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HABITAT USE BY BATS IN A RIPARIAN CORRIDOR OF THE MOJAVE DESERT IN SOUTHERN NEVADA

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We used a combination of capture and acoustic monitoring equipment to examine use of habitat by bats in a desert riparian community in southern Nevada. Each habitat type (riparian marsh, mesquite bosque, riparian woodland, and riparian shrubland) was simultaneously and continuously sampled acoustically in 3- to 5-night increments for 54 nights between June 2000 and January 2001. Fifteen species of bats were detected acoustically, 13 of which were captured using harp traps or mist nets. Five species were not detected frequently enough to be included in statistical analyses. California leaf-nosed bats (*Macrotus californicus*) and Brazilian free-tailed bats (*Tadarida brasiliensis*) were generalists, spending equal amounts of time in each habitat. Western yellow bats (*Lasiurus xanthinus*) and pallid bats (*Antrozous pallidus*) demonstrated strong biases for riparian woodland over the other habitats sampled. The remaining 6 species spent substantially more time in at least 1 of the 4 habitats. Riparian woodlands accounted for more than 50% of all bat activity, whereas riparian marshes were the least used habitat. High species richness and differences in habitat use by most species emphasizes the importance of a diversity of riparian habitats for bats at the study site. The existence of both native and nonnative habitat may elevate bat species richness and increase the degree of differential habitat use to levels higher than would be expected if only native habitat existed at the study site. Understanding differential riparian habitat use by bats in desert ecosystems may have profound management implications.

Key words: acoustic monitoring, community ecology, conservation, echolocation, inventory, Microchiroptera, species richness

Bats are important members of a variety of natural communities, yet many aspects of their basic biology are still unknown because of difficulties encountered in studying volant, nocturnal organisms. Bats have been proposed as good indicators of the integrity of natural communities because they integrate a number of resource attributes (e.g., roosting, watering, and feeding habitats), and thus may show population declines quickly if a resource attribute is missing (Hutson et al. 2001). Yet current knowledge of foraging practices and roost selection is limited for most species, and such knowledge is crucial in order to determine the most appropriate methods of conservation (Fenton 1997; Findley 1993). Ecological factors such as productivity, habitat heterogeneity, and area of available habitat influence structure of bat communities (Crome and Richards 1988; Findley 1993). Management actions may have profound effects on habitat factors and thus on diversity and abundance of bats in a local community.

Changes in hydrology and alteration in composition of vegetative communities along riparian corridors may be expected to affect foraging behavior of bats, but few empirical data exist to assess the magnitude of effects. Some actions, such as riparian restoration resulting in greater structural diversity of a habitat, may be beneficial for many bat species (Fenton 1997). Alternatively, habitat alterations that increase frequency and distribution of monotypic habitats may precipitate a decrease in foraging quality. The ability of bats to move long distances with relatively low energetic cost gives them access to a variety of habitats and decreases their dependence on any one particular area (Campbell et al. 1996; Fenton 1997; Fenton and Rautenbach 1986; Findley 1993). This high vagility also suggests that location of roosting sites and foraging habitats may occur some distance from one another. Previous studies suggest that given access to multiple habitats, individual species will selectively forage in different habitats (Crome and Richards 1988; Findley 1993; Swift and Racey 1983). Thus, changes in

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or manipulations of habitat types may alter the richness and abundance of species in a local assemblage.

Because the vagility of bats provides them with opportunities to sample dispersed and fragmented habitats, using bats to assess integrity of native plant communities may be difficult. Existence of nonnative habitats interspersed among native habitats could potentially increase bat diversity, and favor those species that are able to use small patches of habitat, whereas those species that rely on larger habitat patch size are adversely affected.

Historically, inferences of habitat and resource use have been gained from bats captured in collection devices such as harp traps and mist nets, or from visual observations. However, inferences drawn from net or trap data are biased because different species and individuals are not equally susceptible to capture devices (Kunz and Kurta 1988; O'Farrell and Gannon 1999). Visual observations are even more limited and subject to greater bias. Additionally, capture and visual methods (i.e., observations at water sources and internal cave and mine surveys) can alter behavior of bats (Fenton 1970). Advances in the design of acoustic monitoring equipment over the past decade have provided means to reduce or eliminate many of the problems associated with capture and visual methods.

Acoustic sampling devices provide opportunities to identify free-flying bats (Fenton and Bell 1981; O'Farrell 1997). Current technological advances now allow reliable identification of most species of bats thus far examined (Ochoa et al. 2000; O'Farrell and Miller 1999; O'Farrell et al. 1999). Acoustic detection has proven to be more effective than capture methods for determining presence of many species (Kalko et al. 1996; O'Farrell and Gannon 1999), and provides a number of advantages, including a less-invasive method of collecting species occurrence data, ability to detect free-flying bats outside the reach of conventional sampling methods, potential to record passively (researcher absent) throughout the course of entire nights, and potential to sample multiple locations simultaneously with minimal effort. However, like all sampling methods, acoustic detection of bats has its own set of biases, because some species are diagnosed more easily than others (O'Farrell et al. 1999), and some bats (e.g., California leaf-nosed bat [*Macrotus californicus*] and Townsend's big-eared bat [*Corynorhinus townsendii*]) produce vocalizations of low intensity and are difficult to detect at distances greater than 15 m, whereas bats that produce high-intensity vocalizations may be detected at distances greater than 100 m. Although species identity can usually be determined, acoustic information does not provide sex, age, or reproductive status. Nightly variation in activity patterns of bats must be considered in sampling designs that use acoustic detection, and intensive sampling efforts (>8 consecutive nights) may be required to detect accurate levels of activity (Hayes 1997). A combination of capture devices and acoustic detection can increase the accuracy of species verification within local bat assemblages (O'Farrell and Gannon 1999).

