UNIVERSITY OF COLORADO MUSEUM

EDITOR: SHI-KUEI WU

Natural History Inventory of Colorado, No. 15, pp. 1-83, 19 figures, 9 tables.

Published December 1, 1994

Review Committee:

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ISSN 0890-6882
DISTRIBUTION AND ECOLOGY OF BATS OF COLORADO

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Abstract.—Eighteen species of bats in the families Vespertilionidae and Molossidae are documented from Colorado. Accounts of species include information on foraging and roosting habitat, status and abundance, activity patterns, and reproduction. Records of occurrence are mapped based on examination of some 2110 specimens and review of literature. Summary analyses of population and community ecology, zoogeography, and public health provide a basis for review of conservation and management issues.

INTRODUCTION

A comprehensive account of the distribution and natural history of Coloradan bats is long overdue, but available data still are inadequate to support it. Therefore, this paper is meant as a progress report. The most recent published synopsis of Coloradan mammals (Armstrong, 1972) included detailed distributional and descriptive data on bats, but little information on other aspects of their zoology, and it has been out of print for a number of years.

An updated account of Coloradan bats is timely because over the past two decades there has been a remarkable increase in interest in bats worldwide. This is due in part to their inherent evolutionary and ecological interest, and also to the widely held perception that populations of a number of species are declining dramatically. These declines have been attributed to effects of artificial chemical biocides, habitat disturbance and destruction, and direct impacts, including wanton molestation. Some have estimated that as much as 45 percent of the North American bat fauna is endangered (Tuttle, 1988). However, techniques for the study of bats have improved dramatically since the 1960s, leading to deeper understanding of a number of species and their roles in ecosystems.

In recent decades, popular interest in bats has increased, in part, we suspect, because of the heightened awareness stimulated by such organizations as Bat Conservation International and, locally, the Colorado Bat Society. An increased interest in Coloradan bats seems to have begun with the establishment, in 1970, of a Nongame Wildlife Program in the Colorado Division of Wildlife (CDOW). Armstrong (1972) pointed out the paucity of information on most Coloradan species; in the past two decades, that situation has begun to change. Steven Ellinwood, a graduate student at the University of Northern Colorado, worked on bats in southeastern Colorado in 1977 and 1978, with support from CDOW (Ellinwood, 1978). In 1979, Jerry Freeman began a study of bats statewide, also funded (in part) by CDOW.
Eventually Freeman pursued a concerted field program in Moffat County to test some hypotheses about the ecological structure of an assemblage of species of bats (Freeman, 1984).

A popular-style account of Coloradan bats (Scott et al., 1984) summarized some of the published research to that time, again sponsored by CDOW. The present paper actually was begun as a more technical extension of (and originally as the foundation for) that general-interest publication.

In the past decade there has been research on Brazilian free-tailed bats, *Tadarida brasiliensis*, in the San Luis Valley (Svoboda and Choate, 1987, Freeman and Wunder, 1988). Michael A. Bogan, Robert B. Finley, Jr., and their colleagues from the National Ecology Research Laboratory of the US Fish and Wildlife Service in Fort Collins (subsequently moved to Albuquerque, New Mexico as part of the National Biological Survey) began on-going, long-term studies of bats and other mammals in western Colorado, especially in Dinosaur National Monument and Mesa Verde National Park. James P. Fitzgerald and his students at the University of Northern Colorado have studied bats, especially in northeastern Colorado; Fitzgerald et al. (1989) provided a summary of their results. Carron A. Meaney, then Curator of Mammals at the Denver Museum of Natural History, compiled data on distributions of Coloradan mammals, including bats, for a revision of *Colorado Mammal Distribution, Latilong Study* (Meaney, 1990).

The Colorado Bat Society (CBS) was founded by Rick A. Adams in 1990 to further research and conservation and to increase public appreciation of Coloradan bats. CBS provides speakers, a quarterly newsletter (*The Chiropteran*), members’ meetings, and field trips. Speakers from the Society also visit schools to educate children about the importance of bats. Individuals who wish to learn more about Colorado’s bats or contribute to their study or conservation, might wish to explore membership in CBS (mailing address: 1085-14th Street-Suite 1337, Boulder, CO 80302).

In the summer of 1991, a statewide Bat Population Trend Survey--analogous to the Audubon Society’s highly successful Christmas Bird Counts and based on a method pioneered in Pennsylvania--was initiated, coordinated by David Armstrong and sponsored by CBS. Joseph G. Hall of Grand Junction now is coordinator of the survey. With several summers’ compiled results, this survey could lead to new insight into long-term trends in populations, identify persons willing to do field work on bats, and locate areas of the state worthy of intensive study.

Also in 1991 the Bats/Inactive Mines Project, a potentially very important effort, was begun by CDOW in cooperation with the Mined Land Reclamation Division of the Colorado Department of Natural Resources. It is led by Kirk A. Navo, with the assistance of Connie L. Knapp and Tom Ingersoll, and field consulting by Rick Adams and Jerry Freeman. With the assistance of several dozen trained volunteers, the presence of bats is being documented in abandoned mines slated for closure. If a particular mine is found to provide habitat for bats, a
cooperative effort is undertaken to install a bat-accessible gate on the entrance.

METHODS

Order of treatment and scientific and vernacular nomenclature generally follow Jones et al. (1992). Woodman (1993) suggested changing gender of specific epithets of *Myotis lucifugus*, *M. californicus*, and *M. velifer*, based on the assertion that *Myotis* is a feminine noun. However, a detailed and cogent argument by Pritchard (1994) would seem to leave the situation equivocal, and we have chosen not to depart from traditional and familiar nomenclature without compelling and conclusive reason. Genera are treated in conventional phylogenetic order, and species are ordered alphabetically within genera. Treatment is at the level of species; for data on subspecies, see Armstrong (1972).

Accounts of species are organized as follows: geographic and ecological distribution; status and abundance; daily and seasonal activity patterns; reproduction; records of occurrence (specimens examined, additional records). Elevations are presented in either metric or "English" units without conversion, reflecting original sources (specimen labels or published reports). Foraging behavior and food habits are discussed in the summary section on ecology and zoogeography. We have made no attempt to provide comprehensive reviews of the literature under these headings, especially for areas distant from Colorado. Rather, we emphasize observations in the state, highlighting opportunities for further research. For more comprehensive accounts of general natural history of Coloradan bats, see Fitzgerald et al. (in press). Fortunately, most Coloradan bats (14 of the 18 species known from the state and also the two species treated herein as of possible occurrence) are the subject of accounts in *Mammalian Species*, an occasional series of review articles published by the American Society of Mammalogists. Information on the natural history of Coloradan vertebrates, including bats, is maintained in an electronic "Wildlife Species Database" by the Colorado Division of Wildlife at its Denver headquarters (6060 North Broadway, Denver, CO 80216).

Distributional records are listed by county. Counties are ordered from northwest to southeast, with counties at the same latitude listed westernmost first. Similarly, within counties, localities are ordered from northwest to southeast. This order is used because it imparts geographic coherence to the records (Armstrong, 1972). Figure 1 locates Colorado’s 63 counties. Unless otherwise indicated, specimens examined are in the Zoology Section of the University of Colorado Museum (UCM). Colorado Department of Health is designated herein as CDOH and the Rio Blanco Oil Shale Company as RB. Abbreviations of other collections are conventional (see Yates et al., 1987), as follows: Adams State College Collection (ASCC); American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Colorado National Monument (COLM); Teaching Collection, Department of Biology, Colorado State University (CSUTC); Denver Museum of Natural History (DMNH); Field Museum of Natural History (FMNH); Great Sand Dunes National Monument (GSDNM); Museum of Comparative Zoology, Harvard University (MCZ); Museum of the High Plains (Sternberg Museum), Fort Hays State University (MHP); Museum of Natural History, University of Kansas (KU); Museum of Southwestern Biology, University of New Mexico.
(MSB); Museum of Zoology, University of Michigan (UMMZ); Rocky Mountain National Park (RMNP); United States National Museum (USNM); School of Biological Sciences, University of Kentucky (UKEN); University of Northern Colorado (UNC); Western State College of Colorado (WSC). BS/FC—the Fort Collins collection of the US Fish and Wildlife Service (National Biological Survey)—is being relocated to Albuquerque, where it will be housed in the Museum of Southwestern Biology at the University of New Mexico (M. A. Bogan, pers. comm.). Locality records are mapped, with shaded circles indicating specimens examined, and unshaded circles indicating additional records. Localities too close to other localities to be mapped conveniently are italicized in lists of records of occurrence.
Measurements are not included, inasmuch as Armstrong (1972) provided extensive data, mostly from Coloradan specimens. Also, we do not present a key to species, inasmuch as keys have been published (e.g., Lechleitner, 1969, Armstrong, 1972, Kunz, in press) and a new and reliable key will be available in Fitzgerald et al. (in press). Problematic specimens should be submitted for identification to individuals who have ready access to comparative material in collections (e.g., personnel of the University of Colorado Museum or the Denver Museum of Natural History).

Acknowledgments.—This paper began many years ago as a cooperative effort of Jerry Freeman (then a graduate student) and two colleagues (then undergraduates), Rick Adams and Brad Lengas. Since that beginning, numerous colleagues have furnished unpublished information that is included in this paper. We list these individuals alphabetically because generally we cannot presume to establish a quantitative or qualitative ordering of individuals' contributions: S. J. Bissell, M. A. Bogan, A. Cruz, R. B. Finley, Jr., J. P. Fitzgerald, J. G. Hall, T. Ingersoll, B. Kaeding, C. L. Knapp, D. A. Leatherman, B. W. Lengas, C. A. Meaney, K. A. Navo, S. C. Pedersen, C. Rector, J. D. Taylor. (We note parenthetically that Dr. Steven J. Bissell, of the Colorado Division of Wildlife, clearly would be listed even if we had tried to rank-order our acknowledgments. Steve's contributions to the present effort and to the popularization and conservation of bats in Colorado are numerous, and we all are grateful for his friendship and for his financial support of much work by RAA and JF. Dr. Carron A. Meaney and Dr. Jerry R. Choate read the manuscript and made numerous suggestions for improvement, nearly all of which have been included. (Persistent errors of omission or commission remains our own, of course.)

In addition to the persons listed, we each recall the efforts of numerous unnamed landowners, local wildlife officials, and friends who have contributed to our efforts. Personnel of the Colorado Department of Health have furnished annual reports of numbers of potentially rabid bats turned in by the public and by personnel of various agencies.

We end these grateful acknowledgments with a brief but telling story, to suggest that often expert help and important data turn up in unexpected places. In January, 1990, one of us (DMA) presented an informal program on bats in Cortez. After the presentation, a couple from Mancos came forward to share some of their experiences with bats. A result was that the following day Armstrong and a band of other interested biologists (in which category we advisedly include a number of local ranchers and farmers as well as several state and federal agency personnel) were led to an active gold mine at 9500 ft. in the La Plata Mountains, which resulted in first hibernation records in Colorado for Pipistrellus hesperus and the highest elevation hibernation records to date for Myotis ciliolabrum and Plecotus townsendii anywhere in their ranges.

Colorado has a diverse bat fauna scattered over a complex terrain. A comprehensive, systematic survey of Coloradan bats would be prohibitively expensive. Therefore, observations by all interested naturalists are essential if we are to understand much of the basic biology of these animals. We thank the hundreds of "bat-watchers" around the
state—those we know and those we have yet to meet—and encourage their activities on behalf of Colorado’s native fauna.

ACCOUNTS OF SPECIES

ORDER CHIROPTERA

FAMILY VESPERTILIONIDAE

*Myotis californicus* (Audubon and Bachman), 1842

California Myotis

*Geographic and Ecological Distribution.*—The California myotis ranges from the state of Chiapas, México, to central British Columbia and from the Pacific Coast to western Colorado and south-central New Mexico. Coloradan records all are from lower elevations in the valleys of the Western Slope (Fig. 2). Elevational range is to about 7400 ft.

General habitat of the California myotis in Colorado is semi-desert shrublands and piñon-juniper woodlands. Night roosts include cracks and crevices in cliff faces, caves, mines, tunnels, and abandoned structure. Day roosts are similarly eclectic, and also are known to include tree holes and the space beneath shredding bark.

*Status and Abundance.*—Although the status of the California myotis in Colorado is poorly known, it appears to occur throughout suitable low-elevation, semi-desert habitat on the Western Slope. It seems not to form large colonies at any particular place, so we speculate that it does not face major threats from habitat modification at the present time.

*Daily and Seasonal Activity Patterns.*—Foraging begins at dusk and continues through the night, but there are two pulses of activity (as is typical of temperate zone vespertilionids), early evening and again after midnight (Simpson, 1993).

Winter range and habits of Coloradan animals are unknown, although they do migrate locally to hibernate in a number of other western states (Simpson, 1993), so wintering in Colorado is not out of the question.

*Reproduction.*—Little is known about reproductive patterns of the California myotis. Indications are that males become reproductively active in the fall (Krutzsch, 1954; Barbour and Davis, 1969). Females give birth to a single young each year. Gestation period is not known. Females are known to store sperm through the winter months with fertilization taking place in the spring (Krutzsch, 1954).

In Colorado (Adams, 1988), no pregnant females were collected in June (0/5 specimens) or July (0/10) but one was collected in August (1/1). Embryos were taken from six of 10
females in July. One female caught in June was not pregnant. No positive reproductive data are available for males of this species in Colorado, although Freeman and Adams (1992) reported males with non-scrotal testes from the Peacock and Burnwell mines, La Plata County, in early August.

Records of Occurrence.--Specimens examined, 36, distributed as follows: MOFFAT COUNTY: Holland Draw, 6 mi. W Greystone, T7N, R101W, 3; right bank Yampa River, river mile 24, Big Joe Campground, 6 (BS/FC); left bank Yampa River, river mile 20, Harding Hole, 1 (BS/FC); right bank Yampa River, river mile 34, Haystack Rock, 1 (BS/FC); Pool Creek at Echo Park, 2 (BS/FC); Lily Park, 5 mi. N Elk Springs, T5N, R99W, 4; 12 mi. E Dinosaur, NW 1/4 sec. 15, T3N, R101W, 2 (BS/FC). RIO BLANCO COUNTY: Monument Gulch, 16 mi. NE Rangely, T2N, 99W, 1. GARFIELD COUNTY: 5 1/2 mi. N, 2 mi. W Rifle, 5900 ft., 5 (BS/FC); Rifle, 1. MESA COUNTY: Aspen Street, Fruita, 1. MONTROSE COUNTY: Bedrock, 1; no locality other than County, 1. MONTEZUMA COUNTY: Ashbaugh's Ranch [Moqui], 3 (USNM); Rock Springs, Mesa Verde National Park, 7400 ft., 2 (KU); Loop Road, 1 1/2 mi. S Park Headquarters, 1 (KU); Mesa Verde National Park, 1 (DMNH2).

*Myotis ciliolabrum* (Merriam), 1886

**Western Small-footed Myotis**

*Geographic and Ecological Distribution.*--The small-footed myotis has an apparently disjunct distribution, with a western population (recognized as a distinct species by van Zyll de Jong, 1984) ranging from Zacatecas and Nuevo Leon, México, northward to southern Alberta, and from California to the Plains States (*Myotis ciliolabrum*), and an eastern population (*Myotis leibii*) ranging from the Ozarks eastward to New England and the eastern Great Lakes Region. In Colorado, the species occurs at low to moderate elevations on either side of the Continental Divide (Fig. 3), to as high as about 8000 ft. in the San Luis Valley and to 9500 ft. in the La Plata Mountains.

The small-footed myotis has a wide ecological range, from rock outcrops on open grassland (Robbins et al., 1977) to canyons in the foothills to lower mountains with coniferous woodland (Table 1). Day roosts are various, including cracks and crevices in cliffs, beneath tree bark, in mines and caves, and occasionally in dwellings of humans. Night roosts are under a variety of natural and artificial overhangs. Hibernacula include caves, mines, and tunnels, where the animals hang singly, often in quite exposed situations (Armstrong, 1972), and frequently associated with hibernating Townsend's big-eared bats.

*Status and Abundance.*--The western small-footed myotis has rather wide ecological tolerance and distribution and is an animal encountered fairly consistently in suitable habitats. Its habit of hibernating in rather exposed sites in tunnels and mines may make it more susceptible to wanton molestation than some more retiring species. However, the fact that it does hibernate in Colorado means that steps (like grating mines and tunnels) may be taken to conserve it here with the assurance that these positive efforts will not be "undone" elsewhere, as too frequently occurs with migratory species.

*Daily and Seasonal Activity Patterns.*--*Myotis ciliolabrum* begins to forage well before full dark, but usually not as early as the western pipistrelle. Foraging is biphasic (Table 2). The small-footed myotis is a year-around resident of Colorado. The animals hibernate in caves, mines, and tunnels, where they hang singly or in small clusters. One of us (DMA) observed a small-footed myotis in January in the Red Arrow Mine at 9500 ft. in the La Plata Mountains above Mancos. The bat hung alone but within a few centimeters of clusters of hibernating *Plecotus townsendii*. Air temperature in the 1-2 m high passageways was near freezing, as water dripping from the ceiling was freezing as "stalagmites" on the floor. Armstrong (1972) reported hibernation under similarly rigorous conditions in an irrigation tunnel near Livermore in northern Larimer County; Cramer (1994) collected hibernating animals from the same area.
Warren (1942) found hibernating small-footed myotis in Marchioness Tunnel, Boulder Canyon, in December 1909.

