

Forest Bat Communities in the East Cascade Range, Washington

Abstract

Limited data are available on the occurrence and relative abundance of bat species in Washington. We surveyed forest bat communities on the eastern slope of the Cascade Range in south-central Washington from May through August, 2001 and 2002. We selected two watersheds that differed in range of elevation (760-1260 m vs. 1000-1400 m), contained mixed ownership (public and private), and were subject to forest management practices typical of the ponderosa pine forest zone in eastern Washington. We captured 1057 bats of 11 species over 135 nights of sampling (mean = 2.39 ± 0.23 bats net⁻¹ night⁻¹). Of captures, 65% were adult males, 29% were adult females, and 6% were volant juveniles. Fifteen percent of adult males and 49% of adult females were reproductively active. We first captured pregnant females of myotis species from 3 to 27 June, and reproductive males from 12 July to 4 August. Volant juveniles of myotis species were captured between 25 July and 13 August. We captured more males per female in the high-elevation watershed (3.53) than in the low-elevation watershed (1.58); the proportion of reproductively active females was not different between watersheds. A greater proportion of males were reproductively active in the high-elevation watershed (0.2) than in the low-elevation watershed (0.09). We captured more juveniles and juveniles of more species in the high-elevation watershed. Comparison to other studies showed discrepancies in the relative abundance of fringed myotis and long-legged myotis, suggesting that further study of these species is warranted. These data indicate that management of forest bats should begin to place a greater emphasis on conservation across landscapes.

Introduction

Thirteen species of bats inhabit forests in the Pacific Northwest (Dalquest 1948, Christy and West 1993, Wunder and Carey 1996), making bats among the most diverse taxonomic group of mammals in the region. Information on population status is lacking for most species of forest bats across many regions in the Pacific Northwest, including the eastern Cascades (Forest Ecosystem Management Assessment Team 1993, USDA Forest Service and USDI Bureau of Land Management 1994). Because forest bats switch roosts frequently (Lewis 1995), reliable data from which to assess changes in population size are difficult to acquire (Hayes 2003). *In lieu* of such information, forest resource managers require, at a minimum, basic information on species composition to assess the potential range of impacts that management activities might have on forest bats. Likewise, information on population structure of forest bat communities can provide an improved understanding of differential habitat use among sex and age classes of bats.

Published survey data on bats are scarce for areas east of the Cascade Crest in Washington. The only study published in the primary litera-

ture in which capture data for forest bats in the eastern Cascades are presented is Thomas (1988); 57 bats of five species were captured over two nights in early August, 25% were adult females and 82% of these were reproductively active. Three theses contain bat capture data for forests east of the Cascade Range in Washington. Campbell (1993) captured 114 bats of eight species in the Calispell Basin in the Selkirk Mountains of north-eastern Washington. Thirty-three percent of captures were adult females and 63% of adult females were reproductively active. Frazier (1997) captured 106 bats of 8 species in the Teanaway River Valley in central Washington, and Taylor (1999) captured 234 bats of 12 species in the upper White Salmon River watershed in south-central Washington. Gitzen et al. (2002) captured 81 bats of five species in shrub-steppe habitat, most from a single man-made structure on the Hanford site in eastern Washington. Unfortunately, the latter studies presented no data on population structure or timing of reproductive stages.

Geographic variation in sex and age ratios of bats and adult sex ratios skewed toward males have been reported for many bat species across North America (Kurta and Matson 1980, Schowalter 1980, Thomas 1988, Barclay 1991, Cryan et al. 2000, Zimmerman and Glanz 2000), though the opposite has also been reported (Barclay et al. 1988). Explanations for male-biased sex ratios

¹Author to whom correspondence should be addressed. E-mail: earnhardt2k@yahoo.com

include differential mortality rates between the sexes (Kurta and Matson 1980), climatic factors (Thomas 1988), and elevation (e.g., Allen 1939, Vaughn and Kruttsch 1954, Easterla 1973, Fenton et al. 1980, Thomas 1988, Cryan et al. 2000). Biases inherent to all bat capture methods (Kunz and Brock 1975, Tidemann and Woodside 1978) are overcome within individual studies by using the same methods across study sites. Elevational differences in occurrence between the sexes have been reported (Thomas 1988, Cryan et al. 2000), with proportionally fewer females than males captured at high elevations relative to low elevations. Cryan et al. (2000) suggested that female bats at higher elevations experience greater energetic expenditures than males, limiting the ability of females to forage successfully and locate adequate roosting sites. However, the flexible foraging behavior (i.e., vegetation and ground gleaning) of female western long-eared myotis (*Myotis evotis*) may enable this species to breed successfully in high-elevation habitats in British Columbia (Nagorsen and Brigham 1993).

