He growled a few times and then ran away, carrying an unidentified mammal.

CASE 4.—9 September 1987, 1730 h. M24 was found resting in a rock outcrop. As the observer approached, the marten peered from a crevice before disappearing back into the rocks. After a few seconds he emerged and fled, carrying a chipmunk (*Tamias* spp.).

CASE 5.—22 September 1987, 1300 h. M3 was seen feeding on a freshly killed Blue Grouse (*Dendragapus obscurus*) next

<sup>1</sup>Rocky Mountain Forest and Range Experiment Station, 222 South 22nd St., Laramie, Wyoming 82070.

<sup>2</sup>Pacific Northwest Forest and Range Experiment Station, 3625 93rd Ave., S. W., Olympia, Washington 98502.



to a large log. The marten carried the grouse about 40 m and cached it in branches of a recently felled pine, then retreated to a nearby resting site under a different log. Two Blue Grouse feathers, one Northern Flicker (*Colaptes auratus*) feather, and two Gray Jay (*Perisoreus canadensis*) feathers were found at the entrance to the resting site. After 25 min the marten ran from the den, took the grouse, and headed downslope.

CASE 6.—27 July 1988, 1605 h. The observer heard F28 killing a juvenile Blue Grouse in an alder (*Alnus tenuifolia*) bog. A few minutes later she was observed eating the grouse inside a hollow log approximately 25 m from the kill site. During this time an adult grouse was heard giving the brood-gathering call. When one of the young responded with a call, the marten left the dead grouse in the log and stalked the live young. It located a young grouse in a tree and made an unsuccessful attempt to catch it. Upon returning to the original prey, the marten saw the observer and left without the cached grouse. The prey had been removed from the log by 1400 h the following day.

CASE 7.—31 January 1989, 1240 h. M35 found a piece of beaver meat (trap bait) at our field camp. He carried the meat 15 m away, climbed up a tree, and moved out onto a limb heavily laden with snow. He dug a hole in the snow, placed the meat in it, and then covered the meat with snow before descending the tree. He continued to move about the camp area, searching for additional food.

CASE 8.—26 July 1989, 0710 h. A hidden observer witnessed M35 cache a red squirrel (*Tamiasciurus hudsonicus*) under a shelter at the field camp. After caching, the marten immediately left. Approximately 12 h later (1930 h), M35 was observed retrieving the squirrel.

CASE 9.—3 August 1989, 1050 h. Red squirrels were heard scolding F37 at their midden. At 1115 h the marten was seen at the base of a snag 150 m from the midden. She had a squirrel forearm in her mouth as she ascended into the broken top of the snag. Within moments she descended without the forearm and left the area. Inside the snag was found the squirrel forearm and the hind one-third of a squirrel. Within an hour the marten was out of telemetry range.

## DISCUSSION

For our purposes "caching" is defined as the act of concealing food for later consumption. Marten meet the criteria for "cachers" (Macdonald 1976); viz., they are solitary hunters with fixed home ranges, and they are not large enough to protect their prey from larger scavengers. Our observations show that marten will cache large prey items, and cases 1, 5, and 8 are rare documentation that the same individual that made the cache had subsequently returned to it. In addition, these observations show that sometimes the cache site also serves as a resting site or den. We have also documented hunting behavior that is generally associated with surplus killing.

Small rodents are consumed quickly by marten, and they are not necessarily removed from the kill site (Pulliainen 1981b). However, it has been reported that marten readily carry larger prey from 9 m to several hundreds of meters away from kill sites (Murie 1961, Hargis 1981, Pulliainen 1981b, Raine 1981, Spencer and Zielinski 1983). Our observations (cases 1, 2, 5, 7, 8, 9) demonstrate that marten cache food at varying distances from kill sites, especially if the prey is too large for one meal. We suggest that the removal of prey from capture sites may provide security for marten. The noise of the pursuit and kill (e.g., cases 6 and 9) and the distress calls of the prey could alert competitors or predators to the location of a marten and its kill. This is consistent with observations made by Simon (1980), who found that marten typically consume food in secluded cover.

Cases 2, 3, and 4 are similar to the findings of Pulliainen (1981a), Raine (1981), and Spencer (1981), who also observed that marten sometimes carry prey items to their resting sites. The selection of a resting site may depend upon the proximity to the kill site (Marshall 1951, Buskirk 1984) and the amount of protection afforded. When a marten uses a specific rest site on consecutive days (e.g., Steventon 1979), it may be because of cached food.

In Finland, Pulliainen (1981b) found surplus killing of prey by European pine marten (*M. martes*). Our observations (cases 1, 6, 7, 8, 9) suggest that marten participate in surplus killing. Animals that we observed resumed an apparent foraging activity after caching.

Marten meet the criteria for species prone toward surplus killing, suggested by Oksanen et al. (1985), because they are small members of a predator guild in a cool, dry environment (at least throughout portions of their range). However, there is no evidence suggesting that marten are involved in surplus killing or hoarding to the same extent as other mustelids (e.g., Johnsen 1969 [as cited in Oksanen 1983] reported a stoat's [*Mustela erminea*] single cache of 153 lemmings and a shrew). Important knowledge of marten ecology would be gained if researchers could devise a way to examine the interior of resting sites to determine if food caches vary seasonally.

#### ACKNOWLEDGMENTS

We thank S. W. Buskirk, R. T. Reynolds, and W. D. Spencer for comments on an earlier draft, and K. O. Christensen and L. J. Kelly for manuscript preparation.

#### LITERATURE CITED

- BUSKIRK, S. W. 1983. The ecology of marten in southcentral Alaska. Unpublished dissertation, University of Alaska, Fairbanks. 131 pp.
- . 1984. Seasonal use of resting sites by marten in southcentral Alaska. *Journal of Wildlife Management* 48: 950–953.
- HARGIS, C. D. 1981. Winter habitat utilization and food habits of pine martens in Yosemite National Park. Unpublished thesis, University of California, Berkeley. 57 pp.
- HAWBECKER, A. C. 1945. Activity of the Sierra pine marten. *Journal of Mammalogy* 26: 435.
- MACDONALD, D. W. 1976. Food caching by red foxes and some other carnivores. *Journal of Tierpsychologie* 42: 170–185.
- MARSHALL, W. H. 1951. Pine marten as a forest product. *Journal of Forestry* 49: 899–905.
- MURIE, A. 1961. Some food habits of the marten. *Journal of Mammalogy* 42: 516–521.
- OKSANEN, T. 1983. Prey caching in the hunting strategy of small mustelids. *Acta Zoologica Fennica* 174: 197–199.
- OKSANEN, T., L. OKSANEN, AND S. D. FRETWELL. 1985. Surplus killing in the hunting strategy of small predators. *American Naturalist* 126: 328–346.
- PULLIAINEN, E. 1981a. Winter habitat selection, home range, and movements of the pine marten (*Martes martes*) in a Finnish Lapland forest. Pages 1068–1087 in J. A. Chapman and D. Pursley, eds., *Worldwide furbearer conference proceedings*, Frostburg, Maryland.
- . 1981b. Food and feeding habits of the pine marten in a Finnish Lapland forest in winter. Pages 580–598 in J. A. Chapman and D. Pursley, eds., *Worldwide furbearer conference proceedings*, Frostburg, Maryland.
- RAINE, R. M. 1981. Winter food habits, responses to snow cover and movements of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. Unpublished thesis, University of Manitoba, Winnipeg. 145 pp.
- SIMON, T. L. 1980. An ecological study of the marten in the Tahoe National Forest, California. Unpublished thesis, California State University, Sacramento. 187 pp.
- SPENCER, W. D. 1981. Pine marten habitat preferences at Sagehen Creek, California. Unpublished thesis, University of California, Berkeley. 121 pp.
- SPENCER, W. D., AND W. J. ZIELINSKI. 1983. Predatory behavior of pine martens. *Journal of Mammalogy* 64: 715–717.
- STEVENTON, J. D. 1979. Influence of timber harvesting upon winter habitat use by marten. Unpublished thesis, University of Maine, Orono. 25 pp.
- STORDEUR, L. A. 1986. Marten in British Columbia with implications for forest management. WHR-25. Research Branch, B.C. Ministry of Forests and Land, Victoria, B.C.
- THOMPSON, I. D. 1986. Diet choice, hunting behaviour, activity patterns, and ecological energetics of marten in natural and logged areas. Unpublished dissertation, Queen's University of Kingston, Ontario. 179 pp.