Reproduction.—Present data on the reproductive biology of this species are poor. A single young is thought to be most common. In Colorado (Adams, 1988), embryos were taken from pregnant females in the months of May (1/1 specimens) and June (3/4). Scrotal males were captured in August (6/6) and September (4/5). Adams (1993a) reported lactating females from Colorado National Monument in mid-June, and two pregnant females were captured at the Peacock Mine, La Plata County, in mid-June (Freeman and Adams, 1992).
Records of Occurrence.--Specimens examined, 112, distributed as follows: MOFFAT COUNTY: [Little] Snake River, S of Sunny Peak, 2 (USNM); 2 mi. SE Greystone, 4 (CM); Holland Draw, 6 mi. SW Greystone, T7N, R101W, 3; Echo Park, 10 mi. N Artesia [Dinosaur], 1 (KU); right bank Yampa River, river mile 24, Big Joe Campground, 4 (BS/FC); Yampa River, sec. 7, T6N, R97W, 5800 ft., 1; Lily Park, 5 mi. N Elk Springs, R99W, T7N, 3; 1 mi. SW Cross Mountain, 2 (KU); Elk Springs, 5 mi. SE Elk Springs, R98W, T5N, 6200 ft., 4; 12 mi. E Dinosaur, sec. 15, T3N, R101W, 1 (BS/FC). LARIIMER COUNTY: 27 mi. NNW Fort Collins, 1 (KU); 3 mi. N, 3 1/2 mi. W Livermore, NW 1/4 sec. 18, 1 (BS/FC); sec. 4, T10N, R71W, 1 (KU); T. 10 N, R. 70 W, 6160 ft., 1 (BS/FC); Fort Collins, 2 (1 CU, 1 BS/FC); Corbett Hall, CSU, 1 (CSUTC); 4 mi. SW Fort Collins, 1 (CSUTC). LOGAN COUNTY: Chimney Canon, 10 mi. NE Avalo, 2. RIO BLANCO COUNTY: Monument Gulch, 16 mi. NE of Rangely, R99W, T2N, 1; Dry Fork, White River, 6200 ft., 1 (AMNH); 6 mi. NE Meeker, 1 (CM); Ryan Gulch, NW 1/4 sec. 9, T2S, R98W, 1 (RB); Ryan Gulch, 25 mi. W, 10 mi. S Meeker, 6400 ft., 1 (BS/FC); Ryan Gulch Stock Tank. 24 mi. W, 10 mi. S Meeker, 6500 ft., 2 (BS/FC); Waterhole Ryan School, SE 1/4 sec. 9, T2S, R98W, 2 (RB); Duck Creek Stock Pond, NW 1/4 sec. 7, T1S, R98W, 1 (RB); Little Duck Creek, sec. 10, T1S, R98W, 6200 ft., 2 (BS/FC); Cascade Gulch, sec. 8, T3S, R95W, 2 (BS/FC). GARFIELD COUNTY: Groaning Cave, sec. 19, T4S, R47W, 1 (BS/FC); 3 mi. N Douglas Pass, 7000 ft., 1 (BS/FC); 5 1/2 mi. N, 2 mi. W Rifle, 5900 ft., 5 (BS/FC); 4.6 mi. W Rifle, sec. 14, T6S, R94W, 1 (BS/FC). BOULDER COUNTY: 6570 Old Stage Road, 1; Marchioness Tunnel, 6200 ft., Boulder Canyon, 2; Boulder Canyon, 1. MESA COUNTY: sec. 13, T8S, R102W, 1 (BS/FC); Ute Canyon, T12S, R2W, 4600 ft. (COLM). DOUGLAS COUNTY: 39°28'49"N, 104°55'20"W, 1 (DMNH2). GUNNISON COUNTY: 4 mi. W Sapinerro, 7750 ft., 2 (KU); Dos Rios, 1 (WSC). CHAFFEE COUNTY: Salida, 1. EL PASO COUNTY: Van Andert's Spring, Little Fountain Creek, 1. MONTROSE COUNTY: Jones Summit, Black Canyon of the Gunnison National Monument, 11; Grizzly Gulch, 1; 1/2 mi. SE North Rim Headquarters, Black Canyon of the Gunnison National Monument, 5. SAGUACHE COUNTY: 1 1/2 mi. N Crestone, 8050 ft., 1 (KU). OTERO COUNTY: 30 mi. S La Junta, 1 (DMNH2). MONTEZUMA COUNTY: Rock Springs, 7400 ft., Mesa Verde National Park, 5 (KU); Ruins Road, 1 1/2 mi. S Park Headquarters, 3 (KU); Loop Road, 1 1/2 mi. S Park Headquarters, 4 (KU); Mesa Verde National Park, 1 (DMNH2). LA PLATA COUNTY: Allison, 1 (MSB). CONEJOS COUNTY: La Manga Creek, 3 mi. N, 18 mi. W Antonito, 1 (UKEN); 7 mi. E Antonito, 1 (USNM). LAS ANIMAS COUNTY: 3 1/2 mi. S, 7 1/4 mi. W Guinare, 7940 ft., SW 1/4 sec. 10, T32S, R87W, 1 (BS/FC); abandoned coal mine on CF and I Steel Property, 1 mi. directly S Trinidad, 1920 m, 4 (UNC); near Wooton, 7500 ft., 1 (MSB). BACA COUNTY: Skull Canon, 2 (1 UNC); Holt Canyon, North Spring near Old Rock Quarry, 1 (UNC); Regnier, 1 (DMNH2).

Myotis evotis (H. Allen), 1864

Long-eared Myotis

Geographic and Ecological Distribution.--The long-eared myotis is a bat of western North America, ranging from the Pacific Coast to the Dakotas and Nebraska and from British Columbia to Baja California. In Colorado it occurs in the foothills, plateaus, and lower mountains on both sides of the Continental Divide (Fig. 4) to elevations above 8000 ft. in the San Luis Valley.

The long-eared myotis occurs in coniferous woodlands and forests, especially ponderosa pine and piñon-juniper communities (Table 1). Roosts both day and night include tree hollows, beneath loose bark, abandoned buildings, and mines.

Status and Abundance.--The long-eared myotis is usually found singly or in nursery colonies of a dozen or so individuals. Because it does not seem to congregate in large colonies, it does not appear to be particularly abundant, but it is widespread and tolerant of a variety of roosting sites, so it probably is not especially threatened by present trends in habitat disturbance.

Daily and Seasonal Activity Patterns.--M. evotis generally emerges to feed after full dark, and foraging activity appears to be related to temperature and consequent insect activity (reviewed by Manning and Jones, 1989). One to three individuals used cracks between rough pine roof sheathing on an abandoned bunkhouse on Cedar Creek, west of Loveland, Larimer County, as a night roost, but not at consistent times and by no means every night during the summer (DMA, unpublished). The long-eared myotis is not known to hibernate in Colorado, and it is presumed to be migratory, although the winter range is unknown.

Reproduction.--Freeman and Adams (1992) reported pregnant females from the Peacock Mine, La Plata County, in mid-June and early July. Capture of adult males with scrotal testes and adult females in late July on Sugarloaf Mountain west of Boulder led to speculation (Anonymous, 1993b) that the animals might be breeding in the vicinity.

Records of Occurrence.--Specimens examined, 165, distributed as follows: MOFFAT COUNTY: [Little] Snake River, S of Sunny Peak, 5 (USNM); [Little] Snake River, 2 (1 MCZ, 1 USNM); Alta Vista Ranch, 2 mi. SE Greystone, R100 W, T7N, 1; Holland Draw, 6 mi. SW Greystone, R101W, T7N, 4; right bank Yampa River, river mile 24, Big Joe
Figure 4. Distribution in Colorado of the long-eared myotis, Myotis evotis. (For explanation of symbols and conventions, see Methods.)

Campground, 1 (BS/FC); 1 mi. SW Cross Mountain, 3 (KU); Elk Springs, 5 mi. SE Elk Springs, 6200 ft., 42; 12 mi. E Dinosaur, NW 1/4 sec. 15, T3N, R101W, 1 (BS/FC). ROUTT COUNTY: Sand Mountain, 5 mi. NE Milner, R86W, T7N, 1; Blacktail Mountain, 5 mi. E Oak Creek, R84W, T4N, 1. LARIMER COUNTY: 14 mi. W Fort Collins, 1 (CSUTC); Loveand, 1 (USNM); Hallowell Park, 1 (RMNP); Moraine Park, 5 (RMNP); no locality other than county, 1 (CDOH). RIO BLANCO COUNTY: 6 mi. SW Meeker, R95W, T1N, 4; 10 mi. S, 25 mi. W Meeker, 6400 ft., 2 (BS/FC); Ryan Gulch, 10 mi. S, 24 mi. W Meeker, 6500 ft., 5 (BS/FC); Little Hills Experimental Station, sec. 32, T1N, R96W, 1 (BS/FC); Duck Creek Stock Pond, NW 1/4 sec. 7, T1S, R98W, 1 (RB); Duck Creek Tank, sec. 7, R98W, T1S, 1 (BS/FC); Little Duck Creek, sec. 10, T1S, R98W, 6200 ft., 10 (BS/FC); SE 1/4 sec. 9, T2S,
Little Brown Bat

Geographic and Ecological Distribution.--The little brown myotis ranges widely in North America, from central Alaska across Canada to Newfoundland, southward (except for parts of the central and southern Great Plains) to northern México. The species is widespread in Colorado at moderate elevations, with most records in and near the foothills and lower mountains (Fig. 5), although the extreme elevational record is 11,000 ft. in Lake County.

The little brown bat is broadly distributed ecologically, especially in areas of deciduous woody vegetation, including riparian forests and woodlands and also urban plantings. Known day roosts include buildings (sometimes occupied by humans), beneath bark and in tree holes, and in woodpiles. Hibernacula include caves, mines, and human structures (Table 1).

Status and Abundance.--The little brown bat appears to be less abundant in Colorado than it once was. Of course, this is mere speculation, because the baseline studies of abundance that would allow a definitive statement simply do not exist. What is known is that colonies which were known a quarter century ago now are gone or much reduced in size. Further, one of us (RAA) invested several months without success trying to locate a colony of Myotis lucifugus along the northern Front Range suitable for proposed studies of developmental morphology of flight, research eventually conducted in southeastern Wyoming (Adams, 1989b, 1992a, b, c, 1993b; Adams and Pederson, 1994).

Daily and Seasonal Activity Patterns.--Little brown bats usually forage over water, beginning at dusk. Activity patterns are highly variable over their range (Fenton and Barclay, 1980).

Hibernal activity of the little brown bat is poorly known in the West. Typical hibernacula include caves and mines, but wintering concentrations seldom have been reported. In the eastern United States, the animals undertake only short-distance (local) migrations from summer roosts to hibernacula (Humphrey and Cope, 1976).

Reproduction.--The little brown bat is one of the best studied bats in North America, but there is a general paucity of information on reproductive biology in the western part of its range. Nursery colonies usually are located in and around buildings (Fenton and Barclay, 1980; Wunder and Nash, 1980, 1981) and have been observed to number in the hundreds (Humphrey and Cope, 1976).

Reproductive information on this species in Colorado, compiled from museums, literature, and dissections (Adams, 1988), showed 6 of 13, 0 of 2, and 0 of 14 specimens of females
Figure 5. Distribution in Colorado of the little brown bat, *Myotis lucifugus*. (For explanation of symbols and conventions, see Methods.)

Lactating in June, July, and August, respectively. Males with scrotal testes have been recorded in June (1/1) and July (6/6). Findley (1954) found that in Jackson Hole, Wyoming, one-third of the females had given birth by the first week in July while all others were at or near term. In the Black Hills of Wyoming, seven females and a newborn young were captured on July 4 (Turner, 1974).

Records of Occurrence.—Specimens examined, 243, distributed as follows: MOFFAT COUNTY: 5 mi. SE Elk Springs, 6200 ft., 2. ROUTT COUNTY: Steamboat Springs, 2 (1 USNM); no locality other than county, 2 (CDOH). LARIMER COUNTY: Red Feather Lakes, 4 (UNC); 2 mi. E Wellington, 1 (BS/FC); Town & Country Motel, sec. 24, T7N, R69W, Fort
Collins, 1 (BS/FC); Fort Collins, 45 (1 UNC, 44 MSB); 4 1/2 mi. SW Estes Park, 1 (KU); no locality other than county, 1 (CDOH). WELD COUNTY: canal, 7th Ave. and 17th Street, Greeley, 2 (UNC); TKE House, Greeley, 2 (UNC); 1 mi. S La Salle, 1 (UNC). RIO BLANCO COUNTY: Meeker 2 (USNM); Buford Hatchery, 7000 ft., 1 (BS/FC); Little Hills Research Station, 1.9 mi. S, 15 mi. W Meeker, 1 (CDOW); 1 mi. N, 4 mi. W Rio Blanco, 6900 ft., 2 (BS/FC); Rio Blanco Lake, 1 (CDOW). GARFIELD COUNTY: Groaning Cave entrance, sec. 19, T4S, R87W, 1 (BS/FC); Groaning Cave, SE 1/4 sec. 19, T4S, R87W, 1 (BS/FC); 1 mi. S, 4 mi. W Rifle, 5300 ft., 1 (BS/FC); 39°35'45"N, 107°32'53"W, 1 (DMNH2); no locality other than county, 2 (CDOW). GRAND COUNTY: Arapahoe Valley Lodge, Shadow Mountain National Recreation Area, 1 (RMNP); no locality other than county, 1 (CDOH). SUMMIT COUNTY: no locality other than county, 1 (CDOH). BOULDER COUNTY: 1 1/2 mi. SE Jarnestown, 1; Boulder, 2 (1 CSUTC); Columbine Apartments, 24th St., Boulder, 1 (UNC); 3790 Silverplume Lane, Boulder, 1 (CDOH); no locality other than county, 2 (CDOH). GILPIN COUNTY: Lump Gulch, 1. JEFFERSON COUNTY: Ken-Caryl Ranch, 1; no locality other than county, 2 (CDOW). ADAMS COUNTY: no locality other than county, 1 (CDOH). MESA COUNTY: Ute Canyon, T12S, R2W, 4600 ft. (COLM); Headquarters, Colorado National Monument, 1; Colorado National Monument, 1 (COLM). PITKIN COUNTY: Aspen, 1 (DMNH2). LAKE COUNTY: 9 mi. SW Leadville, 11,000 ft., 2 (KU); Twin Lakes, 9200 ft., 17 (UKEN). PARK COUNTY: no locality other than county, 1 (CDOH). GUNNISON COUNTY: Gunnison, 2 (1 UMMZ, 1 WSC); Taylor Hall, WSC, Gunnison, 1 (WSC). TELLER COUNTY: Woodland Park, 1 (AMNH). EL PASO COUNTY: Fort Carson, 1 (FMNH); no locality other than county, 3 (CDOW). MONTROSE COUNTY: Jones Summit, Black Canyon of the Gunnison National Park, 3; Grizzly Gulch, 2; Black Canyon of the Gunnison National Monument, 2 (1 COLM). SAGUACHE COUNTY: 1 1/2 mi. N Crestone, 8050 ft., 4 (KU); 9 mi. E Center, 18 (AMNH); no locality other than county, 1 (AMNH). PUEBLO COUNTY: Pueblo International Airport, 1 (CDOH); no locality other than county, 3 (CDOW). ALAMOSA COUNTY Mosca Creek, 8800 ft., 1 (GSDNM); S of Great Sand Dunes National Monument, 1 (GSDNM); 1 mi. N, 3 mi. E Mosca, 12 (UKEN); 1 mi. N, 4 mi. E Mosca, 18 (UKEN); 4 mi. E Mosca, 2 (1 USNM); Alamosa, 2 (ASCC). MONTEZUMA COUNTY: 5 mi. N, 2 mi. W Dolores, 6750 ft., 14 (BS/FC). LA PLATA COUNTY: Bell, 13 mi. N Durango, T37N, R9W, 4; Durango, 1 (CDOH). CONEJOS COUNTY: Courthouse, Conejos, 7900 ft., 29 (UKEN); Conejos River, 8300 ft., 1 (USNM). LAS ANIMAS COUNTY: Burro Canyon, sec. 18, T32S, R66W, 7600 ft., 2 (BS/FC); City Park Pond, Trinidad, 1890 m, 1; Trinidad Fire Station #1, 1859 m, 1 (UNC); (Bar) NI Ranch, 1/2 mi. S Stonewall, 2438 m, 12 (UNC); 6 mi. N, 1/2 mi. E Weston, 7350 ft., 1 (BS/FC).


*Myotis thysanodes* Miller, 1897

**Fringed Myotis**

*Geographic and Ecological Distribution.*—The fringed myotis occurs from the Isthmus of Tehuantepec northward to south-central British Columbia and from the Pacific Coast eastward to the Black Hills of South Dakota and Wyoming. Coloradan records are scattered at moderate elevations (about 5000-8000 ft.) on either side of the Continental Divide (Fig. 6).

*Myotis thysanodes* is a species of coniferous woodlands (Table 1) at moderate elevations in mountainous parts of the state. Night and day roosts include caves, mines, and buildings (typically abandoned houses or outbuildings). Hibernacula include caves and buildings elsewhere, but have not been identified in Colorado.

*Status and Abundance.*—The fringed myotis has been considered rare, but as more is known about its habitat, distribution, and habits, it is becoming increasingly clear that it is simply widely dispersed. Nursery colonies of dozens to hundreds of individuals have been encountered elsewhere in the West, but Coloradan observations have almost all been of single individuals.

Daily and Seasonal Activity Patterns.—Foraging is concentrated from about sunset until midnight, and there are no firm reports of the biphasic foraging pattern so typical of temperate zone vespertilionids (O'Farrell and Studier, 1980).

Winter whereabouts of Coloradan fringed myotis are not known, although one would expect the animals to hibernate in the state. Hibernacula elsewhere in the West include caves and buildings, usually within a few kilometers of the summer roost (O'Farrell and Studier, 1980).

Reproduction.—The fringed myotis is a colonial species, forming nursery colonies of up to hundreds of individuals in some cases (O'Farrell and Studier, 1980). Copulation occurs in fall, sperm are stored through the winter months, and fertilization and implantation take place in spring. In New Mexico, parturition began on 25 June and concluded on 7 July; gestation period was estimated to be between 50 and 60 days (O'Farrell and Studier, 1973). Two females collected near Colorado Springs on 18 June (Barbour and Davis, 1969) each carried a
Figure 6. Distribution in Colorado of the fringed myotis, Myotis thysanodes. (For explanation of symbols and conventions, see Methods.)

single embryo (6, 10 mm in crown-rump length). Neither of two males captured by Adams (1990b) in Colorado National Monument in June had scrotal testes. No data other than these are available on this species' reproductive biology in Colorado.

Records of Occurrence.--Specimens examined, 14, distributed as follows: MOFFAT COUNTY: right bank Yampa River, river mile 24, Big Joe Campground, 1 (BS/FC); Elk Springs, 5 mi. SE of Elk Springs, T5N R98W, 6200 ft., 1. LARIMER COUNTY: 1.5 mi. S, 5.6 mi. W Livermore, 6600 ft., SE 1/4 sec. 5, T9N R71W, 1 (BS/FC). RIO BLANCO COUNTY: 6 mi. SW of Meeker, T1N R95W, 2. GARFIELD COUNTY: New Castle, 1 (DMNH2). MESA COUNTY: Ute Canyon, T12S, R2W, 4600 ft. (COLM); West Creek, 4 mi.


*Myotis volans* (H. Allen), 1864

**Long-legged Myotis**

*Geographic and Ecological Distribution.*--The long-legged myotis is a species of western North America, ranging from Veracruz and Jalisco, México, to northern British Columbia and from the Pacific Coast eastward to the Dakotas, Nebraska, and Texas. Coloradan records are from the western three-fifths of the state (Fig. 7), mostly at moderate elevations, but ranging to nearly 11,500 ft. at Glen Cove on Pikes Peak.

The long-legged myotis is typical of coniferous woodland and forest (Table 1), especially ponderosa pine and piñon-juniper communities, although they do range higher into subalpine spruce-fir forest. Roosts include buildings, trees, and crevices in rocks. Mines, tunnels, and natural caves are used as night roosts, but apparently are not especially important as day roosts.