Virtually no data specific to eastern Washington exist on the timing of stages of reproduction; however, historical species accounts and data for a few species from a wider geographic range provide a basis for comparison. Pregnant female western long-eared myotis (*M. evotis*) were reported from mid May through mid July throughout their range (Manning and Jones 1989). Wider temporal variation in pregnancy in long-legged myotis (*M. volans*) is reported (Warner and Czaplewski 1984), ranging from as early as mid April and as late as mid August across studies in Southern California (Dalquest and Ramage 1946), Nevada (Hall 1946), Montana (Jones et al. 1973), Wyoming (Findley 1954), South Dakota (Jones and Genoways 1967), Nebraska (Jones 1964, Czaplewski et al. 1979), and Colorado and New Mexico (Davis and Barbour 1970). Druecker (1972) indicated that parturition in long-legged myotis extended from May through August. Verts and Caraway (1998) report that all adult and most juvenile male long-legged myotis collected in Oregon in August and September were reproductively active.

Timing of reproduction for fringed myotis (*M. thysanodes*) varies little throughout the range of the species (O'Farrell and Studier 1973). Histological examination placed the onset of pregnancy between late April and mid May and parturition

between late June and early July. Pregnant fringed myotis were captured in mid to late June (Barbour and Davis 1969), and lactating individuals in early to mid July (Miller and Allen 1928, Cockrum and Ordway 1959, Easterla 1973). Maser (1998) reported pregnant big brown bats (*Eptesicus fuscus*) in late June, parturition in late June / early July, and lactation as late as early August in the northern United States. Fenton et al. (1980) collected eight pregnant big brown bats on 21 June and two lactating bats on 27 June; Schowalter and Gunson (1979) reported similar dates. While these studies provide valuable information from a wide geographic perspective, data specific to more narrowly-defined regions are needed by land managers charged with conservation of bat species.

In this paper we report the sampling results of two breeding seasons in two forested watersheds on the east side of the Cascade Range in south-central Washington. We assessed species relative abundance, sex ratio, age structure, and timing of reproductive stages. To synthesize available information, we compared our data to completed studies of forest bat communities in eastern Washington and we discuss differences in reported population structure parameters across the region.

Study Area

We surveyed bat communities in the Rock Creek drainage of the Naches River valley and the Oak Creek drainage of the Tieton River valley on the Okanogan-Wenatchee National Forest, along the eastern slopes of the Cascade Range in south-central Washington. In this region, andesite and basalt flows form ridge crests that are dissected by deep valleys (Franklin and Dyrness 1988). Coarse-textured, sandy soils support a narrow 15 to 30-km wide zone of ponderosa pine (*Pinus ponderosa*) forest between 600 and 1200 m in elevation, running north to south and abutting shrub-steppe habitat to the east (Franklin and Dyrness 1988). Ponderosa pine dominates the xeric mid and upper slopes and characterizes this forest zone in southern and central Washington. Grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) grow on more mesic sites (Franklin and Dyrness 1988). The area experiences extremely dry summers and long winters with heavy snowfall. Townships in each study area occur in a checkerboard fashion, with the USDA Forest Service administering public lands on even-numbered sections

and private industry managing forests on odd-numbered sections. We concentrated our sampling in Rock Creek (high-elevation watershed) between 1000 and 1400 m in elevation, and in Oak Creek (low-elevation watershed) between 760 and 1260 m in elevation.

