

EXAMINING PATTERNS OF BAT ACTIVITY IN BANDELIER NATIONAL MONUMENT, NEW MEXICO, BY USING WALKING POINT TRANSECTS

LAURA E. ELLISON,* A. LANCE EVERETTE, AND MICHAEL A. BOGAN

*United States Geological Survey, Fort Collins Science Center, 2150 Centre Avenue, Building C,
Fort Collins, CO 80526 (LEE, ALE)*

*United States Geological Survey, Fort Collins Science Center, Museum of Southwestern Biology,
University of New Mexico, Albuquerque, NM 87131 (MAB)*

**Correspondent: Laura.Ellison@usgs.gov*

ABSTRACT—We conducted a preliminary study using small field crews, a single Anabat II detector coupled with a laptop computer, and point transects to examine patterns of bat activity at a scale of interest to local resource managers. The study was conducted during summers of 1996–1998 in Bandelier National Monument in the Jemez Mountains of northern New Mexico, a landscape with distinct vegetation zones and high species richness of bats. We developed simple models that described general patterns of acoustic activity within 4 vegetation zones based primarily on nightly variation and a qualitative index of habitat complexity. Bat acoustic activity (number of bat passes/point) did not vary dramatically among a limited sample of transects within a vegetation zone during 1996. In 1997 and 1998, single transects within each vegetation zone were established, and bat activity did not vary annually within these zones. Acoustic activity differed among the 4 vegetation zones of interest, with the greatest activity occurring in riparian canyon bottomland, intermediate activity in coniferous forest and a 1977 burned zone, and lowest activity in piñon-juniper woodlands. We identified 68.5% of 2,529 bat passes recorded during point-transect surveys to species using an echolocation call reference library we established for the area and qualitative characteristics of bat calls. Bat species richness and composition differed among vegetation zones. Results of these efforts were consistent with general knowledge of where different bat species typically forage and with the natural history of bats of New Mexico, suggesting such a method might have value for drawing inferences about bat activity in different vegetation zones.

RESUMEN—Condujimos un estudio preliminar usando pequeños equipos de investigadores del campo y un detector Anabat II conectado a una computadora laptop, y transectos de puntos para examinar patrones de actividad de murciélagos en una escala de interés a los gerentes locales de recursos naturales. El estudio fue realizado durante los veranos de 1996–1998 en Bandelier National Monument en las montañas Jemez del norte de Nuevo México (Estados Unidos), un paisaje con distintas zonas de vegetación y altos niveles de riqueza de especies de murciélagos. Desarrollamos modelos simple que describió patrones generales de actividad acústica, basado fundamentalmente en localización del transecto, variación nocturna, y un índice cualitativo de complejidad de hábitat. Actividad acústica de murciélagos (número de veces que pasan murciélagos por un punto) no varió dramáticamente entre un muestreo limitado de transectos en una zona de vegetación durante 1996. En 1997 y 1998 se establecieron transectos múltiples en cada zona de vegetación, y la actividad de murciélagos no varió anualmente entre las zonas. Actividad acústica varió entre las cuatro zonas de vegetación de interés, con la actividad más alta en las zonas bajas riparias de cañón, actividad intermedia en bosque conífero y en una zona quemada en 1977, y la actividad más baja en bosques de piñón-junípero. Identificamos 68.5% de 2,529 pasos de murciélagos registrados durante los muestreos de transectos de puntos usando una gama de llamadas de ecolocación que establecimos para la región y características cualitativas de llamadas de murciélagos. Riqueza y composición de especies de murciélagos difirieron entre zonas de vegetación. Los resultados de estos esfuerzos concordaron con conocimiento general del lugar donde diferentes especies de murciélagos forrajean típicamente y con la historia natural de murciélagos de Nuevo México, sugiriendo que un método tal pueda tener valor para sacar inferencias sobre actividades de murciélagos en diferentes zonas de vegetación.

Acoustic surveys to determine bat activity provide a way to develop balanced field studies addressing patterns of foraging activity on a larger scale than conventional trapping techniques (e.g., mist netting). However, these types of surveys provide only a relative index of bat activity, and they are limited in their accuracy in identifying all species in a community (Fenton et al., 1987). Despite these limitations, acoustic surveys remain one of the few tools available for assessing general bat activity across landscapes (Hayes, 1997; O'Farrell and Gannon, 1999).

Although acoustic surveys have been employed over the past 25 years, methods and study designs used for these surveys have varied dramatically depending on habitat types, landscape attributes, advances in technology, and objectives. The most common methods include stationary points (e.g., Bell, 1980; Fenton, 1982; Crome and Richards, 1988; Thomas and West, 1989; Rydell et al., 1994; Krusic et al., 1996; Hayes, 1997; Grindal and Brigham, 1998; Zielinski and Gellman, 1998; Humes et al., 1999; Kalcounis et al., 1999; Duffy et al., 2000; Sherwin et al., 2000; Seidman and Zabel, 2001; Gannon et al., 2003; Patriquin and Barclay, 2003) and line transects (e.g., Barclay, 1985; Judes, 1989; Rydell, 1991; Blake et al., 1994; Walsh et al., 1995; Vaughan et al., 1997; Glendell and Vaughan, 2002; Russo and Jones, 2003).

Stationary points are commonly set up to collect bat calls remotely, and calls are often stored on magnetic tape with voice-activated cassette recorders (e.g., Krusic et al., 1996; Law and Chidel, 2002; Erickson and West, 2003; Patriquin and Barclay, 2003). This method can be costly, but allows for multiple detectors to be used simultaneously to adequately replicate within and among habitat types or management regimes. Studies using stationary points while actively collecting bat passes either onto a tape recorder or directly onto a laptop computer are less common (e.g., Everette et al., 2001; Hogberg et al., 2002; Gannon et al., 2003). Line transects have been surveyed either on foot while continuously collecting data (Barclay, 1985; Walsh et al., 1995; Vaughan et al., 1997; Glendell and Vaughan, 2002; Russo and Jones, 2003) or by slow-moving vehicle (Rydell, 1991; Russ et al., 2003). Examples of studies using walking point-transects consisting

of survey points spaced at predetermined intervals along a transect exist, but are less common than stationary points or line transects (e.g., Thomas, 1988; Zimmerman and Glanz, 2000; Menzel et al., 2002).