*Status and Abundance.*--The long-legged myotis is widespread across a wide range of elevations in the Colorado mountains and it is the species of bat most predictably encountered in these situations. Roosting in small colonies, it seems to be under no particular threat.

*Daily and Seasonal Activity Patterns.*--*M. volans* feeds, often over water, on a repeated circuit. Foraging begins at dusk and continues through the night, with a peak of activity within 3-4 h after sunset (Warner and Czaplewski, 1984).

The long-legged myotis has yet to be encountered in Colorado in winter, but (based on their behavior elsewhere) hibernacula in caves or mines would be expected in the state. Elsewhere the animals make only short-distance migrations between summer and winter roosts (Schowalter, 1980).
Reproduction.--This species tends to form small maternity colonies up to approximately several dozen individuals. On 8 July, Davis and Barbour (1970) caught 45 females from the Courthouse in Conejos, in the San Luis Valley. Reproductive data collected in Colorado (Adams, 1988) show the proportion of females lactating to be highest in August (16/35 specimens), but they also were present in June (3/29) and July (11/34). Fetuses were taken from females in June (1/10), July (7/16) and in August (6/25). Freeman and Adams (1992) reported a pregnant female from the Peacock Mine, La Plata County, in mid-June. No data are available on the reproductive biology of male long-legged myotis in Colorado.

Records of Occurrence.--Specimens examined, 191, distributed as follows: MOFFAT

Figure 7. Distribution in Colorado of the long-legged myotis, Myotis volans. (For explanation of symbols and conventions, see Methods.)
COUNTY: Holland Draw, 6 mi. SW Greystone, R101W T7N, 2; Alta Vista Ranch, 2 mi. SE of Greystone, R100W T7N, 1; right bank Yampa River, river mile 24, Big Joe Campground, 6 (BS/FC); left bank Yampa River, river mile 20, Harding Hole, 1 (BS/FC); Hell's Canyon, Dinosaur National Monument, 1; Lily Park, 5 mi. N Elk Springs, T5N R99W, 1; Elk Springs, 5 mi. S Elk Springs, T5N R 98W, 6200ft., 1. ROUTT COUNTY: Sand Mountain, 5 mi. NW Milner, R86W T1N, 1; Blacktail Mountain, 5 mi. E Oak Creek, R84W T4N, 1; 5 mi. E Toponas, 1. LARIMER COUNTY: W 1/2, sec. 26, T8N, R73W, 8400 ft., 3 (KU); Fort Collins, 2 (1 CSUTC, 1 CDOH); Aspenglen Campground, 1 (RMNP); Moraine Park, 8200 ft., 1 (KU); YMCA Camp, 1 (RMNP). RIO BLANCO COUNTY: Monument Gulch, 16 mi. NE Rangely, T2N, R99W, 4; 4 mi. S South Fork Campground, sec. 21, T2S, R90W, 1 (BS/FC); NW 1/4 sec. 7, T1S R93W, 1 (RB); Little Duck Creek, sec. 10, T1S R93W, 6200 ft., 4 (BS/FC); Corral Gulch Spring, SE 1/4 sec. 30, T1S R75W, 1 (RB); Ryan Gulch, 24 mi. W, 10 mi. S Meeker, 6500 ft., 5 (BS/FC). GARFIELD COUNTY: 2 mi. E Rio Blanco, 1 (BS/FC); Groaning Cave, sec. 19, T45, R87W 2 (BS/FC); Groaning Cave Entrance, sec. 19, T1S, R88W, 1 (BS/FC); Douglas Pass, 28 mi. N Loma, 1. BOULDER COUNTY: 5 mi. S, 10 mi. W Lyons, 7240 ft., 1 (KU); 3 mi. S, 1/2 mi. W Ward, 9400 ft., 7 (KU); Boulder, 3. GILPIN COUNTY: Rollinsville, 1 (KU); S of Rollinsville, 4 (KU); Lump Gulch, 1. JEFFERSON COUNTY: Evergreen, 1 (CDOH); no locality other than county, 1 (CDOH). MESA COUNTY: De Beque Canon, 1; Grand Junction, 1 (USNM); Grand Mesa, 28 mi. E Grand Junction, 1 (KU); Grand Mesa, 6 mi. E Lands End Observatory, T11S, R96W, 1. PITKIN COUNTY: Aspen, 1 (CDOH). PARK COUNTY: 2.5 mi. E Estabrook, 18 (MHP). DOUGLAS COUNTY: Missouri Gulch, Manitou Experimental Forest, sec. 35, T10S R69W, 1 (BS/FC). DELTA COUNTY: Leroux Creek, 8 mi. NW Hotchkiss, T13S R93W, 3. GUNNISON COUNTY: 9 mi. N Crested Butte, 11,000 ft., 1 (KU); sec. 3, T12S R86W, 8 (RMBL); sec. 3, T13S R86W, 4 (RMBL); Gothic, 2 (1 KU, 1 MSB); 10 mi. up Ohio Creek, 1 (WSC); Ute Hall, WSC Campus, 1 (WSC); Gold Basin, 6 mi. S Gunnison, R1W, T49N, 1; 4 mi. W Sapinero, 7750 ft., 3 (KU). TELLER COUNTY: Glen Cove, 11,450 ft., 1 (UMMZ). EL PASO COUNTY: 412 San Rafael, Colorado Springs, 1 (CDOH). MONTROSE COUNTY: Jones Summit, Black Canyon of the Gunnison National Monument, 6; Grizzly Gulch, 3; 1/2 mi. SE North Rim Headquarters, Black Canyon of the Gunnison National Monument, 6; 1/2 mi. SE North Rim Headquarters, Black Canyon of the Gunnison National Monument, 1; La Sal Creek, 4 mi. W of Bedrock, R19W T47N, 2; Cottonwood Trail, 12 mi. NE of Nucla, T48N R14W, 1; Coventry, 1 (USNM). SAGUACHA COUNTY: Graveyard Gulch, 8 mi. NE Saguache, T45N, R9E, 1; 5 mi. N, 22 mi. W Saguache, 10,000 ft., 1 (KU); Madenos Canon, above Herard's, 8700 ft., 2. HINSDALE COUNTY: Fish Canyon, 11 mi. SE of Powderhorn, R2W T45N, 1. ALAMOSA COUNTY: Great Sand Dunes National Monument, 1 (GSDNM). MONTEZUMA COUNTY: Cahone Canyon, 4 mi. SW Cahone, T39N, R18W, 1; Yellowjacket Canyon, 1 mi. NE Ismay Trading Post, T36N, R20W, 1; Rock Springs, Mesa Verde National Park, 7400 ft., 1 (KU). LA PLATA COUNTY: 26 mi. N Bayfield, 1 (AMNH). ARCHULETA COUNTY: Deep Canon, 2 (MSB). CONEJOS COUNTY: 37° 05' 18"N, 106° 01'14"W, 8 (MSB). LAS ANIMAS COUNTY: junction Plum and Chacuaco creeks, 2 (UNC); 3.5 mi. S, 7 1/4 mi. W Gulnare, 3 (BS/FC); 3.5 mi. S, 7 1/4 mi. W Gulinare, 7940 ft., SW 1/4 sec.10, T32S R67W, 7 (BS/FC); 3.5 mi. S, 7 1/4 mi. W Gulnare, 7900 ft., 9 (BS/FC); Burro Canyon, sec. 18, T32S R66W, 7600 ft., 8 (BS/FC); sec. 18, T32S R66W, 7600 ft., 8 (BS/FC).
ft., 3 (BS/FC); abandoned coal mine, CF and I Steel property, 1 mi. directly N of Trinidad, 1920 m, 2 (UNC); City Park Pond, Trinidad, 1890 m, 1; Trinidad Golf Course, 1; S end, Trinidad Municipal Golf Course, 1920 m, 1; (Bar) NI Ranch, 1/2 mi. S Stonewall, 2438 m, 2; (Bar) NI Ranch, 1 mi. S of Stonewall, 1; Raton Mesa near San Francisco Pass, 2682 m, 2; near Wooton, 7500 ft., 2 (MSB); no locality other than county, 1 (DMNH2).


Myotis yumanensis (H. Allen), 1864

Yuma Myotis

Geographic and Ecological Distribution.—The Yuma myotis occurs from west-central México northward to Colorado and Utah in the interior and to British Columbia along the Pacific Coast. In Colorado, the species is known at moderate elevations on the Western Slope and also on the Eastern Slope south of the Arkansas River (Fig. 8). Maximal elevation is nearly 8000 ft. in the San Luis Valley.

This is a species of forests and woodlands in semi-desert areas of Colorado (Table 1), and its foraging is restricted to riparian corridors of the few major rivers. Day roosts are in crevices and fissures in cliffs, buildings, mines or caves, and in other dark, protected areas, including swallows' nests. Night roosts have been located in buildings and under natural ledges. Nursery colonies have been found in buildings, dams, and caves.

Status and Abundance.—The Yuma myotis seems not to be particularly common even in suitable habitat. They are rather eclectic in their choice of roosting sites, however, and we have no evidence to suggest that they are less abundant than they have been historically.

Daily and Seasonal Activity Patterns.—The Yuma myotis emerges at dusk to forage along streams (Table 2). As many other Coloradan species of Myotis, hibernal habits of M. yumanensis are poorly known. Elsewhere over their range, they make local movements from summer roosts to hibernacula in a variety of dark, cool places: mines, tunnels, caves, and buildings.
Reproduction.--Little is known of this species' reproductive habits. Parturition takes place from late May to mid-July in California and in mid-July in Arizona (Dalquest, 1947). In Colorado (Adams, 1988), testes of one of two and and 19 of 22 specimens of males taken in July and August were scrotal. Davis and Barbour (1970) reported finding a lactating female containing a 22 mm fetus in the Courthouse in Conejos. Ellinwood (1978) captured a lactating female on Carizzo Creek, Baca County, in mid-June. Adams (1990b) reported a maternity colony near the west entrance gate of Colorado National Monument; juveniles were taken over Fruita Reservoir in early August and adult males were also present in the area (Adams, 1993a).
Records of Occurrence.--Specimens examined, 93, distributed as follows: MOFFAT COUNTY: [Little] Snake River, S of Sunny Peak, 2 (USNM); Echo Park, 10 mi. N Artesia (Dinosaur), 1 (KU); Pool Creek at Echo Park, 2 (BS/FC); Lily, 1 (USNM); right bank Yampa River, river mile 24, Big Joe Campground, 9 (BS/FC); Yampa River, sec. 7, T6N, R94W, 5800 ft., 1; Yampa River, sec. 16, T6N, R94W, 5960 ft., 1; 5 mi. SE Elk Springs, T5N R98W, 6200 ft., 1. RIO BLANCO COUNTY: Monument Gulch, 16 mi. NE Rangely, T2N, R99W, 1; Little Hills Game Research Station, 19 mi. S, 15 mi. W Meeker, 1; Douglas Creek, 18 mi. S Rangely, T2S, R101W, 1; attic of deserted house, Rio Blanco Lake, 1. GARFIELD COUNTY: Douglas Pass, 28 mi. N of Loma, T5S, R102W, 1. MESA COUNTY: Highline Lake, 2 (UNC). Fruita Reservoir, 1/4 mi. S W Entrance Gate, sec. 32, T1N, R2W, 4640 ft. (COLM). EL PASO COUNTY: Fort Carson, 1 (MSB). MONROSE COUNTY: La Sal Creek, 4 mi. W Bedrock, T47N, R91W, 3. SAN MIGUEL COUNTY: 1 mi. SW Slick Rock, T44N, R18W, 1. BENT COUNTY: John Martin Dam, 3 mi. S Hasty, T35S R47W, 6. LA PLATA COUNTY: Florida River, 12 mi. S Durango, T33N, R9W, 1; Allison, 2 (MSB). CONEJOS COUNTY: Courthouse, Conejos, 7900 ft., 1 (UKEN); Antonito, T33N, R9E, 1 (MSB). LAS ANIMAS COUNTY: Courthouse, Conejos, 7900 ft., 1 (UKEN); Antonito, T33N, R9E, 1 (MSB). LAS ANIMAS COUNTY: junction of Plum and Chacuaco Creeks, 3 (1 CU, 2 UNC); 3 mi. S Potato Butte, Cottonwood Creek, 41. BACA COUNTY: Cat Creek, 1 mi. S Springfield, 1 (UNC); Carizzo Creek (Miller Myir Ranch), 1372 m, 2; Skull Canon, 4600 ft., 1; Holt Canyon, South Spring, 1311 m, 4; Furnish Canyon, 4600 ft., 1; Sand Canyon West, 1 (UNC); Picture Canyon Spring, 1311 m, SE 1/4 sec. 7, T35S, R47W, 1.

Additional Records: MOFFAT COUNTY: Green River, Dinosaur National Monument (Navo et al., 1992). MESA COUNTY (Adams, 1993a): Lower Tunnel; Devil's Kitchen; West Side Settling Pond, Colorado National Monument. OTERO COUNTY: near mouth of Apishapa Creek (Glass and Baker, 1968). LAS ANIMAS COUNTY (J. R. Choate, pers. comm., unless otherwise noted): Pinon Canyon Maneuver Site, 37°37'03"N, 103°35'45"W; Pinon Canyon Maneuver Site, 37°31'38"N, 103°49'06"W; Pinon Canyon Maneuver Site, UTM: 602600, 4150250; Pinon Canyon Maneuver Site, UTM: 595620, 4142800; Pinon Canyon Maneuver Site, UTM: 599160, 4140640; Cow Canyon, 16 mi. SW Kim, T34S, R56W (J. Freeman, 1981).

Lasiurus borealis (Müller), 1776

Red Bat

Geographic and Ecological Distribution.--The red bat occurs throughout most of temperate and tropical North America except in the Rocky Mountains and the Great Basin, from northern Saskatchewan south to Tierra del Fuego in Argentina and Chile. In Colorado, all records are from the Eastern Slope (Fig. 9).

Red bats occur in deciduous forest (Table 1), especially forest-edge situations. They roost hanging from branches, often within 5 m of the ground. On its range in eastern Colorado suitable habitat is mostly limited to riparian corridors and urban, ornamental woodland. David A. Leatherman (Colorado State Forest Service, pers. comm.) furnished a noteworthy
Figure 9. Distribution in Colorado of the red bat, Lasiurus borealis. (For explanation of symbols and conventions, see Methods.)

photograph (taken 28 August 1990) of a red bat whose uropatagium had become tangled on a barbed wire fence in dry rangeland at a place 8/10 mi. S of Villagreen, Las Animas Co.

**Status and Abundance.**—There is no indication that red bats ever have been abundant in Colorado. Certainly suitable deciduous forest habitat is better developed in the state today than it ever was prior to the advent of urbanization and irrigated agriculture on the eastern plains (Fitzgerald et al., in press). Therefore, one might expect populations to be increasing, as have populations of other riparian forest mammals, such as fox squirrels (*Sciurus niger*) and raccoons (*Procyon lotor*) (Fitzgerald et al., in press), and deciduous forest birds (Knopf, 1986).
Daily and Seasonal Activity Patterns.—Knowledge of the red bat in Colorado is based wholly on chance encounters with individuals, rather than systematic study. Shump and Shump (1982a) reviewed the literature, noting that foraging begins 1-2 h after sunset, later than that of sympatric vespertilionids other than *Lasiurus cinereus*, and is biphasic, corresponding with insect activity.

In Colorado, where it is at the margin of its range at this latitude, the winter habits of the red bat are unknown. Based on its biology elsewhere, however, one would expect migration to the south and east. Where the animals overwinter is generally unknown even for the abundant populations of midwestern United States.

Reproduction.—Males may copulate with females while in flight (see Barbour and Davis, 1969), in August and September. Sperm is stored throughout the winter in the uterus with actual fertilization occurring in spring. Parturition takes place in the latter part of May in Illinois (Layne, 1958) and Indiana (Mumford, 1973). Litters range in number from one to five (Shump and Shump, 1982a) averaging about 2.3 young per female (Constantine, 1966a).

No females in breeding condition have been collected in Colorado, but Ellinwood (1978) captured a lactating female in Picture Canyon, Baca County, in early June, leading him to surmise that at least some red bats rear young in the state. A male with scrotal testes was captured in August, whereas one taken in September was non-scrotal.

Records of Occurrence.—Specimens examined, 10, distributed as follows: WELD COUNTY: Greeley, 2 (1 UNC). BOULDER COUNTY: CU Boulder Campus, 18th and Colorado, Boulder, 1; no locality other than county, 1 (CDOH). DENVER COUNTY: no locality other than county, 1 (CDOH). PUEBLO COUNTY: no locality other than county, 1 (CDOH). KIOWA COUNTY: no locality other than county, 1 (CDOH). PROWERS COUNTY: no locality other than county, 2 (CDOH). BACA COUNTY: Picture Canyon Spring, 4206 ft., 1 (UNC).


*Lasiurus cinereus* (Palisot de Beauvois), 1796

Hoary Bat

Geographic and Ecological Distribution.—The hoary bat is the most widespread of American bats, ranging from coast to coast and from Southampton Island, Hudson Bay, southward to Argentina and Chile. Furthermore, this is the only land mammal native to Hawaii. In Colorado, the hoary bat occurs statewide, at least as migrants (Fig. 10). Highest elevational
records are above 9,000 ft., although a specimen (DMNH2) labeled "Loveland Pass" may not actually have been taken at the Pass, which is nearly 12,000 ft. high and well above timberline.

This is a tree-roosting bat, inhabiting a variety of forests and woodlands (Table 1), including deciduous forests of the plains as well as montane and subalpine coniferous and deciduous forests. The animals roost singly in trees both day and night.

Status and Abundance.—This is a widespread species of generally solitary habits and it is observed rather consistently. It does not seem to be particularly susceptible to disturbance on the Coloradan portion of its range. However, the status of the species is likely to be influenced only partly by conditions here, inasmuch as females mostly are migrating through the state, and the males only summer here. Conditions on the nursery range to the north and the unknown winter breeding and/or hibernation range to the south would seem to be critical to the welfare of the species.

Daily and Seasonal Activity Patterns.—Hoary bats emerge to feed in full darkness, usually after most other vespertilionids except for the plecotines (Table 2). Hoary bats are suspected to be strongly migratory, but their winter range is unknown (Shump and Shump, 1982b). Both males and females are known in migration in Colorado (May-June and August-September), but in summer most animals found are males, as females apparently have moved farther north to deliver and rear the young.

Reproduction.—Little is known about the reproductive habits and patterns of the hoary bat. Twins are usual. In Colorado (Adams, 1988) pregnant females were collected in June (4/11 specimens) and July (3/9). None of the females collected in August, September, and October, was pregnant (0/6, 0/2, 0/4, respectively). Scrotal males have been collected from June through October with the highest proportion observed in August (14/14).