Methods

We used mist nets to capture bats, and we sampled on most nights from 22 May to 17 August 2001 and 1 June to 16 August 2002. We placed nets across and around ephemeral ponds and in areas of pooled water along small streams. We sampled 9 locations in Rock Creek and 18 in Oak Creek with a variety of nets used at capture sites. Nets were 3 m tall and 3, 6, 9, 12, or 18 m long and comprised 36-mm mesh. In general, we alternated sampling between watersheds and chose capture sites opportunistically. We opened nets ~ 15 min prior to local sunset and monitored nets until 2400 or 0100 hours PDT.

We identified bats to species and aged them using ossification of the epiphyseal cartilage in the finger joints (Anthony 1988). We noted the presence of descended testes in males, and the presence of a fetus (pregnant), exposed or swollen teats (lactating), or exposed but not swollen teats (post-lactating) in females (Racey 1988). We marked the dorsal surface of a wing with a spot of liquid paper to aid in identification of individuals recaptured the same night.

We tested for differences in sex ratio and the proportion of reproductively active adults between

watersheds using a Chi-square test of proportions, with significance determined at $P = 0.05$. Data for capture success rates are presented as mean (\pm SE). We also provide a qualitative evaluation of similarities and differences in reported population structure parameters from the limited number of published studies conducted in forest habitat on the east side of the Cascade Crest in Washington.

Results

We set mist nets on 70 nights for a total of 274 net nights in 2001 and on 65 nights for a total of 224 net nights in 2002. Overall capture success was 2.39 ± 0.23 bats net⁻¹ night⁻¹. We captured 1057 individuals of 11 species. Likelihood of capture varied within watersheds with four capture sites in the high-elevation watershed and five capture sites in the low-elevation watershed showing particularly high rates of capture success. The western long-eared myotis, long-legged myotis, and fringed myotis were the most abundant species (Table 1). Big brown bats, silver-haired bats (*Lasionycteris noctivagans*), and California myotis (*M. californicus*) also were frequently captured. We captured both sexes of all species except for the silver-haired bat, hoary bat (*Lasiurus cinereus*), and Townsend's big-eared bat (*Corynorhinus townsendii*). The absence of female silver-haired bats, despite the capture of 81 males, was unexpected; however, we captured a single juvenile male silver-haired bat on 2 August 2001 in Rock Creek. Sixty-six percent of all bats were adult males and 29% were adult females. Twenty-nine

TABLE 1. Bat species captured in mist nets in Kittitas and Yakima counties, Washington, 2001 and 2002. The number of adults is indicated, with the number of volant young in parentheses.

Species	Males	Females	Total	Relative Abundance (%)
Western long-eared myotis	268 (11)	107 (3)	375 (14)	36.8
Long-legged myotis	53 (11)	82 (18)	135 (29)	15.5
Fringed myotis	97 (7)	32 (1)	129 (8)	13.0
Big brown bat	100 (1)	23 (0)	123 (1)	11.7
Silver-haired bat	81 (1)	0 (0)	81 (1)	7.8
California myotis	42 (1)	36 (0)	78 (1)	7.5
Western small-footed myotis	26 (0)	14 (0)	40 (0)	3.8
Yuma myotis	9 (5)	4 (0)	13 (5)	1.7
Little brown myotis	5 (0)	7 (0)	12 (0)	1.1
Hoary bat	11 (0)	0 (0)	11 (0)	1.0
Townsend's big-eared bat	0 (0)	1 (0)	1 (0)	0.1
Totals	692 (37)	306 (22)	998 (59)	100.0

TABLE 2. Timing of the stages of reproduction for select species of bats based on dates of mist net captures in Kittitas and Yakima counties, Washington, 2001 and 2002. Dates for pregnancy, lactation, and post-lactation are the earliest and latest recorded captures of each species, and dates for descended testes and volant young are the earliest dates of capture.

Species	Pregnancy	Lactation	Post-lactation	Descended testes	Volant young
Western long-eared myotis	5 Jun – 25 Jul	8 Jul – 5 Aug	1 Aug – 12 Aug	12 Jul	2 Aug
Long-legged myotis	3 Jun – 4 Aug	6 Jul – 8 Aug	31 Jul – 13 Aug	12 Jul	25 Jul
Fringed myotis	24 Jun – 26 Jun	3 Jul – 12 Aug	7 Aug – 12 Aug	30 Jul	2 Aug
California myotis	22 Jun – 5 Jul	21 Jul – 1 Aug	12 Aug	12 Jul	13 Aug
Western small-footed myotis	27 Jun – 5 Jul	1 Aug – 3 Aug	7 Aug – 12 Aug	4 Aug	— ^a
Big brown bat	23 May – 12 Aug	30 Jul – 2 Aug	7 Aug – 16 Aug	12 Jul	12 Aug
Silver-haired bat ^b	—	—	—	12 Jul	2 Aug

^a Volant young of this species were not captured.

