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Source: Monographs of the Western North American Naturalist, 5(1) : 1-19

Published By: Monte L. Bean Life Science Museum, Brigham Young University

URL: https://doi.org/10.3398/042.005.0101

Monographs of the Western North American Naturalist 5, © 2011, pp. 1–19

BATS OF MESA VERDE NATIONAL PARK, COLORADO: COMPOSITION, REPRODUCTION, AND ROOSTING HABITS

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ABSTRACT.—We determined the bat fauna at Mesa Verde National Park (Mesa Verde) in 2006 and 2007, characterized bat elevational distribution and reproduction, and investigated roosting habits of selected species. We captured 1996 bats of 15 species in mist nets set over water during 120 nights of sampling and recorded echolocation calls of an additional species. The bat fauna at Mesa Verde included every species of bat known west of the Great Plains in Colorado, except the little brown bat (*Myotis lucifugus*). Some species showed skewed sex ratios, primarily due to a preponderance of males. Thirteen species of bats reproduced at Mesa Verde. Major differences in spring precipitation between the 2 years of our study were associated with differences in reproductive rates and, in some species, with numbers of juveniles captured. Reduced reproductive effort during spring drought will have a greater impact on bat populations with the forecasted increase in aridity in much of western North America by models of global climate change. We radiotracked 46 bats of 5 species to roosts and describe the first-known maternity colonies of spotted bats (*Euderma maculatum*) in Colorado. All 5 species that we tracked to diurnal roosts relied almost exclusively on rock crevices rather than trees or snags, despite the presence of mature forests at Mesa Verde and the use of trees for roosts in similar forests elsewhere by some of these species. Comparisons with past bat surveys at Mesa Verde and in surrounding areas suggest no dramatic evidence for effects of recent stand-replacing fires on the composition of the bat community.

Key words: bats, Chiroptera, reproduction, roosts, drought, fires, climate change.

Several species of western bats are of conservation concern and were former candidates for listing under the U.S. Endangered Species Act (O'Shea et al. 2003). Thus a fundamental objective of resource managers interested in bats is to inventory the bat fauna in specific management areas (e.g., Kuenzi et al. 1999, Morrell et al. 1999, Chung-MacCoubrey 2005). Managers may also wish to determine whether an area supports reproductively active bats, what habitat features bats use for roosts, and how bats are affected by landscape-level changes in habitat (e.g., Lacki et al. 2007b). We undertook a study at Mesa Verde National Park, Colorado, with such objectives in mind.

Mesa Verde National Park has suffered dramatic landscape alterations from droughts and stand-replacing wildfires since 1989 (Floyd et al. 2003, 2004, 2006). Large tracts of piñon-juniper woodlands were destroyed, and trees in such woodlands can provide important roosts for bats (Chung-MacCoubrey 2003a, 2003b). The long-term effects of droughts and large fires on western bat communities have not been well addressed (Fisher and Wilkinson 2005). The effects of drought and fire on bat faunas is of concern given projections of climate change models for greater aridity in much of western North America (Holden et al. 2007, Seager et al. 2007, Barnett et al. 2008). We sought comparative evidence for such effects from our survey, past surveys at Mesa Verde National Park (Chung-MacCoubrey and Bogan 2003), and surveys done in nearby regions of the Four Corners states (e.g., Mollhagen and Bogan 1997, Morrell et al. 1999, Chung-MacCoubrey 2005).

STUDY AREA

Mesa Verde is a large (53,870-ha), southward-sloping cuesta in southwestern Colorado intersected by numerous canyons. Mesa Verde National Park (herein referred to as Mesa Verde) occupies 21,433 ha of the cuesta and spans an elevational range of 1835 m to 2612 m (Floyd et al. 2003). We categorized sites where we captured bats above or below the midpoint of this range (2223 m) as higher elevation

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(2311 m or higher) or lower elevation (2165 m or lower). Vegetation types at Mesa Verde range from high-desert shrublands to pockets of montane forests, but the area is dominated by piñon-juniper woodlands (Floyd et al. 2003). Climate is temperate and semiarid, with average monthly maximums of 29 °C in July and –8 °C in January; precipitation has high interannual variability, but most falls as monsoon rains in July and August and as snow in March (Doesken and McKee 2003). The 3 months with lowest precipitation are April, May, and June, with June the driest month of the year (Doesken and McKee 2003). Drought coupled with mature, dense forests resulted in large wildfires that have burned extensive tracts of piñon-juniper woodlands since 1989 (over 70% of the park area) (Floyd et al. 2003, 2006, Romme et al. 2003). The landscape history, ecology, and natural history of Mesa Verde are reviewed in the volume edited by Floyd (2003).

METHODS

We sampled the bat fauna in 2006 and 2007 by setting mist nets (Avinet, Inc., Dryden, NY) over or along margins of water sources used by bats. We sampled 11 such sites, ranging in elevation from 1890 m to 2361 m, all within park boundaries except the Bear Track stock tank located immediately adjacent on Bureau of Land Management property. Logistic and access considerations dictated that most sampling (83% of nights) took place at 3 sewage treatment lagoons: Cedar Tree Tower lagoon (UTM 723204 E, 4119490 N; NAD83 datum) on lower Chapin Mesa, upper Morefield Canyon lagoon (729092 E, 4128479 N), and Far View lagoon (722669 E, 4126030 N) on upper Chapin Mesa above Little Soda Canyon. In both years, we also sampled at the base of a cliff (724412 E, 411634 N) a drainage tunnel frequented by bats early at night (perhaps for water) and a fourth sewage lagoon on Wetherill Mesa (719103 E, 4128479 N). In 2006, we netted bats at the Far View Visitor Center (721940 E, 4126169 N) at a stairwell used as a night roost and at Bear Track stock tank (724436 E, 4131913 N). In 2007, we netted bats at 3 seepage and runoff pools in Soda Canyon (723711 E, 4119868 N) and Rock Canyon (719479 E, 4115672 N; 719456 E, 4115598 N).

We report effort as “net-nights”—the total linear lengths of nets deployed each night divided by 12 m, the typical length of nets. We determined sex and reproductive condition of each bat captured following criteria in Racey (1988) and determined age (adult or volant juvenile) based on ossification of phalangeal epiphyses (Anthony 1988). Netting began on 17 May in both years and ended on 23 August in 2006 and 17 August in 2007. Personnel who handled bats wore leather gloves, had pre-exposure rabies prophylaxis, and followed capture and handling procedures approved by the Institutional Animal Care and Use Committee of the U.S. Geological Survey, Fort Collins Science Center. We released bats on-site after capture and handling. We retained 15 voucher specimens of 8 species in the U.S. Geological Survey collection at the Museum of Southwestern Biology (MSB), University of New Mexico, Albuquerque. Nomenclature of bats follows regional manuals (Armstrong et al. 1994, Fitzgerald et al. 1994), with recent exceptions. We use *Parastrellus hesperus* for the canyon bat (Hoofer et al. 2006), *Corynorhinus townsendii* for Townsend’s big-eared bat (Tumlinson and Douglas 1992, Bogdanowicz et al. 1998), and *Myotis occultus* for the occult myotis (Piaggio et al. 2002). We identified occult myotis captured in this study based on appearance (reddish brown pelage and missing or displaced upper premolars; Hoffmeister 1986) of occult myotis from elsewhere in southern Colorado (Piaggio et al. 2002), but we retained voucher specimens for future study.

Selected bats were radio-tagged soon after capture to determine locations of daytime roosts. We used miniature radio-transmitters tuned to 164–165 MHz (Holohil Systems Ltd., Woodlawn, Ontario, Canada; Blackburn Transmitters, Nacogdoches, TX). We focused tracking on reproductive females to find maternity colonies. Transmitters weighed 0.32–0.78 g and were deployed on bats only when the transmitter weighed ≤5% of the bat’s body weight (Aldridge and Brigham 1988, Neubaum et al. 2005). After trimming a small patch of fur to within 1 mm of the skin, transmitters were attached to the midscapular region of the dorsum using surgical adhesive (Skin-Bond, Smith & Nephew, Largo, FL). Bats were held for 30 minutes after transmitter attachment to ensure adhesion. We used scanning-telemetry receivers (R-1000, Communication Specialists, Inc., Orange, CA) and monitored signals from vehicles with roof-mounted 5-element Yagi antennas and on foot using collapsible 3-element Yagi antennas. In 2007, we augmented searches with 2 tracking flights in a Cessna 182 fixed-wing aircraft with antennas mounted on the wing struts. When we detected radio signals of tagged bats, we zeroed in and tried to determine their exact location. In most cases, we could not reach the origins of transmitter signals because of cliffs and inaccessible canyons. When we could not get within 5 m of the roost, we took multiple bearings on the signals and estimated locations by triangulation. We attempted to locate tagged bats daily for the life of each transmitter (8–14 days). Upon finding a bat roost, we recorded structure type (e.g., building, rock crevice, or tree) and qualitative descriptions of the roost structure and surrounding area. When practical, we sat outside of roosts at dusk and counted the number of bats that emerged. At roosts of spotted bats (*Euderma maculatum*), we observed bats and counted the number of individuals heard making audible calls as they left crevice entrances.

We recorded echolocation calls and searched for distinctive acoustic properties of additional species not captured in nets. We recorded ultrasonic calls of bats from sunset to sunrise on 10 nights each month in June, July, and August 2006 at 4 randomly selected stations on Chapin Mesa. We used AnaBat™ II bat detectors with programmable zero-crossing analysis interface modules (AnaBat™ CF Storage ZCAIM; Titley Electronics, NSW, Australia). Detectors were placed in weatherproof boxes oriented in random directions and angled 45° to a reflective polycarbonate-plastic surface. Detectors were precalibrated to minimize variation in zone of reception among units. We used Analook for Windows [software], version 3.20 (http://users.lmi.net/corben/anabat.htm), to analyze call recordings, and we categorized them by species, based on qualitative and quantitative features documented in libraries of species-specific echolocation calls (O'Farrell et al. 1999, Everette et al. 2001, Ellison et al. 2005; C. Corben and M. O'Farrell, O'Farrell Biological Consulting, unpublished data 2007). We did not attempt to distinguish between calls from silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*). We defined a "bat pass" as a sequence of ≥ 2 call pulses produced by a single bat from the moment it was detected until it left the range of detection (Thomas 1988). Detections of <2 call pulses were not used.