Received 23 May 1990  
 Revised 7 February 1991  
 Accepted 12 February 1991





## HOLOCENE PREDATION OF THE UINTA GROUND SQUIRREL BY A BADGER

Michael E. Nelson<sup>1</sup>

In 1985 J. H. Madsen, Jr., then the state paleontologist of Utah, collected several fossil bones at an elevation of 1524 m in Morgan County, Utah (Utah Antiquities locality 42Mo029v). The specimens were recovered from a large burrow intruded into shoreline sands deposited by Pleistocene Lake Bonneville. All fossils were found in a single pocket that probably represents the distal end of a burrow of the North American badger, *Taxidea taxus*. The specimens consist of (1) numerous post-cranial elements of a juvenile badger and (2) several bones, including a right dentary, of the Uinta ground squirrel, *Spermophilus armatus*. Many of the ground squirrel bones are crushed or broken, a condition also noted by Long and Killingley (1983) in their study of badger prey.

*Taxidea taxus* is virtually an exclusive carnivore and does not eat significant amounts of plant material (Ewer 1973). Rodents are the most common prey, but the animals are not adverse to eating a variety of other vertebrates and arthropods (Long and Killingley 1983). Messick and Hornocker (1981) noted that Townsend ground squirrels, *Spermophilus townsendi*, are the most important prey species of badgers in southwestern Idaho. The animals either burrow after the active squirrels, catch them hibernating in their burrows, or opportunistically wait at a burrow entrance (Balph 1961). Badgers also will eat carrion and sometimes make food caches (Snead and Hendrickson 1942).

Postdeath disturbance of the bones probably accounts for missing elements of both *Taxidea* and *Spermophilus*. All preserved bones show extensive gnawing by small rodents; mice and other rodents commonly

occupy badger burrows after the structures are deserted (Choate 1989, personal communication).

Part of the badger pelvis was sacrificed for a radiocarbon date completed by Tandem Accelerator Mass Spectrometry at the Laboratory of Isotope Geochemistry, University of Arizona. The date of  $2790 \pm 74$  yr. B.P. (AA-2514) suggests that Holocene diets of Utah badgers were similar to their extant counterparts. The remains of the ground squirrel may represent the last meal of the badger.

All specimens are accessioned into the Sternberg Memorial Museum at Fort Hays State University (FHSM VP-10648 [ground squirrel] and FHSM VP-10649 [badger]). I thank Dr. Dave Gillette (Utah Antiquities), James H. Madsen (DINOLAB), and John Lund (FHSU).

### LITERATURE CITED

- BALPH, D. F. 1961. Underground concealment as a method of predation. *Journal of Mammalogy* 42: 423-424.
- EWER, R. F. 1973. The carnivores. Cornell University Press, Ithaca, New York. 494 pp.
- LONG, C. A., AND C. A. KILLINGLEY. 1983. The badgers of the world. Charles C. Thomas, Publisher, Springfield, Illinois. 404 pp.
- MESSICK, J. P., AND M. G. HORNOCKER. 1981. Ecology of the badger in southwestern Idaho. *Wildlife Monographs* No. 3. 53 pp.
- SNEAD E., AND G. O. HENDERSON. 1942. Food habits of the badger in Iowa. *Journal of Mammalogy* 45: 380-391.

Received 16 January 1991

Accepted 28 January 1991

<sup>1</sup>Department of Earth Sciences, Fort Hays State University, Hays, Kansas 67601-4099.



## PATTERNS OF MICROHABITAT USE BY *SOREX MONTICOLUS* IN SUMMER

Mark C. Belk<sup>1,2</sup>, Clyde L. Pritchett<sup>1</sup>, and H. Duane Smith<sup>1</sup>

*Sorex monticolus* is found from Alaska to Mexico in a variety of montane and boreal habitats (Hennings and Hoffmann 1977). In previous characterizations of microhabitat used by this species, few measures of physical or vegetative structure were significantly correlated with captures of *S. monticolus*. Typically, only some measure of near-ground cover (or related variables) is significantly associated with abundance. *Sorex monticolus* favors habitats with dense ground cover but seems to have few other microhabitat requirements (Hawes 1977, Terry 1981, Gunther et al. 1983, Reichel 1986, Doyle 1989).

In most montane areas the annual cycle of snow accumulation and melting, followed by herbaceous growth and decay, causes large-scale changes in the near-ground environment. During summer rapid herbaceous growth greatly increases the area covered by dense, near-ground vegetation. Previous studies of microhabitat use by *S. monticolus* have not addressed temporal changes in habitat use relative to this change in available cover (Terry 1981, Doyle 1989).

During summer 1986, in conjunction with a study of microhabitat use by rodents in a montane area, we recorded 104 captures of shrews in Sherman live traps. These shrews all appeared similar, and 17 specimens, retained for positive identification, subsequently were identified as *S. monticolus*. Given the possibility that some of the shrews captured may have been another species, we used a binomial probability to calculate the proportion of the 104 captures that could be regarded as *S. monticolus*; at a .05 level of confidence at least 85% of shrews captured were *S. monticolus*. Based on this, we feel confident that the majority, if not all, of the shrews captured were *S. monticolus*. In this paper we examine tem-

poral patterns of microhabitat use by these shrews during summer in relation to changes in microhabitat.

### STUDY AREA AND METHODS

The study site (111°37'N, 40°26'W) is on the east slope of Mount Timpanogos at an elevation of about 2400 m in Utah County, Utah. The habitat includes stands of aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) interspersed with herbaceous meadows and shrub-dominated ridges (principally snowberry, *Symphoricarpos albus*). Three trap grids were located in separate areas considered similar in overall habitat structure. Each grid covered 1 ha and contained 100 trap stations arranged in 10 rows of 10 each. Two folding Sherman traps were placed at each station, and stations were 10 m apart. Grids were trapped in a rotating fashion (see Belk et al. 1988 for details). Trapping began in early June, immediately after snowmelt, and continued until mid-September, resulting in 13,800 trap nights.