Resource managers might be interested in bat activity trends and habitat use on specific management areas at a landscape level, but they are frequently limited by available people, equipment, and time. For example, it might not be possible for a land manager to purchase an adequate number of detectors to simultaneously monitor multiple stationary points for bat activity or to provide the labor necessary for reviewing large numbers of bat calls. The aim of our study, therefore, was to examine the feasibility of using walking point-transects to describe patterns of bat activity among different vegetation zones in Bandelier National Monument, New Mexico. The models we developed to describe bat activity in this park were not meant to be predictive of habitat use by bats on a large scale, but simply meant to describe patterns at a scale of interest to resource managers.

METHODS—Study Area—The study area was located in northern New Mexico in Bandelier National Monument and Los Alamos National Laboratory, approximately 40 km northwest of Santa Fe, New Mexico (Fig. 1). These 2 areas were located on the Pajarito Plateau on the southeastern slope of the Jemez Mountains. Bandelier National Monument comprised approximately 13,215 ha ranging from 1,620 to 3,050 m elevation. Los Alamos National Laboratory adjoined Bandelier to the northeast and encompassed 11,132 ha ranging from 1,950 to 2,300 m elevation. The study area included several distinct vegetation zones (Allen, 1989), and 15 species of bats are known to exist in the area (Bogan et al., 1998).

Point Transect Surveys—Our approach was to conduct a pilot study to assess variation in bat activity among transects in distinct vegetation zones in a single summer (1996) using designated hiking trails in Bandelier National Monument. We used trails to establish transects because they allowed for ease of traveling at night, were conveniently recognized by managers, and were easily located on the landscape for future sampling. In 1997 and 1998, we selected single transects in each vegetation zone to assess the potential for quantitatively describing bat activity using generalized linear models that also incorporated several other features likely to be associated with bat acoustic activity. Strict inferences from these surveys are limited to these particular transects in this land-

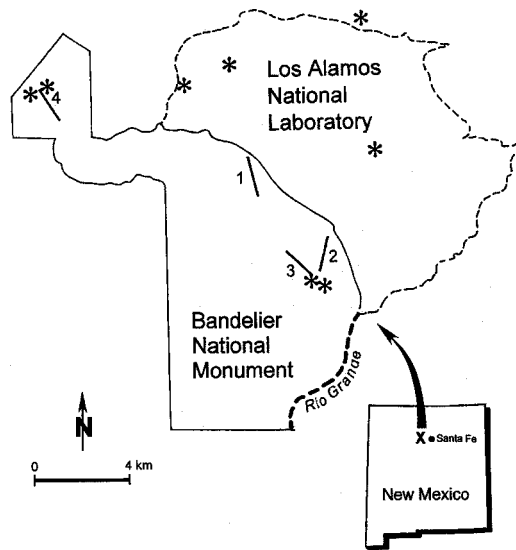


FIG. 1—Location of the study area, the 4 permanent point transects surveyed for nightly and annual variation (1 = Fire, 2 = Piñon-Juniper, 3 = Riparian, and 4 = Conifer), and mist-netting sites (*) in Bandelier National Monument and Los Alamos National Laboratory, Los Alamos County, New Mexico, where bat surveys were conducted during June through August in 1996, 1997, and 1998.

scape. This approach, however, did not assess potential differential activity among vegetation zones by bats according to species or species groups. Therefore, we also qualitatively identified bat calls to species or species group based on acoustic characteristics using a reference call library we established for the study area, investigated simple patterns of species richness and distribution along the different transects, and compared these patterns with general knowledge of the natural history of the bats of New Mexico (Findley et al., 1975).

We selected transects along hiking trails in 4 distinct vegetation zones: 1) lower elevation riparian and canyon bottom vegetation zone, consisting of narrowleaf cottonwood (*Populus angustifolia*), willows (*Salix*), western boxelder (*Acer negundo*), numerous shrubs, and scattered ponderosa pine (*Pinus ponderosa*) at ca. 1,900 m elevation; 2) La Mesa fire zone, a 6,266-ha area of ponderosa pine forest that burned in 1977, resulting in an open shrub habitat with scattered stands of ponderosa pine at ca. 2,200 m; 3) piñon-juniper (*Pinus edulis* and *Juniperus monosperma*) zone at ca. 2,000 m; and 4) mixed coniferous forest zone consisting of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), white fir (*Abies concolor*), limber pine (*Pinus flexilis*), and quaking aspen (*Populus tremuloides*) at ca. 2,750

m. Hereafter, these vegetation zones will be referred to as Riparian, Fire, Piñon-Juniper, and Conifer.

We surveyed 11 point-transects along hiking trails in Bandelier National Monument during the summer of 1996 to establish patterns of variation in bat activity among transects in the 4 vegetation zones. We chose these transects randomly from all available hiking trails. There were 5 Riparian, 2 Fire, 2 Piñon-Juniper, and 2 Conifer transects. Transects during this first summer consisted of a variable number of points ranging from 6 to 14. We then randomly chose one transect out of each vegetation zone to replicate nightly and annually in 1997 and 1998. We surveyed these 4 “permanent” transects during the same moon phase, and we replicated them for 3 consecutive nights to sample night-to-night or temporal variability. In 1996, we conducted all surveys from June through early August in an attempt to avoid periods of migration. In 1997 and 1998, we surveyed from mid July to early August. We did not survey transects during rainfall when bat activity can be suppressed (Fenton, 1970; Bell, 1980).