Data Analysis

We provide simple descriptive summary statistics, percentages, and community indices based on capture data. To compare proportions among categorical data sets, we provide 95% confidence intervals (CI) and assess degree of overlap. For contrasting sex ratios, we expected CIs to overlap 0.5 if sex ratios of males to females were equal. We also used logistic regression (PROC GENMOD, SAS Institute, Inc. 2003) coupled with an information-theoretic approach to select between competing explanatory models (Burnham and Anderson 2002) and test the biological hypotheses that reproductive rates varied between 2006 and 2007; the 2 years differed greatly in amount of spring precipitation and community productivity.

We compared the proportions of reproductive females in each year using 2 models. Under the general model, the probability of a female being reproductive was allowed to vary between the 2 years; whereas under the constrained model, the probability of a female being reproductive was assumed to be constant between the 2 years. Models were ranked using Akaike's information criterion corrected for sample size (AIC_c) (Burnham and Anderson 2002). We also calculated AIC_c differences (Δ_i = difference in AIC_c score between the *i*th and the top-ranked model) and Akaike weights (w_i = probability that the *i*th model is the best approximating model among candidate models). The model with the lowest AIC_c score was assumed to be the best-fitting model (Burnham and Anderson 2002).

Reproductive rate is the life history trait of bats most likely to vary with environmental conditions (Barclay et al. 2004). Reproductive rates were calculated as the proportion of adult females captured that were pregnant, lactating, or postlactating within a time period defined by the recognition of the first pregnant and last lactating female of any species. Limiting rates to this period should reduce incorrect field diagnoses (e.g., pregnant bats with small fetuses not detectable by palpation earlier in the season or postlactating bats with regression of teats miscategorized as nonreproductive later in the season). Spring precipitation data were obtained for the Mesa Verde station from the National Climatic Data Center (http://cdo.ncdc.noaa.gov/ancsum/ACS). Comparisons of reproduction, relative abundances, and sex ratios of bats between 2006 and 2007 are limited to data from sites that were sampled in both years.

We compare the bat fauna at Mesa Verde with other regional bat faunas reported in the literature. We limit such comparisons to other studies based on captures of bats in mist nets over water or similar high-use areas but not to those studies based on captures at colonies or on echolocation recordings. To conduct these comparisons, we calculated 4 community indices: species richness (the number of species detected), Jaccard's index of community similarity, Simpson's diversity index, and evenness of distribution of individuals among species based on Simpson's index. We calculated Jaccard's index as $J = C/(A + B - C)$, where C is the number of species in common between the faunas of 2 regions, A is the number of species in one region, and B is the number of species in the other region (Magurran 1988). We express Simpson's index as $1 - D$, where $D = [\sum n(n - 1)]/[N(N - 1)]$, n is the number of individuals in each species, and N is the total number of individuals captured (Magurran 1988). Evenness of the distribution of individuals among species is expressed by the formula $(1/D)/S$, where S is the number of species in the bat fauna. A number of alternative metrics of species richness, diversity, and evenness are available in the ecological literature, each with its own advantages and biases. Their properties are discussed by Magurran (1988, 2004), and their application to bat studies is reviewed by Kingston (2009).

We used a comparative approach to search for evidence of major impacts of recent extensive fires on bat fauna. We compared the relative abundances of species and the aforementioned community indices with those of other surveys using similar methods elsewhere in the Four Corners states within about 375 km of Mesa Verde. These comparisons did not present major difficulties in determining species' taxonomic identity. One possible exception was distinguishing between *M. occultus* and *Myotis lucifugus* (little brown bat) on the basis of geographic distribution. However, only 2 of these other studies reported either species. In one study (Coconino Plateau, Arizona; Morrell et al. 1999), identity of *M. occultus* is supported by the literature on distribution (Hoffmeister 1986), and in the other (Moffat County, Colorado, 330 km north of Mesa Verde; Freeman 1984), identity of *M. lucifugus* is likewise supported by the literature (Armstrong 1972, Armstrong et al. 1994, Fitzgerald et al. 1994).

We also compared our results with those of a previous survey at Mesa Verde in 1989–1994 (Chung-MacCoubrey and Bogan 2003) conducted before the most extensive burns. Our ability to make comparisons with the 1989–1994 survey was limited because those results were primarily from different locations and emphasized small pools in canyons (perhaps biased towards maneuverable species that are more likely to drink at sources with small surface areas) sampled mostly in late July through August. These small pools have since filled with silt from postfire runoff or dried due to prolonged drought, and we were thus unable to repeat sampling at most of the same sites. However, we were able to make comparisons with the 1989–1994 results from netting at or within 2.5 km of the Morefield Canyon site. Additionally, in 2007, we sampled a permanent seepage pool in Soda Canyon on 6 nights; the configuration for netting at this site was similar to the configuration at sites sampled in 1989–1994. We used Jaccard's index and rankings of the most abundant species to make qualitative comparisons with findings of the 1989–1994 surveys of bats at these locations. Original data from the 1989–1994 surveys reported by Chung-MacCoubrey and Bogan (2003) are available through the MSB (http://arctos.database.museum/home.cfm).

In describing relative abundances of bats at Mesa Verde, we arbitrarily use the term "common" for species that account for ≥10% of total captures, "uncommon" for species that account for 2%–9% of total captures, and "rare" for species that account for ≤1% of total captures. To our knowledge, standardized uses for these terms in bat studies are not available in the literature.

RESULTS

Faunal Composition and Adult Sex Ratios

We captured 1996 bats of 15 species at Mesa Verde (Table 1) during 120 nights of sampling (58 nights in 2006 and 62 nights in 2007, for a total of 1082 12-m net-nights). The same 15 species were detected in both years, with similar relative abundances (other than a shift in proportions of silver-haired bats; Table 1). Relative abundances of species at sites sampled in common in both years were similar to relative

TABLE 1. Species and numbers of bats captured at Mesa Verde National Park, Colorado, in 2006 and 2007. Percentages of column totals are given in parentheses. Captures at sites in common in 2006–2007 do not include bats that were captured at sites sampled in only 1 of the 2 years.

Species	Total bats captured	Captured in 2006	Captured in 2007	Captures at sites in common 2006–2007
Antrozous pallidus	5 (<1%)	1 (<1%)	4 (<1%)	3 (<1%)
Corynorhinus townsendii	13 (<1%)	6 (<1%)	7 (<1%)	10 (<1%)
Eptesicus fuscus	203 (10%)	85 (9%)	118 (11%)	182 (10%)
Euderma maculatum	10 (<1%)	4 (<1%)	6 (<1%)	10 (<1%)
Lasionycteris noctivagans	227 (11%)	135 (15%)	92 (8.5%)	227 (12%)
Lasiurus cinereus	51 (2.5%)	12 (1%)	39 (4%)	47 (3%)
Myotis californicus	99 (5%)	25 (3%)	74 (7%)	96 (5%)
Myotis ciliolabrum	199 (10%)	73 (8%)	126 (12%)	193 (10%)
Myotis evotis	286 (14%)	137 (15%)	149 (14%)	227 (12%)
Myotis occultus	100 (5%)	60 (7%)	40 (4%)	100 (5%)
Myotis thysanodes	41 (2%)	19 (2%)	22 (2%)	33 (2%)
Myotis volans	643 (32%)	322 (35%)	321 (30%)	609 (33%)
Myotis yumanensis	18 (1%)	7 (<1%)	11 (1%)	16 (<1%)
Parastrellus hesperus	81 (4%)	18 (2%)	63 (6%)	68 (4%)
Tadarida brasiliensis	20 (1%)	6 (<1%)	14 (1%)	20 (1%)
TOTAL	1996	910	1086	1841

abundances at all sites (including sites sampled in only one year) in either year, suggesting no strong site differences that would bias annual results. Differences in monthly level of effort between years were also minor, at 1–3 nights per site per month in May–July each year. The long-legged myotis (*Myotis volans*) was the most frequently captured bat and accounted for about one-third of the total bats captured (Table 1). Other common species (≥10% of captures) were long-eared myotis (*Myotis evotis*), silver-haired bats, big brown bats, and western small-footed myotis (*Myotis ciliolabrum*). Five species were rarely captured, each accounting for ≤1% of the total (Table 1): pallid bats (*Antrozous pallidus*), Townsend's big-eared bats, spotted bats, Yuma myotis (*Myotis yumanensis*), and Brazilian free-tailed bats (*Tadarida brasiliensis*). Other species were uncommon, including migratory hoary bats (*Lasiurus cinereus*), taken primarily in late spring and early summer; 86% of silver-haired bats and 67% of hoary bats were captured by 30 June in both years, although only 47% of nights sampled were before 30 June. We recorded 15,389 echolocation call files in 2006 and identified 12,888 of them to species or species group. All calls that we identified were attributed to species also captured in mist nets, with the exception of the big free-tailed bat (*Nyctinomops macrotis*). We recorded 698 passes of big free-tailed bats in 2006 during the months of June (389 passes in 8 nights), July (96 passes in 7 nights), and August (213 passes in 8 nights), but no bats of this species were captured.

Disproportionate adult sex ratios occurred in some species of bats. These patterns included more males than females in big brown bats, hoary bats, silver-haired bats, western small-footed myotis, canyon bats, and Brazilian free-tailed bats, but more females than males in long-legged myotis (Table 2). Patterns in sex ratios were consistent between the 2 years at sites sampled in common, except for long-eared myotis, which shifted from more males than females in 2006 to more females than males in 2007 (Table 2). With the exception of long-eared myotis, the proportions of sexes within species in the 2 elevational categories (≤2165 m or ≥2311 m) did not differ strongly between years at Mesa Verde (Table 3). Sex ratios within species also were the same, with broadly overlapping CIs in both elevational categories. The one exception was for long-eared myotis, which had a preponderance of males at higher elevations and females at lower elevations (Table 3). A seeming tendency toward more females at lower elevations was also indicated at pools in Rock Canyon and Soda Canyon (elevations 1899–2103 m), sampled only in 2007. At Rock Canyon we captured 2 lactating female pallid bats (the only pallid bats captured at Mesa Verde). We also captured 9 female canyon bats at Rock Canyon (8 lactating) and only 2 males. In contrast, we captured 64 adult canyon bats over both years at all other sites, and 56 were male. At Soda Canyon, we caught 6 adult female fringed myotis (*Myotis thysanodes*), 4 of which were reproductive, whereas all other sites

TABLE 2. Comparison of adult sex ratios and proportions of adults that were male in 2006 and 2007 (May–August both years) at selected sites at Mesa Verde National Park, Colorado. Only bats at locations sampled in common in the 2 years are included. M = males, F = females, CI = 95% confidence interval.