Nineteen habitat variables were measured at each trap site characterizing live woody structure (trees and shrubs), dead woody structure (fallen logs), and herbaceous cover and height (see Belk et al. 1988 for details). Five variables were correlated with shrew captures at the .10 level of significance during at least one month. These variables—percent canopy cover, average overstory tree size, average understory tree size, density of fallen logs, and number of woody species—were analyzed with principal-components analysis (SAS Institute, Inc. 1985). Two components had eigenvalues greater than one, but shrews exhibited little variation of habitat use on the second component (all means near

<sup>1</sup>Department of Zoology, Brigham Young University, Provo, Utah 84602.

<sup>2</sup>Present address: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802.



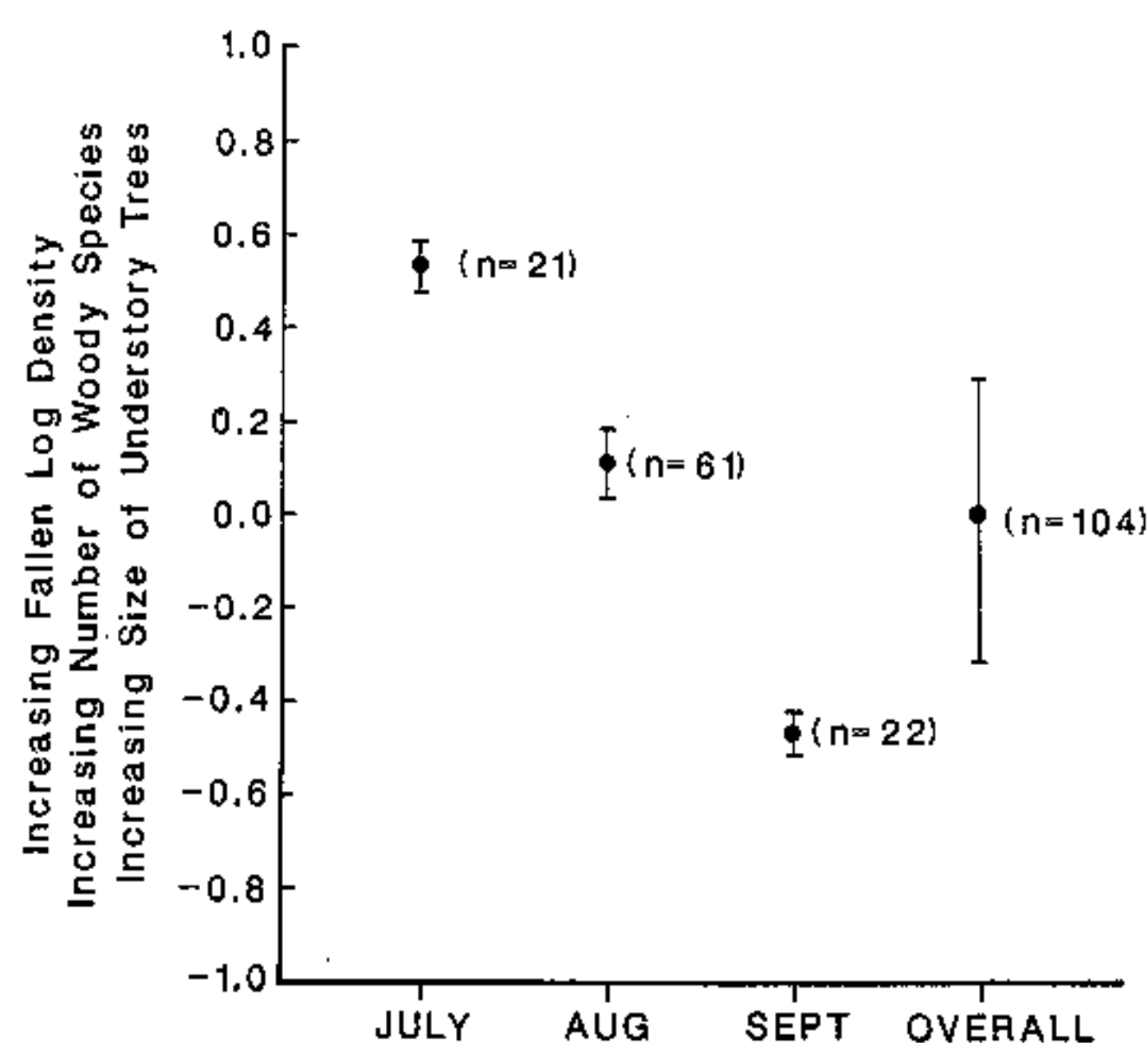


Fig. 1. Distribution of means and 95% confidence intervals of habitat use by shrews on the first principal component for July, August, September, and the entire summer combined.

zero). Accordingly, habitat use by shrews was interpreted only on the first principal component. This component (variable loadings in parentheses) described a gradient of increasing density of fallen logs (0.596), increasing number of woody species (0.628), and increasing size of understory trees (0.415).

### RESULTS

No shrews were captured in June; 21, 61, and 22 captures of shrews were recorded for July, August, and September, respectively. Mean habitat use for the entire summer plotted on the first component appeared no different from a random sample (Fig. 1). However, investigation of habitat use partitioned by months revealed temporal variation in habitat use (Fig. 1). Thus, the pattern of habitat use generated from the entire sample was an artifact caused by averaging over time. Habitat used by shrews for each month was much less variable (variance ranged from 0.03 to 0.07) than simulated random samples, with sample sizes about equal to those observed for shrews (variance ranged from 1.28 to 1.81 for five simulations). Thus, it appears that shrews were using the habitat nonrandomly, and observed patterns of variation were not merely artifacts of limited samples.

Habitat use in July was characterized by

areas with higher densities of fallen logs, greater numbers of woody species, and larger size of understory trees. This was characteristic of shrubby areas in earlier stages of succession. In August mean habitat use was close to the overall mean of available habitat, representing areas with intermediate values of habitat variables. In September shrews used habitat with lower densities of fallen logs, fewer numbers of woody species, and smaller understory trees, representing areas dominated by climax aspen stands (Fig. 1).

### DISCUSSION

No variable or combination of variables was characteristic of habitat used by shrews across all months. Rather, since characteristics of woody vegetation changed little during the summer, it appears shrews are responding to temporal change in the near-ground environment caused by rapid herbaceous growth during early to mid-summer (occurring first in open areas), followed by dessication and matting down of herbaceous growth as autumn approaches. In early summer, soon after snowmelt, areas lacking woody vegetation were mostly bare, having only a thin, compacted layer of litter. Correspondingly, habitat used by shrews included woody ground cover such as fallen logs and shrubs. At the height of the summer season, a few weeks later, herbaceous growth 0.5–1.5 m high covered the entire study area, and most of the habitat was probably suitable for use by shrews. By September herbaceous growth persisted in mesic sites under dense canopies provided by aspen stands, but herbaceous cover in open areas was declining. Accordingly, habitat used by shrews shifted toward areas dominated by mature aspen stands. Such tracking of ground cover by *S. monticolus* accords with previous descriptions of microhabitat use by this species (Terry 1981, Doyle 1989).