We used the Anabat II bat detector (Titley Electronics, Ballina, New South Wales, Australia) interfaced with an IBM-compatible laptop computer using a zero-crossings analysis interface module (ZCAIM) to produce frequency-time displays. We viewed these displays directly in the field as bats were detected, and we saved them as files on the laptop computer with file information such as date, transect name, and pertinent comments (O’Farrell, 1997). We controlled for variation in detection range and sensitivity among detectors by using the same detector unit, laptop, and ZCAIM for all surveys. Sensitivity of the detector was set to 6 and the ZCAIM sensitivity was set to its maximum. Batteries in both the ZCAIM and the detector were changed every other night.

Each annually replicated transect consisted of 10 flagged points and was 2.25 km in length. Points within all transects were separated by 250 m to minimize the chance of double-counting bats. Two observers walked each transect, and each survey began directly after the first bat was detected or 0.5 h after sunset (whichever occurred first) and continued until 2 to 3 h past sunset. We sampled at each point for 5 min. During each 5-min point, we tallied bat passes and assigned an initial species identification as they were saved on the laptop computer. We defined a “bat pass” to be a continuous sequence of ≥ 2 call pulses given by a single bat from the moment it was first detected until it traveled beyond the range of detection (Thomas, 1988). Detections of < 2 call pulses and detections with no visible call structure were not used for species identification or statistical analyses. We assumed the number of bat passes collected per point were independent events. In addition to recording number of bat passes, at

TABLE 1—Table of model results by vegetation zone for Bandelier National Monument, New Mexico, 1997 and 1998. Numbers of bat passes (Passes) were modeled by date, a structural complexity index (Clutter), temperature (Temp), year, cloud cover (Skies), and wind speed (Wind). The model incorporating date and clutter was the best model chosen to explain bat activity in all vegetation zones, AIC_c values are reported, and delta AIC_c values are in parentheses.

Model (Passes~)	Riparian	Conifer	Fire	Piñon-Juniper
Date + Clutter	277.6 (0)	370.8 (0)	513.9 (0)	256.9 (0)
Date + Clutter + Year + Skies + Temp + Wind	289.1 (11.5)	373.6 (2.8)	541.7 (27.8)	260.5 (3.6)
Date + Temp	304.1 (26.5)	383.6 (12.8)	541.9 (28.0)	263.2 (6.3)
Clutter	399.1 (121.5)	410.3 (39.5)	547.8 (33.9)	259.2 (2.3)
Date	552.4 (274.8)	409.0 (38.2)	545.9 (32.0)	265.2 (8.3)

each point we recorded a beginning time, temperature, wind speed, cloud cover, and an index of 3-dimensional habitat complexity, or clutter. The structural complexity index was a qualitative measure. It ranged from 0 to 4, with 0 corresponding to no structural interference within a 50-m hemispheric radius of the detector (open habitat, such as in the Fire zone) and 4 corresponding to 76 to 100% interference (dense vegetation or narrow canyon topography, such as in the Riparian zone). A structural complexity index of 1 represented 1 to 25% clutter within a 50-m radius of the detector, a 2 was 26 to 50% clutter, and a 3 was 51 to 75% clutter. Structural complexity included both vegetation and topographical components.

We used generalized linear models in S-Plus (Statistical Sciences, 1995) to estimate bat activity within each vegetation zone in relation to date within a year, year, time (begin time for each point survey), weather variables (temperature, wind speed, and cloud cover), and structural complexity. We chose this modeling strategy so that in the future, resource managers could repeat our methods and observe which variables in the model change over time. Because count data are not distributed normally, we used the Poisson distribution to model the number of bat passes (Neter et al., 1996). We screened data for outliers, influential observations, and multicollinearity prior to data analysis. We chose the most parsimonious model using Akaike's Information Criterion (AIC_c), a criterion for model selection based on information theory, which penalizes the model fit (maximized log-likelihood) by twice the number of parameters (Venables and Ripley, 1994). We used the analysis of deviance table (with chi-squared approximation test) to examine significant components of the model. For reporting comparisons in mean number of bat passes among vegetation zones and structural complexity indices, we calculated standard errors from the mean square error of the selected model and the appropriate sample sizes. We analyzed 1996 pilot data first to determine how

much variation there was among transects within a vegetation zone, and then analyzed 1997 and 1998 data for the final analysis.

Species Identification—We developed a call reference library by recording vocalizations from bats captured with mist-nets at 8 water sources around Bandelier National Monument and Los Alamos National Laboratory from May to July 1996 as part of an ongoing project to document bat species in the area (Fig. 1). We released each bat in an open area near the capture site, but far enough in distance from the water source to minimize the potential for interference from other foraging bats. Three people participated in recordings: one spotlighted the bat as it flew on release, one released the bat, and one recorded the calls. We saved an average of 2 files from every hand-released bat, and we retained files for the call library if they contained greater than 2 search-phase orientation calls, were not contaminated by calls from other bats, and had no excessive background noise.

We recorded 12 species of bats and 198 calls from hand releases (Table 1), and we made additional recordings of free-flying *Euderma maculatum* (spotted bat), *Tadarida brasiliensis* (Brazilian free-tailed bat), and *Pipistrellus hesperus* (western pipistrelle). The most frequently recorded species were *Eptesicus fuscus* (big brown bat), *Antrozous pallidus* (pallid bat), *Myotis volans* (long-legged myotis), and *Lasiorycteris noctivagans* (silver-haired bat). The number of representative calls in the library was a reflection of mist-net captures; species more difficult to capture lacked good representation in the library.

We used a combination of criteria to identify calls to species following recommendations of O'Farrell (1997) and O'Farrell et al. (1999). We compared all saved files qualitatively with the known, catalogued calls from our reference library using Anulook software (version 3.5). Characteristics used as reference points included shape of the call, characteristic frequency, maximum and minimum frequency, bandwidth, and duration of individual call pulses. The

first separation was to classify calls into their characteristic frequency, and then because several species have the same frequency, we separated them further by using the shape of the call. As an example, both *Myotis yumanensis* and *M. californicus* echolocate at 50-kHz, but *M. yumanensis* calls have a distinctive “lazy S” shape, whereas *M. californicus* calls tend to be more linear and of shorter duration (O’Farrell et al., 1999). We made no further quantification, and we did not use all calls for identification purposes. We assigned calls not readily identified to species to 1 of 2 groupings: low-frequency group (generally 20 to 30 kHz bats) or *Myotis* group (generally >30 kHz bats). We assumed that calls collected in each species or species group had an equal capture probability.