Species	M:F 2006	M:F 2007	% Male 2006 (CI)	% Male 2007 (CI)
Antrozous pallidus	1:0	2:0	100 (5–100)	100 (20–100)
Corynorhinus townsendii	2:4	2:2	33 (6–76)	50 (9–91)
Eptesicus fuscus	79:6	90:5	93 (85–97)	95 (88–98)
Euderma maculatum	1:3	1:5	25 (1–78)	17 (1–64)
Lasionycteris noctivagans	130:5	87:3	96 (91–98)	97 (90–99)
Lasiurus cinereus	12:0	31:2	100 (70–100)	94 (78–99)
Myotis californicus	11:14	36:33	44 (25–65)	52 (40–64)
Myotis ciliolabrum	45:27	80:37	62 (50–73)	68 (59–76)
Myotis evotis	77:56	32:54	58 (49–66)	37 (27–48)
Myotis occultus	24:34	13:21	41 (29–55)	38 (23–56)
Myotis thysanodes	12:7	2:7	63 (39–83)	22 (4–60)
Myotis volans	70:239	53:197	23 (18–28)	21 (16–27)
Myotis yumanensis	4:3	3:5	57 (20–88)	38 (10–74)
Parastrellus hesperus	13:1	42:7	93 (64–100)	86 (72–94)
Tadarida brasiliensis	6:0	13:1	100 (52–100)	93 (64–100)

combined yielded only 4 reproductive female fringed myotis in 2007; other sites with reproductive female fringed myotis were also at lower elevations.

Comparisons with Other Bat Faunal Surveys

The 4 most abundant species at Morefield Canyon in 2006–2007 were long-eared myotis (25% of captures, $n = 78$), long-legged myotis (24%, $n = 75$), occult myotis (19%, $n = 61$), and silver-haired bats (16%, $n = 50$). Rankings at Morefield Canyon in 1989–1994 were similar (but proportions differed), with long-eared myotis (48%, $n = 41$), long-legged myotis (27%, $n = 23$), silver-haired bats (6%, $n = 5$), and California myotis (*Myotis californicus;* 5%, $n = 4$) as the most abundant species. Relative abundance was greater for occult myotis at Morefield Canyon in our study (1%, $n = 1$ in 1989–1994). Only 4 of the 61 occult myotis captured at Morefield Canyon in 2006–2007 were caught during the month of July. The rank order at Morefield Canyon is different than at Mesa Verde in that long-legged myotis was not the most abundant species either in 2006–2007 or in 1989–1994.

Sampling over small pools in the earlier work and sampling over larger ponds in our study resulted in different biases in rank orders of relative abundance. In 2007, we sampled over the small pool in Soda Canyon on 6 nights and obtained relative rankings of the various species that were similar to rankings from the park-wide 1989–1994 surveys: long-eared myotis (61%, $n = 50$), long-legged myotis (24%, $n = 20$), fringed myotis (7%, $n = 6$), and Townsend's big-eared bats (2%, $n = 2$). Park-wide rankings in the 1989–1994 surveys were as follows: long-eared myotis (40%, $n = 71$), long-legged myotis (30%, $n = 53$), Townsend's big-eared bats (11%, $n = 20$), and fringed myotis (5%, $n = 7$). Based on Jaccard's index of similarity, the bat fauna at Soda Canyon was more similar to that of the 1989–1994 surveys ($J = 0.73$) than to the overall bat fauna at Mesa Verde in 2006–2007 ($J = 0.40$).

Five surveys in the Four Corners states conducted within 375 km of Mesa Verde captured bats in mist nets over water at comparable elevations, most including piñon-juniper woodlands (Table 4). Species composition of the bat fauna at Mesa Verde is very similar to the composition at all of these areas. Species richness at our study area is identical to species richness at 3 other areas and higher than species richness at 2 areas (both primarily in piñon-juniper woodlands). Simpson indices indicate that Mesa Verde is intermediate in diversity and evenness. Two of three species not documented at Mesa Verde have distributions that do not include Colorado (*Idionycteris phyllotis* in Utah and Arizona, and *Myotis auriculus* in Arizona); a third species (little brown bat, *Myotis lucifugus*) was found only at the Moffat County, Colorado, comparison site. Based on Jaccard's index, the bat fauna of Mesa Verde is most similar to the bat fauna of the 2 geographically closest areas previously surveyed: the Henry Mountains in Utah and the Jemez Mountains in New Mexico (Table 4). If migratory tree bats (hoary and silver-haired bats) are removed from consideration because of irregular capture biases during migration peaks, the 3

TABLE 3. Numbers of adult bats captured and proportion that were male at capture sites lower (≤2165 m) or higher (≥2311 m) in elevation at Mesa Verde National Park, Colorado, 2006 and 2007. Data from all sites and dates are included. CI = 95% confidence interval.

	Lower sites (2006)		Higher sites (2006)		Lower sites (2007)		Higher sites (2007)	
Species	*n*	% Male (CI)	*n*	% Male (CI)	*n*	% Male (CI)	*n*	% Male (CI)
Antrozous pallidus	1	100 (5–100)	0	—	3	33 (2–87)	1	100 (5–100)
Corynorhinus townsendii	4	25 (1–78)	2	50 (3–97)	7	43 (12–80)	0	—
Eptesicus fuscus	47	96 (84–99)	38	89 (74–97)	98	95 (88–98)	18	94 (71–100)
Euderma maculatum	1	0 (0–95)	3	33 (2–87)	1	0 (0–95)	5	20 (1–70)
Lasionycteris noctivagans	34	97 (83–100)	101	96 (90–99)	44	95 (83–99)	46	98 (87–100)
Lasiurus cinereus	7	100 (56–100)	5	100 (46–100)	27	96 (79–100)	10	90 (54–99)
Myotis californicus	22	45 (25–67)	3	33 (2–87)	66	48 (36–61)	6	83(36–99)
Myotis ciliolabrum	50	62 (47–75)	23	65 (43–83)	113	65 (55–73)	9	78 (40–96)
Myotis evotis	27	22 (9–43)	109	65 (55–74)	97	12 (7–21)	37	65 (47–79)
Myotis occultus	0	—	58	41 (29–55)	1	0 (0–95)	33	39 (23–58)
Myotis thysanodes	7	43 (12–80)	12	75 (43–93)	17	18 (5–44)	0	—
Myotis volans	133	29 (22–38)	177	18 (13–25)	201	22 (17–28)	77	17 (10–28)
Myotis yumanensis	3	66 (13–98)	4	50 (9–91)	9	56 (23–85)	1	0 (0–95)
Parastrellus hesperus	10	90 (54–99)	4	100 (40–100)	60	73 (60–84)	0	—
Tadarida brasiliensis	5	100 (46–100)	1	100 (5–100)	14	93 (64–100)	0	—

most common species in most study areas are long-legged myotis, long-eared myotis, and big brown bats. This is true in 4 of the 6 study areas, including Mesa Verde (Table 4), and perhaps in a fifth (the California myotis and western small-footed myotis were treated as a single species in one study). In the remaining 2 study areas, at least 2 of the 3 most abundant species at Mesa Verde (long-legged myotis, long-eared myotis, and big brown bats) were among the top 3 most abundant species (exclusive of migratory tree bats; Table 4). The proportions of California myotis and western small-footed myotis among the other Four Corners study areas each varied from <1% to 13% (Table 4); at Mesa Verde, the relative abundances of these 2 species were similar: 5% (California myotis) and 10% (western small-footed myotis). Three other species uncommon at Mesa Verde (occult myotis, canyon bats, and fringed myotis) were also typically uncommon at most other study areas. The occult myotis was only present at one other area (Coconino Plateau, relative abundance 13%), the canyon bat was present at 3 of the 6 areas at relative abundances of <1% to 11%, and the fringed myotis was present at all areas but always at a low relative abundance (<1% to 8%, Table 4). Rare species at Mesa Verde were similarly rare or uncommon in most of these other faunas (Table 4). Big free-tailed bats were only captured in one of the other studies and constituted only 1% of the total bats. Townsend's big-eared bat and the spotted bat always made up <1% to 3% of the total bats in all studies. Pallid bats made up 4% or less in all other regional studies, and Brazilian free-tailed bats made up ≤1% in 5 of the 6 studies; the Yuma myotis represented 2% or less of the total captures in all 6 studies.

Bat Reproduction and Spring Precipitation

Spring precipitation differed markedly between the 2 years, with higher precipitation in 2007 (Table 5). Much more precipitation fell in April and May 2007 than in April and May 2006. In April 2007 total precipitation was 1.6 times as high as in April 2006, and it was slightly higher than the monthly median and mean for April 1949–2005 (but within the 95% confidence limits). Total precipitation in May 2007 was more than 25 times that in May 2006 and much higher than typical for May in the 1949–2005 data set (Table 5). Precipitation in June varied less between the 2 study years.

TABLE 4. Comparative characteristics and results of 6 surveys of bat faunas within 375 km of Mesa Verde National Park, Colorado. Surveys sampled bats by capturing them in mist nets (Freeman [1984] includes 74 based on observation). All study areas were within similar elevation ranges, and most included piñon-juniper woodlands. The value of Jaccard's index was based on similarity with the Mesa Verde bat fauna. ND = not determined.