Comparison of patterns of microhabitat use between shrews and four species of rodents (*Peromyscus maniculatus*, *Zapus princeps*, *Clethrionomys gapperi*, and *Microtus montanus*) in the same area reveals a strong contrast. Rodent abundance was strongly correlated with 13 habitat variables, and rodents showed strong patterns of habitat partitioning based on these variables (Belk et al. 1988).

Shrew captures were weakly correlated with only five variables and showed relatively little variation on these variables. In this study area coexistence of several rodents may necessitate habitat partitioning, whereas *S. monticolus* appears to be the only shrew in the area (at least other species are rare). However, even when other species of shrews are present, *S. monticolus* is only weakly associated with measurements of physical or vegetative structure (Terry 1981, Doyle 1989). In conclusion, use of microhabitat by *S. monticolus* is strongly affected by temporal variation in distribution of ground cover, and this should be taken into account in future studies of microhabitat use and partitioning by shrews.

#### ACKNOWLEDGMENTS

We thank the Associated Students of Brigham Young University and the Department of Zoology for financial support. We also thank J. Stoddard, D. Thurber, R. Rasmussen, and K. Hovorka for help with fieldwork. J. Lawson and R. Chessier helped with statistical procedures; J. Coleman drew the figure. Data analysis and manuscript preparation were supported by the U.S. Department of Energy (Contract DE-AC09-76SROO-819) through the Savannah River Ecology Laboratory's Graduate Research Participation Program and by a fellowship to MCB from Oak

Ridge Associated Universities Graduate Research Participation Program.

#### LITERATURE CITED

- BELK, M. C., H. D. SMITH, AND J. LAWSON. 1988. Use and partitioning of montane habitat by small mammals. *Journal of Mammalogy* 69: 688-695.
- DOYLE, A. T. 1989. Use of riparian and upland habitats by small mammals. *Journal of Mammalogy* 70: 14-23.
- GUNTHER, P. M., B. S. HORN, AND G. D. BABB. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade mountains. *Northwest Science* 57: 32-44.
- HAWES, M. L. 1977. Home range, territoriality, and ecological separation in sympatric shrews, *Sorex vagrans* and *Sorex obscurus*. *Journal of Mammalogy* 58: 354-367.
- HENNINGS, D., AND R. S. HOFFMANN. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. *Occasional Papers, Museum of Natural History, University of Kansas* 68: 1-35.
- REICHEL, J. D. 1986. Habitat use by alpine mammals in the Pacific Northwest. *Arctic and Alpine Research* 18: 111-119.
- SAS INSTITUTE, INC. 1985. SAS user's guide: statistics. Version 5. SAS Institute, Inc., Cary, North Carolina. 956 pp.
- TERRY, C. J. 1981. Habitat differentiation among three species of *Sorex* and *Neurotrichus gibbsi* in Washington. *American Midland Naturalist* 106: 119-125.

Received 18 September 1990

Revised 8 January 1991

Accepted 28 January 1991





---

**T H E**

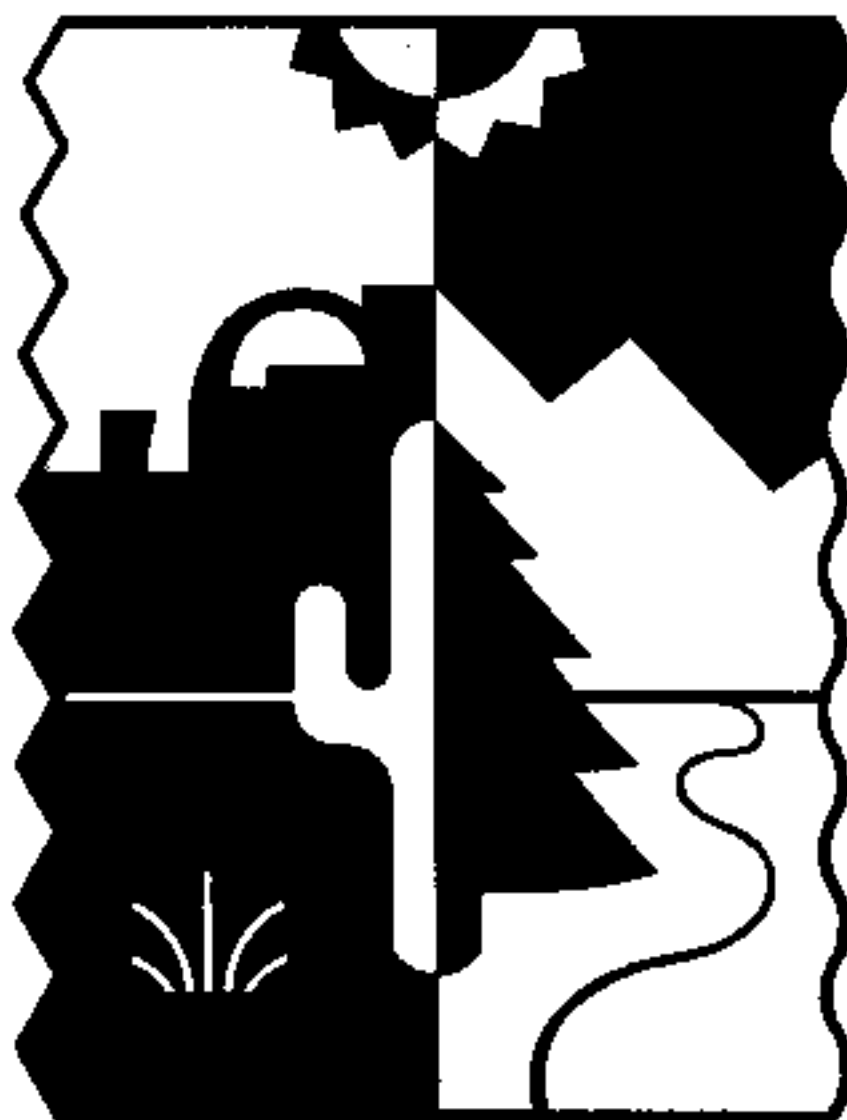
---

**G R E A T B A S I N**

---

**N A T U R A L I S T**

---



---

VOLUME 50 — 1990

---

BRIGHAM YOUNG UNIVERSITY

---

# INDEX

## GREAT BASIN NATURALIST

### Volume 50

Taxa described as new to science in this volume appear in **bold type** in this index.