^b Adult females of this species were not captured.

percent of all adults were reproductively active, including 15% of adult males and 49% of adult females.

We restrict our report of the timing of reproductive stages to those species for which we captured 10 or more individuals. We captured 14 pregnant western long-eared myotis between early June and late July, 18 pregnant long-legged myotis between early June and early August, two pregnant fringed myotis in late June, and nine pregnant big brown bats between late May and mid August (Table 2). We captured 25 lactating western long-eared myotis between early July and early August, 19 lactating long-legged myotis between early July and early August, 11 lactating fringed myotis between early July and mid August, and six lactating big brown bats between late July and early August (Table 2). Fifty-six percent of all adult females captured on or after 18 June showed evidence of reproductive activity (i.e., pregnant, lactating, or post-lactating). Reproductively active males of six species (western long-eared myotis, long-legged myotis, California myotis, big brown bat, silver-haired bat, and hoary bat) were each first captured on 12 July in 2002.

We captured volant young of each species except the hoary bat, western small-footed myotis (*M. ciliolabrum*), little brown myotis (*M. lucifugus*), and Townsend's big-eared bat (Table 1). Only 5.6% of all captures were juveniles; volant juveniles constituted 19% of all captures on or after 1 August. Forty-nine percent of all juveniles captured were long-legged myotis. Thirty-seven percent of juveniles captured were female. The earliest capture dates for volant young were 9 July

for Yuma myotis (*M. yumanensis*) and 25 July for long-legged myotis.

We captured 517 bats over 67 nights of sampling in the high-elevation watershed (mean = 2.37 ± 0.29 bats net⁻¹ night⁻¹), and 540 bats over 68 nights of sampling in the low-elevation watershed (mean = 2.42 ± 0.35 bats net⁻¹ night⁻¹). Long-legged myotis and silver-haired bats were more abundant in the high-elevation watershed, whereas fringed myotis were more abundant in the low-elevation watershed (Table 3). A difference in adult sex ratio of bat species between watersheds where a sufficient number of both sexes was captured was evident for long-legged myotis and fringed myotis. More males were captured per female in the high-elevation watershed than in the low-elevation watershed ($P < 0.001$). The proportion of reproductively active adult females did not differ between the high-elevation watershed and the low-elevation watershed; however, the proportion of reproductively active adult males was greater in the high-elevation watershed than in the low-elevation watershed ($P < 0.001$). We captured slightly more juveniles and juveniles of more species in the high-elevation watershed than in the low-elevation watershed.

Discussion

We captured each of the 11 bat species noted to use Washington forests as primary or secondary habitat by Dalquest (1948), all but one species predicted to occur in the Pacific Northwest by Christy and West (1993), and all but two species noted to use forest canopies in the Pacific Northwest (Wunder and Carey 1996). We did not capture

TABLE 3. Number of adult (juvenile) bats captured in mist nets, with adult sex ratio (no. males / females) by species and watershed in Kittitas and Yakima counties, Washington, 2001 and 2002.

Species	High-elevation watershed		Low-elevation watershed		Totals	
	Adults (juveniles)	M:F	Adults (juveniles)	M:F	Adults (juveniles)	M:F
Western long-eared myotis	144 (6)	2.89	231 (8)	2.30	375 (14)	2.50
Long-legged myotis	96 (15)	0.92	39 (14)	0.22	135 (29)	0.65
Fringed myotis	33 (4)	4.50	96 (4)	2.69	129 (8)	3.03
Big brown bat	61 (0)	11.20	62 (1)	2.44	123 (1)	4.35
Silver-haired bat ¹	72 (1)	—	9 (0)	—	81 (1)	—
California myotis	35 (1)	10.67	43 (0)	0.30	78 (1)	1.17
Western small-footed myotis	22 (0)	10.00	18 (0)	0.50	40 (0)	1.86
Yuma myotis	8 (5)	— ²	5 (0)	0.25	13 (5)	2.25
Little brown myotis	6 (0)	1.00	6 (0)	0.50	12 (0)	0.71
Hoary bat ¹	7 (0)	—	4 (0)	—	11 (0)	—
Townsend's big-eared bat ²	1 (0)	—	0 (0)	—	1 (0)	—
Combined	485 (32)	3.53 ^a	513 (27)	1.58 ^b	998 (59)	2.26

¹ Males only.