Records of Occurrence.—Specimens examined, 187, distributed as follows: MOFFAT COUNTY: Castle Park, Dinosaur National Monument, 1; Elk Springs, 5 mi. SE Elk Springs, R98W, T5 N, 6200 ft., 7. LARIMER COUNTY: 1 mi. S, 3 mi. E Fort Collins, 2 (1 CSUTC, 1 UMMZ); no locality other than county, 6 (CDOH). WELD COUNTY: Highline Canal where crosses 18th St., 1; 1215 14th St., Greeley, 1; no locality other than county, 2 (CDOH). MORGAN COUNTY: no locality other than county, 3 (CDOH). RIO BLANCO COUNTY: W of Rangely, sec. 4, T1N, R102W, 5300 ft. 1 (BS/FC); Little Duck Creek, sec. 10, T1S R98W, 2 (BS/FC); Corral Gulch Springs, SE 1/4 sec. 30, T. 1 S, R. 98 W, 1 (RB); 3 1/2 mi. W Rio Blanco, 5 (BS/FC). GARFIELD COUNTY: Trappers Lake, 9600 ft., 1; 2 mi. E Rio Blanco, 7500 ft., 3 (BS/FC); 3 mi. N Douglas Pass, 7000 ft., 1 (BS/FC); 28 mi. N Loma, Douglas Pass, R102W, T5S, 1; 5 1/2 mi. N, 2 mi. W Rifle, 5900 ft., 3 (BS/FC); New Castle, 1 (DMNH2); Government Creek, 3.4 mi. N Rifle, 5900 ft., 3 (BS/FC); 1 mi. E Rulison, 3; 3 mi. S Silt, R92W, T65S, 1; no locality other than county, 2 (CDOH). GRAND COUNTY: no locality other than county, 1 (CDOH). BOULDER COUNTY: 7 mi. NE Boulder, 1; Valmont Road, Boulder, 1; Boulder, 3; S of Boulder, 1; no locality other than county, 6 (1 USNM, 5
Figure 10. Distribution in Colorado of the hoary bat, Lasiurus cinereus. (For explanation of symbols and conventions, see Methods.)

MONTROSE COUNTY: Jones Summit, Black Canyon of the Gunnison National Monument, 2; Black Canyon of the Gunnison National Monument, 1 (COLM); Cottonwood Trail, 12 mi. NE Nucla, R14W, T48N, 2; 4 mi. W Bedrock, La Sal Creek, R19W, T47N, 2. OURAY COUNTY: Billy Creek Refuge, 10 mi. N Ridgway, T47N R8W, 5. PUEBLO COUNTY: no locality other than county, 1 (CDOH). OTERO COUNTY: no locality other than county, 1 (CDOH). PROWERS COUNTY: no locality other than county, 1 (CDOH). MONTEZUMA COUNTY: 4 mi. SW Cahone, Cahone Canyon, R18W, T39N, 2; McElmo Canyon, 11 mi. W Cortez, R18W, T36N, 1; 1/2 mi. N North Rim, Chapin Mesa, Mesa Verde National Park, 1 (KU). LA PLATA COUNTY: Allison, 2 (MSB). ARCHULETA COUNTY: Deep Canon, 5 (MSB). LAS ANIMAS COUNTY: City Park Pond, Trinidad, 1 (UNC); 1/2 mi. S Stonewall, (Bar) NI Ranch, 2438 m, 2 (UNC); Mesa de Maya, 12 mi. SW Kim, R54W, T34S, 1; near Wooton, 7500 ft., 3 (MSB). BACA COUNTY: South Spring near Old Homestead, Holt Canyon, 1 (UNC).


Lasionycteris noctivagans (Le Conte), 1831

Silver-haired Bat

Geographic and Ecological Distribution.--The silver-haired bat ranges from coast to coast in the United States and southern Canada, and from southern Alaska to the Mexican border. The animals occur essentially statewide in Colorado, at least in migration (Fig. 11). A species of forested areas (Table 1), silver-haired bats roost in cavities and beneath loose bark of both deciduous and coniferous trees, at elevations to 10,000 ft. Also, individuals occasionally are found in buildings, woodpiles, and similar cultural situations, especially during migration.

Status and Abundance.--This is a widespread and widely dispersed species; therefore it tends to be encountered in consistent but low numbers. Other than the generalized habitat modification that accompanies human population growth and economic development, there are no known threats to this species. However, we note quickly that this statement could easily be based on ignorance rather than real insight. Silver-haired bats have often been encountered roosting behind the loose bark of old aspen trees, where they would seem to be cryptically protected by a dappled dorsal pelage the colors of shadow and frost. In Colorado's aspen
woodlands, trees with peeling bark are typical of "overmature" stands. The possibility—as yet uninvestigated—exists that the widespread practice of clear-cutting aspen (and thereby encouraging young, even-aged stands) is reducing a preferred roosting site for silver-haired bats.

*Daily and Seasonal Activity Patterns.*—Silver-haired bats usually emerge late to feed (Table 2), usually later than sympatric species other than *Lasiurus cinereus*. Feeding is probably biphasic in Colorado as has been detailed elsewhere (Kunz, 1982).

The silver-haired bat appears to be migratory, and there are no Coloradan records from the winter months. Where Coloradan animals spend the winter is unknown, as migration in
Lasionycteris noctivagans is poorly understood (Kunz, 1982).

Reproduction.--Reproductive data are scarce on this species throughout its range. Specimens of females (and sample size) available from Colorado by month are: March (1), June (1), August (4), September (11), October (8); none is labeled as pregnant. Scrotal males have been collected in Colorado in June (7/9 specimens), August (13/13), September (9/10), and October (3/8) (Adams, 1988).

Records of Occurrence.--Specimens examined, 191, distributed as follows: MOFFAT COUNTY: 6 mi. SW Greystone, Holland Draw, R101W, T7N, 1; right bank Green River, river mile 235, Pot Creek, 1 (BS/FC); Elk Springs, 5 mi. SE Elk Springs, R98W, T5N, 2. ROUTT COUNTY: Blacktail Mountain, 5 mi. E Oak Creek, T4N, R84W, 1. JACKSON COUNTY: North Park, 10,000 ft., 1 (USNM). LARIMER COUNTY: sec. 3 T. 8 N, R. 70 W, 5500 ft., 1 (CSUTC); Fort Collins, 1; Loveland, 1. WELD COUNTY: sec. 21 T4N, R62W, 1 (UNC); Quarry [not found], 1 (DMNH2); no locality other than county, 4 (CDOH). RIO BLANCO COUNTY: Ute Creek, 8000 ft., 1 (AMNH); White River Plateau, 25 mi. SE Meeker, 8500 ft., 1 (USNM); Corral Gulch Spring, SE 1/4 sec. 30, T1S, R98W, 1 (RB); 1 mi. N, 4 mi. W Rio Blanco, 6900 ft., 1 (BS/FC); 3 1/2 mi. W Rio Blanco, 1 (BS/FC); no locality other than county, 2 (CDOH). GARFIELD COUNTY: West Fork Elk Creek, 8 mi. above New Castle, 7722 ft., 1 (USNM); Douglas Pass, 28 mi. N Loma, T5S, R102W, 1; 5 1/2 mi. N, 2 mi. W Rifle, 5900 ft., 6 (BS/FC); 1 mi. E Rulison, T6S, R94W, 3. SUMMIT COUNTY: no locality other than county, 1 (CDOH). BOULDER COUNTY: Boulder, 1; Pine Street, Boulder, 1; 3250 O'Neal Circle, Boulder, 1; 1111-125th Street, Boulder, 1; no locality other than county, 20 (CDOH). JEFFERSON COUNTY: 6148 Iris Way, Arvada, 1; 2368 Ward Road, 1; no locality other than county, 7 (CDOH). ADAMS COUNTY: Barr, 1 (DMNH2); 1753 E 46th Drive, 1 (CDOH); 14505 Country Hill Drive, 1 (CDOH); 4801 E 72nd Street, 1 (CDOH); no locality other than county, 8 (CDOH). DENVER COUNTY: Denver, 3 (1 CSUTC, 1 DMNH2); 1347 S Grant, 1 (CDOH); Denver City Park, 1 (DMNH2); no locality other than county, 8 (CDOH). ARAPAHOE COUNTY: no locality other than county, 12 (CDOH). WASHINGTON COUNTY: Eastern Colorado Range Experiment Station [17 mi. N Akron], 1 (CSUTC). MESA COUNTY: Fruita Reservoir, 1/4 mi S W Entrance Gate, sec. 32, T1N, R2W, 4640 ft. (COLM); Ute Canyon, T12S, R2E, 4600 ft. (COLM); 4 mi. NE Gateway, West Creek, R103W, T15S, 1; no locality other than county, 6 (CDOH). PARK COUNTY: 2 1/2 mi. S Estabrook, 18 (MHP); GUNNISON COUNTY: Gold Basin, 6 mi. S Gunnison, T49N R1W, 1; 4 mi. W Sapinero, 7750 ft., 1 (KU). CHAFFEE COUNTY: Salida, 7050 ft., 13 (2 AMNH); Poncha Creek, 9 mi. SW Salida, 8000 ft., 3 (KU). TELLER COUNTY: Trout Creek, Manitou Experimental Forest, sec. 10, T11S, R69W, 5 (BS/FC); Green Mountain Falls, 7535 ft., 1. EL PASO COUNTY: Glen Eyrie, 1; no locality other than county, 13 (CDOH). MONTROSE COUNTY: N Rim, Black Canyon of the Gunnison National Monument, 1; Grizzly Ridge, NW 1/4 sec. 33, T50N, R7W, 7960 ft., 1; 4 mi. W Bedrock, La Sal Creek, R19W, T47N, 2; 12 mi. NE Nucla, Cottonwood Trail, 2. OURAY COUNTY: 10 mi. N Ridgway, Billy Creek Refuge, R8W, T45N, 1. PUEBLO COUNTY: no locality other than county, 7 (CDOH). HINSdale COUNTY: Fish Canyon, 11 mi. SE Powderhorn, R2W, T45N, 2. ALAMOSA COUNTY: 1 1/2 mi. W Alamosa, 1 (ASCC). OTERO COUNTY: 12
mi. S Rocky Ford, 1 (CSUTC); 4 mi. SW Timpas, 1. MONTEZUMA COUNTY: 4 mi. SW Cahone, Cahone Canyon, R18W, T39N, 1; 11 mi. W Cortez, McElmo Canyon, R18W, T36N, 2; 1 mi. NE of Ismay Trading Post, Yellowjacket Canyon, T36N, R20W, 1; 9 mi. SW Towaoc, Mountain Ute Indian Reservation, R19W, T34N, 3. LA PLATA COUNTY: Florida, 2 (AMNH); 12 mi. S Durango, Florida River, 2; Bondad, 1 (DMNH2). BACA COUNTY: Picture Canyon Spring, 1311 m, 1.


*Pipistrellus hesperus* (H. Allen), 1864

**Western Pipistrelle**

*Geographic and Ecological Distribution.*—The western pipistrelle occurs from Jalisco and Baja California, México, northward to Washington, and from California eastward to southeastern Oklahoma. Coloradan animals occur at moderate elevations of the western and southeastern parts of the state (Fig. 12). Most records are from below 7000 ft., although the extreme elevation reported is a hibernaculum at 9500 ft.

This is a bat of woodlands and shrublands in canyon country (Table 1), where it roosts both day and night beneath boulders or in cracks and crevices of rock faces. It has been suggested (Barbour and Davis, 1969) that western pipistrelles use burrows of such rodents as kangaroo rats.

*Status and Abundance.*—The western pipistrelle appears to be rather common in suitable habitat. Its generally solitary habits would seem to protect it from undue impact from local disturbance.

*Daily and Seasonal Activity Patterns.*—The western pipistrelle usually is the first bat to emerge to feed often in late afternoon, well before dusk (Table 2), although in Colorado National Monument they are commonly taken late, after 2300 h, along Ute Canyon. Fluttering along cliff faces or among píñons and desert shrubs, they can be mistaken at first glance for large moths. Activity seems to be biphasic and the second phase may continue past dawn. Western pipistrelles are not strongly migratory, generally staying year-around in the same general area. Hibernating animals have seldom been encountered, although one of us (DMA) observed them in hibernation in January in mines above Mancos, in the La Plata Mountains. For a description of one of those hibernacula, see the account of *Myotis ciliolabrum*.

*Reproduction.*—Maternity colonies of up to a dozen individuals have been reported, but pregnant, solitary females have also been found (Koford and Koford, 1948). The discovery of
Figure 12. Distribution in Colorado of the western pipistrelle, Pipistrellus hesperus (round symbols), and the eastern pipistrelle, Pipistrellus subflavus (square symbol). (For further explanation of symbols and conventions, see Methods.)

an infant bat on the floor of an abandoned house in Rio Blanco County was the first direct evidence of reproduction in Colorado (Scott et al., 1984). Adams (1990b, 1993a) reported a lactating female from Colorado National Monument in early July.

Records of Occurrence.—Specimens examined, 61, distributed as follows: MOFFAT COUNTY: right bank Yampa River, river mile 34, Haystack Rock, 1 (BS/FC); RIO BLANCO COUNTY: Douglas Creek, 18 mi. S Rangely, R101W, T2S, 2; Rio Blanco Lake, 1 (CDOW); GARFIELD COUNTY: 5 1/2 mi. N, 2 mi. W Rifle, 5900 ft., 1 (BS/FC); Rifle, 1 (USNM); 1 mi. S, 4 mi. W Rifle, 5300 ft., 1 (BS/FC); West Salt Creek, 19 mi. NW Mack, T7S, R104W,
8. MESA COUNTY: Stateline, 1 (CM); 1/2 mi. S Fruita, 1; 1 mi. SW Fruita, 1 (DMNH2); Lower Fruita Reservoir, 1; Fruita Reservoir, 1/4 mi. S W Entrance Gate, sec. 32, T11N, R2W, 4640 ft. (COLM); North Monument Canyon, Colorado National Monument, 1; Headquarters Colorado Monument, 5 (3 COLM); Colorado National Monument, 2; Grand Junction, 4 (USNM). DELTA COUNTY: Escalante Creek, 14 mi. SW Delta, T51N, R13W, 1.

MONTROSE COUNTY: 1/4 mi. N North Rim Entrance, Black Canyon of the Gunnison National Monument, 1; La Sal Creek, 4 mi. W Bedrock, R19W, T47N, 1; Bedrock, 1; Tabeguache Creek, 8 mi. NW Nucla, 1 (USNM). OTERO COUNTY: Rock Crossing, 30 mi. S La Junta, 1; no locality other than county, 1 (DMNHZ). MONTEZUMA COUNTY: Ashbaugh's Ranch [Moqui], 1 (USNM); Ruins Road, 1 mi. S Headquarters, 6900 ft., Mesa Verde National Park, 1 (KU); Loop Road, 1 1/2 mi. S Headquarters, 2 (KU); Mesa Verde National Park, 1 (DMNH2); Yellowjacket Canyon, 1 mi. NE Ismay Trading Post, R20W, T36N, 4; McElmo Canyon, 11 mi. W Cortez, R18W, T36N, 1; Four Corners, 8 (DMNHZ).

LAS ANIMAS COUNTY: junction Plum and Chacuaco creeks, 1524 m, 5 (4 UNC).


Pipistrellus subflavus (F. Cuvier), 1832

Eastern Pipistrelle

Geographic and Ecological Distribution.--The eastern pipistrelle occurs from Nova Scotia and Minnesota southward through eastern and central United States and along the Caribbean Coast of Mexico to Guatemala and Belize. A single record of an individual from Greeley documents the species in Colorado (Fig. 12). That locality is nearly 500 km from the previously known margins of its conterminous range in north-central Kansas, eastern Nebraska, and the Texas Panhandle (Hall, 1981). This is a bat of open deciduous woodland (Table 1).

Status and Abundance.--Unknown; the animal taken at Greeley may have been a disoriented wanderer.

Daily and Seasonal Activity Patterns.--P. subflavus emerges early to forage in clearings and over water (Table 2). Eastern pipistrelles appear to undertake only short migrations to the hibernaculum. This fact makes the lone Coloradan record particularly intriguing, because local migrants in eastern Nebraska or central Kansas would hardly be expected to wander the great distance to north-central Colorado.

Records of Occurrence.--Specimens examined, none.

Additional Record: Greeley (Fitzgerald et al., 1989).
**Eptesicus fuscus** (Palisot de Beauvois), 1796

**Big Brown Bat**

**Geographic and Ecological Distribution.**—The big brown bat is a widespread species, ranging from coast to coast in the United States and from northern Alberta southward to northern South America. In Colorado, these bats occur statewide in suitable habitat (Fig. 13), at elevations to about 10,000 ft.

**Eptesicus fuscus** occurs across a wide range of habitats (Table 1), and they seem to be especially common in urban settings, clearly one of our most familiar “neighborhood bats” (Tuttle, 1988). They often roost in buildings, even while occupied by humans. Virtually any other concealed roost may be used however, including caves, tunnels, mines, or tree hollows.

**Status and Abundance.**—The big brown bat is widespread and may be common locally. Its habit of roosting in buildings, even while occupied by people, predisposes it to human disturbance, including deliberate eradication.

**Daily and Seasonal Activity Patterns.**—Big brown bats emerge to feed at dusk or just after full darkness (Table 2). The peak of foraging occurs within the first hour of activity (Kurta and Baker, 1990).

Considering its general abundance and the geographic extent of the range of the big brown bat, remarkably little is known about its winter activity. The animals appear to winter in the general vicinity of the summer roost, but hibernacula have seldom been found. Armstrong (1972) reported hibernating animals from a diversion tunnel in the North Poudre drainage northwest of Livermore, and occasionally the animals are encountered in winter in attics.

**Reproduction.**—Data from Colorado indicate that females lactate in June, July, and August. Highest percentage of lactating females was in July (24/38 specimens), followed by June (11/39), and August (12/56) (Adams, 1988). None of 15 females caught in April, May, and September was lactating, but sample sizes were small for these months (2, 11, and 2, respectively). Adams (1990b, 1993a) captured pregnant and lactating females and juveniles in Colorado National Monument in mid-June and early July, and Freeman and Adams (1992) captured a lactating female at the Peacock Mine, La Plata County, in early July.

Most males with scrotal testes were collected in August (44/46 specimens). However, scrotal males also were captured in April (2/2 specimens), May (1/1), June (17/25), July (46/60), and September (1/1). Testes descend in juvenile males, but histological inspection indicates no spermatogenesis the first year (Adams, 1988). In Maryland, by contrast, all males observed reached full maturity their first summer (Christian, 1956).

**Records of Occurrence.**—Specimens examined, 527, distributed as follows: MOFFAT COUNTY: 2 mi. SE Greystone, 4 (CM); Alta Vista Ranch, 2 mi. SE Greystone, R100W, T7N.
Figure 13. Distribution in Colorado of the big brown bat, Eptesicus fuscus. (For explanation of symbols and conventions, see Methods.)