- A plasma protein marker for population genetic studies of the desert tortoise (*Xerobates agassizi*), 1
- Allred, Kelly W., article by, 73
- Amy, Penny S., and Deborah A. Hall, note by, 289
- Anderson, Gary A., Jack E. Williams, Mark A. Stern, and Alan V. Munhall, article by, 243
- Apa, Anthony D., Daniel W. Uresk, and Raymond L. Linder, article by, 107
- Asquith, Adam, article by, 135
- Bats in Spotted Owl pellets in southern Arizona, 197
- Beard, James M., and Harold M. Tyus, article by, 33
- Belk, Mark C., Clyde L. Pritchett, and H. Duane Smith, note by, 387
- Berna, Howard, J., article by, 161
- Bibliography of Nevada and Utah vegetation description, 209
- Birds of a shadscale (*Atriplex confertifolia*) habitat in east central Nevada, 289
- Black-tailed prairie dog populations one year after treatment with rodenticides, 107
- Blackburn, Wilbert H., and M. Karl Wood, article by, 41
- Bone chewing by Rocky Mountain bighorn sheep, 89
- Bourgeron, P. S., L. D. Engelking, J. S. Tuhy, and J. D. Brotherson, article by, 209
- Britton, Carlton M., Guy R. McPherson, and Forrest A. Sneva, article by, 115
- Brotherson, J. D., P. S. Bourgeron, L. D. Engelking, and J. S. Tuhy, article by, 209
- Buchholz, Todd D., William C. McComb, and James R. Sedell, article by, 273
- California Gull populations nesting at Great Salt Lake, Utah, 299
- Chapman, Joseph A., and Kenneth L. Cramer, article by, 361
- Chapman, Joseph A., Kenneth L. Cramer, and A. Lee Foote, note by, 283
- Cole, David N., article by, 321
- Conservation status of threatened fishes in Warner Basin, Oregon, 243
- Cox, George W., article by, 21
- Cramer, Kenneth L., and Joseph A. Chapman, article by, 361
- Cramer, Kenneth L., A. Lee Foote, and Joseph A. Chapman, note by, 283
- Dam-site selection by beavers in an eastern Oregon basin, 273
- Deisch, Michele S., Daniel W. Uresk, and Raymond L. Linder, article by, 347
- Distribution of limber pine dwarf mistletoe in Nevada, 91
- Doescher, Paul S., Richard F. Miller, Jianguo Wang, and Jeff Rose, article by, 9
- Duncan, Russell B., and Ronnie Sidner, note by, 197
- Ecological review of black-tailed prairie dogs and associated species in western South Dakota, 339
- Ectomycorrhizal formation by *Pisolithus tinctorius* on *Quercus gembelii* × *Quercus turbinella* hybrid in an acidic Sierra Nevada minesoil, 367
- Edminster, Carleton B., Robert L. Mathiasen, and Frank G. Hawksworth, articles by, 67, 173
- Effect of backpack radio transmitter attachment on Chukar mating, 379
- Effects of burning and clipping on five bunchgrasses in eastern Oregon, 115
- Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the Southwest, 173
- Effects of nitrogen availability on growth and photosynthesis of *Artemisia tridentata* ssp. *wyomingensis*, 9
- Effects of prairie dog rodenticides on deer mice in western South Dakota, 347
- Eimeria* sp. (Apicomplexa: Eimeriidae) from Wyoming ground squirrels, *Spermophilus elegans*, and white-tailed prairie dogs, *Cynomys leucurus*, in Wyoming, 327
- Elliott, Charles L., and Richard Guetig, article by, 63
- Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado, 333
- Engelking, L. D., P. S. Bourgeron, J. S. Tuhy, and J. D. Brotherson, article by, 209
- Esox lucius* (Esocidae) and *Stizostedion vitreum* (Percidae) in the Green River basin, Colorado and Utah, 33
- Evans, Howard E., note by, 193
- Flinders, Jerran T., Bartel T. Slaugh, Jay A. Roberson, and N. Paul Johnston, note by, 379
- Foliage biomass and cover relationships between tree- and shrub-dominated communities in pinyon-juniper woodlands, 121
- Food caching and handling by marten, 381
- Foote, A. Lee, Kenneth L. Cramer, and Joseph A. Chapman, note by, 283
- Forage quality of rillscale (*Atriplex suckleyi*) grown on amended bentonite mine spoil, 57
- Form and dispersion of Mima mounds in relation to slope steepness and aspect on the Columbia Plateau, 21
- Formation of *Pisolithus tinctorius* ectomycorrhizae on California white fir in an eastern Sierra Nevada minesoil, 85
- Fresquez, P. R., article by, 167
- Fungi associated with soils collected beneath and between pinyon and juniper canopies in New Mexico, 167
- Galatowitsch, S. M., article by, 181