² Females only.

^{a,b} Sex ratios with different letters are different at $P < 0.05$.

the western red bat (*Lasiurus blossevillii*), a species rarely encountered outside established populations in northern California and Utah (Nagorsen and Brigham 1993), or Keen's long-eared myotis (*Myotis keenii*), a species believed to be restricted to the coastal forests of western Washington and British Columbia (van Zyll de Jong 1979, Nagorsen and Brigham 1993). Fringed myotis and Townsend's big-eared bat are considered to be of highest concern by the Western Bat Working Group, a forum comprising the region's leading bat experts. Thus, the prevalence of fringed myotis, especially in the low-elevation watershed, was noteworthy. Moreover, the western long-eared myotis, long-legged myotis, and Yuma myotis, each captured in this study, are designated as warranting closer attention due to the limited data available on their biology, habitat needs, and population status (Forest Ecosystem Management Assessment Team 1993, USDA Forest Service and USDI Bureau of Land Management 1994). Data from our study (Table 1) indicate that the western long-eared myotis and long-legged myotis are abundant species in at least some forested regions, and the fringed myotis can be locally abundant, east of the Cascade Range in Washington.

All bat capture methods are subject to bias (Kunz and Brock 1975, Tidemann and Woodside 1978). Common among the studies conducted in forests of eastern Washington that we reviewed was the use of mist nets, harp traps, or both placed

in travel corridors or locations where bats acquire water and food (Thomas 1988, Campbell 1993, Frazier 1997, Taylor 1999; Table 4). We observed that species richness of bat communities increased with greater sampling effort across studies, but patterns in relative abundance fluctuated among locations (Table 4). Western long-eared myotis, the most frequently captured species in our study, was relatively less common in comparative studies with the exception of Taylor (1999). Occurrence of long-legged myotis was inconsistent, as they were common in our study and studies by Frazier (1997) and Taylor (1999), but absent in captures of Campbell (1993) and the two nights of capture in early August in Thomas (1988). These differences in abundance of long-legged myotis among study locations suggest that further investigation is warranted. Although relatively common in our study, fringed myotis were scarce or absent in the other study locations. We surmise that important habitat elements for this species (e.g., rock outcrops) that were present in the watersheds we examined may be absent near the other study locations.

Sex and age ratios showed geographic variation; however, some of these patterns likely were artifacts of differences in the duration and timing of sampling effort among studies. For example, we captured a lower percentage of reproductive females than did Thomas (1988), and we captured a lower percentage of reproductively active adults

TABLE 4. Author, location, capture effort, mean elevation, and species list (with relative abundance ranks) for studies east of the Cascade Crest in Washington.

Author	Thomas (1988)	Campbell (1993)	Frazier (1997)	Taylor (1999)	This study
Location	Southeast Cascades	Selkirk Mountains	Teanaway Valley	White Salmon R.	Naches / Tieton
Capture effort	2 nights	78 nights	65 nights	unreported	135 nights
Mean elevation	500 m	1300 m	675 m	850 m	1000 m
Western long-eared myotis	yes (5)	yes (6)	yes (4)	yes (2)	yes (1)
Long-legged myotis	—	—	yes (1)	yes (1)	yes (2)
Fringed myotis	—	—	—	yes (8)	yes (3)
Big brown bat	yes (3)	yes (7t)	yes (7t)	yes (4)	yes (4)
Silver-haired bat	—	yes (1)	—	yes (9t)	yes (5)
California myotis	—	yes (2)	yes (5)	yes (6)	yes (6)
Western small-footed myotis	yes (2)	yes (3)	yes (6)	yes (7)	yes (7)
Yuma myotis ^a	—	yes (5)	yes (3)	yes (3) ^a	yes (8)
Little brown myotis ^a	yes (1)	yes (4)	yes (2)	yes (3) ^a	yes (9)
Hoary bat	yes (4)	yes (7t)	yes (7t)	yes (9t)	yes (10)
Townsend's big-eared bat	—	—	—	yes (8)	yes (11)
Keen's myotis ^b	—	—	—	yes (5)	—

^a Species considered indistinguishable by Taylor (1999).