Feature or species	Mesa Verde National Park, CO	Coconino Plateau, AZ[a]	Henry Mountains, UT[b]	Jemez Mountains, NM[c]	Gallinas–San Mateo Mountains, NM[d]	Moffat County, CO[e]
Species	15	15	15	15	10	11
Bats captured	1996	1684	572	1532	1669	546
Index of diversity	0.83	0.84	0.89	0.73	ND	0.73
Index of evenness	0.40	0.40	0.63	0.25	ND	0.34
Jaccard's index	1.00	0.76	0.88	0.88	ND	0.63
Km to Mesa Verde	0	375	220	240	350	330
Years surveyed	2 (2006–2007)	3 (1993–1995)	4 (1993–1996)	3 (1995–1997)	5 (1995–1999)	3 (1979–1981)
Capture sites	13	31	22	28	15	3
Nights	121	59	ca. 33	105	77	63
Elevation range (m)	1890–2361	2018–2572	1260–3078	1738–2774	2133–2682	2100
Antrozous pallidus	5 (<1%)	41 (2%)	20 (3%)	67 (4%)	11 (<1%)	19 (3%)
Corynorhinus townsendii	13 (<1%)	2 (<1%)	16 (3%)	7 (<1%)	0	5 (<1%)
Eptesicus fuscus	203 (10%)	390 (23%)	94 (16%)	156 (10%)	678 (41%)	23 (4%)
Euderma maculatum	10 (<1%)	0	1 (<1%)	12 (<1%)	0	0
Idionycteris phyllotis	0	26 (2%)	9 (2%)	0	0	0
Lasionycteris noctivagans	227 (11%)	70 (4%)	71 (12%)	745 (49%)	39 (2%)	13 (2%)
Lasiurus cinereus	51 (3%)	43 (3%)	2 (<1%)	120 (8%)	19 (1%)	48 (9%)
Myotis auriculus	0	56 (3%)	0	0	0	0
Myotis californicus	99 (5%)	8 (<1%)	44 (8%)	11 (<1%)	343 (21%)[f]	44 (8%)
Myotis ciliolabrum	199 (10%)	17 (1%)	8 (1%)	86 (6%)	—[f]	72 (13%)
Myotis evotis	286 (14%)	269 (16%)	75 (13%)	106 (7%)	270 (16%)	257 (47%)
Myotis lucifugus	0	0	0	0	0	5 (<1%)
Myotis occultus	100 (5%)	224 (13%)	0	0	0	0
Myotis thysanodes	41 (2%)	122 (7%)	34 (6%)	69 (5%)	126 (8%)	3 (<1%)
Myotis volans	643 (32%)	400 (24%)	71 (12%)	101 (7%)	175 (10%)	57 (10%)
Myotis yumanensis	18 (1%)	3 (<1%)	13 (2%)	13 (<1%)	1 (<1%)	0
Nyctinomops macrotis	0 (detected)	0	0	15 (1%)	0	0
Parastrellus hesperus	81 (4%)	0	64 (11%)	10 (<1%)	0	0
Tadarida brasiliensis	20 (1%)	4 (<1%)	50 (9%)	14 (1%)	7 (<1%)	0

[a] Morrell et al. (1999), Rabe et al. (1998a).

[b] Mollhagen and Bogan (1997).

[c] Bogan et al. (1998).

[d] Chung-MacCoubrey (2005).

[e] Freeman (1984).

[f] *Myotis californicus* and *Myotis ciliolabrum* were combined because of identification difficulty.

TABLE 5. Monthly precipitation totals (cm; April–August, 2006 and 2007) and summary statistics for spring and summer precipitation (cm) at Mesa Verde National Park, Colorado, 1949–2005. Data for 1977 were unavailable.

Time period	Statistic	April	May	June	July	August
2006	Total	2.2	0.3	2.2	3.8	4.6
2007	Total	3.6	7.2	0.7	6.2	8.3
1949–2005	Mean	3.2	2.7	1.5	4.4	5.1
1949–2005	95% CL	2.6, 3.8	2.0, 3.3	1.1, 2.0	3.6, 5.2	4.3, 5.8
1949–2005	Median	2.8	2.4	0.7	4.0	4.8

Thirteen species of bats at Mesa Verde showed evidence of reproduction, with no evidence of female reproduction detected in hoary bats or silver-haired bats. We first detected pregnancy in bats on 22 June in 2006 and 18 June in 2007; we noted the last lactating bat on 22 July in 2006 and 25 July in 2007; and we caught the first volant juvenile on 15 July 2006 and 22 July 2007. Therefore, we limited comparisons of reproductive rates between years to bats captured from 18 June to 26 July in either year to minimize incorrect field diagnoses, and we limited comparisons to species with sample sizes ≥5 females each year. Reproductive rates in 3 species of bats (western small-footed myotis, long-eared myotis, and long-legged myotis) were higher in 2007 than in 2006, with little or no overlap in CIs and high support by AIC_c for the general logistic regression models for between-year differences (Tables 6, 7). Models wherein proportions were constrained to be equal had greater support in California myotis, fringed myotis, and occult myotis (Table 7). Occult myotis had high reproductive rates in both years. We also captured fewer volant juvenile bats in 2006 than in 2007. In 2006, we captured 6 juveniles of 3 species on 16 nights between 15 July and 15 August (0.4 juveniles per night). In 2007, we captured 68 juveniles of 8 species on 23 nights between the same dates (3.0 juveniles per night).

Roosts of Bats

We radio-tagged 73 bats of 7 species and were successful in finding general roost locations of 46 individuals of 5 species, including long-eared myotis, occult myotis, fringed myotis, long-legged myotis, and spotted bats (Table 8). We were unable to find any daytime roosts of the Yuma myotis or Townsend's big-eared bats that we tagged, but we occasionally detected radio signals from them at night while they were in flight over the mesa tops.

Most bats roosted in rock crevices, but a few also used other structures. Long-legged myotis, fringed myotis, and spotted bats roosted exclusively in rock crevices within steep canyon slopes and cliff faces. Two female long-eared myotis roosted in trees: one nonreproductive female roosted in juniper snags, downed logs, and live trees north of Mesa Verde; and the other roosted for one day in a juniper snag on an unburned part of Chapin Mesa. The latter incident was our only observation of a reproductive female bat roosting in a tree in piñon-juniper woodlands of Mesa Verde. All other female long-eared myotis ($n = 17$) roosted in rock crevices in canyons, often close to the ground (more detailed analyses of roosts used by long-eared myotis are reported by Snider [2009]). The inaccessibility of roosts used by other species precluded our ability to gather detailed information on their characteristics. In most cases, we tracked radio signals to cliff faces but could not determine the exact locations of roosting bats. Rock crevices used by long-legged myotis tended to be in canyon walls between 2 and 15 m in height. On one occasion, we were able to observe an emergence flight of 131 individuals, presumably members of a maternity colony. Signals of spotted bats always were detected from >10 m to 15 m high on sheer cliff faces, but by watching and listening to emerging bats at dusk, we determined the precise location and characteristics of 2 widely separated roosts of spotted bats. In these cases, 18 and 12 bats were seen and heard emerging from long vertical crevices in high walls of Echo Cliffs in Navajo Canyon and in Soda Canyon, respectively. Spotted bats began emerging just before dark (making observation difficult), and emergence of all individuals took about 25–35 minutes. Emergences were followed by calling sounds from spotted bats circling in the air near the roost entrance; during these observations, we heard what sounded like pairs of bats flying together, perhaps mother and young. Some bats were clearly observed circling at the roost and did not leave the area until joined by a second bat leaving the roost. The

TABLE 6. Between-species comparison of reproductive rates of adult female bats captured at Mesa Verde National Park, Colorado, from 18 June to 26 July, in 2006 and 2007. Only species with sample sizes ≥5 adult females were included. Reproductive rates were based on total bats diagnosed as pregnant, lactating, or postlactating as a proportion of all adult females sampled and diagnosed during the 18 June to July 26 time period. To assure comparability between the 2 sampling years, only bats sampled at locations in common in both 2006 and 2007 were included.

Species	Repro rate 2006 (%)	CI (%)	*n*	Repro rate 2007 (%)	CI (%)	*n*
Myotis californicus	64	32–88	11	69	48–85	26
Myotis ciliolabrum	30	13–54	20	63	42–80	27
Myotis evotis	34	22–56	32	69	53–82	42
Myotis occultus	89	51–99	9	77	46–94	13
Myotis thysanodes	33	6–76	6	60	17–93	5
Myotis volans	27	21–34	180	68	59–76	122

TABLE 7. Rankings by Akaike's information criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002) of top logistic regression models (PROC GENMOD in SAS Institute, Inc. 2003) comparing proportions of reproductive female bats caught at Mesa Verde National Park, Colorado, in 2006 with proportions in 2007, based on sites sampled in common between the 2 years. Symbols: K = number of parameters in the model; Δ_i = difference in AIC_c value between the i^{th} and top-ranked model; w_i = Akaike weight (probability that the i^{th} model is the best approximating model among the candidate models). Under the general model, the probability of a female being reproductive was allowed to vary between the 2 years, whereas under the constrained model, the probability of a female being reproductive was assumed to be constant between the 2 years.

Analysis and model	K	AIC_c	Δ_i	w_i
Myotis californicus reproductive rates in 2006 vs. 2007				
Constrained	1	48.63	0.00	0.76
General	2	50.98	2.35	0.24
Myotis ciliolabrum reproductive rates in 2006 vs. 2007				
General	2	62.36	0.00	0.91
Constrained	1	67.05	4.69	0.09
Myotis evotis reproductive rates in 2006 vs. 2007				
General	2	97.32	0.00	0.97
Constrained	1	104.15	6.83	0.03
Myotis occultus reproductive rates in 2006 vs. 2007				
Constrained	1	23.06	0.00	0.72
General	2	24.96	1.89	0.28
Myotis thysanodes reproductive rates in 2006 vs. 2007				
Constrained	1	17.60	0.00	0.76
General	2	19.86	2.26	0.24
Myotis volans reproductive rates in 2006 vs. 2007				
General	2	367.70	0.00	1.00
Constrained	1	415.88	48.18	0.00

occult myotis was the only species at Mesa Verde that did not consistently roost in rock crevices during summer. In early summer, a pregnant female moved between a building in the Mancos Valley and a rock crevice and ponderosa pine snag in Morefield Canyon, whereas all other tagged female occult myotis roosted in buildings in the Mancos Valley.