- George, Sarah B., and Mark A. Ports, note by, 93  
 Glenn, James L., Richard C. Straight, and Jack W. Sites, Jr., article by, 1  
 Guetig, Richard, and Charles L. Elliott, article by, 63  
 Hall, Deborah A., and Penny S. Amy, note by, 289  
 Hawksworth, Frank G., Robert L. Mathiasen, and Carleton B. Edminster, articles by, 67, 173  
 Hawksworth, Frank G., and Robert L. Mathiasen, note by, 91  
 Henry, Stephen E., Martin G. Raphael, and Leonard F. Ruggiero, note by, 381  
 Holocene predation of the Uinta ground squirrel by a badger, 385  
 Home range and activity patterns of black-tailed jackrabbits, 249  
 Humpback chub (*Gila cypha*) in the Yampa and Green rivers, Dinosaur National Monument, with observations on roundtail chub (*G. robusta*) and other sympatric fishes, 257  
 Infection of young Douglas-firs by dwarf mistletoe in the Southwest, 67  
 Influence of soil frost on infiltration of shrub coppice dune and dune interspace soils in southeastern Nevada, 41  
 Jehl, Joseph R., Jr., Don S. Paul, and Pamela K. Yochem, note by, 299  
 Johnston, Paul, Bartel T. Slauch, Jerran T. Flinders, and Jay A. Roberson, note by, 379  
 Joyal, Elaine, note by, 373  
 Karp, Catherine A., and Harold M. Tyus, article by, 257  
 Keating, K. A., note by, 89  
 Lessard, E. D., and J. M. Schmid, article by, 333  
 Linder, Raymond L., Anthony D. Apa, and Daniel W. Uresk, article by, 107  
 Linder, Raymond L., Michele S. Deisch, and Daniel W. Uresk, article by, 347  
 Longitudinal development of macroinvertebrate communities below oligotrophic lake outlets, 303  
 Management of endangered Sonoran topminnow at Bylas Springs, Arizona: description, critique, and recommendations, 265  
 Marsh, Paul C., and W. L. Minckley, article by, 265  
 Mathiasen, Robert L., Carleton B. Edminster, and Frank G. Hawksworth, articles by, 67, 173  
 Mathiasen, Robert L., and Frank G. Hawksworth, note by, 91  
 Mayfly growth and population density in constant and variable temperature regimes, 97  
 McComb, William C., James R. Sedell, and Todd D. Buchholz, article by, 273  
 McPherson, Guy R., Carlton M. Britton, and Forrest A. Sneva, article by, 115  
 Medica, Philip A., note by, 83  
 Medin, Dean E., note by, 295  
 Menkens, George E., Jr., Larry M. Shults, Robert S. Seville, and Nancy L. Stanton, article by, 327  
 Microbiology and water chemistry of two natural springs impacted by grazing in south central Nevada, 298  
 Miller, Richard F., Paul S. Doescher, Jianguo Wang, and Jeff Rose, article by, 9  
 Minckley, W. L., and Paul C. Marsh, article by, 265  
 Minshall, G. Wayne, and Christopher T. Robinson, article by, 303  
 Munhall, Alan V., Jack E. Williams, Mark A. Stern, and Gary A. Anderson, article by, 243  
 Natural hybrid between the Great Plains toad (*Bufo cognatus*) and the red-spotted toad (*Bufo punctatus*) from central Arizona, 371  
 Nelson, Michael E., note by, 385  
 New distribution records of spider wasps (Hymenoptera, Pompilidae) from the Rocky Mountain states, 193  
 New Mexico grass types and a selected bibliography of New Mexico grass taxonomy, 73  
 New variety of *Oxytropis campestris* (Fabaceae) from the Columbia Basin, Washington, 373  
 Noteworthy mammal distribution records for the Nevada Test Site, 83  
 Observations on the dwarf shrew (*Sorex nanus*) in northern Arizona, 161  
 On the typification of *Oxytropis borealis* DC., 355  
*Oxytropis borealis* var. *australis*, 359  
*Oxytropis borealis* var. *hudsonica* (Greene) Welsh, 357  
*Oxytropis borealis* var. *sulchurea* (Pors.) Welsh, 358  
*Oxytropis borealis* var. *viscidi* (Nutt.) Welsh, 358  
*Oxytropis campestris* var. *wanapum*, 373  
 Patten, Duncan T., and Juliet C. Stromberg, article by, 47  
 Patterns of microhabitat use by *Sorex monticolus* in summer, 387  
 Paul, Don S., Joseph R. Jehl, Jr., and Pamela K. Yochem, note by, 299  
 Pollination experiments in the *Mimulus cardinalis*-*M. lewisii* complex, 155  
 Ports, Mark A., and Sarah B. George, note by, 93  
 Pritchett, Clyde L., Mark C. Belk, and H. Duane Smith, note by, 387  
 Rader, Russell B., and James V. Ward, article by, 97  
 Raphael, Martin G., Stephen E. Henry, and Leonard F. Ruggiero, note by, 381  
 Reproduction of three species of pocket mice (*Perognathus*) in the Bonneville Basin, Utah, 361  
 Roberson, Jay A., Bartel T. Slauch, Jerran T. Flinders, and N. Paul Johnston, note by, 379  
 Robinson, Christopher T., and G. Wayne Minshall, article by, 303  
 Rose, Jeff, Paul S. Doescher, Richard F. Miller, and Jianguo Wang, article by, 9  
 Ruggiero, Leonard F., Stephen E. Henry, and Martin G. Raphael, note by, 381  
 Schmid, J. M., and E. D. Lessard, article by, 333  
 Sedell, James R., William C. McComb, and Todd D. Buchholz, article by, 273  
 Seed production and seedling establishment of a Southwest riparian tree, Arizona walnut (*Juglans major*), 47  
 Seville, Robert S., Larry M. Shults, Nancy L. Stanton, and George E. Menkens, Jr., article by, 327  
 Sharps, Jon C., and Daniel W. Uresk, article by, 339  
 Shults, Larry M., Robert S. Seville, Nancy L. Stanton, and George E. Menkens, Jr., article by, 327  
 Sidner, Ronnie, and Russell B. Duncan, note by, 197  
 Sites, Jack W., Jr., James L. Glenn, and Richard C. Straight, article by, 1  
 Slauch, Bartel T., Jerran T. Flinders, Jay A. Roberson, and N. Paul Johnston, note by, 379  
 Slauson, William L., Charles W. Welden, and Richard T. Ward, article by, 313  
 Small mammal records from Dolphin Island, the Great Salt Lake, and other localities in the Bonneville Basin, Utah, 283  
 Smith, David R., note by, 287  
 Smith, Graham W., article by, 249  
 Smith, H. Duane, Mark C. Belk, and Clyde L. Pritchett, note by, 387  
 Sneva, Forrest A., Carlton M. Britton, and Guy R. McPherson, article by, 115



- Sorex preblei* in the northern Great Basin, 93
- Spatial pattern and interference in piñon-juniper woodlands of northwest Colorado, 313
- Sprouting and seedling establishment in plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*), 201
- Stanton, Nancy L., Larry M. Shults, Robert S. Seville, and George E. Menkens, Jr., article by, 327
- Stern, Mark A., Jack E. Williams, Alan V. Munhall, and Gary A. Anderson, article by, 243
- Straight, Richard C., James L. Glenn, and Jack W. Sites, Jr., article by, 1
- Stromberg, Juliet C., and Duncan T. Patten, article by, 47
- Sullivan, Brian K., note by, 371
- Summer food habits of coyotes in Idaho's River of No Return Wilderness Area, 63
- Tausch, R. J., and P. T. Tueller, article by, 121
- Taxonomy and variation of the *Lopidea nigridia* complex of western North America (Heteroptera: Miridae, Orthotylinae), 135
- Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park, 321
- Tueller, P. T., and R. J. Tausch, article by, 121
- Tuhy, J. S., P. S. Bourgeron, L. D. Engelking, and J. D. Brotherson, article by, 209
- Two pronghorn antelope found locked together during the rut in west central Utah, 287
- Tyus, Harold M., and James M. Beard, article by, 33
- Tyus, Harold M., and Catherine A. Karp, article by, 257
- Uresk, Daniel W., Anthony D. Apa, and Raymond L. Linder, article by, 107
- Uresk, Daniel W., Michele S. Deisch, and Raymond L. Linder, article by, 347
- Uresk, Daniel W., and Jon C. Sharps, article by, 339
- Using the original land survey notes to reconstruct pre-settlement landscapes in the American West, 181
- Vickery, Robert K., Jr., article by, 155
- Voorhees, Marguerite E., article by, 57
- Walker, R. F., notes by, 85, 367
- Walton, T. P., C. L. Wambolt, and R. S. White, article by, 201
- Wambolt, C. L., T. P. Walton, and R. S. White, article by, 201
- Wang, Jianguo, Paul S. Doescher, Richard F. Miller, and Jeff Rose, article by, 9
- Ward, James V., and Russell B. Rader, article by, 97
- Ward, Richard T., Charles W. Welden, and William L. Slauson, article by, 313
- Welden, Charles W., William L. Slauson, and Richard T. Ward, article by, 313
- Welsh, Stanley L., article by, 355
- White, R. S., C. L. Wambolt, and T. P. Walton, article by, 201
- Williams, Jack E., Mark A. Stern, Alan V. Munhall, and Gary A. Anderson, article by, 243
- Wood, M. Karl, and Wilbert H. Blackburn, article by, 41
- Yochem, Pamela K., Don S. Paul, and Joseph R. Jehl, Jr., note by, 299