We examined patterns of species richness and composition among the 4 vegetation zones. For examining patterns of species composition, we classified each bat pass into 1 of 3 groupings: low-frequency group, *Myotis* group, or audible group. We used only those species common to all 4 vegetation zones for this grouping because not all bat species were found in every zone. The low-frequency group included the following species: *Eptesicus fuscus*, *Lasiurus cinereus* (hoary bat), and *Tadarida brasiliensis*. The *Myotis* group included *Myotis ciliolabrum* (western small-footed bat), *M. evotis* (long-eared myotis), *M. thysanodes* (fringed myotis), and *M. volans*. The audible group consisted of *Euderma maculatum* and *Nyctinomops macrotis* (big free-tailed bat). We compared proportions of bat passes within these 3 groupings among vegetation zones using the *G*-test, or the log-likelihood ratio chi-square test for homogeneity of proportions (Sokal and Rohlf, 1981).

RESULTS—Point Transect Surveys—During the 1996 pilot season, bat activity did not vary by transect within a vegetation zone (*Deviance* = 121.95, *df* = 4, *P* = 0.13 for Riparian; *Deviance* = 63.91, *df* = 1, *P* = 0.67 for Conifer; *Deviance* = 47.20, *df* = 1, *P* = 0.33 for Piñon-Juniper; and *Deviance* = 81.90, *df* = 1, *P* = 0.46 for Fire). Bat activity was consistently highest in the Riparian zone, averaging 7.0 ± 0.9 SE (*n* = 82) per point, similar in Conifer (mean = 2.1, SE = 0.8, *n* = 18) and Fire (mean = 2.5, SE = 0.5, *n* = 26), and the lowest amount of activity was found in the Piñon-Juniper (mean = 1.7, SE = 0.5, *n* = 23).

A total of 2,529 bat passes was collected during 1996, 1997 and 1998 (1,223 in Riparian, 558 in Fire, 519 in Conifer, and 229 in Piñon-Juniper). The models selected with AIC_c that parsimoniously explained most of the variation in bat activity were ones that included tempo-

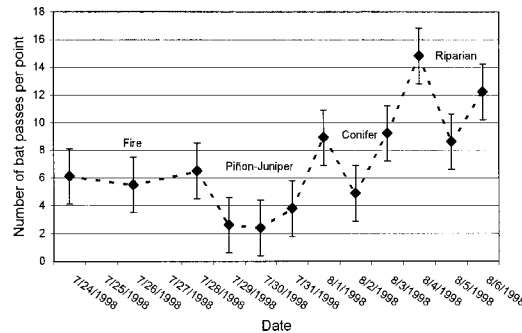


FIG. 2—Bat activity levels (number of bat passes per point) by date in 4 main vegetation zones in Bandelier National Monument, Los Alamos County, New Mexico, during the summer of 1998.

ral variability (date) and structural complexity at a point ($\text{Passes} \sim \text{Date} + \text{Clutter}$) (Table 1). In the Riparian zone, structural complexity was the most important determinant of bat activity (*Deviance* = 155.27, *df* = 1, *P* < 0.01). In the Conifer, Fire, and Piñon-Juniper zones, temporal variability was the most important factor determining amount of bat activity (*Deviance* = 24.3, *df* = 5, *P* < 0.01 for Conifer; *Deviance* = 23.2, *df* = 6, *P* < 0.01 for Fire; and *Deviance* = 12.3, *df* = 5, *P* < 0.01 for Piñon-Juniper). Bat activity did not vary significantly by year, cloud cover, temperature, or wind.

As in the 1996 pilot study, we found the greatest amount of bat activity in the Riparian zone. Number of bat passes per point averaged 9.7 ± 0.8 SE (*n* = 126) in Riparian. Conifer and Fire transects had similar levels of activity (mean = 6.6, SE = 0.6, *n* = 78 for Conifer and mean = 5.6, SE = 0.6, *n* = 99 for Fire), and Piñon-Juniper had the lowest activity (mean = 2.8, SE = 0.3, *n* = 83).

Considerable temporal variability in bat activity within a vegetation zone was illustrated by consecutive-night surveys conducted in 1998 (Fig. 2); a similar pattern of temporal variability in bat activity was found in 1996 and 1997. The mean number of bat passes varied most dramatically for Conifer and Riparian vegetation zones (mean = 4.9 to 9.2 and mean = 8.6 to 14.8, respectively). Night-to-night variability was not as dramatic for Fire and Piñon-Juniper vegetation zones (mean = 5.5 to 6.4 and mean = 2.4 to 3.8, respectively).

Structural complexity within a vegetation zone contributed to the variability in bat activ-