The distribution of sites used by roosting bats varied with species at Mesa Verde. Roosts of long-eared myotis and long-legged myotis were found throughout the study area. Roosts of other bat species were more limited in distribution, with occult myotis roosting only in Morefield Canyon and in the Mancos River Valley, fringed myotis only roosting in Soda Canyon near the southern end of Mesa Verde (perhaps biased by tagging location), and spotted bats only roosting in steep-walled canyons on the southern end of Mesa Verde. Reproductive female bats were found roosting in all parts of the study area within about 15 km of capture sites, but roosts tended to be at lower elevations in canyons and outer slopes of the cuesta (Table 8). Only 2 roosts used by a pregnant long-legged bat on sequential days were situated in what we considered higher elevations of Mesa Verde (≥2311 m).

The distance that bats traveled from tagging sites to subsequent roosts was variable (<1 km–14 km; Table 8). Spotted bats and occult myotis traveled the longest distances, and long-eared myotis and fringed myotis traveled the shortest

TABLE 8. Summary of female bats marked with miniature radio-transmitters during the summers of 2006 and 2007 at Mesa Verde National Park, Colorado, grouped by species and reproductive status. Values in parentheses indicate the number of individuals successfully followed to roost sites (roost sites for others were not located). Also listed are average distances moved between capture sites and daytime roosts, as well as average elevations of roost sites.

	Reproductive status						
Species	Unknown	Pregnant	Lactating	Postlactating	Total	Mean distance (km) to roost ± SD	Mean elevation (m) of roost ± SD
Myotis evotis	5 (2)	3 (0)	21 (16)	3 (1)	32 (19)	2.3 ± 1.8	2146 ± 135
Myotis occultus	—	4 (4)	1 (0)	—	5 (4)	6.8 ± 5.3	2107 ± 122
Myotis thysanodes	1 (0)	—	5 (3)	—	6 (3)	2.7 ± 2.3	1997 ± 37
Myotis volans	—	14 (9)	5 (5)	—	19 (14)	3.8 ± 3.3	2108 ± 152
Myotis yumanensis	—	1 (0)	—	—	1 (0)	—	—
Corynorhinus townsendii	1 (0)	—	2 (0)	—	3 (0)	—	—
Euderma maculatum	2 (2)	1 (1)	4 (3)	—	7 (6)	10.8 ± 3.8	1968 ± 44
TOTAL	9 (4)	23 (14)	38 (27)	3 (1)	73 (46)	—	—

distances. We also observed interspecific variation in the degree to which bats switched roosts from day to day. Long-eared myotis frequently switched roosts, with an average of 2.3 roosts (1–7 roosts per individual, SD = 2.1) discovered per bat followed. The occult myotis also switched roosts frequently, with an average of 2.0 roosts (1–3 roosts per bat, SD = 0.8). Our observations suggest that other species switched roosts less often, if at all, with <2 roosts found or suspected per individual tracked.

DISCUSSION

Faunal Composition and Adult Sex Ratios

Sixteen species of bats occur at Mesa Verde. The bat fauna in 2006 and 2007 included every species of bat known west of the Great Plains in Colorado, except for the little brown bat (Armstrong et al. 1994, Fitzgerald et al. 1994). Our results illustrate the value of conducting thorough contemporary faunal surveys of management areas of interest. The first faunal list of bats at Mesa Verde documented 8 species based on 25 specimens (Anderson 1961): California myotis, long-eared myotis, western small-footed myotis, fringed myotis, long-legged myotis, big brown bats, Townsend's big-eared bats, and Brazilian free-tailed bats. The list increased by 2 species with the inclusion of canyon bats and hoary bats in 1963 and 1964 (based on 4 specimens—Douglas 1967). The Mesa Verde bat fauna was again surveyed in 1989–1994 (Chung-MacCoubrey and Bogan 2003). This effort resulted in capture of 177 bats of 11 species, adding 3 additional species: pallid bats, silver-haired bats, and occult myotis. In addition, 3 skulls of spotted bats were found in spotted owl (*Strix occidentalis*) pellets, and spotted bat calls were heard at night, although no bats were captured (Chung-MacCoubrey and Bogan 2003). The fauna we documented in 2006 and 2007 added captures of spotted bats, Yuma myotis, the first canyon bats since 1963, and the first Brazilian free-tailed bats since 1936 (Anderson 1961, Chung-MacCoubrey and Bogan 2003); we also documented big free-tailed bats by acoustic recordings.

The occurrence of spotted bats at Mesa Verde is noteworthy. This species was first found in Colorado in 1982, but its range in Colorado was thought to be restricted to the northwestern corner of the state. There were published records for just 3 specimens, all from northwestern Colorado (Finley and Creasy 1982, Bogan et al. 1988). Past observational records of spotted bats in Colorado were acoustically-based foraging-habitat surveys in the northwestern part of the state (Navo et al. 1992, Storz 1995). We provide new distribution records and the first documentation of spotted bat maternity colonies in Colorado, as well as new information on locations and sizes of maternity colonies. To our knowledge, only one other study has observed maternity colonies of this species anywhere in western North America (Bogan et al. 1998), and our findings are consistent with that report. Records of other species are less noteworthy, although the higher number of big free-tailed bat calls in June differs from most past acoustic and capture records for this species in Colorado, which document more numerous calls in July and August (Navo and Gore 2001). The bat fauna at Mesa Verde contains species that are continental migrants, species with affinities for more-arid southwestern ecosystems (e.g., canyon bats, pallid bats, and Yuma myotis; Barbour and Davis 1969), species with more-montane affinities and distributions that tend to extend further northward (e.g., long-eared myotis, long-legged myotis, and fringed myotis; Barbour and Davis 1969), and species found throughout much of western North America (e.g., big brown bats, spotted bats, Townsend's big-eared bats, and western small-footed myotis; Barbour and Davis 1969). We suggest that the high species diversity of bats at Mesa Verde is a result of elevational zonation and topographical diversity. Although Mesa Verde is dominated by piñon-juniper woodland, the elevational zonation provides gradients in temperature and aridity, creating habitats that range from high-desert shrubland to pockets of montane forest; and the area has a complex topography with numerous cliffs and canyons (Floyd et al. 2003). Areas in North America with high topographical diversity have high bat diversity because such areas have abundant roosting opportunities for bats in crevices of cliff faces, canyon walls, and rock outcroppings (Humphrey 1975).

Based on captures in mist nets (Table 1), we also characterize the fauna as composed of 5 common species (each ≥10% of total captures), 5 uncommon species (each 2%–9% of total captures), and 5 rare species (each ≤1% of total captures). The 5 common species of bats at Mesa Verde (Table 1) are typical of mid-elevation forested sites in the Rocky Mountain and south-western states (Table 4; Jones 1965, Findley et al. 1975, Hoffmeister 1986). The 5 rare species can be categorized chiefly as inhabitants of zones that are warmer, more arid, or of lower elevation (pallid bats, Yuma myotis, and Brazilian free-tailed bats; Findley et al. 1975, Hoffmeister 1986) or species that may be more adept at maneuvering and avoiding nets (spotted bat and Townsend's big-eared bat)—habits that make them less likely to be captured. The 5 uncommon species are a mixed group and include species that can be categorized as (1) bats of more arid lowlands (California myotis and canyon bat; Armstrong et al. 1994, Fitzgerald et al. 1994), (2) bats typical of the zones in which we sampled but migratory (e.g., hoary bat) and not commonly captured in Colorado except during migration (Armstrong et al. 1994, Fitzgerald et al. 1994), or (3) bats typical but uncommon in Colorado and in some areas of other Four Corners states (fringed myotis; Table 4; Armstrong et al. 1994, Fitzgerald et al. 1994), except perhaps in areas near buildings used as roosts (e.g., occult myotis; Davis and Barbour 1970). Colonies of big free-tailed bats are generally limited to areas of the southwestern U.S. with deep canyons and cliff walls (Bogan et al. 1998, Corbett et al. 2008).

Comparisons with Other Bat Faunal Surveys

Piñon-juniper woodland is the dominant vegetation at Mesa Verde, and some stands are centuries old (Floyd et al. 2004). Fires dramatically reduced the extent of these woodlands between the 1989–1994 surveys by Chung-MacCoubrey and Bogan (2003) and ours. Fires in 1996, 2000, 2002, and 2003 burned 15,663 ha—about 73% of the park area and more than 3 times the total area burned in the preceding 100 years (Floyd et al. 2004, 2006). This large disturbance may have affected availability of prey or roosts (in other areas, some of the same species of bats found at Mesa Verde use crevices and cavities in piñon and juniper trees as sites for maternity roosts—Chung-MacCoubrey 2003a, 2003b), in turn causing shifts in species composition or in relative abundance in the bat fauna. We attempted to assess these effects by comparing our results with those from the 1989–1994 surveys and with similar bat studies in nearby regions of the other Four Corners states. Our 2006–2007 rankings of species at Morefield Canyon were similar with the 1989–1994 rankings and with rankings in abundance at Soda Canyon, a site we sampled in 2007 with a similar configuration to sites sampled at Morefield Canyon in 1989–1994. Given the biases and unknown factors that can influence bat faunal surveys (e.g., Larsen et al. 2007, Kingston 2009), these data do not provide strong evidence for changes in bat fauna between the 1989–1994 survey and our study.

Similarly, we saw no evidence for major differences between the bat fauna at Mesa Verde and the bat faunas at other regional study areas with different and less extensive recent fire histories (Table 4). Compared to these other areas, Mesa Verde had identical or higher species richness and intermediate diversity and evenness of bat fauna. Species composition at Mesa Verde was most similar to the 2 geographically closest areas; and, excluding migratory tree bats, the 3 most abundant species were generally the same in most of these surveys (long-legged myotis, long-eared myotis, and big brown bats). These 3 species are typically considered to be "forest bats" (Barclay and Kurta 2007, Lacki et al. 2007a, 2007b). Forest bats remain among the most common species at Mesa Verde, and the relative abundances of uncommon and rare species of bats are similar to those at the other well-studied locations in the region (Table 4). Thus we find no evidence that the bat fauna at Mesa Verde is grossly dissimilar to the faunas in the other regional studies, despite the recent history of extensive fires.