## TABLE OF CONTENTS

Volume 50

No. 1 – March 1990

### Articles

A plasma protein marker for population genetic studies of the desert tortoise ( <i>Xerobates agassizi</i> ) . . . . . James L. Glenn, Richard C. Straight, and Jack W. Sites, Jr.	1
Effects of nitrogen availability on growth and photosynthesis of <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> . . . . . Paul S. Doescher, Richard F. Miller, Jianguo Wang, and Jeff Rose	9
Form and dispersion of Mima mounds in relation to slope steepness and aspect on the Columbia Plateau. . . . . George W. Cox	21
<i>Esox lucius</i> (Esocidae) and <i>Stizostedion vitreum</i> (Percidae) in the Green River basin, Colorado and Utah. . . . . Harold M. Tyus and James M. Beard	33
Influence of soil frost on infiltration of shrub coppice dune and dune interspace soils in southeastern Nevada . . . . . Wilbert H. Blackburn and M. Karl Wood	41
Seed production and seedling establishment of a Southwest riparian tree, Arizona walnut ( <i>Juglans major</i> ) . . . . . Juliet C. Stromberg and Duncan T. Patten	47
Forage quality of rillscale ( <i>Atriplex suckleyi</i> ) grown on amended bentonite mine spoil . . . . . Marguerite E. Voorhees	57
Summer food habits of coyotes in Idaho's River of No Return Wilderness Area . . . . . Charles L. Elliott and Richard Guetig	63
Infection of young Douglas-firs by dwarf mistletoe in the Southwest. . . . . Robert L. Mathiasen, Carleton B. Edminster, and Frank G. Hawksworth	67
New Mexico grass types and a selected bibliography of New Mexico grass taxonomy . . . . . Kelly W. Allred	73

### Notes

Noteworthy mammal distribution records for the Nevada Test Site. . . . . Philip A. Medica	83
Formation of <i>Pisolithus tinctorius</i> ectomycorrhizae on California white fir in an eastern Sierra Nevada minesoil . . . . . R. F. Walker	85
Bone chewing by Rocky Mountain bighorn sheep . . . . . K. A. Keating	89
Distribution of limber pine dwarf mistletoe in Nevada . . . . . Robert L. Mathiasen and Frank G. Hawksworth	91
<i>Sorex preblei</i> in the Northern Great Basin . . . . . Mark A. Ports and Sarah B. George	93

No. 2 – June 1990

### Articles

Mayfly growth and population density in constant and variable temperature regimes . . . . . Russell B. Rader and James V. Ward	97
--	----

Black-tailed prairie dog populations one year after treatment with rodenticides . . . . .	Anthony D. Apa, Daniel W. Uresk, and Raymond L. Linder	107
Effects of burning and clipping on five bunchgrasses in eastern Oregon . . . . .	Carlton M. Britton, Guy R. McPherson, and Forrest A. Sneva	115
Foliage biomass and cover relationships between tree- and shrub-dominated communi- ties in pinyon-juniper woodlands . . . . .	R. J. Tausch and P. T. Tueller	121
Taxonomy and variation of the <i>Lopidea nigridia</i> complex of western North America (Heteroptera: Miridae, Orthotylinae) . . . . .	Adam Asquith	135
Pollination experiments in the <i>Mimulus cardinalis</i> – <i>M. lewisii</i> complex . . . . .	Robert K. Vickery, Jr.	155
Observations on the dwarf shrew ( <i>Sorex nanus</i> ) in northern Arizona. . . . .	Howard J. Berna	161
Fungi associated with soils collected beneath and between pinyon and juniper canopies in New Mexico . . . . .	P. R. Fresquez	167
Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the Southwest. . . . .	Robert L. Mathiasen, Frank G. Hawksworth, and Carleton B. Edminster	173
Using the original land survey notes to reconstruct presettlement landscapes in the American West. . . . .	S. M. Galatowitsch	181
<b>Notes</b>		
New distribution records of spider wasps (Hymenoptera, Pompilidae) from the Rocky Mountain states . . . . .	Howard E. Evans	193
Bats in Spotted Owl pellets in southern Arizona . . . . .	Russell B. Duncan and Ronnie Sidner	197

## No. 3 – October 1990

### Articles

Sprouting and seedling establishment in plains silver sagebrush ( <i>Artemisia cana</i> Pursh. ssp. <i>cana</i> ) . . . . .	C. L. Wambolt, T. P. Walton, and R. S. White	201
Bibliography of Nevada and Utah vegetation description . . . . .	P. S. Bourgeron, L. D. Engelking, J. S. Tuhy, and J. D. Brotherson	209
Conservation status of threatened fishes in Warner Basin, Oregon . . . . .	Jack E. Williams, Mark A. Stern, Alan V. Munhall, and Gary A. Anderson	243
Home range and activity patterns of black-tailed jackrabbits . . . . .	Graham W. Smith	249
Humpback chub ( <i>Gila cypha</i> ) in the Yampa and Green rivers, Dinosaur National Monu- ment, with observations on roundtail chub ( <i>G. robusta</i> ) and other sympatric fishes . . . . .	Catherine A. Karp and Harold M. Tyus	257
Management of endangered Sonoran topminnow at Bylas Springs, Arizona: description, critique, and recommendations . . . . .	Paul C. Marsh and W. L. Minckley	265
Dam-site selection by beavers in an eastern Oregon basin . . . . .	William C. McComb, James R. Sedell, and Todd D. Buchholz	273

### Notes

Small mammal records from Dolphin Island, the Great Salt Lake, and other localities in the Bonneville Basin, Utah . . . . .	Kenneth L. Cramer, A. Lee Foote, and Joseph A. Chapman	283
--	--	-----



Two pronghorn antelope found locked together during the rut in west central Utah . . . .	David R. Smith	287
Microbiology and water chemistry of two natural springs impacted by grazing in south central Nevada . . . . .	Deborah A. Hall and Penny S. Amy	289
Birds of a shadscale ( <i>Atriplex confertifolia</i> ) habitat in east central Nevada . . . . .	Dean E. Medin	295
California Gull populations nesting at Great Salt Lake, Utah . . . . .	Don S. Paul, Joseph R. Jehl, Jr., and Pamela K. Yochem	299

#### No. 4 – December 1990

#### Articles

Longitudinal development of macroinvertebrate communities below oligotrophic lake outlets . . . . .	Christopher T. Robinson and G. Wayne Minshall	303
Spatial pattern and interference in piñon-juniper woodlands of northwest Colorado. . . .	Charles W. Welden, William L. Slauson, and Richard T. Ward	313
Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. . . . .	David N. Cole	321
<i>Eimeria</i> sp. (Apicomplexa: Eimeriidae) from Wyoming ground squirrels, <i>Spermophilus elegans</i> , and white-tailed prairie dogs, <i>Cynomys leucurus</i> , in Wyoming. . . . .	Larry M. Shults, Robert S. Seville, Nancy L. Stanton, and George E. Menkens, Jr.	327
Emergence, attack densities, and host relationships for the Douglas-fir beetle ( <i>Dendroctonus pseudotsugae</i> Hopkins) in northern Colorado. . . . .	E. D. Lessard and J. M. Schmid	333
Ecological review of black-tailed prairie dogs and associated species in western South Dakota. . . . .	Jon C. Sharps and Daniel W. Uresk	339
Effects of prairie dog rodenticides on deer mice in western South Dakota . . . . .	Michele S. Deisch, Daniel W. Uresk, and Raymond L. Linder	347
On the typification of <i>Oxytropis borealis</i> DC. . . . .	Stanley L. Welsh	355
Reproduction of three species of pocket mice ( <i>Perognathus</i> ) in the Bonneville Basin, Utah . . . . .	Kenneth L. Cramer and Joseph A. Chapman	361