1: Douglas Spring, 1; Holland Draw, 6 mi. SW Greystone, R101W, T7N, 7; right bank Green River, river mile 235, Pot Creek, 2 (BS/FC); right bank Green River, river mile 230 1/2, Rippling Brook, 1 (BS/FC); right bank Yampa River, river mile 24, Big Joe Campground, 1 (BS/FC); Castle Park, Dinosaur National Monument, 5; N bank Yampa River, 4 mi. NW Cross Mountain, 1 (AMNH); Lily Park, 5 mi. N Elk Springs, R99W, T5N, 2; 5 mi. SE Elk Springs, R98W, T5N, 6200 ft., 7. ROUTT COUNTY: Sand Mountain, 5 mi. NW of Milner, 1; Steamboat Springs, 1 (USNM). LARIMER COUNTY: Phantom Cayon, North Fork Poudre River, 6300 ft., 1; 1 1/2 mi. S, 6 mi. W Livermore, T9N, R71W, SE 1/4 sec. 5, 6600 ft., 1 (BS/FC); Laporte, 1; 1 mi. N, 5 mi. E Fort Collins, 1 (BS/FC); Fort Collins, 5015 ft., 25 (CSUTC); 502 Gordon St., Fort Collins, 1 (BS/FC); 2911 Parker Ave., Fort Collins, 1; CSU
MONTEZUMA COUNTY: Cahone Canyon, 4 mi. SW Cahone, T39N, R18W, 1; McElmo Canyon, 11 mi. W Cortez, T36N, R18W, 1; Rock Springs, Mesa Verde National Park, 1 (KU). LA PLATA COUNTY: Florida, 1 (AMNH); Florida River, 12 mi. S Durango, T33N, R9W, 1. ARCHULETA COUNTY: Deep Canon, 1 (MSB); no locality other than county, 2 (CDOH). LAS ANIMAS COUNTY: Timpas Creek, 1524 m, 2 (UNC); junction of Plum and Chacuacho creeks, 44 (42 UNC); Burro Canyon, sec. 18, T32S, R66W, 7600 ft., 4 (BS/FC); City Park Pond, Trinidad, 1890 m, 6 (UNC); pond at S end, Trinidad Municipal Golf Course, 1920 m, 2 (UNC); no locality other than county, 1 (CDOH). BACA COUNTY: 2 mi. N, 19 mi. W Campo, 1 (KU).


_Euderma maculatum_ (J. A. Allen), 1891

**Spotted Bat**

*Geographic and Ecological Distribution.*—The spotted bat is a species of western interior North America, with records of occurrence scattered from Montana to Querétaro, México, and from southern California to New Mexico. There is a single Coloradan specimen (Fig. 14), but there are recent indications that the species occurs rather widely on the Western Slope, based in part on documentation of echolocatory calls (Navo et al., 1992; Storz, in press). The animals have been reported mostly from ponderosa pine and pinion-juniper woodlands (Table 1), where they forage over open meadows. Roosts are in cracks in cliffs.
Status and Abundance.—The spotted bat has long been considered to be rare. However, there is now some suggestion (see Navo et al., 1992) that the species was simply rarely encountered with conventional methods of monitoring bats. With the advent of electronic “bat detectors” which sometimes permit discrimination of species-specific echolocatory sounds, reports of spotted bats from western Colorado are becoming more frequent and widespread (Navo et al., 1992; Storz, in press). Of course, great care must be taken to discriminate calls of spotted bats from those of other species with low-frequency calls and similar habitat preferences (Antrozous pallidus and Idionycteris phyllotis, in particular).

Daily and Seasonal Activity Patterns.—Spotted bats emerge to feed later than any sympatric species, generally after midnight (Storz, in press). Nothing is known about winter habits of Coloradan spotted bats. Even where the biology of the species is better known, there are virtually no data on hibernation (see Schmidly, 1991, for example), although the presumption is that they are generally sedentary, as are other plecotine bats.

Reproduction.—Meager evidence suggests that spotted bats bring forth a single young in May
or mid-June (Watkins, 1977). No reproductive information is available on this species in Colorado. However, lactating females were taken by Findley and Jones (1965) on June 23, and 30 and July 1 in New Mexico. Parturition appears to take place before mid-June (Watkins, 1977).

**Records of Occurrence.**--Specimens examined, 1, as follows: MOFFAT COUNTY: Old Headquarters Area, Brown's Park National Wildlife Refuge, 1630 m, 1 (BS/FC).

Additional Records: MOFFAT COUNTY (Dinosaur National Monument--Navo et al., 1992): Vermillion Creek; Gates of Lodore; Pot Creek; Limestone Creek; Echo Park; Canyon Overlook, ca. 10 km S Echo Park.

**Plecotus townsendii** Cooper, 1837

**Townsend's Big-eared Bat**

**Geographic and Ecological Distribution.**--Townsend's big-eared bat appears to have a disjunct distribution. The bulk of the range is in western North America, from British Columbia to Oaxaca, México, but there are outlying populations in the Ozarks and the Ohio Valley. The species occurs in western, central, and southeastern Colorado (Fig. 15), at elevations to at least 9500 ft.

Biotic communities inhabited by Townsend's big-eared bat are diverse (Table 1), including coniferous forest and woodland, deciduous riparian woodland, and semidesert and montane shrublands. More important than vegetation surely is physical habitat, especially the presence of caves or mines suitable for day and night roosting and for hibernation.

**Status and Abundance.**--There has been concern about the status of Townsend's big-eared bat in Colorado because the subspecies of the West Coast (P. *t. townsendii*) has been designated by the U. S. Fish and Wildlife Service as a "Category 2" candidate species for listing under the Endangered Species Act, and *P. *t. ingens* of the southeastern United States is an endangered species (50 C.F.R. 17.11 and 17.12, August 1993). This is a cave- and mine-roosting species. On one hand, such colonies (of dozens to hundreds of individuals) are particularly susceptible to disturbance. On the other hand, species with such a contagious pattern of dispersion can be protected by rather simple means, such as placing grates on mines or caves. Hence, this species is quite appropriately a principal focus of the Bats/Inactive Mines Project of the Colorado Division of Wildlife.

**Daily and Seasonal Activity Patterns.**--*P. townsendii* generally emerges late to feed (Table 2), as late or later than *Lasius cinereus*, but not as late as *Euderma maculatum*. The animals hibernate near their summer range. They have been encountered in March in irrigation diversion tunnels in Larimer County along with *Myotis ciliolabrum* and *Eptesicus fuscus* (Armstrong, 1972). In January some 190-200 Townsend's big-eared bats were located in a working gold mine in eastern Montezuma County, in the La Plata Mountains above Mancos,
hanging in clusters of 2 to 20 individuals in the company of *M. ciliolabrum* and *Pipistrellus hesperus* (DMA, unpublished). In an inactive mine nearby were 12 *P. townsendii* and one western pipistrelle (DMA, unpublished). Also in January, seven hibernating big-eared bats (five in one cluster, two in another) were located in a coal mine in Simon Draw, NE of Cortez.

**Reproduction.**—In Colorado, very little is known about reproductive habits and patterns. All 12 females captured at the Salida Mine in Chaffee County on 19 June were pregnant or lactating, all nine adult females captured there on 29 July were lactating, as was one of eight females captured there 26 August (Freeman and Adams, 1992). Four of six females captured
at the Peacock Mine, La Plata County, in mid-June were pregnant (Freeman and Adams, 1992).

**Records of Occurrence.**--Specimens examined, 129, distributed as follows: MOFFAT COUNTY: 6 mi. SW Greystone, R101W, T7N, 1; right bank Yampa River, river mile 24, Big Joe Campground, 6 (BS/FC); Castle Park, Dinosaur National Monument, 1; 5 mi. SE Elk Springs, R98W, T5N, 6200 ft., 1. LARIMER COUNTY: Cherokee Park, 1; 5 mi. NW Livermore, 6700 ft., 1 (CSUTC); 34 mi. NW Fort Collins, 1 (CSUTC); 22 mi. NW Fort Collins, 1 (CSUTC); 20 mi. NW Fort Collins, 12 (CSUTC); 1/4 mi. N Owl Canyon Store, 1 (CSUTC); limestone cave, Owl Canyon, 2 (CSUTC); 11 mi. N Fort Collins, 1 (UNC); sec. 20, T9N, R73W, 1 (CSUTC); 9 mi. N, 5 mi. W Fort Collins, 1 (CSUTC); N of Fort Collins, Poudre Canyon, 1 (UNC); Rustic, 8000 ft., 2 (CSUTC); 26 mi. W Laporte, 7000 ft., 1 (CSUTC); 14 mi. W Laporte, 2 (CSUTC); 12 mi. W Laporte, 1 (CSUTC); Sevenmile Creek, 40 mi. W Fort Collins, 2 (CSUTC); 14 1/2 mi. W Fort Collins, 6500 ft., 1 (CSUTC); 14 mi. W Fort Collins, 1 (CSUTC); Fort Collins, 1 (CSUTC); Masonville, 2 (CSUTC). RIO BLANCO COUNTY: 16 mi. NE of Rangely, R99W, T2N, 1; 5 mi. N, 10 mi. W Rangely, 5800 ft., 1 (KU); Spring Cave near Buford, 1. GARFIELD COUNTY: 19 mi. NE Mack, West Salt Creek, R104W, T7S, 2; Fairy Cave, Iron Mountain, near Glenwood Springs, 1; Hubbard's Cave, 1/2 mi. S Shoshone Power Plant, Glenwood Canyon, 4; 3 mi. S Silt, R92W, T6S, 2; no locality other than county, 1 (CDOH). EAGLE COUNTY: Fulford Cave, NW 1/4, sec. 36, T6S R83W, 1 (BS/FC); Upper Entrance Fulford Cave, sec. 35, R83W, T6S, 1 (BS/FC). BOULDER COUNTY: 12 mi. W Lyons, 7760 ft., 1; 1 mi. S, 5 mi. W Boulder, 1; Boulder Canyon, 7000 ft., 1. CLEAR CREEK COUNTY: 2 mi. NW Idaho Springs, 1. JEFFERSON COUNTY: Golden, 21 (DMNH2); Red Rocks Park, 10 (8 DMNH2, 2 KU); no locality other than county, 1 (CDOH). MESA COUNTY: no locality other than county, 1 (CDOH). GUNNISON COUNTY: Gothic, 1 (MSB). EL PASO COUNTY: Cave of the Winds, 1 (AMNH); Colorado Springs, 4 (AMNH). FREMONT COUNTY: 10 mi. N Canon City, 1; Fly Cave, 10. PUEBLO COUNTY: Swallows, 1 (SCSC). Buelah, 1. MONTEZUMA COUNTY: 1 mi. NE Ismay Trading Post, R20W, T36N, 1; Rock Springs, 7400 ft., Mesa Verde National Park, 1 (KU); Square Tower House, 6700 ft., 1 (KU). LA PLATA COUNTY: 18 mi. S of Hesperus, McDermott Arroyo, R20W, T36N, 1; Conejos County: Manassa, 1 (GSDNM). LAS ANIMAS COUNTY: abandoned coal mine on CF and I Property, 1 mi. S Trinidad, 1920 m, 2 (UNC). BACA COUNTY: Jimmie Creek, 1 (DMNH2); 2 mi. N, 19 mi. W Campo, 1 (KU); copper mine, Skull Canyon, 1 (UNC); copper mine on Walt Dunlop Ranch, 1372 m, 1 (UNC).


Antrozous pallidus (Le Conte), 1856

Pallid Bat

Geographic and Ecological Distribution.--The pallid bat is a species of western North America, ranging from southern British Columbia to Querétaro, México, and from California eastward to Oklahoma and Kansas. Coloradan records all are from western or southeastern parts of the state (Fig. 16), generally below 6000 ft. in elevation. Pallid bats are essentially desert mammals, occupying a variety of shrub and woodland community-types (Table 1). Roosts are known to occur in crevices, shallow caves or rock shelters, and buildings.

Status and Abundance.--The pallid bat is widespread and not uncommonly encountered in suitable semidesert habitat. However, because of their low-altitude flight and seemingly rather poor ability to avoid mistnets, the animals may be captured in disproportionately large numbers, relative to some sympatric species. Day roosting and nursery colonies are rather small and well-dispersed. Hibernacula have yet to be located in Colorado.

Daily and Seasonal Activity Patterns.--Pallid bats begin to forage after full dark, feeding on or near the ground (Table 2), and then enter communal night roosts. A second foraging bout occurs before movement to the day-roost. Actual emergence time varies seasonally (reviewed by Hermanson and O'Shea, 1983).

Hibernacula have not been located in Colorado, but based on their behavior elsewhere, probably they are not strongly migratory, and they likely hibernate in Colorado in caves, mines, tunnels, or even buildings.

Reproduction.--Little is known about reproduction in this species despite much research on other aspects of natural history. In Colorado, copulation occurs in the fall, followed by sperm storage until spring when ovulation, fertilization, and implantation take place. Gestation is approximately 9 weeks. Specimen data show pregnant females to have been collected in June (5/17 specimens), July (14/16), and August (12/13). Fetuses were collected from 8/17 females in June whereas 0/16 females were pregnant in July (Adams, 1988). There are no data on male reproductive biology in Colorado.

Records of Occurrence.--Specimens examined, 69, distributed as follows: MOFFAT COUNTY: Alta Vista Ranch, 2 mi. SE Greystone, T7N, R100W, 20; Big Joe Campground, right bank Yampa River, river mile 24, 2 (BS/FC); Harding Hole, left bank Yampa River, river mile 20, 1 (BS/FC); Castle Park, Dinosaur National Monument, 2; Elk Springs, 5 mi. SE Elk Springs, T5N, R98W, 18. RIO BLANCO COUNTY: Monument Gulch, 16 mi. NE Rangely, 5; W of Rangely, sec. 4, T1N, R102W, 1 (BS/FC). GARFIELD COUNTY: 3.4 mi.
Figure 16. Distribution in Colorado of the pallid bat, Antrozous pallidus. (For explanation of symbols and conventions, see Methods.)

N Rifle on Government Creek, 3 (BS/FC); 19 mi. NW Mack, W of Salt Creek, T7S, R104W, 2. MESA COUNTY: E of Monument Canon, 4800 ft., Colorado National Monument, 2; no locality other than county, 1 (CDOH). DELTA COUNTY: no locality other than county, 1 (CDOH). OTERO COUNTY: 3 mi. NW Higbee, 4300 ft., 1 (KU). ARCHULETA COUNTY: Chimney Rock, T34N, R4W, 1 (MSB); Deep Canon, 1 (MSB). LAS ANIMAS COUNTY: Cobert Canyon, 16 mi. SW Kim, 4. BACA COUNTY: Picture Canyon Spring, 1311 m, 5 (UNC).

Additional Records: GARFIELD COUNTY: 7 mi. W Rifle (Cary, 1911). MESA COUNTY: 39°03'39"N, 108°33'07"W (Natural Heritage Inventory—MSB); Crevasse (Cary, 1911); 5 mi. E
FAMILY MOLOSSIDAE

Tadarida brasiensis (I. Geoffroy St.-Hilaire), 1824

Brazilian Free-tailed Bat

Geographic and Ecological Distribution.--A widespread species, the Brazilian free-tailed bat ranges from southern Chile and Argentina northward to southern Oregon and central Colorado. Coloradan records are scattered in and near the mountains on both sides of the Continental Divide (Fig. 17), but the only known colony is in the Sangre de Cristo Range above the San Luis Valley. This is the northernmost colony of the species, located in an abandoned mine above Villa Grove. The mine is surrounded by open montane forest. The animals exit to forage over the wetlands and agricultural fields of the San Luis Valley to the south and west.

Status and Abundance.--Capture of a very recently lactating female at Colorado National Monument suggests the presence of a maternity colony in or near the Grand Valley (Adams, 1990b). However, at the present time, the only known colony of the Brazilian free-tailed bat in Colorado is in the San Luis Valley. Composition of the colony is biased strongly toward males through most of each summer. Arrival of females and juveniles late in the season suggests that there may be a maternity colony in the vicinity (Svoboda and Choate, 1987). Maximal numbers (in round thousands) per year have been estimated by various means as follows: 1978, 50; 1979, 75; 1980, 100; 1981, 86 (Freeman and Wunder, 1988); 1982, 154; 1983 (107) (Svoboda and Choate, 1987); 1989, 132 (Adams, 1989a). In recent years there has been no consistent attempt to monitor this colony for population changes annually, although that is certainly to be encouraged.

Daily and Seasonal Activity Pattern.--Brazilian free-tailed bats begin to emerge from the Orient Mine at about 2030 h, the exit flight—in the tight, cylindrical formation typical of the species—taking about 40 minutes. The animals return to the mine in a dispersed pattern from
Figure 17. Distribution in Colorado of the Brazilian free-tailed bat, *Tadarida brasiliensis*. (For explanation of symbols and conventions, see Methods.)

all directions, mostly between 2300 and 0430 hr (Freeman and Wunder, 1988).

The colony of Brazilian free-tailed bats in the Orient Mine begins to form in mid-June and has mostly left by late September (Freeman and Wunder, 1988). Winter range is unknown, although populations which summer elsewhere in the West are known to winter in México (Svoboda et al., 1985; Wilkins, 1989).

*Reproduction.*—This species is renowned for forming very large nursery colonies. Mating probably takes place to the south of Colorado; a few young, however, have been found within
the state. None of the few adult females taken in the months of June (0/1 specimens), September (0/1), or October (0/2) were pregnant or lactating (Adams, 1988). In addition, none of the males taken in June (n = 1), September (n = 1), October (n = 2) were in reproductive condition. Lactating females were captured at the Orient Mine in 1978, and post-lactating females were taken in 1979 (Freeman and Wunder, 1988). An additional lactating female was captured in late July, 1993 (JF, unpublished). Four pregnant females were captured in 1980 and juveniles were taken in 1978, 1979, and 1981 (Freeman and Wunder, 1988) and 1982 and 1983 (Svoboda and Choate, 1987). A recently lactating female was captured at Colorado National Monument (Adams, 1990b).

**Records of Occurrence.**--Specimens examined, 79, distributed as follows: GARFIELD COUNTY: New Castle, 5. MESA COUNTY: Lower Car Tunnel, 2.2 mi. SE W Entrance Gate, sec. 32, TIS, R2W, 5000 ft. (COLM); Grand Junction, 1; no locality other than county, 4 (CDOH). DOUGLAS COUNTY: no locality other than county, 1 (CDOH). GUNNISON COUNTY: WSC Campus, 1 (WSC); Wildwood Trailer Park, 2 (WSC). SAGUACHE COUNTY: near Mineral Hot Springs, 1 (GSDNM); Orient Mine, 7 mi. E junction Hwy. #15 and Hwy. #17, 60. OTERO COUNTY: no locality other than county, 1 (CDOH). LAS ANIMAS COUNTY: City Pond Park, Trinidad, 1890 m, 1 (UNC). BACA COUNTY: Walsh, 1.