Our findings of disproportionate sex ratios favoring males in several bat species suggest that for such species, the upper reaches of canyons and mesa tops that characterize much of Mesa Verde may be at elevations too high and too cool to be favorable for female reproduction. Results of tracking bats to roosts at Mesa Verde (see below) also indicate that females avoid roosting on mesa tops and within the upper elevations of Mesa Verde during summer. Lower elevations provide warmer roosts for female bats to rear young, whereas higher elevations can allow deeper daily torpor for males and nonreproductive females (see review in Weller et al. 2009). Sex ratios of silver-haired bats and hoary bats in their summer distributions are consistent with continental patterns, with males found primarily in mountainous areas of the Rocky Mountains and females found at lower elevations to the north and east (Cryan 2003). Reproductive female Brazilian free-tailed bats are not common in Colorado and usually favor lower, warmer, and more-southern locations for formation of maternity colonies (Freeman and Wunder 1988, Fitzgerald et al. 1994). Big brown bats are widespread in Colorado; but there is increasing evidence that female big brown bats use the lower, warmer elevations to form maternity colonies (often in buildings), while males use higher, cooler elevations in summer—with both sexes hibernating in rock crevices at cooler elevations in winter (Neubaum et al. 2006).

Our netting results coupled with radio-tracking suggest a similar pattern for female occult myotis at Mesa Verde. We found little or no evidence for reproductive females at higher-elevation sites in the canyon bat, California myotis, western small-footed myotis, and occult myotis. Although reproductive female long-eared myotis were captured at higher-elevation sites at Mesa Verde, these sites generally had a greater abundance of adult males, and most roosts used by females were at lower elevations. The pattern for much of Mesa Verde to serve as habitat primarily for males and nonreproductive females of some species in summer is similar to patterns that have been noted at higher elevations in other areas of western North America (e.g., Grinnell 1918, Vaughan 1954, Fenton et al. 1980, Cryan et al. 2000).

At other study areas, researchers have also noted a preponderance of males at higher elevations in various species, including the California myotis, western small-footed myotis, and Yuma myotis (see review in Cryan et al. 2000 and citations below). Evidence for consistent use of netting sites at all elevations at Mesa Verde by reproductive females was strong only for the long-legged myotis. The long-legged myotis was also the only species that had adequate sample sizes with sex ratios skewed in favor of females. Long-legged myotis can be abundant in higher-elevation forests in Colorado, where sex ratios skewed toward females have been noted (all nonreproductive; Storz and Williams 1996). However, results of our study indicate that although female long-legged myotis frequent high-elevation habitats to forage and drink, based on radio-tracking, they did not show a greater tendency than other species to roost at higher elevations.

Bat Reproduction and Spring Precipitation

Findings regarding bat reproduction in relation to spring precipitation may have implications for populations of western bats in the future because climate change models project reduced spring moisture in large areas of western North America (Seager et al. 2007, Barnett et al. 2008, McAfee and Russell 2008). The effects of variable spring and summer weather on reproduction in western bats have not been well documented. Grindal et al. (1992) and Lewis (1993) reported an association between lengthy cool, rainy periods (precluding foraging) and decreased female reproductive success in 3 species of western bats. Spring drought has been suggested to lower reproduction of some species of western bats in only one other study (Bogan et al. 1998).

Between-year differences in female reproduction of some bat species at Mesa Verde paralleled differences in primary productivity of vegetation and a corresponding relative abundance of insects. Late spring and summer growth of herbaceous vegetation at Mesa Verde was greater in 2007 than in 2006 and was accompanied by a 1.6-times-greater abundance of nocturnal insects in 2007 (including coleopterans and lepidopterans), with marked differences in insect abundance by mid-June (Snider 2009). These differences occurred in areas that had recent fires (in 2002) as well as in unburned areas. Drought has been experimentally shown to reduce insect abundance (Frampton et al. 2000). Decreased abundance of nocturnal flying insects during drought has been reported in Arizona (Hovorka 1996); and reproduction is enhanced in insectivorous birds in areas with greater abundances of insects and other invertebrates (Burke and Nol 1998, Zanette et al. 2000). Curtailed reproduction in insectivorous bats during drought years has been noted in Australia (Rhodes 2007); and in some areas of the world, bat reproduction is thought to be timed with increases in food abundance associated with seasonally predictable rainfall (e.g., Fleming et al. 1972, McWilliam 1987, Bernard and Cumming 1997).

Insectivorous bats in temperate areas have physiological mechanisms that can facilitate curtailment of reproduction. They mate in autumn or winter, and sperm is stored in the female reproductive tract until ovulation in spring. Females under environmental stress can forego ovulation, fail to implant fertilized embryos, or resorb embryos (Racey and Entwistle 2000). Adult females in temperate areas thus act like “income” breeders in that they rely on food resources to support developing young during late gestation and lactation. Food resources are acquired more or less simultaneously to these phases of reproduction (Henry et al. 2002).

The 3 months with the lowest average precipitation at Mesa Verde National Park are April, May, and June—with June being the driest (Doesken and McKee 2003). These spring months may be critical for reproduction in bats because they are the period when bats leave hibernation and when fetuses develop in adult females. Births occur in mid- to late June, followed by the heavy nutritional demands of lactation over the subsequent 3–5 weeks. We conclude that increases in spring precipitation at Mesa Verde in 2007 resulted in conditions more favorable for reproduction in some species of bats than conditions in 2006. The literature for most species of bats that reproduce at Mesa Verde shows higher rates of reproduction elsewhere compared to our observations in 2006, also supporting our conclusion that reproduction in 2006 was lower than normal (e.g., Jones 1964, Easterla 1973, Barclay 1991, Morrell et al. 1999, Lacki and Baker 2007). Two of the species that did not show reduced reproduction in 2006 were the California myotis and the occult myotis. The California myotis may be more adapted to arid habitats than the other species of myotis we captured (Hoffmeister 1986), and radio-tracking showed that reproductive female occult myotis moved from Mesa Verde to lower elevations in the irrigated Mancos Valley, where precipitation effects may be ameliorated by human-subsidized water development and irrigation. The long-eared myotis also showed a shift in elevational distribution of the sexes in 2007 as well as increased reproduction.

Prolonged, multiyear droughts with reduced reproduction could have an additive impact on reducing growth rates in populations of bats and would likely lead to lower abundances of at least some species in some areas of western North America. Climate-change models suggest continued warming in western North America, with faster spring snowmelt and altered hydrology (Christensen and Lettenmaier 2007, Barnett et al. 2008). Current precipitation projections of global climate-change models for the broad southwestern region include a high likelihood for increased periods of aridity that will be more extensive than in the past (Seager et al. 2007). Decreased spring precipitation has occurred in the southwestern United States for the last 20 years (Holden et al. 2007) and will be a feature of future climate trends throughout the western United States (McAfee and Russell 2008). Given the differences in reproduction seen at Mesa Verde between the dry spring of 2006 and the moist spring of 2007, model projections for climate change have negative implications for reproduction, abundance, and perhaps even the continued presence of some species of bats. An increase in aridity also adds to the importance of managing for accessible drinking water to maintain high-diversity bat faunas in western North America (Adams and Hayes 2008).

Roosting Habits

Our radio-tracking results revealed very limited use of trees as roosts by the species of forest bats we followed. Many of these species tend to be roost generalists. In other parts of their ranges, long-eared myotis, fringed myotis, and long-legged myotis form summer colonies in trees, rock crevices, and buildings (e.g., Barbour and Davis 1969, Ormsbee and McComb 1998, Cryan et al. 2001, Chung-MacCoubrey 2003a, 2003b, 2005, Solick and Barclay 2006, Lacki and Baker 2007). We found all 3 species using mostly rock crevices at Mesa Verde, despite reports that they primarily roost in trees in some other forested regions, including piñon-juniper woodlands of west central New Mexico (Chung-MacCoubrey 2003a, 2003b, 2005). Piñon-juniper woodlands at Mesa Verde are among the oldest on the continent (Floyd et al. 2003), and structural characteristics of these ancient trees are likely as amenable to bats as the structure of younger forests of this type elsewhere. The older trees common at Mesa Verde may provide even better potential roosts for bats, with their complex, twisted trunks and limbs and deep cracks and pockets. However, our results suggest that females of the species we followed might generally prefer rock crevices over trees as summer roosts at Mesa Verde when both types of structures are available. The only other study that investigated use of roosts by bats in piñon-juniper woodlands took place in a landscape with much less exposed rock than exists at Mesa Verde (A. Chung-MacCoubrey personal communication). Differences observed between our study and those of Chung-MacCoubrey (2003a, 2003b, 2005) likely relate to the relative availability of rock crevices and trees suitable as roosts.

Many species of bats in western North America rely on rock crevices as roosting sites, but the extent of use and requisite characteristics of such sites are poorly understood (Bogan et al. 2003, Neubaum et al. 2006). Researchers working in other forested regions also noted the predominant use of rock crevices by long-eared myotis (Chruszcz and Barclay 2002, Rancourt et al. 2005, Solick and Barclay 2006) and fringed myotis (Cryan et al. 2001, Lacki and Baker 2007). Although long-legged myotis are known to form maternity colonies in rock crevices (Ormsbee and McComb 1998, Cryan et al. 2001, Baker and Lacki 2006), their exclusive use of rock crevices in forested habitats has not been previously reported. Our results from Mesa Verde indicate that use of trees as roosts by certain species of bats may not be extensive when suitable rock crevices are abundant. Bats generally tend to show greater fidelity to permanent roosts than temporary roosts (Lewis 1995) and thus may prefer more stable roost structures and microclimates in rock over those in trees. Preference for rock over tree roosts does not, however, indicate that Mesa Verde's piñon-juniper woodlands are not an important resource to bats. The woodlands host an abundant and diverse assemblage of insects on which bats forage (Snider 2009).

Bats spend the majority of their time sequestered in day roosts, and availability of suitable roosts is a major factor influencing bat populations (Kunz 1982). This work represents the first targeted research into use of daytime roosts by bats at Mesa Verde and emphasizes the importance of site-specific studies of roosting habits of bats. Spotted bats were the only species we tracked that exhibited consistent use of the same type of roost structure across their entire range. Only spotted bats are known to roost in crevices of high cliff faces; but because roosts are typically high above the ground (Leonard and Fenton 1983, Wai-Ping and Fenton 1989, Rabe et al. 1998b), observations at roosts are lacking (but see Bogan et al. 1998). Other species followed to roosts used a wider variety of structures but did not exploit trees at Mesa Verde to the degree they seem to in other regions. Thus, generalizations about the roosting habits of forest bats should be treated cautiously. Although radio-tracking studies of this kind are labor intensive, the knowledge gained is essential for the effective management of habitat for bats in specific areas.