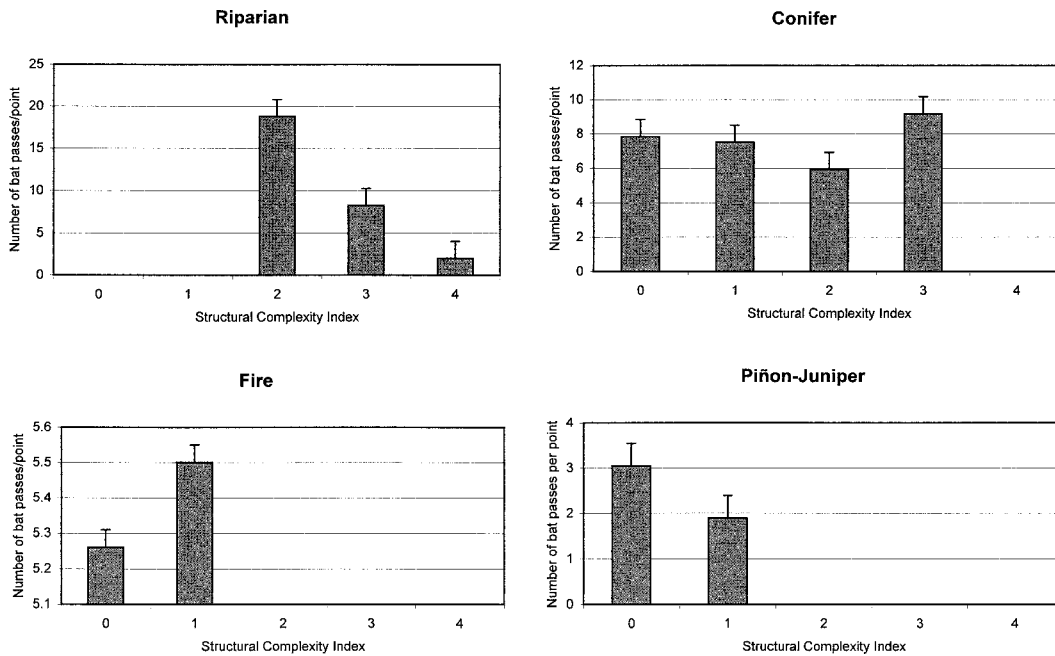


FIG. 3—Bat activity levels by structural complexity index and vegetation zone in Bandelier National Monument, Los Alamos County, New Mexico, during the summers of 1996, 1997, and 1998. Structural complexity indices were 0 = none, 1 = 1 to 25%, 2 = 26 to 50%, 3 = 51 to 75%, and 4 = 76 to 100%. (Bars are standard errors calculated from the fitted statistical model.)

ity (Fig. 3). In the Riparian zone, bat activity was greatest at points with a structural complexity of 2, averaging 14.0 ± 1.9 SE ($n = 33$) bat passes per point. There was less activity at points with a structural complexity of 3 (mean = 8.8, SE = 0.9, $n = 48$) and 4 (mean = 4.3, SE = 0.9, $n = 13$). In Conifer, bat activity was evenly distributed among 4 structural complexity indices (mean = 8.5, SE = 1.4, $n = 18$ for a structural complexity of 0; mean = 6.5, SE = 1.3, $n = 22$ for a structural complexity of 1; mean = 5.3, SE = 0.8, $n = 31$ for a structural complexity of 2; and mean = 8.6, SE = 1.8, $n = 7$ for a structural complexity of 3). In the Fire zone, a more open vegetation community than Riparian and Conifer, bat activity was slightly greater at points with a structural complexity of 1 (mean = 6.9, SE = 0.7, $n = 20$) than at points with a structural complexity of 0 (mean = 5.3, SE = 0.7, $n = 79$). In Piñon-Juniper, bat activity was slightly greater at open points (mean = 3.3, SE = 0.5, $n = 39$) than at points with a structural complexity of 1 (mean = 2.2, SE = 0.3, $n = 44$).

Species Identification—Of the 2,529 bat passes

recorded, 1,732 (68.5%) were identified to species, 453 (17.9%) were identified to 3 species groupings (low-frequency group, *Myotis* group, or audible group), and the remaining 344 (13.6%) were not used for identification purposes (Table 2).

Bat species richness differed among the 4 vegetation zones. The Riparian was the richest with 14 species detected. In both Fire and Piñon-Juniper, 13 species were detected, and 11 species were detected in the Conifer. Species common to all 4 vegetation zones were *M. ciliolabrum*, *M. evotis*, *M. thysanodes*, *M. volans*, *L. cinereus*, *E. fuscus*, *E. maculatum*, *T. brasiliensis*, and *N. macrotis*. *Myotis yumanensis* (yuma myotis) was detected only in the Riparian and Fire zones, *P. hesperus* was detected in all zones but the Conifer, *Corynorhinus townsendii* (Townsend's big-eared bat) was detected in Riparian and Piñon-Juniper, and *A. pallidus* was identified in all vegetation zones except for Conifer. In Riparian and Piñon-Juniper, the most frequently detected species was *T. brasiliensis* (Table 2). *Euderma maculatum* was the most fre-

TABLE 2—Number of bat passes per vegetation zone identified to species in Bandelier National Monument, Los Alamos County, New Mexico, during the summers of 1996, 1997, and 1998. Number of reference recordings made for the library are in parentheses directly following species name. Comparisons also are made to independent qualitative descriptions of distributions for these species by Findley et al. (1975). (The Fire transects were located in the ponderosa pine zone.)

Species	Total	Vegetation zone				Findley et al. (1975)
		Riparian	Conifer	Fire	Piñon-Juniper	
<i>Myotis californicus</i> (2)	45	38	0	3	4	Ponderosa pine and below
<i>M. ciliolabrum</i> (19)	235	85	82	51	17	Spruce-fir and below
<i>M. evotis</i> (23)	58	38	12	6	2	Ponderosa pine and above
<i>M. thysanodes</i> (6)	43	22	15	4	2	Ponderosa pine and below
<i>M. volans</i> (27)	135	69	39	20	7	Ponderosa pine and above
<i>M. yumanensis</i> (2)	194	190	0	2	0	Permanent water sources and below coniferous forest
<i>Lasiurus cinereus</i> (8)	6	2	3	1	1	Throughout all elevations in high mountains
<i>Lasionycteris noctivagans</i> (24)	1	0	1	0	0	
<i>Pipistrellus hesperus</i> (0)	31	25	0	3	3	Cliffs below ponderosa pine
<i>Eptesicus fuscus</i> (53)	128	60	9	50	9	Ponderosa pine
<i>Euderma maculatum</i> (0)	327	94	84	115	34	Piñon-juniper and above
<i>Corynorhinus townsendii</i> (1)	3	2	0	0	1	All elevations
<i>Antrozous pallidus</i> (31)	41	24	0	12	5	Ponderosa pine and below, near rock outcrops
<i>Tadarida brasiliensis</i> (0)	455	211	74	110	60	Piñon-juniper and below
<i>Nyctinomops macrotis</i> (2)	30	5	18	6	1	Below ponderosa pine
Low-frequency group	88	33	26	20	9	
<i>Myotis</i> group	349	160	95	69	25	
Audible group	16	8	4	4	0	
Total identified calls (198)	1,732	865	339	383	145	
Total unused calls	344	157	57	82	50	
Total calls collected	2,529	1,223	519	558	229	

quently detected species in the Conifer and Fire zones.