*Nyctinomops macrotis* (Gray), 1839

**Big Free-tailed Bat**

*Geographic and Ecological Distribution.*--The big free-tailed bat (sometimes included in the genus *Tadarida*, but see P. W. Freeman, 1981b) occurs from Uruguay and Argentina northward through the Greater Antilles and southern México to Colorado and Utah. On the northern fringe of its range (as in Colorado—see Fig. 18) records are scattered and few, and they probably represent wandering individuals or disoriented migrants.

Records of the big free-tailed bat in Colorado are from a variety of habitats, mostly in open country at moderate elevations (to about 7700 ft.), including grasslands, shrublands, and woodlands (Table 1).
Status and Abundance.—The big free-tailed bat seems to be of only sporadic and occasional occurrence in Colorado (as elsewhere at the northern limits of its range), and there is no evidence that there are breeding colonies in the state. Milner et al. (1990) reviewed the literature on the species.

Daily and Seasonal Activity Patterns.—In Texas, big free-tailed bats initiate foraging late in the evening (Schmidly, 1991). Probably the big free-tailed bat is only an occasional resident of Colorado and wintering in the state seems unlikely. Neither the origin nor the winter range of animals captured in Colorado is known.
Reproduction.--Colorado probably is not within the breeding range of N. macrotis.

Records of Occurrence.--Specimens examined, 3, distributed as follows: LINCOLN COUNTY: no locality other than county, 1 (CDOH). GUNNISON COUNTY: Western State College Campus, 1 (WSC). EL PASO COUNTY: Cheyenne Canon, Colorado Springs, 1 (DMNH2).


SPECIES OF POSSIBLE OCCURRENCE

Armstrong (1972) considered three species of bats to be “of probable occurrence” in Colorado, based on their known geographic and ecological distribution in adjacent states. Of those, Euderma maculatum has been documented, and apparently is fairly widespread on the Western Slope at moderate elevations, although actual specimens or captures still are few. The occurrence of two additional species—Myotis velifer and Idionycteris phyllotis—remains a possibility.

Myotis velifer (J. A. Allen), 1890—Cave Myotis.—Armstrong (1972) noted that the cave myotis was of probable occurrence in Colorado. However, the intervening years have made that seem to us somewhat less likely. In particular, Ellinwood (1978) did a thorough reconnaissance survey of bats of southeastern Colorado under the guidance of J. P. Fitzgerald and the sponsorship of CDOW. That survey did not reveal the presence of the cave myotis, although confirmation of the occurrence of Myotis velifer in Colorado was a goal of the study. The record of the cave myotis nearest Colorado is from a place 8 mi. SE Kenton, Cimarron Co., Oklahoma (Caire et al., 1990), which is only about 16 km from the Colorado boundary. The locality is on the Black Mesa, which continues into Colorado (where it is generally continuous with the Mesa de Maya). Records in other states nearest Colorado [approximate distance (in kilometers) from Colorado in brackets] are: Meade County, Kansas [240] (Jones et al., 1967), Lincoln County, New Mexico [420] (Findley et al., 1975), Potter County, Texas [180] (Schmidly, 1991), and Yavapai County, Arizona [350] (Hall, 1981). Fitch et al. (1981) reviewed the literature on the cave myotis.

Idionycteris phyllotis (G. M. Allen), 1916—Allen’s Big-eared Bat.—We suspect that Allen’s Big-eared Bat occurs in the canyon country of lower elevations of southwestern Colorado. Documented localities of occurrence nearest Colorado are from San Juan County, Utah, specifically a place 5 mi. N Blanding (Black, 1970) and in the Needles District of Canyonlands National Park (Armstrong, 1974, 1982). Czaplewski (1983) reviewed the rather meager literature on this poorly known species.
ECOLOGY AND ZOOGEOGRAPHY OF COLORADAN BATS

Ecology and biogeography are closely related fields of study; both seek to understand the distribution and abundance of organisms, and in some definitions the principal distinction between them is one of scale. Ecology describes and attempts to comprehend local patterns of distribution in space and time, and biogeography studies patterns of regional, continental, or global scale and longer term. The emerging field of landscape ecology is bridging any remaining gap between the fields by studying patterns and process at intermediate scales and explicitly (and importantly) including humans and their cultures as components of ecosystems, participants influential on a geological scale.

Ecology of Coloradan Bats

Ecology is the study of populations of organisms and their relationships to each other and to their physical environment. As such it studies the dynamics of species populations, communities, and ecosystems. Ecology includes much of what once was called natural history, and autecological data on habitats, food habits, activity patterns, and reproduction are presented in accounts of individual species. The purposes of this section are to summarize briefly and to seek generalities about ecology of Coloradan bats.

Colorado's 18 species of bats are a diverse lot. What can be said about them in general? Bats in the temperate zone mostly face a common set of fundamental challenges. They are small in size which by itself means that they have a large surface area:volume ratio with a consequent propensity for heat loss. The extent of the wing and tail membranes add to that problem. Further, powered flight of a heavier-than-air craft is an energy-demanding process. Gram-for-gram, bats need lots of energy resources.

However, bats in the temperate zone face seasonal (and even daily) absence of food resources. Three responses to that absence have evolved: daily torpor, hibernation, and migration (and combinations of the responses—migration to hibernate, for example). These adaptations are physiologically demanding, of course, and this exacerbates the problems outlined above. Temperate zone bats in general are organisms operating near their limits of tolerance; they are "pushing the envelope," to borrow an image from the aerospace field.

It is easy to imagine that "bats are bats." Quite the contrary, despite obvious similarities in structure and function (reflecting phylogeny and the constraints of flight), the evolutionary "solutions" to the challenges outlined above differ from one species to the next. Bats are no more "all alike" than are rodents (from pocket mice and porcupines to beavers) "all the same." Bats are ecologically diverse. Coloradan bats differ in daily and seasonal activity, day- and night-roosting habits, foraging strategies (time, height, habitat, technique), and usual prey. Some are sedentary, some make local movements, and others are strongly migratory. Some are tied to a very narrow range of habitats, whereas others are broadly tolerant. We summarize some of the natural history variables in tables 1 and 2.
Table 1 is a compilation of data on habitats of Coloradan bats, both general habitat use and specific day- and night-roosting sites. No particular pattern emerges from those data, except to say that Colorado's bat fauna requires a diversity of habitats. The conservation message is that one cannot deal with bats as a group, but only with bats as local species populations and as occupants of--and integral components of--particular habitats.

Table 2 summarizes aspects of foraging ecology of Coloradan bats. Again, it is difficult to abstract a generalization from this table, except to note the diversity of food habits and foraging strategies. We return to this table beyond, however, in a brief consideration of community and guild structure.

Both tables 1 and 2 present qualitative data on the niches (habitat, food) of the species in question. One of the important products of studies of species' niche dimensions is to suggest where competition and natural selection may have helped to shape species' adaptations, hence allowing coexistence.

Competition is a contest between individuals (or populations) for resources that are in limiting supply. Competition has been a fundamental concept in ecological thinking since the time of Darwin and often has been thought to be an effective force structuring communities of organisms. The only study to address this fundamental aspect of biology for Coloradan bats was conducted in northwestern Colorado and detailed in a doctoral dissertation (Freeman, 1984). The general objective of the study was to characterize some niche dimensions of co-existing species (the local assemblage) and to test whether those niche dimensions reflect present or past competitive interactions. Specifically, multivariate analyses of morphological and ecological data were used to define niches of an assemblage of 11 coexisting species of bats from a site near Elk Springs, Moffat County. These analyses are summarized in Figure 19, a composite projection of 11 species into a 3-dimensional ecospace based upon the first principal components from separate analyses of (A) morphology, (B) foraging area, and (C) food habits.

Principal components analysis of 22 characters was used to define morphological niches. Three components explained 84 percent of the variance and suggested the following broad niche dimensions: (I) size, (II) foraging style and method of food capture, and (III) food hardness.

The structure of the assemblage reflected phylogenetic relationships; congeneric species were closely clustered and non-congeners were situated on the edge of assemblage morphospace, a result consistent with those of similar analyses on other assemblages of bats (Findley and Wilson, 1982; Findley and Black, 1984; Findley, 1993). Did this pattern reflect competition?
Table 1. Comparative summary of habitat characteristics of Coloradan bats.

<table>
<thead>
<tr>
<th>Species</th>
<th>General Habitat</th>
<th>Roost Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Day</td>
</tr>
<tr>
<td>Myotis californicus</td>
<td>semidesert woodlands, shrublands</td>
<td>crevices, mines, caves, tree</td>
</tr>
<tr>
<td></td>
<td></td>
<td>hollows</td>
</tr>
<tr>
<td>Myotis ciliolabrum</td>
<td>woodland, shrublands</td>
<td>buildings, mines,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>crevices, under rocks</td>
</tr>
<tr>
<td>Myotis evotis</td>
<td>coniferous woodland</td>
<td>under bark, in mines, buildings</td>
</tr>
<tr>
<td>Myotis lucifugus</td>
<td>riparian deciduous woodland: urban areas</td>
<td>attics, mines, buildings</td>
</tr>
<tr>
<td>Myotis thysanodes</td>
<td>coniferous woodland</td>
<td>crevices, trees, caves</td>
</tr>
<tr>
<td>Myotis volans</td>
<td>deciduous, coniferous woodland</td>
<td>rock fissures; under bark, in</td>
</tr>
<tr>
<td></td>
<td></td>
<td>buildings</td>
</tr>
<tr>
<td>Myotis yumanensis</td>
<td>coniferous woodland, semidesert shrub, riparian</td>
<td>crevices, mines, caves, buildings</td>
</tr>
<tr>
<td></td>
<td>woodland</td>
<td></td>
</tr>
<tr>
<td>Lasius borealis</td>
<td>riparian deciduous forest</td>
<td>deciduous trees</td>
</tr>
<tr>
<td>Lasius cinereus</td>
<td>coniferous, deciduous woodland, forest</td>
<td>trees</td>
</tr>
<tr>
<td>Lasionycteris noctivagans</td>
<td>coniferous, deciduous forest</td>
<td>trees, behind bark, open caves</td>
</tr>
</tbody>
</table>
Table 1, continued. *Comparative summary of habitat characteristics of Coloradan bats.*

<table>
<thead>
<tr>
<th>Species</th>
<th>General Habitat</th>
<th>Day</th>
<th>Night</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pipistrellus hesperus</em></td>
<td>woodland, semidesert shrublands</td>
<td>crevices, caves, mines, other mammals' burrows, buildings</td>
<td>crevices, caves, mines, buildings</td>
</tr>
<tr>
<td><em>Pipistrellus subflavus</em></td>
<td>deciduous woodland</td>
<td>trees, buildings</td>
<td>mines, crevices, caves</td>
</tr>
<tr>
<td><em>Eptesicus fuscus</em></td>
<td>riparian deciduous woodland, urban areas</td>
<td>buildings, caves, crevices</td>
<td>buildings, mines, caves, tree hollows</td>
</tr>
<tr>
<td><em>Euderma maculatum</em></td>
<td>coniferous woodland, canyons</td>
<td>cliffs</td>
<td>unknown</td>
</tr>
<tr>
<td><em>Plecatus townsendi</em></td>
<td>woodland, shrubland</td>
<td>mines, caves, structures</td>
<td>mines, caves, structures</td>
</tr>
<tr>
<td><em>Antrozous pallidus</em></td>
<td>semidesert shrubland, woodland</td>
<td>caves, mines, structures, crevices</td>
<td>crevices, ledges, buildings</td>
</tr>
<tr>
<td><em>Tadarida brasiliensis</em></td>
<td>semidesert shrubland</td>
<td>caves, mines</td>
<td>none</td>
</tr>
<tr>
<td><em>Nyctimomops macrotis</em></td>
<td>semidesert shrubland</td>
<td>crevices in cliffs, buildings</td>
<td>unknown</td>
</tr>
</tbody>
</table>
Table 2. Comparative summary of foraging characteristics of Coloradan bats.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Foraging</th>
<th>Food</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myotis californicus</em></td>
<td>over shrubs, woodland, cliff faces, stock tanks, arroyos</td>
<td>slow, maneuverable pursuit</td>
<td>moths, flies, spiders</td>
</tr>
<tr>
<td><em>Myotis ciliolabrum</em></td>
<td>among boulders, shrubs</td>
<td>maneuverable pursuit</td>
<td>flies, small beetles, winged ants</td>
</tr>
<tr>
<td><em>Myotis evotis</em></td>
<td>over water near trees, forest gaps</td>
<td>gleaner</td>
<td>beetles, moths, flies</td>
</tr>
<tr>
<td><em>Myotis lucifugus</em></td>
<td>over water, clearings</td>
<td>erratic pursuit, repeated circuit</td>
<td>moths, aquatic insects</td>
</tr>
<tr>
<td><em>Myotis thysanodes</em></td>
<td>over shrubs, woodland</td>
<td>gleaner, slow, maneuverable</td>
<td>moths, beetles, phalangerids, ants, caddisflies, wasps</td>
</tr>
<tr>
<td><em>Myotis volans</em></td>
<td>over ponds, streams, forest edges, gaps</td>
<td>relaxed pursuit on repeated circuit</td>
<td>dusk to 1-2 hr after sunset, dusk</td>
</tr>
<tr>
<td><em>Myotis yumanensis</em></td>
<td>along streams</td>
<td>direct pursuit</td>
<td>duss</td>
</tr>
<tr>
<td><em>Lasiurus borealis</em></td>
<td>over and among trees, clearings</td>
<td>strong, straight</td>
<td>moths, flies, beetles, aquatic</td>
</tr>
</tbody>
</table>

Notes:
- Habitat: Where the bat forages.
- Style: How the bat forages.
- Height: Average height of foraging in meters.
- Time: The time of day the bat is most active for foraging.
- Food: Types of insects that the bat forages for.
Table 2. continued. Comparative summary of foraging characteristics of Coloradan bats.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Style</th>
<th>Height</th>
<th>Time</th>
<th>Food</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lasius cinereus</td>
<td>forest openings, edge</td>
<td>fast, straight</td>
<td></td>
<td>full dark</td>
<td>moths, small bats</td>
</tr>
<tr>
<td>Lasionycteris noctivagans</td>
<td>over clearings, ponds in forests</td>
<td>repeated circuit</td>
<td>1-6 m</td>
<td>late (full dark)</td>
<td>moths, flies, beetles</td>
</tr>
<tr>
<td>Pipistrellus hesperus</td>
<td>canyon rims, woodland</td>
<td>slow, flutery, maneuverable pursuit</td>
<td>2-15 m</td>
<td>early (still light), dawn</td>
<td>aquatic insects, moths, beetles, flies, ants</td>
</tr>
<tr>
<td>Pipistrellus subflavus</td>
<td>open woodlands, over water</td>
<td>maneuverable pursuit</td>
<td>2-10 m</td>
<td>early</td>
<td>moths, beetles, flies</td>
</tr>
<tr>
<td>Eptesicus fuscus</td>
<td>open areas</td>
<td>strong, straight &quot;figure-8&quot;</td>
<td>6-10 m</td>
<td>dusk</td>
<td>larger insects, especially beetles</td>
</tr>
<tr>
<td>Euderma maculatum</td>
<td>open meadows in canyons</td>
<td>maneuverable pursuit</td>
<td>5-20 m</td>
<td>late</td>
<td>moths</td>
</tr>
<tr>
<td>Plecotus townsendii</td>
<td>near shrubs, over water, forest gaps</td>
<td>gleaner</td>
<td>1-5 m</td>
<td>late</td>
<td>moths, flies, beetles, aquatic insects</td>
</tr>
<tr>
<td>Antrozous pallidus</td>
<td>on or near ground in open shrublands</td>
<td>individual pursuit</td>
<td>0-3 m</td>
<td>full dark near or on ground</td>
<td>beetles, crickets, scorpions, small bats, mice</td>
</tr>
<tr>
<td>Tadarida brasiliensis</td>
<td>over fields, shrublands</td>
<td>strong, fast</td>
<td>6-25 m</td>
<td>dusk</td>
<td>moths</td>
</tr>
<tr>
<td>Nyctinomops macrotis</td>
<td>shrublands, cliffs, in canyons</td>
<td>strong, fast</td>
<td></td>
<td>full dark</td>
<td>moths</td>
</tr>
</tbody>
</table>
The niche-variation model (Van Valen, 1967) holds that species on the edge of assemblage morphospace should be more variable morphologically than those in the center due to competitive release. To test this idea, Euclidean distances were computed between individuals of each species and between all pairs of species based on each individual's or species' factor score on each of the three principal components (niches). No significant correlation was found between mean intraspecific Euclidean distance of a species and the mean distance of that species from all other species in the assemblage. In other words, species in the center of assemblage morphospace were as variable as species on the edge.

Null models were also used to test for the possibility of competition in the assemblage. Matrices of Euclidean distance based on species' factor scores were compared to a matrix of "random" assemblages of 11 and of seven species described by factor scores selected at
random. No significant differences were found between Euclidean distances for either the 11 species of the entire assemblage or for the set of seven species clustered closely at the center of morphospace when compared to "random" assemblages of species, suggesting a lack of structure in the assemblage.

Three ecological attributes of the species of the assemblage were determined: diet, foraging area, and activity period. Activity periods did not distinguish species. Foraging areas of species (Table 3) tended to be quite plastic; all species used several foraging categories. Foraging behavior in the assemblage (as judged from field observation of flight patterns) seemed to be quite opportunistic although each species had a characteristic mode.

Table 3. **Percentage use of five foraging habitats by 11 species of bats in the vicinity of Elk Springs, Moffat County (Freeman, 1984).**

<table>
<thead>
<tr>
<th>Species (sample size)</th>
<th>Over water</th>
<th>Forest</th>
<th>Rock/Cliff</th>
<th>Arroyo</th>
<th>Open Areas</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myotis ciliolabrum</em> (18)</td>
<td>22.2</td>
<td>44.5</td>
<td>16.7</td>
<td>16.7</td>
<td></td>
</tr>
<tr>
<td><em>Myotis californicus</em> (14)</td>
<td>14.3</td>
<td>28.6</td>
<td>28.6</td>
<td>28.6</td>
<td></td>
</tr>
<tr>
<td><em>Myotis volans</em> (19)</td>
<td>15.8</td>
<td>26.3</td>
<td>5.3</td>
<td>51.6</td>
<td></td>
</tr>
<tr>
<td><em>Myotis lucifugus</em> (3)</td>
<td>33.3</td>
<td></td>
<td>33.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myotis evotis</em> (74)</td>
<td>51.3</td>
<td>6.7</td>
<td>10.8</td>
<td>31.1</td>
<td></td>
</tr>
<tr>
<td><em>Myotis thysanodes</em> (3)</td>
<td>33.3</td>
<td></td>
<td>33.3</td>
<td>33.3</td>
<td></td>
</tr>
<tr>
<td><em>Lasionycteris noctivagans</em> (6)</td>
<td>16.7</td>
<td></td>
<td>16.7</td>
<td>67.7</td>
<td></td>
</tr>
<tr>
<td><em>Plecotus townsendii</em> (5)</td>
<td>60.0</td>
<td></td>
<td>20.0</td>
<td>20.0</td>
<td></td>
</tr>
<tr>
<td><em>Lasiurus cinereus</em> (9)</td>
<td>22.2</td>
<td>11.1</td>
<td></td>
<td>77.8</td>
<td></td>
</tr>
<tr>
<td><em>Eptesicus fuscus</em> (8)</td>
<td>33.3</td>
<td></td>
<td>66.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antrozous pallidus</em> (19)</td>
<td></td>
<td></td>
<td></td>
<td>100.0</td>
<td></td>
</tr>
</tbody>
</table>

To obtain a niche dimension for foraging, principal component analysis was performed on the foraging data. The first principal component explained 72 percent of the variance. Position of each species on this component is shown in Figure 19 (axis B). Observations of this niche dimension and knowledge of foraging patterns indicated a gradient of habitat complexity for each species. Complex habitats demanding greater maneuverability were used by species located statistically on the far end of the component, whereas species in more open areas are placed on the near end of the component.