#### Notes

Ectomycorrhizal formation by <i>Pisolithus tinctorius</i> on <i>Quercus gambelii</i> × <i>Quercus turbinella</i> hybrid in an acidic Sierra Nevada minesoil . . . . .	R. F. Walker	367
Natural hybrid between the Great Plains toad ( <i>Bufo cognatus</i> ) and the red-spotted toad ( <i>Bufo punctatus</i> ) from central Arizona. . . . .	Brian K. Sullivan	371
New variety of <i>Oxytropis campestris</i> (Fabaceae) from the Columbia Basin, Washington . . . . .	Elaine Joyal	373
Effect of backpack radio transmitter attachment on Chukar mating. . . . .	Bartel T. Slauch, Jerran T. Flinders, Jay A. Roberson, and N. Paul Johnston	379
Food caching and handling by marten. . . . .	Stephen E. Henry, Martin G. Raphael, and Leonard F. Ruggiero	381
Holocene predation of the Uinta ground squirrel by a badger . . . . .	Michael E. Nelson	385
Patterns of microhabitat use by <i>Sorex monticolus</i> in summer. . . . .	Mark C. Belk, Clyde L. Pritchett, and H. Duane Smith	387



## INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

**SUBMIT MANUSCRIPTS** to James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, Utah 84602. A cover letter accompanying the manuscript must include phone number(s) of the author submitting the manuscript; it must also provide information describing the extent to which data, text, or illustrations have been used in other papers or books that are published, in press, submitted, or soon to be submitted elsewhere. Authors should adhere to the following guidelines; manuscripts not so prepared may be returned for revision.

**CONSULT THE MOST RECENT ISSUE** of this journal for general style and format. Also refer to the *CBE Style Manual*, 5th edition (Council of Biology Editors, 9650 Rockville Pike, Bethesda, MD 20814 USA; \$24).

**TYPE AND DOUBLE SPACE** all materials, including literature cited, table headings, and figure legends. Avoid hyphenated words at right-hand margins: Underline words to be printed in italics. Use standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides.

**SUBMIT 3 COPIES** of the manuscript. Number all pages and assemble each copy separately: title page, abstract and key words, text, acknowledgments, literature cited, appendices, tables, figure legends, figures.

**TITLE PAGE** includes an informative title no longer than 15 words, names and addresses of authors, a running head of fewer than 40 letters and spaces, footnotes to indicate change of address and author to whom correspondence should be addressed if other than the first author.

**ABSTRACT** states the purpose, methods, results, and conclusions of the research. It is followed by 6–12 key words, listed in order of decreasing importance, to be used for indexing.

**TEXT** has centered main headings printed in all capital letters; second-level headings are centered in upper- and lowercase letters; third-level headings begin paragraphs.

**VOUCHER SPECIMENS.** Authors are encouraged to designate, properly prepare, label, and deposit high-quality voucher specimens and cultures documenting their research in an established permanent collection, and to cite the repository in publication.

**REFERENCES IN THE TEXT** are cited by author and date: e.g., Martin (1989) or (Martin 1989). Multiple citations should be separated by commas and listed in chronological order. Use "et al." after name of first author for citations having more than two authors.

**ACKNOWLEDGMENTS**, under a centered main heading, include special publication numbers when appropriate.

**LITERATURE CITED**, also under a centered main heading, lists references alphabetically in the following formats:

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. *Journal of Wildlife Management* 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 in S. T. A. Pickett and P. S. White, eds., *The ecology of natural disturbance and patch dynamics*. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984. *Forest entomology: ecology and management*. John Wiley and Sons, Inc., New York. 669 pp.

**TABLES** are double spaced on separate sheets and designed to fit the width of either a single column or a page. Use lowercase letters to indicate footnotes.

**PHOTOCOPIES OF FIGURES** are submitted initially with the manuscript; editors may suggest changes. Lettering on figures should be large enough to withstand reduction to one- or two-column width. Originals must be no larger than 22 × 28 cm.

**NOTES.** If your manuscript would be more appropriate as a short communication or note, follow the above instructions but do not include an abstract.

**A CHARGE** of \$45 per page is made for articles published; the rate for subscribers will be \$40 per page. However, manuscripts with complex tables and/or numerous half-tones will be assessed an additional charge. Reprints may be purchased at the time of publication (an order form is sent with the proofs).

### FINAL CHECK:

- Cover letter explains any duplication of information and provides phone number(s)
- 3 copies of the manuscript
- Conformity with instructions
- Photocopies of illustrations



**CONTENTS****Articles**

- Longitudinal development of macroinvertebrate communities below oligotrophic lake outlets. . . . . Christopher T. Robinson and G. Wayne Minshall **303**
- Spatial pattern and interference in piñon-juniper woodlands of northwest Colorado . . . . . Charles W. Welden, William L. Slauson, and Richard T. Ward **313**
- Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. . . . . David N. Cole **321**
- Eimeria* sp. (Apicomplexa: Eimeriidae) from Wyoming ground squirrels, *Spermophilus elegans*, and white-tailed prairie dogs, *Cynomys leucurus*, in Wyoming . . . . . Larry M. Shults, Robert S. Seville, Nancy L. Stanton, and George E. Menkens, Jr. **327**
- Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado . . . . . E. D. Lessard and J. M. Schmid **333**
- Ecological review of black-tailed prairie dogs and associated species in western South Dakota. . . . . Jon C. Sharps and Daniel W. Uresk **339**
- Effects of prairie dog rodenticides on deer mice in western South Dakota. . . . . Michele S. Deisch, Daniel W. Uresk, and Raymond L. Linder **347**
- On the typification of *Oxytropis borealis* DC. . . . . Stanley L. Welsh **355**
- Reproduction of three species of pocket mice (*Perognathus*) in the Bonneville Basin, Utah . . . . . Kenneth L. Cramer and Joseph A. Chapman **361**

**Notes**

- Ectomycorrhizal formation by *Pisolithus tinctorius* on *Quercus gambelii* × *Quercus turbinella* hybrid in an acidic Sierra Nevada minesoil. . . . . R. F. Walker **367**
- Natural hybrid between the Great Plains toad (*Bufo cognatus*) and the red-spotted toad (*Bufo punctatus*) from central Arizona . . . . . Brian K. Sullivan **371**
- New variety of *Oxytropis campestris* (Fabaceae) from the Columbia Basin, Washington . . . . . Elaine Joyal **373**
- Effect of backpack radio transmitter attachment on Chukar mating . . . . . Bartel T. Slauch, Jerran T. Flinders, Jay A. Roberson, and N. Paul Johnston **379**
- Food caching and handling by marten . . . . . Stephen E. Henry, Martin G. Raphael, and Leonard F. Ruggiero **381**
- Holocene predation of the Uinta ground squirrel by a badger . . . . . Michael E. Nelson **385**
- Patterns of microhabitat use by *Sorex monticolus* in summer . . . . . Mark C. Belk, Clyde L. Pritchett, and H. Duane Smith **387**