^b Species reported (Taylor 1999) outside its known range in coastal Washington and British Columbia (van Zyll de Jong 1979, Nagorsen and Brigham 1993).

than did Campbell (1993), who sampled only after 1 July during a single season. Regardless, patterns of adult sex ratios across studies can still be compared if the methods employed were the same and, therefore, the biases consistent among studies. We found males were more abundant than females (Table 5) as did Thomas (1988) and Campbell (1993). We captured no female silver-haired bats in eastern Washington; however, in Manitoba 90% of all silver-haired bats captured were female (Barclay et al. 1988). This anomaly between these two studies may be an artifact of differences in the timing of capture relative to the timing of migration, a result of local habitat differences, or representative of a geographic variation in the occurrence of the sexes in silver-haired bats. Our results across all species support hypotheses for elevational differences between the sexes (Thomas 1988, Cryan et al. 2000), with proportionally fewer females than males captured in the high-elevation watershed relative to the low-elevation watershed (Table 3). The timing of reproduction in female forest bats in eastern Washington varied widely, both within and among species; however, the data reported here generally fall within the time frames reported for these bats in other regions of North America.

The onset of reproduction occurs in male bats in autumn in the Pacific Northwest; however, data on male reproductive condition are scarce for most

TABLE 5. Percentage of adult male, adult female, and volant juvenile bats, and the percentage of reproductively active adult male and female bats from studies east of the Cascade Crest in Washington. Sex ratio of adults also is provided.

Study	Thomas (1988) ^a	Campbell (1993) ^a	This study
Capture effort	2 nights	78 nights	135 nights
All captures	n = 57	n = 114	n = 1057
Adult males	38	54	65
Adult females	25	33	29
Volant juveniles	37	12	6
Adults only	n = 36	n = 100	n = 998
Reproductive males	n/a	47	15
Reproductive females	82	63	49
Adult sex ratio (M:F)	2.18	1.63	2.26

^a Percentages derived from data in Thomas (1988) and Campbell (1993).

of the bat species captured in this study, with the most extensive data available for the long-legged myotis. Spermatogenesis begins in long-legged myotis in August in New Mexico (Warner and Czaplewski 1984) and all adult and most juvenile male long-legged myotis become reproductively active in August in Oregon (Verts and Caraway 1998). Large testes and small dark epididymides were noted for individuals captured on 17 August but regressed testes and large, pale

epididymides were noted for those captured on 21 September. Schowalter (1980) found spermatozoa in the uterus of a female taken on 21 September in Alberta. Based on consistent data between consecutive breeding seasons in our study, we place the onset of reproductive activity in male long-legged myotis earlier in the summer in eastern Washington than that reported in other portions of its range.

Our comparison of results from geographically-separated studies across eastern Washington demonstrates the existence of variation in the relative abundance of several forest bat species. Thus, conclusions drawn solely on the data we collected on the Okanogan-Wenatchee National Forest would have provided an incorrect and incomplete picture of bat species abundance in the eastern Washington. For example, fringed myotis were relatively common (Table 1), especially in the low-elevation watershed; however, no other study reported this species to be common and most recorded no individual of this species. Examination of other studies confirmed that fringed myotis are rare in eastern Washington; thus, this species requires further study and careful consideration in forest management planning.

Differences in the relative abundance of long-legged myotis among studies was particularly puzzling, as this species was common in three of the five studies we compared but absent in two

others. Whether this pattern reflects differences in sampling effort among studies, or differences in habitat suitability remains unclear. More data on the habitat requirements of long-legged myotis, across multiple geographic locations, are needed. We encourage future studies that assess long-legged myotis habitat selection and landscape-scale variation in their abundance in forests of the Pacific Northwest.