Diet was determined by stomach content analysis (Table 4), which revealed highly variable diets; only *L. cinereus* and *A. pallidus* seemed to be somewhat specialized. *L. cinereus* is known to have a strong predilection for moths and *A. pallidus* was probably using its most available food resource—ground-dwelling beetles and orthopterans. Generally bats seemed to
Table 4. Percentage frequency in stomach analysis of various orders of insects by each of 11 species of bats near Elk Springs, Moffat County (Freeman, 1984). (Abbreviations of species are generic initial and first three letters of specific epithet.)

<table>
<thead>
<tr>
<th>Insect Order</th>
<th>Species of Bat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mcil</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>15.1</td>
</tr>
<tr>
<td>Diptera</td>
<td>7.5</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>34.0</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>5.7</td>
</tr>
<tr>
<td>Homoptera</td>
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<td>Orthoptera</td>
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<td>Other</td>
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take insects relative to their availability. Variability and unpredictability of insect taxa in terms of number, diversity, and biomass may lead bats to maintain generalized food habits.

Principal components analysis of the food data provided food niche dimensions, the first component of which (axis C, Fig. 19) explained 65 percent of the total variance. This component had significant positive factor-loading for Lepidoptera and Trichoptera and significant negative loading for Coleoptera and Orthoptera. These pairs of insect orders contrast significantly in body hardness. Species of bats tending toward soft diets were plotted at one end of the component, whereas species tending toward hard diets were placed on the other end.

Figure 19 suggests that morphology predicts ecological relationships. Freeman (1984) tested a series of hypotheses; results indicated that morphological resemblance among species was correlated with dietary resemblance and foraging resemblance among species.

To examine competitive interactions based on ecological data, randomized food resource matrices were generated. Distributions of Euclidean distances from the random matrices were compared to the distribution of Euclidean distances from the assemblage's food data matrix.
No significant differences were found to indicate competition for food in the assemblage, which lives in an environment with variable and unpredictable food resources.

Likewise the niche variation model failed to indicate competition for food because no significant correlation was found between each species' nearest neighbor distance in food space and its dietary diversity. Species that were similar in food usage did not show lower dietary diversity.

Although insect number, biodiversity, and biomass appeared to be variable and unpredictable, an average hardness index of insects (P. Freeman, 1981a; Freeman, 1984) was relatively constant across all habitats during 16 sampling periods. This may explain the importance of food hardness as a niche dimension. Perhaps bats are cuing on this dependable quality of their food in order to exploit the prey base efficiently. Effective exploitation of prey may be critical to bats in the study area, which are living in a cool and unpredictable environment (Freeman, 1984) in which energetic costs are high.

Bats have low reproductive potential. They probably are kept below their carrying capacity by unpredictable environments and therefore are not in equilibrium with their food resources. Competitive interactions do not seem to structure local bat assemblages (for a review, see Findley, 1993). Habitat complexity and the availability of appropriate roost sites may be the limiting factors influencing species' distributions (Humphrey, 1975; Adams, 1990).

The general conclusion of Freeman's study was that competition could not be demonstrated under present circumstances. However, there were differences in patterns of habitat utilization and foraging behavior, which may have reflected "ghosts of competition past," or adjustments to competition elsewhere. Species were, in fact, distinct from each other and they were, in effect, "avoiding" interaction to a significant extent by distinctive ecology and behavior.

Freeman's work underscored the importance of looking carefully at the structural relationships of niches of a local assemblage of bats before assuming that the local fauna comprises a "community," in any formal ecological sense (which implies a history of competitive or other symbiotic interaction with mutual adjustments of niche dimensions). Indeed, to examine situations where there is likely to be on-going competition, one ought to look beyond the concept of "biotic community" to the ecological "guild." Historically, a guild was an organized group of artisans involved in a particular trade. In ecology, the term guild (as defined by Root (1967) and reviewed by Simberloff and Dayan (1991) carries an analogous connotation. A guild is a group of species exploiting a similar range of resources in similar ways. It is within a guild that one might expect on-going competition to occur or past competition to be reflected. Studies of guilds of Coloradan bats have not been undertaken, nor have the even more important studies been done of guilds that transcend taxonomy. One could define the guild of nocturnal, aerial insectivores in deciduous riparian woodland. The guild would include not only red bats, and big and little brown bats, but also common nighthawks (Caprimulgiformes: *Chordeiles minor*). Is that guild structured, and if so, in what pattern and by what processes? Pallid bats forage at or near ground-level and may be as likely

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to compete with grasshopper mice (*Onychomys*) as with other bats or birds, but is their common resource in limiting supply? Western pipistrelles and California myotis emerge at dusk to feed along canyon walls and over rivers flowing through arid country, overlapping in time with other aerial insectivores like swallows and swifts. Do limited resources structure that guild? Like most of the intriguing questions that could be answered by studying Colorado's fauna closely, the questions have not been asked.

No "assembly rules" (Diamond, 1975) or "management guilds" (Severinghaus, 1981) have been proposed for assemblages of bats. Of course, our ignorance of details of the community ecology of bats does not mean that conservation and management decisions are impossible; for the time-being, decisions can be made on the basis of our growing knowledge of autecology.

**Zoogeography of Coloradan Bats**

Biogeography is the study of patterns in the distribution of species; zoogeography is the branch of biogeography that deals with the distribution of animals. The fundamental observations of biogeography are that some species are widespread and others have very local distributions, but all species reach geographic limits. No species has the range of genetic information to provide it the capability to survive everywhere under all conditions. Biogeography describes patterns in the limits of species and seeks to understand the underlying ecological and/or historical bases for those patterns. One might suppose that bats, with their capacity for flight, would be wide-ranging species, perhaps without any particular pattern. That is not the case, however. Indeed, bats exhibit rather strong patterns of distribution, which are especially marked in an area of high topographic and ecological relief, as is Colorado.

Armstrong (1972) identified three broad approaches to zoogeographic analysis—ecological, ecogeographic, and areographic—and analyzed distribution of Coloradan mammals (as then known) by each approach. To some extent patterns of distribution of Coloradan bats are a microcosm of the overall distribution of mammals, but bats do show enough zoogeographic peculiarities to warrant brief analysis of their own.

*Ecological biogeography* analyzes patterns of distribution in terms of biotic communities, ecosystem-types, stand-types, life-zones, or some other system of discrete subdivisions of the landscape. Often these units are defined by ecological relationships and species composition and they are described by the vegetation of the site. This is practical because the plant species composition of a community changes less rapidly than does that of animals, and further, plants are more readily visible than are many animals or microbes.

Table 5 indicates distribution of Coloradan bats in terms of the 14 ecological community-types identified by Armstrong (1972). This is a coarse-grained, broad-scale analysis. In fact, on a fine scale we suspect that most temperate zone bats—as insectivores—**are**
Table 5  Ecological distribution of Colorado bats in 14 community-types (after Armstrong, 1972). LEGEND: 1 = Subhumid Grassland; 2 = Plains Wetlands; 3 = Deciduous Riparian Woodland; 4 = Saxicoline Brush; 5 = Sagebrush; 6 = Semidesert Shrub; 7 = Piñon-Juniper Woodland; 8 = Ponderosa Pine Woodland; 9 = Montane Forest; 10 = Mountain Meadow; 11 = Subalpine forest; 12 = Highland Streambank; 13 = Aspen Woodland; 14 = Alpine tundra, fellfield.

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<td>Myotis lucifugus</td>
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<td>Lasionycteris noctivagans</td>
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<td>Nyctinomops macrotis</td>
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**TOTALS**

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Adams (1990a) emphasized ecological distribution in an account of biogeography of Coloradan bats. He concluded that piñon-juniper woodlands supported more species of bats than other Coloradan habitats. That is reflected in Table 5. Further, Adams noted that some quite widespread community-types (e.g., plains grassland) in Colorado had very few species of bats, whereas some community-types of more restricted extent (e.g., piñon-juniper woodland, sagebrush) supported more species of bats. Obviously those patterns have implications for conservation.

Despite these caveats, the distribution of Coloradan bats does reflect broadscale patterns in the living landscape. Of major biotic community-types, only alpine tundra is typically without bats (although some bats do forage and roost high in subalpine forest, near timberline). Beyond that, no habitat-type in Colorado is without bats, at least occasionally, although open grasslands have few species, and piñon-juniper woodlands have many.

Adams (1990b, 1993a) identified Colorado National Monument, west of Grand Junction, as a particularly rich area. This is due to the mosaic of foraging habitats present in a restricted area, a plethora of roosting habitat in the landscape, and also probably to direct access to the "bat-rich" environments downstream in the Colorado drainage, in the canyon country of southeastern Utah (Armstrong, 1982).

The pattern of species richness is an important feature of biogeography. To this end, the Colorado Division of Wildlife has compiled distribution of vertebrates in the state in a series of "latilong" studies, in which occurrence of species is plotted in geographic blocks 1 degree of latitude by 1 degree of longitude (areas of roughly 3500 square miles = 9100 square kilometers). The latilong notion takes good advantage of the fact that Colorado is essentially a rectangle, seven degrees wide by four degrees high and has purely political boundaries. The
most recent such study for mammals in the state's 28 latilong blocks was edited by Meaney (1990).

Of course, a latilong study *per se* ignores ecological distribution; the strictly geometric latilong blocks bear no necessary relationship to ecological pattern. However, the various latilong studies produced by CDOW have also included information on ecological distribution of species across the state.

Table 6 indicates numbers of species of bats within each latilong block. Tabulation was deliberately conservative. A grid of latilong blocks was superimposed over the "dot maps" of species occurrence presented in this paper. If a dot occurred in a block the species was tallied in that block (if the supposed and therefore shaded range of a species was included a block but there was no actual record, it was not tallied in that block). A dot falling on a latilong boundary and not clearly attributable to one block or the other was tallied in both blocks.

Table 6. *Numbers of species of bats reported per latilong block.* (For definition, see text; after Meaney, 1990).

<table>
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<tr>
<th>Boundary Degrees N Latitude</th>
<th>Boundary Degrees W Longitude</th>
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<td>41-40</td>
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<td>40-39</td>
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<td>39-38</td>
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<td>38-37</td>
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The pattern that emerges here probably is real—within the crude limits of the analysis—and it is important in two respects. On one hand, as a matter of pure science, it reflects the ecological and historical distribution of species of bats, as we shall see. On the other, as a matter of management concern, it suggests in broad terms where bats live and therefore where protection is essential.

Blocks with the fewest species doubtless represent areas where further survey is needed. Probably every latilong block—even those on the eastern plains—provides habitat for four or
five species of bats, at least in migration and at least occasionally. Blocks with highest numbers of reported species tend to include localities that have been well sampled and they also tend to encompass considerable ecological heterogeneity, providing habitat for a variety of specialized bats as well as for broadly tolerant species.

Ecogeographic analysis lies at the interface of ecology and geography, and attempts to recognize and describe distinctive regional landscapes. Dice (1943) recognized ecogeographic biotic provinces of North America, and Udvardy (1975) mapped analogous units on a global scale. Based on both semi-quantitative and graphical analyses of distributional limits of Coloradan mammals, Armstrong (1972) abstracted a hierarchical arrangement of broad faunal areas and subordinate faunal districts. Because few bats occur statewide, the Chiroptera contributed to the ecogeographic pattern that Armstrong (1972) described. Table 7 includes a rough tabulation of bat species richness in each mammalian faunal district.

Five species (*Myotis ciliolabrum*, *M. lucifugus*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, and *Eptesicus fuscus*) range essentially statewide in suitable habitat. (The few available records of *Nyctinomops macrotis* also are scattered widely, but apparently represent wandering individuals). All other species reach obvious limits in the state. Highest species richness is in the lower elevational faunal districts of the Western Slope—corresponding to the Yampa-White, Grand (Colorado, Lower Gunnison), and Dolores-San Juan valleys. Each of these streams has carved major or minor canyons as it exits the Southern Rockies and enters the Wyoming Basin or Colorado Plateau, and these dissected landscapes provide abundant habitat for bats.

Another point of interest in this table is the strong similarity in bat faunas between the lower elevation districts on the Western Slope, the Raton Section, and the San Luis Valley. This similarity is largely due to the common presence of species of Mexican affinities, as revealed by areographic analysis.

Areography considers the shape and size of species' geographic ranges. Armstrong (1972) analyzed shapes of continental ranges of Colorado mammals and attributed species to nine distinctive faunal elements, with a tenth category of species too widespread to identify with any particular areographic element. Table 7 expands on that earlier analysis, to incorporate species then unknown in Colorado or too poorly known to include. Interestingly, four of the areographic faunal elements identified by Armstrong (1972) contribute no bats to the Coloradan fauna. The Cordilleran and Boreo-Cordilleran elements include species of northern and western affinities, and the absence of bats in these elements of the fauna is not surprising, as bats are essentially a tropical and subtropical group, dependent for success in the temperate zone on seasonal resources and hibernation. The Campestrian element has no bats, and again that is not surprising; the essentially 2-dimensional environment of the Great Plains provides little suitable roosting habitat for bats, except for places where the predominant vegetation is interrupted by riparian corridors. The Yuman faunal element is poorly represented in Colorado. This is, roughly speaking, a fauna which centered in the Sonoran Desert. There are bats in this element (Armstrong, 1977, in press), but those species simply have not reached.
Table 7. Distribution of bats in Colorado in nine ecogeographic faunal districts and association of species with five areographic faunal elements (for definitions, see text) Abbreviations—ECOGEOGRAPHIC FAUNAL DISTRICTS: N = Northern Great Plains; SP = South Platte Valley; A = Arkansas Valley; R = Raton; RM = Rocky Mountains; SL = San Luis Valley; W = Wyoming Basin; GV = Grand Valley; DS = Dolores-San Juan. AREOGRAPHIC FAUNAL ELEMENTS: W = Widespread; E = Eastern; G = Great Basin; Ch = Chihuahuan; N = Neotropical.

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<tr>
<th>Species</th>
<th>Faunal District</th>
<th>Faunal Element</th>
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<td>N</td>
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<td>Myotis californicus</td>
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<td>Myotis ciliolabrum</td>
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<td>Lasius cinereus</td>
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<td>Lasionycteris noctivagans</td>
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<td>Eptesicus fuscus</td>
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<td>Nyctinomops macrotis</td>
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TOTAL SPECIES  4  8  7  12  10  10  14  15  14  5  2  2  8  1
Colorado, having met their limits in western interior United States in southwestern Utah (Armstrong, 1977) or even farther to the south and west (Armstrong, in press).

Table 7 indicates that eight of 18 Coloradan bats (44 percent) represent a Chihuahuan faunal element, species that share a geographic range in northern interior Mexico. (Parenthetically, we note that both species of possible occurrence but as yet undocumented in Colorado—Allen's big-eared bat and the cave myotis—also are Chihuahuan species; hence fully half of Colorado's potential bat fauna has strong affinities with northern México.) Chihuahuan species overall (and Chihuahuan species of bats in particular) are especially characteristic of the Raton, San Luis Valley, Dolores-San Juan, Grand Valley, and Wyoming Basin faunal districts (Table 7 and Armstrong, 1972). The importance of Chihuahuan species in roughland and semidesert environments in Colorado is even greater than the crude analyses of this paper would suggest. A narrow band of foothills habitats (a band too narrow to be reflected in a statewide vegetation map and completely obscured at the level of a latilong study) extends northward from the Raton Section along the Front Range and the Laramie Mountains. Local populations of such Chihuahuan species of the fringed and long-eared myotis occur in these habitats and enrich the fauna of the foothills, making them distinct from the mountains to the west and the plains to the east (Armstrong, 1992).

COLORADAN BATS IN RELATION TO PUBLIC HEALTH

Most people consider bats to be important carriers and reservoirs of disease. Their concerns, however, may be based more upon misconception than reality. Tuttle and Kern (1981) sampled natural populations of bats and re-evaluated data previously published by others, concluding that bats are not especially important reservoirs of zoonotic diseases. Other experts on bat-borne diseases agree (see Constantine, 1988, for review). Recent data suggest that less than 0.5 percent of bats contract rabies and experts now believe that many bats considered rabid in earlier studies were actually infected by other viruses such as the Rio Bravo virus, which is harmless to bats and humans but fatal to mice, which succumb exhibiting rabies-like symptoms (Constantine, 1988; Tuttle, 1988).

Only two bat-borne diseases, rabies and histoplasmosis, are currently considered to be potential hazards to human health. Histoplasmosis is a fungal disease found in soils enriched by feces of bats and birds. Human infections are usually asymptomatic or appear as a mild respiratory infection. Histoplasmosis is usually transmitted through inhalation of airborne spores in closed areas such as caves. Probability of inhalation of spores under these conditions is enhanced where the humidity may be high, suspending the spores in air (Tuttle and Kern, 1981).

Unlike histoplasmosis, rabies is a viral infection which, if not treated quickly, leads to death. The virus is usually transmitted in saliva of an infected animal, usually by way of a bite. Beyond a certain stage of incubation within the host animal, there is no known cure. The rabies virus is potentially capable of infecting any mammal, although incidence tends to be highest in carnivores (Bell and Moore, 1971; Constantine, 1988).
Because North American bats are insectivorous or nectarivorous, not carnivorous, it is not clearly understood how the rabies virus enters bat populations. Once the virus is contracted by an individual, however, it can potentially be spread through aggressive interactions to other colony members in the late stages of infections or by attacks of rabid individuals on other bats flying in the same area (Bell, 1980).

Over the past decade, two questions concerning bats and public health have been of paramount importance: (1) can bats be carriers of rabies without themselves being killed by the virus? and (2) are bats major vectors of rabies to wildlife? In the past, the presumed answer to both of these questions has been affirmative. Data to support the assertions, however, are inconclusive at best. Bats appear to be similar to other wildlife species and to humans, becoming victims rather than sources of further infection (Constantine, 1988).