General patterns of species composition differed among the 4 vegetation zones (Fig. 4). Proportions of total bat passes in low frequency, *Myotis*, and audible groupings differed by vegetation zone ($G = 99.82$, $df = 6$, $P < 0.001$). More than half the bat passes along the Riparian and Conifer transects were in the *Myotis* group (55.3% and 53.2%, respectively), with lower proportions of bat passes in the low fre-

quency and audible groups. Along the Fire and Piñon-Juniper transects, bat passes were more evenly distributed among the 3 groups.

DISCUSSION—The models we developed to explain bat activity patterns in the 4 vegetation zones in Bandelier National Monument included both temporal and spatial components. Activity varied by date (night-to-night variation) and structural complexity within a vegetation zone. We found substantially greater amounts

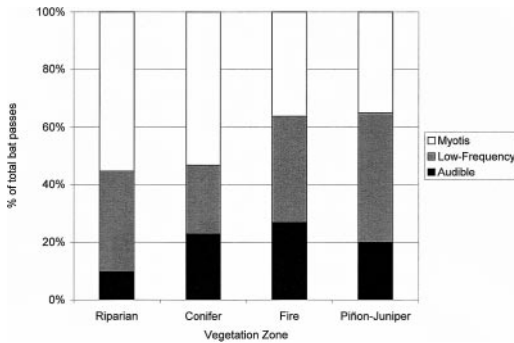


FIG. 4—Bat species composition among the 4 vegetation zones in Bandelier National Monument, Los Alamos County, New Mexico, during the summers of 1996, 1997, and 1998.

of activity in the Riparian zone compared to the 3 upland zones. Bell (1980) observed a similar pattern in southeastern Arizona. He found significantly higher bat activity levels in riparian forest than either desert or juniper-scrub habitats using point-transect methods.

Temporal or night-to-night variability in bat activity by point and transect was a significant component of our activity models. Hayes (1997) also found that total activity of bats at a site varied substantially among nights in the Oregon Coast Range. This has important consequences for design of acoustic surveys. As fewer nights are surveyed, there is an increased chance that estimates of activity will be biased and seeming differences or similarities between areas and years could actually be a product of temporal variation. Hayes (2000) recommended replicating survey-nights per site a minimum of 6 nights to adequately quantify bat activity, which we were unable to accomplish with our limited field crew.

Spatial variability within a vegetation zone was also a significant component of our activity models; our index of structural complexity seemed to explain some of the variation in bat passes per point. Structural clutter influences bat activity patterns because less maneuverable species might be restricted in their ability to forage in more cluttered environments (Mackey and Barclay, 1989; Brigham et al., 1992; Grindal, 1995). This can be particularly true for small bats; artificial clutter has been shown to negatively affect the foraging activity of *Myotis* (Brigham et al., 1997). Clutter also might influence the detection range of bat detectors.

It is likely that the detection range was greater in the more open Fire and Piñon-Juniper zones than in the more spatially complex Riparian and Conifer zones, which would bias our results. More studies are needed to determine detection probabilities of the Anabat system in relation to structural complexity.

Species richness and diversity were higher in the Riparian zone versus the other 3 zones. The linear characteristics of the canyon bottoms combined with the availability of a perennial stream (Frijoles Creek) providing water and emergent insects, as well as the availability of multiple roosting sites in both vegetation and along cliff faces could explain this pattern. This was contrary to what Bell (1980) found in southeastern Arizona where, unlike bat activity, species diversity was lower in riparian forest than in desert and juniper-scrub habitats.

Patterns of species composition among the 4 zones, with a significantly larger proportion of the *Myotis* group in the Riparian and Conifer zones and smaller proportions in the Fire and Piñon-Juniper, might be explained, in part, by the differences in structural complexity. Generally, the *Myotis* species common to all 4 zones are small bats with broad wings (low aspect ratio) and are able to forage in more cluttered habitats, whereas the larger bats in our low-frequency group have higher aspect ratios and forage in more open areas (Vaughan, 1970; Crome and Richards, 1988). However, this hypothesis could be confounded by the detection range of the Anabat detector. Only bats that fly within range of the Anabat microphone will provide a call sequence of sufficient quality for identification to species, and this range of detection can differ by species. Hence, our survey technique might positively bias detections toward louder bats and negatively bias detections for quieter species (*Myotis*). Therefore, our assumption that calls collected in each species or species group had an equal probability of detection was probably not supported in this study.

Our indices of bat activity by vegetation zone for various species showed the relatively high importance of riparian zones (Table 2). The importance of riparian zones to insectivorous birds in the Southwest is also well recognized (Stamp, 1978; Strong and Bock, 1990; Skagen et al., 1998). The activity we observed also agreed with qualitative characterizations by re-

gional mammal experts (Findley et al., 1975). The most notable exceptions to these characterizations were the greater activity of big free-tailed bats and Brazilian free-tailed bats at higher elevation habitats. These are the only 2 molossid bats in the group, and both have high aspect ratio wings that enable travel over greater distances in shorter times. Both also have colonial roosts in the region within 10 km of the Fire and Conifer transects (Bogan et al., 1998), and the colony of Brazilian free-tailed bats is located less than 0.5 km from the Riparian transect.