Acknowledgements

Funding and support was provided by the Northwest Bat Cooperative, Bat Conservation International, Inc., and the Department of Agriculture, University of Kentucky. We thank E. Carnahan, A. Christensen, G. Falxa, M. Neutzmann, K. Nye, C. Phifer, C. Reber, and M. Toncray for assistance in the field. Access to watersheds and logistical support were provided by P. Forbes, Okanogan-Wenatchee National Forest, L. Hicks, Plum Creek Timber Company, and J. McGowan, Oak Creek Wildlife Management Area. J. Erickson and P. Forbes provided comments on earlier drafts. This investigation is connected with a project of the Kentucky Agricultural Experiment Station (KAES No. 03-09-061) and is published with the approval of the director. Methods used in this study were approved by the Institutional Animal Care and Use Committee, University of Kentucky (IACUC No. 00219A2001).

Literature Cited

- Allen, G. M. 1939. Bats. Dover Publications, New York.
- Anthony, E. L. P. 1988. Age determination in bats. Pages 47-58 In T. H. Kunz (editor), Ecological and Behavioral Methods for the Study of Bats, Smithsonian Institution Press, Washington, D.C.
- Barbour, R. W., and W. H. Davis. 1969. Bats of America. University of Kentucky Press, Lexington, Kentucky.
- Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. *Journal of Animal Ecology* 60:165-178.
- Barclay, R. M. R., P. A. Faure, and D. R. Farr. 1988. Roosting behavior and roost selection by migrating silver-haired bats (*Lasiurus noctivagans*). *Journal of Mammalogy* 69:821-825.
- Campbell, L. A. 1993. Bat diversity and habitat use in managed forests of northeastern Washington. M.S. Thesis, Washington State University, Pullman, Washington.
- Christy, R., and S. D. West. 1993. Biology of bats in Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-308. Pacific Northwest Research Station, Portland, Oregon.
- Cockrum, E. L., and E. Ordway. 1959. Bats of the Chiricahua Mountains, Cochise County, Arizona. American Museum, No. 1938.
- Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy* 81:719-725.
- Czaplewski, N. J., J. P. Farney, J. K. Jones, Jr., and J. D. Dreucker. 1979. Synopsis of bats of Nebraska. Texas Tech University, Occasional Papers of the Museum 61:1-24.
- Dalquest, W. W. 1948. Mammals of Washington. University of Kansas, Lawrence, Kansas. Publication of the Museum of Natural History 2:1-444.
- Dalquest, W. W., and M. C. Ramage. 1946. Notes on the long-legged bat (*Myotis volans*) at Old Fort Tejon and vicinity, California. *Journal of Mammalogy* 27:60-63.
- Davis, W. H., and R. W. Barbour. 1970. Life history data on some southwestern *Myotis*. *Southwestern Naturalist* 15:261-273.
- Druecker, J. D. 1972. Aspects of reproduction in *Myotis volans*, *Lasiurus noctivagans*, and *Lasiurus cinereus*. Ph.D. Dissertation, University of New Mexico, Albuquerque, New Mexico.