The reliance of most bats at Mesa Verde on crevices in rocks and cliffs for roosts would suggest that a warming and more arid climate would not greatly impact bat roosting habitat in summer, although choice of specific roosts might shift upward in elevation as preferred temperature regimes also shift upward. The current pattern of sex-biased elevational distributions could also change with a warming climate; it is possible that bat species more typical of arid lowlands will increase in abundance. Additionally, almost nothing is known about overwintering habits of most bats that use Mesa Verde during the summer. It is likely that some may overwinter by hibernating in inconspicuous rock crevices at higher elevations, similar to big brown bats on the eastern slope of the Rocky Mountains (Neubaum et al. 2006). For example, we suspect that the female occult myotis we followed during early summer between natural roosts at Mesa Verde and a building in the Mancos Valley may have been in transition from winter to summer quarters. If hibernating sites at upper elevations warm at sufficient depth from the surface, then such sites may become unsuitable as hibernacula because bats would expend more metabolic energy at higher overwinter hibernacula temperatures.

ACKNOWLEDGMENTS

G. San Miguel and M. Colyer of Mesa Verde National Park facilitated many of our activities and provided logistical support. P. Stevens and J. Godbey at the U.S. Geological Survey provided administrative guidance. M. Bogan provided advice, background, and data from the 1989–1994 surveys and confirmed identification of *Myotis californicus* and *M. ciliolabrum.* C. Ramotnik provided curatorial assistance. M. O'Farrell aided in identifying AnaBat call recordings. Field assistance was provided by K. Briones, R. Choi, A. Gann, L. Gayton, J. Lamb, J. Much, M. Neubaum, E. Tuttle, D. Sparks, S. Peurach, C. Cooke, E. Mering, and A. Chung-MacCoubrey. Tracking flights were piloted by D. Gregg of Gregg Flying Service. Use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The manuscript was improved by comments from S. Peurach, M. Bogan, and 2 anonymous reviewers.

LITERATURE CITED

ADAMS, R.A., AND M.A. HAYES. 2008. Water availability and successful lactation by bats as related to climate change in arid regions of western North America. Journal of Animal Ecology 77:1115–1121.

ALDRIDGE, H.D.J.N., AND R.M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. Journal of Mammalogy 69:379–382.

ANDERSON, S. 1961. Mammals of Mesa Verde National Park, Colorado. University of Kansas Publications, Museum of Natural History 14:29–67.

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, DC.

ARMSTRONG, D.M. 1972. Distribution of mammals in Colorado. Monograph of the Museum of Natural History, The University of Kansas 3:1–415.

ARMSTRONG, D.M., R.A. ADAMS, AND J. FREEMAN. 1994. Distribution and ecology of bats of Colorado. Natural History Inventory of Colorado, University of Colorado Museum 15:1–83.

BAKER, M.D., AND M.J. LACKI. 2006. Day-roosting habitat of female long-legged myotis in ponderosa pine forests. Journal of Wildlife Management 70:207–215.

BARBOUR, R.W., AND W.H. DAVIS. 1969. Bats of America. University of Kentucky Press, Lexington, KY.

BARCLAY, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology 60:165–178.

BARCLAY, R.M.R., AND A. KURTA. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pages 17–59 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, editors, Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, MD.

BARCLAY, R.M.R., J. ULMER, C.J.A. MACKENZIE, M.S. THOMPSON, L. OLSON, J. MCCOOL, E. CROPLEY, AND G. POLL. 2004. Variation in the reproductive rate of bats. Canadian Journal of Zoology 82:688–693.

BARNETT, T.P., D.W. PIERCE, H.G. HIDALGO, C. BONFILS, B.D. SANTER, T. DAS, G. BALA, A.W. WOOD, T. NOZAWA, A.A. MIRIN, D.R. CAYAN, AND M.D. GETTINGER. 2008. Human-induced changes in the hydrology of the western United States. Science 319:1080–1083.

BERNARD, R.T.F., AND G.S. CUMMING. 1997. African bats: evolution of reproductive patterns and delays. Quarterly Review of Biology 72:253–274.

BOGAN, M.A., P.M. CRYAN, E.W. VALDEZ, L.E. ELLISON, AND T.J. O'SHEA. 2003. Western crevice and cavity-roosting bats. Pages 69–77 *in* T.J. O'Shea, and M.A. Bogan, editors, Monitoring trends in bat populations of the United States and territories—problems and prospects. U.S. Geological Survey, Biological Resources Discipline, Information and Technology Report USGS/BRD/ITR 2003-0003.

BOGAN, M.A., R.B. FINLEY JR., AND S.J. PETERSBURG. 1988. The importance of biological surveys in managing public lands in the western United States. Pages

254–261 *in* R.C. Szaro, K.E. Severson, and D.R. Patton, editors, Management of amphibians, reptiles, and small mammals in North America. General Technical Report RM-166, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

BOGAN, M.A., T.J. O'SHEA, P.M. CRYAN, A.M. DITTO, W.H. SHAEDLA, E.W. VALDEZ, K.T. CASTLE, AND L.E. ELLISON. 1998. A study of bat populations at Los Alamos National Laboratory and Bandelier National Monument, Jemez Mountains, New Mexico. Los Alamos National Laboratory General Technical Report LA-UR-98-2418, Los Alamos, NM.

BOGDANOWICZ, W., S. KASPER, AND R.D. OWEN. 1998. Phylogeny of plecotine bats: reevaluation of morphological and chromosomal data. Journal of Mammalogy 79:78–90.

BURKE, D.M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. Auk 115:96–104.

BURNHAM, K.P., AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, NY.

CHRISTENSEN, N.S., AND D.P. LETTENMAIER. 2007. A multimodel ensemble approach to assessment of climate change impacts on the hydrology and water resources of the Colorado River Basin. Hydrology and Earth System Sciences 11:1417–1434.

CHRUSZCZ, B.J., AND R.M.R. BARCLAY. 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis,* roosting in rock crevices. Functional Ecology 16:18–26.

CHUNG-MACCOUBREY, A., AND M.A. BOGAN. 2003. Bats of the piñon-juniper woodlands of southwestern Colorado. Pages 131–149 *in* M.L. Floyd, editor, Ancient piñon-juniper woodlands: a natural history of Mesa Verde country. University Press of Colorado, Boulder, CO.

CHUNG-MACCOUBREY, A.L. 2003a. Ecology and management of bats in pinyon-juniper woodlands of west-central New Mexico. Doctoral dissertation, University of New Mexico, Albuquerque, NM.

______. 2003b. Monitoring long-term reuse of trees by bats in pinyon-juniper woodlands of New Mexico. Wildlife Society Bulletin 31:73–79.

______. 2005. Use of pinyon-juniper woodlands by bats in New Mexico. Forest Ecology and Management 204:209–220.

CORBETT, R.J.M., C.L. CHAMBERS, AND M.J. HERDER. 2008. Roosts and activity areas of *Nyctinomops macrotis* in northern Arizona. Acta Chiropterologica 10:323–330.

CRYAN, P.M. 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. Journal of Mammalogy 84:579–593.

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.

CRYAN, P.M., M.A. BOGAN, AND G.M. YANEGA. 2001. Roosting habits of four bat species in the Black Hills of South Dakota. Acta Chiropterologica 3:43–52.

DAVIS, W.H., AND R.W. BARBOUR. 1970. Life history data on some southwestern *Myotis.* Southwestern Naturalist 15:261–273.

DOESKEN, N.J., AND T.B. MCKEE. 2003. The climate history of southwestern Colorado. Pages 247–258 *in* M.L. Floyd, editor, Ancient piñon-juniper woodlands: a natural history of Mesa Verde country. University Press of Colorado, Boulder, CO.

DOUGLAS, C. 1967. New records of mammals from Mesa Verde National Park, Colorado. Journal of Mammalogy 48:322–323.

EASTERLA, D.A. 1973. Ecology of the 18 species of Chiroptera at Big Bend National Park, Texas. Northwest Missouri State University Studies 34:1–165.

ELLISON, L.E., A.L. EVERETTE, AND M.A. BOGAN. 2005. Examining patterns of bat activity in Bandelier National Monument, New Mexico, by using walking point transects. Southwestern Naturalist 50:197–208.

EVERETTE, A.L., T.J. O'SHEA, L.E. ELLISON, L.A. STONE, AND J.L. MCCANCE. 2001. Bat use of a high-plains urban wildlife refuge. Wildlife Society Bulletin 29:967–973.

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., A.H. HARRIS, D.E. WILSON, AND C. JONES. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque, NM.

FINLEY, R.B., AND J. CREASY. 1982. First specimen of the spotted bat (*Euderma maculatum*) from Colorado. Great Basin Naturalist 42:360.

FISHER, J.T., AND L. WILKINSON. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review 35:51–81.

FITZGERALD, J.P., C.A. MEANEY, AND D.M. ARMSTRONG. 1994. Mammals of Colorado. Denver Museum of Natural History and University of Colorado Press, Boulder, CO.

FLEMING, T.H., E.T. HOOPER, AND D.E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. Ecology 53:555–569.

FLOYD, M.L., EDITOR. 2003. Ancient piñon-juniper woodlands: a natural history of Mesa Verde country. University Press of Colorado, Boulder, CO.

FLOYD, M.L., D.D. HANNA, AND W.H. ROMME. 2003. Introduction and overview. Pages 1–10 *in* M.L. Floyd, editor, Ancient piñon-juniper woodlands: a natural history of Mesa Verde country. University Press of Colorado, Boulder, CO.

______. 2004. Historical and recent fire regimes in piñon-juniper woodlands on Mesa Verde, Colorado, USA. Forest Ecology and Management 198:269–289.