Studies of rabies infections in bats in Asia, Africa, and Europe showed the virus to be rare (Meredith et al., 1971; Tignor et al., 1977). Recently, rabies-related viruses have been isolated from bats in Africa and Europe (Constantine, 1988). In the United States, records spanning more than 30 years showed only nine cases of human rabies with suspected contractions from bats (Greenhall, 1982). Infection rates in bats collected from wild populations in North America were less than 0.5 percent (Tuttle and Kern, 1981). Many of the reported human exposures to rabies via bats was through the mishandling of grounded, partially paralyzed individuals (Tuttle and Kern, 1981). Constantine (1979) stated that rabies outbreaks in bat populations other than vampire bats "either do not occur or must be rare." Moreno and Baer (1980), Bell et al. (1962), and Constantine (1979) all refuted previous ideas that bats are "high-risk" carriers of rabies and that bats survive rabies infection better than other mammals. Rather, they provided data which suggested strongly that bats survive rabies infections no better than any other mammal and succumb quickly to the effects of the virus.

Laboratory rats were infected when bitten by rabid bats (Bell, 1959; Bell et al., 1962; Bell et al., 1969; Reagan et al., 1957). Burns et al. (1958), however, observed no infection in white mice, monkeys, and guinea pigs after repeated biting by rabid bats. Studies involving carnivores bitten by rabid bats showed transmission to be difficult with only rare cases of infection (Constantine et al., 1968; Constantine et al., 1966; Constantine, 1966). Although results of these laboratory studies are variable, most data indicate that rabies transmission from bats to other wildlife is both difficult and rare (Tuttle and Kern, 1981). Kurta (1979) found no evidence of elevated incidence of rabies in terrestrial wildlife in areas of high occurrence of bat rabies in Michigan.

Intraspecific transmission of a virus coupled with the absence of interspecific transmission, except for rare, "dead-end" infections, is referred to as "compartmentalization" (Winkler, 1975). Compartmentalization is the rule for rabies in bats. Constantine (1988) estimated that only about one in 1000 clinically normal bats is infected with rabies in most of North America.
Bat Rabies in Colorado

Although rabies is known to occur in Coloradan bats, the incidence of occurrence has not been clearly determined. Data on rabies infections in bats and other animals, including domestic pets, are collected by the Colorado Department of Health (CDOH). Bats analyzed for rabies infection by the CDOH represent instances of contact between bats and humans or their pets. In most cases, individuals tested for rabies infection were found sick or dead.

Methods.--We compiled data from Colorado Department of Health (CDOH) records spanning 10 years (1976 through 1985). The data allowed us to calculate frequency of incidence of rabies per species of bat per year. Spearman Rank Correlation Analysis was used to test the relationship between percentage of infected individuals per species and both average body size and sample size for each species. Species with low sample sizes (<20 over the decade—Antrozous pallidus, Plecotus townsendii, and Tadarida macrotis) were excluded from the analysis to avoid effects of sampling error. Species included in the analysis were: Myotis lucifugus, Myotis evotis, Lasionycteris noctivagans, Eptesicus fuscus, Lasiurus borealis, Lasiurus cinereus, and Tadarida brasiliensis.

Results.—Incidence of rabies-infected individuals showed interspecific variability as well as year-to-year intraspecific variability (Table 8). Myotis lucifugus showed a consistently low frequency of rabies infection, whereas Myotis evotis was high in some years. Other species had no incidence. Highest levels of year-to-year variation were exhibited by M. evotis and Lasiurus cinereus. The former species showed no incidence in most years, but jumped to 75 percent in 1980; the latter had infection rates ranging from 13 percent in 1980 to 51 percent in 1984. Small sample size in M. evotis may be responsible for high variation from year-to-year.

Total percentages for each species indicate that L. cinereus had the highest incidence of rabies (35 percent) over the 10-year period. Eptesicus fuscus had the second highest incidence (15 percent). Spearman Rank Correlation Analysis showed that frequency of infected individuals was highly correlated with average body length ($r = 0.782$). Frequency of rabies-positive individuals was not highly correlated with sample size ($r = 0.252$).

Discussion.--For field data to be useful they must tell us something about the natural history of the organism(s) under study. For data to be considered valid as an accurate depiction of the natural world, they must be collected under unbiased circumstances. Conclusions from biased data are not valid.

Information presented here suggests that reports of incidence of rabies in bats in Colorado are invalid due to unconsciously biased collection of these data, a conclusion similar to that of a worldwide review (Constantine, 1988). In the present study, data compiled from CDOH records showed a positive correlation of increasing incidence of rabies with an increase in average species' body size. This could be interpreted to mean that the larger a bat the greater its risk of rabies infection, a conclusion that makes little obvious biological sense. Smaller
Table 8. Number of bats, by species per year, infected by rabies virus, number of bats submitted for testing, and percentage infected, summed to 10-year cumulative total. Compiled from CDOH records.

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<td><em>Myotis lucifugus</em></td>
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<td>5</td>
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<td>4</td>
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<tr>
<td></td>
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<td>(7%)</td>
<td>(8%)</td>
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<td>(3%)</td>
<td>(9%)</td>
<td>(0%)</td>
<td>(7%)</td>
</tr>
<tr>
<td><em>Myotis evotis</em></td>
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<td>0</td>
<td>3</td>
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<td>0</td>
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<td>(0%)</td>
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<td>(0%)</td>
<td>(0%)</td>
<td>(50%)</td>
<td>(0%)</td>
<td>(3%)</td>
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<tr>
<td><em>Lasiurus borealis</em></td>
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<td>0</td>
<td>0</td>
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<td>(0%)</td>
<td>(50%)</td>
<td>(0%)</td>
<td>(15%)</td>
</tr>
<tr>
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<td>17</td>
<td>16</td>
<td>5</td>
<td>12</td>
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<td>(33%)</td>
<td>(51%)</td>
<td>(40%)</td>
<td>(34%)</td>
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<tr>
<td><em>Lasionycteris noctivagans</em></td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>2</td>
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<td>3</td>
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<td>(2%)</td>
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<td>(3%)</td>
<td>(9%)</td>
<td>(7%)</td>
<td>(3%)</td>
<td>(6%)</td>
<td>(3%)</td>
<td>(0%)</td>
<td>(4%)</td>
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<tr>
<td><em>Eptesicus fuscus</em></td>
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<td>23</td>
<td>15</td>
<td>26</td>
<td>31</td>
<td>17</td>
<td>25</td>
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<td>(19%)</td>
<td>(14%)</td>
<td>(11%)</td>
<td>(15%)</td>
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<td><em>Plecotus townsendii</em></td>
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<td><em>Antrozous pallidus</em></td>
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<tr>
<td><em>Tadarida brasiliensis</em></td>
<td>1</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
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<td>(0%)</td>
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<td>(0%)</td>
<td>(0%)</td>
<td>(11%)</td>
<td>(0%)</td>
<td>(1%)</td>
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<tr>
<td><em>Nyctinomops macrotis</em></td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<td>(0%)</td>
<td>(0%)</td>
<td>(0%)</td>
<td>(3%)</td>
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</tbody>
</table>

69
species tend to be colonial whereas larger species tend to be more solitary. Potential for
disease transmission is higher among colonial mammals. Therefore rabies incidence and
transmission should be highest among the smaller-sized, colonial bat species. Data from
CDOH do not support this prediction; in fact, they contradict it. Because the number of bats
obtained per species did not correlate strongly with the percentage incidence of rabies, we can
disregard sample size as a bias. Rather, there appears to be a bias concerning average species
body size and collection procedures.

Large bats tend to roost in open areas such as under shingles on houses, branches and bark of
trees, and cliff overhangs. Smaller species tend to occupy more secluded places such as attics
or deep, narrow crevices. Larger species roosting in open, urban areas are more likely to be
found and taken in for examination than are secretive species (96 percent of individuals
examined by us from the CDOH had an associated street address, suggesting roosting in close
proximity to humans). Likewise, larger bats are more easily observed when either sick or
dying or dead. Furthermore, tree-roosting species, which tend to be relatively larger, are more
easily captured (dead or alive) by domestic animals, especially cats, and brought to an
unsuspecting owner. Largest sample size collected was for Eptesicus fuscus, a common,
large-sized, tree-roosting bat, whereas one of the smaller sample sizes collected was of Myotis
lucifugus, a generally common, small-sized, attic-roosting bat. Little brown bats commonly
live in large colonies in well-hidden roosts. It is curious why so few little brown bats were
obtained relative to big brown bats, a larger, less colonial, similarly abundant species of
similar habitats. Differences in roosting ecology and body size may play an important role in
determining the availability of specimens obtained by CDOH.

In addition, we note that the CDOH tested mostly animals that already were sick or dead.
Because these individuals became sick or died from some cause, it is not surprising that a
high percentage of them were infected with rabies, because rabies is one of the few diseases
that affects bats.

Current knowledge of rabies infections in bats in Colorado is poor because the data base is
poor. This leads us to a series of recommendations. First, studies should be made of enzootic
disease in natural populations. Deliberate, statistically defensible sampling of bat populations
must be undertaken to provide an accurate picture of the incidence of bat rabies. In addition,
ecological aspects of species must be taken into account when evaluating data and discussing
disease transmission and public health. Further, we suggest that bats tested for rabies by the
CDOH be identified to species by experts and that voucher specimens be prepared and
curated to allow future re-examination and verification. At present, some bats (for example,
species of Myotis) are not keyed to species and are treated together statistically despite their
quite different natural histories.

CONSERVATION AND MANAGEMENT OF COLORADAN BATS

The topography of Colorado is diverse and, as a consequence, so is its ecology. Seventeen
species of bats are known to occur in Colorado, each with a unique geographic distribution
reflecting its particular ecology and history. Further, each species exhibits its own pattern of relative abundance; some are observed commonly, whereas others seem to be quite rare, or occur only as accidental or wandering individuals.

For most of the species in Colorado we have few baseline data on local population numbers or relative abundance across their ranges. For conservation efforts to be effective, baseline data must be acquired on species diversity (richness and evenness) in communities. Although some research has focused on bats, there is much to be learned before a statewide conservation plan can be designed and implemented. There is a dilemma among bat biologists in Colorado who today share a “feeling” that populations of most species are probably in serious decline, but have few or no hard data to support this assertion. With the benefit of clear hindsight it is easy to see that if data on population numbers had been collected beginning decades ago, we would now have a much better understanding of the status of Coloradan bat populations. Clearly, however, conservation cannot wait for exhaustive research. A first priority must be to assure the on-going viability of bat populations. Sheffield et al. (1992) provided guidelines for the protection of bat roosts in a statement approved by the Board of Directors of the American Society of Mammalogists in 1987.

Over the past several years, various projects have been initiated to solve the problem of the paucity of data and to conserve bat populations. In May 1990, The Colorado Bat Society (CBS) was founded. Conservation efforts by CBS range from consulting with people experiencing problems with bats to promoting the building and hanging of bat houses in natural habitats and urban areas when appropriate. In 1991 the Society initiated an Annual Bat Trend Survey. One of us (DMA) designed and coordinated the project through 1992. In 1993, Joe Hall of Grand Junction became statewide coordinator for the project (Hall, 1994b). The purpose of the Survey is four-fold: 1) to involve the public with bat conservation and appreciation by teaching them how to observe the bats foraging in their neighborhoods; 2) to begin to gather long overdue data on bat “hotspots” which could be monitored for population fluctuations; 3) to identify suitable locations for CBS field trips; and 4) to identify possible research sites for qualified specialists. In 1991, 27 observers throughout the state covering five of 28 “latilong blocks” (see Table 9) filed complete observation forms. In 1992, the number of observers increased to more than 100 statewide covering 12 of 28 latilong blocks. Table 9 presents data from the first three years of the survey.

The Colorado Division of Wildlife (CDOW) initiated and coordinates the “Bats/Inactive Mines Project.” The importance to the health of bat populations of deep natural caverns and mines and other artificial tunnels and caves has been firmly established. Inactive mines provide subterranean microclimates buffered from outside conditions and conducive to habitation by bats. Some species congregate in large numbers within mine shafts which they use as maternity sites and/or hibernacula. Because of the apparent importance of these types of caverns to bats, the CDOW Bats/Inactive mines project has focussed on locating shafts housing significant populations and then installing grates to prevent human entry while allowing for access by bats. The project consists of two stages. First, volunteers (of whom nearly 400 had been trained by 1993--Navo, 1993), armed with bat detectors, visit mines
Table 9. Three-year summary of Colorado Bat Trend Surveys, 1991-1993, by latilong block. Number tabulated is average number of passes tallied in two night's observations (n = number of observers in latilong block in parentheses). Compiled by J. G. Hall and D. M. Armstrong; also see Hall (1994).

<table>
<thead>
<tr>
<th>Block</th>
<th>Counties</th>
<th>1991 (n)</th>
<th>1992 (n)</th>
<th>1993 (n)</th>
</tr>
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<tr>
<td>4</td>
<td>Larimer, Boulder</td>
<td>51.8 (7)</td>
<td>51.5 (12)</td>
<td>85.2 (6)</td>
</tr>
<tr>
<td>5</td>
<td>Weld</td>
<td>94.0 (1)</td>
<td>144.9 (5)</td>
<td>226.8 (4)</td>
</tr>
<tr>
<td>8</td>
<td>Mesa</td>
<td>125.7 (3)</td>
<td>310.5 (6)</td>
<td>271.4 (11)</td>
</tr>
<tr>
<td>10</td>
<td>Pitkin</td>
<td>---------</td>
<td>245.0 (1)</td>
<td>---------</td>
</tr>
<tr>
<td>11</td>
<td>Jefferson, Boulder</td>
<td>34.2 (7)</td>
<td>55.7 (8)</td>
<td>204.3 (3)</td>
</tr>
<tr>
<td>12</td>
<td>El Paso, Boulder, Denver</td>
<td>---------</td>
<td>114.6 (3)</td>
<td>208.0 (4)</td>
</tr>
<tr>
<td>18</td>
<td>Chaffee, Fremont</td>
<td>---------</td>
<td>61.0 (2)</td>
<td>---------</td>
</tr>
<tr>
<td>19</td>
<td>El Paso, Pueblo</td>
<td>19.0 (2)</td>
<td>18.9 (26)</td>
<td>23.3 (18)</td>
</tr>
<tr>
<td>21</td>
<td>Prowers</td>
<td>---------</td>
<td>123.0 (1)</td>
<td>---------</td>
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<tr>
<td>23</td>
<td>La Plata</td>
<td>---------</td>
<td>268.0 (1)</td>
<td>28.0 (1)</td>
</tr>
<tr>
<td>24</td>
<td>Rio Grande</td>
<td>---------</td>
<td>21.0 (1)</td>
<td>---------</td>
</tr>
<tr>
<td>26</td>
<td>Las Animas</td>
<td>---------</td>
<td>6.0 (2)</td>
<td>---------</td>
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</table>

scheduled for closure by the Mined Land Reclamation Division (MLRD, Colorado Department of Natural Resources). They monitor the entrance to the mine, recording the number of passes by exiting bats. They also tally the number and frequency of echolocatory calls. If significant numbers of bats are detected, experienced bat biologists visit the shaft to trap bats, identify them, and collect data on the size of the population(s), the type of colony (bachelor, nursery, hibernacular, etc.), and the reproductive condition of individuals (see Freeman and Adams, 1992). If the site is deemed significant, a “bat-friendly” grate is installed. The Colorado Bat Society provided modest monetary support for this project.
The Bats/Inactive Mines Project has focussed especially on the presence of Townsend's Big-eared bat (*Plecotus townsendii*), a Colorado "species of special concern." This species is known to reside in mines; the Californian subspecies (*P. t. townsendii*--a Category 2 "candidate" taxon under the federal Endangered Species Act) is thought to be threatened due to mine closure and destruction. Closure of abandoned mines is a practice necessary to protect the public from entering dangerous shafts. Typically, mines are sealed shut with concrete and/or rubble. Depending upon the time of year that closure is done, the practice may either entomb the bats already inside the mine or preclude bats' access to traditional maternity roosts or hibernacula. As of 1993, 13 mine portals in Colorado have been fitted with bat-friendly grates (Navo, 1993). Shafts so far grated function as maternity roosts and/or hibernacula for *Myotis lucifugus, M. evotis, M. volans, M. ciliolabrum, M. thysanodes, M. californicus, E. fuscus,* and/or *P. townsendii* (Navo, 1993).

The impact of standard mine-closure practices on bat populations in Colorado has never been assessed. However, in 1992, about 600 shafts in the state were scheduled for closure by MLRD. This large number of closures suggests that the impact on bat populations due to this procedure may be significant.

In addition to mines, bats also utilize the few natural caves in Colorado. A recent survey by two of us (RAA and JF) of several caves known historically to house *P. townsendii* proved disturbing. At only one of the five caves visited were relatively high numbers of *P. townsendii* (n = 26 passes) observed. This cave is on private property and public access is tightly controlled by the landowner. The other sites are located on public land and are frequented by hikers and spelunkers. These sites had relatively low numbers of *P. townsendii* present, suggesting the possibility of human impact. This survey was conducted over a 12-day period in June and population numbers at any of these caves may fluctuate seasonally. Therefore, Adams and Freeman (1993) suggested more intensive observations at these sites before recommendations concerning their protection be made.

In accounts of individual species we make comments on status and abundance. Usually these comments are based on speculation and casual observation and they should be taken with due caution. Colorado provides an example of a general paradox in knowing and protecting bats. Species that appear to be common often are those that form large nursery of hibernating colonies, especially in buildings, mines, caves, or other situations readily accessible to humans. Based on casual observation, we are likely to characterize such species as "abundant." But that abundance may be more obvious than real. Further, if roosting sites are readily accessible to humans for observation, then they also may be readily disturbed, accidentally or wantonly. Hence, populations of these conspicuous species--the little and big brown bat, Brazilian free-tailed bat, and Townsend's big-eared bat, for example--may be especially vulnerable to encroachment.

Successful conservation programs are based on both research and education. Through the efforts of various organizations and governmental agencies we have begun to make strides towards conservation of Coloradan bats on both fronts. Still, knowledge of the population
ecology of bats in Colorado is rather rudimentary (although emerging data indicate that many species are in trouble). Much more needs to be known before we can begin to understand the consequences of past and current human impacts and thereby build a comprehensive plan for the future conservation of bats in Colorado. While that research is progressing, tremendous opportunities exist for education at all levels, both informal efforts—through the Colorado Bat Society, museums, nature centers, and other organizations—as well as the formal curriculum of the schools. Deeper understanding (based on research) and increased public support (based on effective educational programs) together will lead to appropriate stewardship of the Coloradan landscape to preserve its fascinating fauna of bats.

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