Design of Acoustic Surveys—The point transect technique we used during this study to examine bat activity patterns has advantages and disadvantages over line transects and stationary points. In open habitats, walking line-transects while continuously collecting data is useful method for sampling an area for wildlife abundance, particularly for bird surveys, because more time is spent actually surveying and more of the landscape can be covered (Bollinger et al., 1988). Conversely, during point-transect surveys, more time is spent traversing between and locating sampling points, less time is actually spent surveying, and less area is covered (see Buckland et al., 1993). In our study area, walking point-transects were more practical than line transects; the terrain made it nearly impossible to traverse a straight line safely in the dark while also viewing frequency-time displays on the computer screen and recording vocalizations of incoming bats. We attempted to account for the higher night-to-night variability of point transects by repeating each transect 3 consecutive nights during each year of the study.

A passive monitoring design allows multiple systems to be operated simultaneously, but increases costs for purchasing additional detector units to cover a habitat type or feature sufficiently with replication. Correction factors also are needed to account for variability in sensitivity of individual detectors (Larson and Hayes, 2000). Walking point-transects allow a greater amount of land to be surveyed with fewer detectors, which in some cases might be more cost-effective. Field survey time is increased with passive monitoring, but only at the expense of sifting through large quantities of tape-recorded or downloaded material. Tape recording is still commonly used in

acoustic surveys, but this method can introduce significant distortion and background noise that reduces the ability to make species identifications compared with directly recording onto a laptop computer (O'Farrell et al., 1999). Compact flash cards and the new Anabat CF storage ZCAIM were not available during our study, but many studies are now using this technology, which circumvents problems with tape recordings. However, using laptop computers in the field not only allows an observer to actively count bat passes at each point, but the observer also can examine the incoming calls and follow bats with the detector microphone to maximize the number of calls that can be used for identification purposes. Choice of survey technique also depends on the landscape attributes of the study area and the bat community.

In our study, we examined the feasibility of point transects using a limited number of Anabat detectors and field personnel to determine whether reliable patterns of bat activity would emerge. Despite our inherent problems with pseudoreplication due to small field crews and a limited budget, we were able to develop a simple model of bat activity and to describe patterns of species detection that were consistent with knowledge of the natural history of bats of New Mexico and factors likely to influence bat acoustic activity. The technique and modeling strategy we used can be repeated in the future by resource managers and can be used to determine which environmental variables contributing to bat activity change over time. However, without additional sampling and further replication among vegetation zones, our level of inference remains limited to transects surveyed within this particular landscape. Such a level of inference might be acceptable to local resource managers, but gaining a broader understanding of habitat use by bats based on acoustic activity will require substantially greater effort regardless of the sampling technique. For this reason, it would be valuable to conduct future experiments that compare several sampling designs (i.e., point transects, stationary points, line transects) concurrently. Characterization of habitat use also should include replication of sampling in vegetation zones across regions as well as within landscapes, account for species differences in detectability based on call intensities, develop

species rarefaction curves to support design criteria (such as duration of time at each point, particularly if certain species are of special interest; Fenton et al., 1987), and increase the reference call collection to encompass the full range of variability in echolocation traits.

We are indebted to S. Fettig and K. Beeley of Banderlier National Monument and T. S. Foxx and D. C. Keller of Los Alamos National Laboratory for their support and advice during this project. We also thank I. Ahlén, B. S. Cade, M. B. Fenton, W. L. Gannon, M. J. O'Farrell, T. J. O'Shea, and several anonymous reviewers for their comments on previous drafts of this paper. C. Baxter, K. Castle, A. Ditto, and S. Flick provided invaluable assistance in the field, and J. Arentz helped with statistical advice.

LITERATURE CITED

- ALLEN, C. D. 1989. Changes in the landscape of the Jemez Mountains, New Mexico. Unpublished Ph.D. dissertation, University of California, Berkeley.
- BARCLAY, R. M. R. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasiomyotis noctivagans*) bats and the consequence for prey selection. *Canadian Journal of Zoology* 63:2507–2515.
- BELL, G. P. 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology* 58:1876–1883.
- BLAKE, D., A. M. HUTSON, P. A. RACEY, J. RYDELL, AND J. R. SPEAKMAN. 1994. Use of lamplit roads by foraging bats in southern England. *Journal of Zoology* 234:453–462.
- BOGAN, M. A., T. J. O'SHEA, P. M. CRYAN, A. M. DITTO, W. H. SCHAEDELA, E. W. VALDEZ, K. T. CASTLE, AND L. E. ELLISON. 1998. A study of bat populations at Los Alamos National Laboratory and Banderlier National Monument, Jemez Mountains, New Mexico. Technical Report LA-UR-98-2418, Los Alamos National Laboratory, Los Alamos, New Mexico.
- BOLLINGER, E. K., T. A. GAVIN, AND D. C. MCINTYRE. 1988. Comparison of transects and circular-plots for estimating bobolink densities. *Journal of Wildlife Management* 52:777–786.
- BRIGHAM, R. M., H. D. J. N. ALDRIDGE, AND R. L. MACKEY. 1992. Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. *Journal of Mammalogy* 73:640–645.
- BRIGHAM, R. M., S. D. GRINDAL, M. C. FIRMAN, AND J. L. MORISSETTE. 1997. The influence of structural clutter on activity patterns of insectivorous bats. *Canadian Journal of Zoology* 75:131–136.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, United Kingdom.
- CROME, F. H. J., AND G. C. RICHARDS. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* 69:1960–1969.
- DUFFY, A. M., L. F. LUMSDEN, C. R. CADDLE, R. R. CHICK, AND G. R. NEWELL. 2000. The efficacy of Anabat ultrasonic detectors and harp traps for surveying microchiropterans in southeastern Australia. *Acta Chiropterologica* 2:127–144.
- ERICKSON, J. L., AND S. D. WEST. 2003. Associations of bats with local structure and landscape features of forested stands in western Oregon and Washington. *Biological Conservation* 109:95–102.
- 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. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Canadian Journal of Zoology* 48:847–851.
- FENTON, M. B. 1982. Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, North Queensland. *Australian Journal of Zoology* 30:417–425.
- FENTON, M. B., D. C. TENNANT, AND J. WYSZECKI. 1987. Using echolocation calls to measure the distribution of bats: the case of *Euderma maculatum*. *Journal of Mammalogy* 68:142–144.
- FINDLEY, J. S., A. H. HARRIS, D. E. WILSON, AND C. JONES. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque.
- GANNON, W. L., R. E. SHERWIN, AND S. HAYMOND. 2003. On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. *Wildlife Society Bulletin* 31:45–61.
- GLENDELL, M., AND N. VAUGHAN. 2002. Foraging activity of bats in historic landscape parks in relation to habitat composition and park management. *Animal Conservation* 5:309–316.
- GRINDAL, S. D. 1995. Impacts of forest harvesting on habitat use by foraging bats in southern British Columbia. Unpublished M.S. thesis, University of Regina, Regina, Saskatchewan, Canada.
- GRINDAL, S. D., AND R. M. BRIGHAM. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. *Journal of Wildlife Management* 62:996–1003.
- HAYES, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy* 78:514–524.
- HAYES, J. P. 2000. Assumptions and practical implications in the design and interpretation of echo-