FLOYD, M.L., D. HANNA, W.H. ROMME, AND T.E. CREWS. 2006. Predicting and mitigating weed invasions to restore natural post-fire succession in Mesa Verde National Park, Colorado, USA. International Journal of Wildland Fire 15:247–259.

FRAMPTON, G.K., P.J. VAN DEN BRINK, AND P.J.L. GOULD. 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain. Journal of Applied Ecology 37:865–883.

FREEMAN, G.E. 1984. Ecomorphological analysis of an assemblage of bats: resource partitioning and competition. Doctoral dissertation, University of Colorado, Boulder, CO.

FREEMAN, J., AND L. WUNDER. 1988. Observations at a colony of the Brazilian free-tailed bat (*Tadarida brasiliensis*) in southern Colorado. Southwestern Naturalist 33:102–104.

GRINDAL, S.D., T.S. COLLARD, R.M. BRIGHAM, AND R.M.R. BARCLAY. 1992. The influence of precipitation on reproduction by *Myotis* bats in British Columbia. American Midland Naturalist 128:339–344.

GRINNELL, H.W. 1918. A synopsis of the bats of California. University of California Publications in Zoology 17:223–404.

HENRY, M., D.W. THOMAS, R. VAUDRY, AND M. CARRIER. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy 83:767–774.

HOFFMEISTER, D.F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, AZ.

HOLDEN, Z.A., P. MORGAN, M.A. CRIMMINS, R.K. STEINHORST, AND A.M.S. SMITH. 2007. Fire season precipitation variability influences fire extent and severity in a large southwestern wilderness area, United States. Geophysical Research Letters 34 (L16708): 1–5.

HOOFER, S.R., R.A. VAN DEN BUSSCHE, AND I. HORACEK. 2006. Generic status of the American pipistrelles (Vespertilionidae) with description of a new genus. Journal of Mammalogy 87:981–992.

HOVORKA, M.D. 1996. The impacts of livestock grazing on Sonoran desertscrub vegetation, insect, and insectivorous bat communities. Master's thesis, York University, North York, Ontario, Canada.

HUMPHREY, S.R. 1975. Nursery roosts and community diversity of Nearctic bats. Journal of Mammalogy 56: 321–346.

JONES, C. 1964. Distribution and ecology of the bats of the Mogollon Mountains area. Doctoral dissertation, University of New Mexico, Albuquerque, NM.

______. 1965. Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. Tulane Studies in Zoology 12: 93–100.

KINGSTON, T. 2009. Analysis of species diversity of bat assemblages. Pages 195–215 *in* T.H. Kunz and S. Parsons, editors, Ecological and behavioral methods for the study of bats. 2nd edition. Johns Hopkins University Press, Baltimore, MD.

KUENZI, A.J., G.T. DOWNARD, AND M.L. MORRISON. 1999. Bat distribution and hibernacula use in west central Nevada. Great Basin Naturalist 59:213–220.

KUNZ, T.H. 1982. Roosting ecology of bats. Pages 1–55 *in* T.H. Kunz, editor, Ecology of bats. Plenum Press, New York, NY.

LACKI, M.J., S.K. AMELON, AND M. BAKER. 2007a. Foraging ecology of bats in forests. Pages 83–127 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, editors, Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, MD.

LACKI, M.J., AND M.D. BAKER. 2007. Day roosts of female fringed myotis (*Myotis thysanodes*) in xeric forests of the Pacific Northwest. Journal of Mammalogy 88: 967–973.

LACKI, M.J., J.P. HAYES, AND A. KURTA, EDITORS. 2007b. Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, MD.

LARSEN, R.J., K.A. BOEGLER, H.H. GENOWAYS, W.P. MASEFILED, R.A. KIRSCH, AND S.C. PEDERSEN. 2007. Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). Acta Chiropterologica 9:423–435.

LEONARD, M.L., AND M.B. FENTON. 1983. Habitat use by spotted bats (*Euderma maculatum,* Chiroptera: Vespertilionidae): roosting and foraging behaviour. Canadian Journal of Zoology 61:1487–1491.

LEWIS, S.E. 1993. Effect of climatic variation on reproduction by pallid bats. Canadian Journal of Zoology 71: 1429–1433.

______. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76:481–496.

MAGURRAN, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

______. 2004. Measuring biological diversity. Blackwell Publishing Company, Oxford, United Kingdom.

MCAFEE, S.A., AND J.L. RUSSELL. 2008. Northern Annular Mode impact on spring climate in the western United States. Geophysical Research Letters 35(L17701):1–5.

MCWILLIAM, A.N. 1987. The reproductive and social biology of *Coleura afra* in a seasonal environment. Pages 324–350 *in* M.B. Fenton, P. Racey, and J.M.V. Rayner, editors, Recent advances in the study of bats. Cambridge University Press, Cambridge, United Kingdom.

MOLLHAGEN, T.R., AND M.A. BOGAN. 1997. Bats of the Henry Mountains region of southeastern Utah. Occasional Papers Museum Texas Tech University 170:1–13.

MORRELL, T.E., M.J. RABE, J.C. DEVOS JR., H. GREEN, AND C.R. MILLER. 1999. Bats captured in two ponderosa pine habitats in north-central Arizona. Southwestern Naturalist 44:501–506.

NAVO, K.W., AND J.A. GORE. 2001. Distribution of the big free-tailed bat (*Nyctinomops macrotis*) in Colorado. Southwestern Naturalist 46:370–376.

NAVO, K.W., J.A. GORE, AND G.T. SKIBA. 1992. Observations on the spotted bat, *Euderma maculatum,* in northwestern Colorado. Journal of Mammalogy 73:547–551.

NEUBAUM, D.J., M.A. NEUBAUM, L.E. ELLISON, AND T.J. O'SHEA. 2005. Survival and condition of big brown bats (*Eptesicus fuscus*) after radiotagging. Journal of Mammalogy 86:95–98.

NEUBAUM, D.J., T.J. O'SHEA, AND K.R. WILSON. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. Journal of Mammalogy 87:470–479.

O'FARRELL, M.J., B.W. MILLER, AND W.L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. Journal of Mammalogy 80:11–23.

ORMSBEE, P.C., AND W.C. MCCOMB. 1998. Selection of day roosts by female long-legged myotis in the central Oregon Cascade Range. Journal of Wildlife Management 62:596–603.

O'SHEA, T.J., M.A. BOGAN, AND L.E. ELLISON. 2003. Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. Wildlife Society Bulletin 31:16–29.

PIAGGIO, A.J., E.W. VALDEZ, M.A. BOGAN, AND G.S. SPICER. 2002. Systematics of *Myotis occultus* (Chiroptera: Vespertilionidae) inferred from sequences of two mitochondrial genes. Journal of Mammalogy 83:386–395.

RABE, M.J., T.E. MORRELL, H. GREEN, J.C. DEVOS JR., AND C.R. MILLER. 1998a. Characteristics of ponderosa pine snag roosts used by reproductive bats in Northern Arizona. Journal of Wildlife Management 62:612–621.

RABE, M.J., M.S. SIDERS, C.R. MILLER, AND T.K. SNOW. 1998b. Long foraging distance for a spotted bat (*Euderma maculatum*) in northern Arizona. Southwestern Naturalist 43:266–286.

RACEY, P.A. 1988. Reproductive assessment in bats. Pages 31–46 *in* T.H. Kunz, editor, Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC.

RACEY, P.A., AND A.C. ENTWISTLE. 2000. Life-history and reproductive strategies of bats. Pages 363–414 *in* E.G. Crichton and P.H. Krutzsch, editors, Reproductive biology of bats. Academic Press, San Diego, CA.

RANCOURT, S.J., M.I. RULE, AND M.A. O'CONNELL. 2005. Maternity roost site selection of long-eared myotis, *Myotis evotis.* Journal of Mammalogy 86:77–84.

RHODES, M. 2007. Roost fidelity and fission-fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). Journal of Mammalogy 88:1252–1260.

ROMME, W.H., S. OLIVA, AND M.L. FLOYD. 2003. Threats to the piñon-juniper woodlands. Pages 339–360 *in* M.L. Floyd, editor, Ancient piñon-juniper woodlands: a natural history of Mesa Verde country. University Press of Colorado, Boulder, CO.

SAS INSTITUTE, INC. 2003. SAS Online Doc 9.1. SAS Institute, Inc., Cary, NC.

SEAGER, R., M. TING, I. HELD, Y. KUSHNIR, J. LU, G. VECCHI, H.-P. HUANG, N. HARNIK, A. LEETMAA, N.-C. LAU, C. LI, J. VELEZ, AND N. NAIK. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

SNIDER, E. 2009. Post-fire insect communities and roost selection by western long-eared myotis (*Myotis evotis*) in Mesa Verde National Park, Colorado. Master's thesis, University of Colorado, Fort Collins, CO.

SOLICK, D.I., AND R.M.R. BARCLAY. 2006. Thermoregulation and roosting behavior of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta. Canadian Journal of Zoology 84:589–599.

STORZ, J.F. 1995. Local distribution and foraging behavior of the spotted bat (*Euderma maculatum*) in northwestern Colorado and adjacent Utah. Great Basin Naturalist 55:78–83.

STORZ, J.F., AND C.F. WILLIAMS. 1996. Summer population structure of subalpine bats in Colorado. Southwestern Naturalist 41:322–324.

THOMAS, D.W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management 52:619–626.

TUMLINSON, R., AND M.E. DOUGLAS. 1992. Parsimony analysis and the phylogeny of the plecotine bats (Chiroptera – Vespertilionidae). Journal of Mammalogy 73:276–285.

VAUGHAN, T.A. 1954. Mammals of the San Gabriel Mountains of California. University of Kansas Publications, Museum of Natural History 7:513–582.

WAI-PING, V., AND M.B. FENTON. 1989. Ecology of spotted bat (*Euderma maculatum*) roosting and foraging behavior. Journal of Mammalogy 70:617–622.

WELLER, T.J., P.M. CRYAN, AND T.J. O'SHEA. 2009. Broadening the focus of bat conservation and research in the USA for the 21st century. Endangered Species Research 8:129–145.

ZANETTE, L., P. DOYLE, AND S.M. TREMONT. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. Ecology 81:1654–1666.

Received 12 May 2009
Accepted 11 February 2010
Early online 5 January 2011