- Easterla, D. A. 1973. Ecology of the 18 species of Chiroptera at Big Bend National Park, Texas: parts 1 and 2. *Northwest Missouri State University Studies* 34:1-165.
- Fenton, M. B., C. G. van Zyll de Jong, G. P. Bell, D. B. Campbell, and M. LaPlante. 1980. Distribution, parturition dates, and feeding of bats in south-central British Columbia. *Canadian Field-Naturalist* 94:416-420.
- Findley, J. S. 1954. Reproduction in two species of *Myotis* in Jackson Hole, Wyoming. *Journal of Mammalogy* 35:434.
- Forest Ecosystem Management Assessment Team. 1993. Forest ecosystem management: An ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. U.S. Government Printing Office 1993-793-071.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.
- Frazier, M. W. 1997. Roost site characteristics of the long-legged myotis (*Myotis volans*) in the Teanaway River Valley of Washington. M.S. Thesis, University of Washington, Seattle, Washington.
- Gitzen, R. A., J. L. Erickson, and S. D. West. 2002. Bat activity and species occurrence on the Hanford site in eastern Washington. *Northwestern Naturalist* 83:35-46.
- Hall, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley, California.
- Hayes, J. P. 2003. Habitat ecology and conservation of bats in western coniferous forests. Pages 81-119 *In* C. J. Zabel and R. G. Anthony (editors), *Mammal Community Dynamics in Coniferous Forests: Management and Conservation Issues in Western North America*. Cambridge University Press.
- Jones, J. K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas, Publications of the Museum of Natural History 16:1-356.
- Jones, J. K., Jr., and H. H. Genoways. 1967. Annotated checklist of bats from South Dakota. *Transactions of the Kansas Academy of Science* 70:184-196.
- Jones, J. K., Jr., R. P. Lampe, C. A. Spemath, and T. H. Kunz. 1973. Notes on the distribution and natural history of bats in southern Montana. *Texas Tech University, Occasional Papers of the Museum* 15:1-12.
- Kunz, T. H., and C. E. Brock. 1975. A comparison of mist nets and ultrasonic detectors for monitoring flight activity of bats. *Journal of Mammalogy* 56:907-911.
- Kurta, A., and J. O. Matson. 1980. Disproportionate sex ratio in the big brown bat (*Eptesicus fuscus*). *American Midland Naturalist* 104:367-369.
- Lewis, S. E. 1995. Roost fidelity of bats: a review. *Journal of Mammalogy* 76:481-496.
- Manning, R. W., and J. K. Jones, Jr. 1989. *Myotis evotis*. *Mammalian Species* 329:1-5.
- Maser, C. 1998. Mammals of the Pacific Northwest: from the coast to the high Cascades. Oregon State University Press, Corvallis, Oregon.
- Miller, G. S., Jr., and G. M. Allen. 1928. The American bats of the genera *Myotis* and *Pipistrellus*. *Bulletin of the U.S. National Museum* 144:1-218.
- Nagorsen, D. W., and R. M. Brigham. 1993. Bats of British Columbia. University of British Columbia Press, Vancouver, British Columbia.
- O'Farrell, M. J., and E. H. Studier. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology* 54:18-30.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-45 *In* T. H. Kunz (editor), *Ecological and Behavioral Methods for the Study of Bats*, Smithsonian Institution Press, Washington, D.C.
- Schowalter, D. B. 1980. Swarming, reproduction, and early hibernation of *Myotis lucifugus* and *Myotis volans* in Alberta. *Journal of Mammalogy* 61:350-354.
- Schowalter, D. B., and J. R. Gunson. 1979. Reproductive biology of the big brown bat (*Eptesicus fuscus*) in Alberta. *Canadian Field-Naturalist* 93:243-251.
- Taylor, J. A. 1999. Roost-site and habitat selection of the long-legged myotis (*Myotis volans*) in a managed landscape of the eastern Cascade range. M.S. Thesis, Michigan State University, East Lansing, Michigan.
- Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* 52:619-626.
- Tidemann, C. R., and D. P. Woodside. 1978. A collapsible bar-trap and a comparison of results obtained with the trap and with mist-nets. *Australian Wildlife Research* 5:355-362.
- USDA Forest Service and USDI Bureau of Land Management. 1994. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the Northern Spotted Owl. Unpublished report on file at USDA Forest Service, Portland, Oregon.
- van Zyll de Jong, C. G. 1979. Distribution and systematic relationships of long-eared *Myotis* in western Canada. *Canadian Journal of Zoology* 57:987-994.
- Vaughn, T. A., and P. H. Krutzsch. 1954. Seasonal distribution of the hoary bat in southern California. *Journal of Mammalogy* 35:431-432.
- Verts, B. J., and L. N. Caraway. 1998. Land Mammals of Oregon. University of California Press, Berkeley, California.
- Warner, R. M., and N. J. Czaplewski. 1984. *Myotis volans*. *Mammalian Species* 224:1-4.
- Wunder, L., and A. B. Carey. 1996. Use of the forest canopy by bats. *Northwest Science* 70:79-85.
- Zimmerman, G. S., and W. E. Glanz. 2000. Habitat use by bats in eastern Maine. *Journal of Wildlife Management* 64:1032-1040.

Received 28 May 2003

Accepted for publication on 29 February 2004