- location-monitoring studies. *Acta Chiropterologica* 2:225–236.
- HOGBERG, L. K., K. J. PATRIQUIN, AND R. M. R. BARCLAY. 2002. Use by bats of patches of residual trees in logged areas of the boreal forest. *American Midland Naturalist* 148:282–288.
- HUMES, M. L., J. P. HAYES, AND M. W. COLLOPY. 1999. Bat activity in thinned, unthinned, and old-growth forests in western Oregon. *Journal of Wildlife Management* 63:553–561.
- JUDES, U. 1989. Analysis of the distribution of flying bats along line-transects. In: V. Hanak, I. Horaček, and J. Gaisler, editors. *European bat research 1987*. Charles University Press, Praha, Czech Republic. Pages 311–318.
- KALCOUNIS, M. C., K. A. HOBSON, R. M. BRIGHAM, AND K. R. HECKER. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy* 80:673–682.
- KRUSIC, R. A., M. YAMASAKI, C. D. NEEFUS, AND P. J. PEKINS. 1996. Bat habitat use in White Mountain National Forest. *Journal of Wildlife Management* 61:625–631.
- LARSEN, D. J., AND J. P. HAYES. 2000. Variability in sensitivity of Anabat II detectors and a method of calibration. *Acta Chiropterologica* 2:209–213.
- LAW, B., AND M. CHIDEL. 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology* 39:605–617.
- MACKAY, R. L., AND R. M. R. BARCLAY. 1989. The influence of physical clutter and noise on the activity of bats over water. *Canadian Journal of Zoology* 67:1167–1170.
- MENZEL, M. A., T. C. CARTER, J. M. MENZEL, W. M. FORD, AND B. R. CHAPMAN. 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management* 162:209–218.
- NETER, J., M. H. KUTNER, C. J. NACHTSHEIM, AND W. WASSERMAN. 1996. *Applied linear statistical models*, fourth edition. Times Mirror Higher Education Group, Inc., Chicago, Illinois.
- O'FARRELL, M. J. 1997. Use of echolocation calls for the identification of free-flying bats. *Transactions of the Western Section of the Wildlife Society* 33: 1–8.
- O'FARRELL, M. J., AND W. L. GANNON. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy* 80: 24–30.
- 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.
- PATRIQUIN, K. J., AND R. M. R. BARCLAY. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. *Journal of Applied Ecology* 40: 646–657.
- RUSS, J. M., M. BRIFFA, AND W. I. MONTGOMERY. 2003. Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *Journal of Zoology* 259:289–299.
- RUSSO, D., AND G. JONES. 2003. Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26:197–209.
- RYDELL, J. 1991. Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. *Holarctic Ecology* 14:203–207.
- RYDELL, J., A. BUSHBY, C. C. COSGROVE, AND P. A. RACEY. 1994. Habitat use by bats along rivers in northeast Scotland. *Folia Zoologica* 43:417–424.
- SEIDMAN, V. M., AND C. J. ZABEL. 2001. Bat activity along intermittent streams in northwestern California. *Journal of Mammalogy* 82:738–747.
- SHERWIN, R. E., W. L. GANNON, AND S. HAYMOND. 2000. The efficacy of acoustic techniques to infer differential use of habitat by bats. *Acta Chiropterologica* 2:145–153.
- SKAGEN, S. K., C. P. MELCHER, W. H. HOWE, AND F. L. KNOPF. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. *Conservation Biology* 12:896–909.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*, second edition. W. H. Freeman and Company, New York.
- STAMP, N. E. 1978. Breeding birds of riparian woodlands in southcentral Arizona. *Condor* 80:64–71.
- STATISTICAL SCIENCES. 1995. *S-Plus guide to statistical and mathematical analysis*, version 3.3. StatSci, Inc., Seattle, Washington.
- STRONG, T. R., AND C. E. BOCK. 1990. Bird species distribution patterns in riparian habitats in southeastern Arizona. *Condor* 92:866–885.
- THOMAS, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management* 52:619–626.
- THOMAS, D. W., AND S. D. WEST. 1989. *Sampling methods for bats*. United States Forest Service, General Technical Report PNW-GTR-243.
- VAUGHAN, N., G. JONES, AND S. HARRIS. 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *Journal of Applied Ecology* 34:716–730.
- VAUGHAN, T. A. 1970. Flight patterns and aerodynamics. In: W. A. Wimsatt, editor. *Biology of bats*, volume I. Academic Press, New York. Pages 195–216.
- VENABLES, W. N., AND B. D. RIPLEY. 1994. *Modern applied statistics with S-Plus*. Springer-Verlag, New York.

WALSH, A. L., S. HARRIS, AND A. M. HUTSON. 1995. Abundance and habitat selection of foraging vespertilionid bats in Britain: a landscape-scale approach. *Symposium of the Zoological Society of London* 67:325–344.

ZIELINSKI, W. J., AND S. T. GELLMAN. 1999. Bat use of

remnant old-growth redwood stands. *Conservation Biology* 13:160–167.

Submitted 20 January 2004. Accepted 6 October 2004.
Associate Editor was Cody W. Edwards.