Most studies investigating differential habitat use by bats have been conducted in forest ecosystems (e.g., Barclay 1991; Brigham et al. 1997; Crome and Richards 1988; Kalcounis et al. 1999; Swift and Racey 1983). To our knowledge, no studies to date have examined differential use of habitat by individual bat species in a desert environment. Riparian communities nested within desert ecosystems offer crucial foraging and roosting habitat for both migratory and nonmigratory wildlife species. Because animals tend to congregate in these areas, riparian corridors offer an excellent location to study resource partitioning. Our study was designed to investigate habitat use by bats within a representative range of riparian habitats along the Muddy River drainage nested within the Mojave Desert in southern Nevada. Specific objectives of this study were to assess the current assemblage of bat species inhabiting the study area and to evaluate overall patterns of habitat use within riparian habitat types.

MATERIALS AND METHODS

Study area.—The study area included 22.5 km of the Muddy River drainage in upper Moapa Valley, Clark County, Nevada. Currently, 4 distinct habitat types are associated with the Muddy River floodplain in upper Moapa Valley: riparian woodland, mesquite bosque, riparian shrubland, and riparian marsh (Nature Conservancy 1999). These habitats intermingle in a mosaic fashion throughout the floodplain, which encompasses approximately 3,116 ha, has been highly disturbed as a result of long-standing flood control measures and livestock grazing, and contains a mix of native and nonnative flora. Plant nomenclature follows Hickman (1993).

Riparian woodlands along the Muddy River floodplain in the vicinity of our study site consist of 2 types: monotypic stands of California fan palms (*Washingtonia filifera*) and mixed stands of deciduous Fremont cottonwood (*Populus fremontii*), velvet ash (*Fraxinus velutina*), and Gooddings black willow (*Salix gooddingii*); combined they currently represent less than 1% of the total riparian habitat. Riparian woodland habitats mature at approximately 15 m in height. Mesquite bosques are comprised primarily of native screwbean mesquite (*Prosopis pubescens*) and honey mesquite (*Prosopis glandulosa*), and mature at approximately 5 m in height. Small shrubs, grasses, and succulents dominate the understory. This habitat is recovering in much of the floodplain where agriculture and grazing has ceased and at present represents 20% of the total riparian habitat. Riparian shrublands are composed of monotypic stands of arrowweed (*Pluchea sericea*) and quailbush (*Atriplex lentiformis*) as tall as 2 m. This is the largest habitat type and occupies an estimated 50% of the riparian habitat. Riparian marshes are about 1 m in height and are dominated by mixed sedges (*Carex*, *Eleocharis*, and *Juncus*), southern cattail (*Typha domingensis*), yerba mansa (*Anemopsis californica*), paintbrush (*Castilleja*), and grasses (Nature Conservancy 1999). This habitat accounts for approximately 5% of the riparian habitat. Remaining acreage of the floodplain is reported to have been mesquite bosque habitats historically, but these were drained and cleared for grazing purposes decades ago. Currently these grazing lands consist of Bermuda grass (*Cynodon dactylon*) and other distichous type grasses, mixed herbs and weeds, and open ground. The upper Moapa Valley floodplain is surrounded by typical Mojave Desert creosote (*Larrea tridentata*) scrub habitat.

Inventory.—Historical data for bats, including museum records and published accounts, identified relatively few species as occurring in Moapa Valley. No thorough or systematic inventories were previously conducted in the study area, and information available on species richness was generated from observations from anecdotal historical surveys. In this study, capture surveys were conducted to compliment acoustic sampling in developing a thorough inventory of the species assemblage in the study area, and to allow for comparison between the 2 techniques in their ability to detect species presence. Double-frame harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and mist nets (Avinet Inc., Dryden, New York) were deployed in suspected flyways in 3 of the 4 habitat types, at an abandoned mine, and over 3 open-water sources from March 2000 through April 2001.

Riparian woodland habitat (riparian woodland site 1) was sampled at approximately 30-day intervals using 2 harp traps, placed side-by-side, in an observed flyway. Voucher specimens of all species captured are deposited in the New Mexico Museum of Natural History.

During this study, animals were handled humanely following guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998), and methods used for handling bats in this study conform to guidelines set forth by the Institutional Animal Care and Use Committee at the University of Nevada, Las Vegas.

Acoustic sampling.—In addition to collecting general site inventory data using various capture methods, we quantified habitat use patterns for each species using acoustic sampling methods. Three sites were selected within each habitat type for acoustic monitoring. Reference to riparian woodland habitat in this study refers directly to monotypic California palm stands. Monotypic stands of California palms were selected to represent the riparian woodland habitat type and comprise the greatest acreage of riparian woodland in the study area. However, it is important to note that habitat use inside the California palm habitat is not necessarily representative of habitat use in the cottonwood and velvet ash assemblages. Each sampling location was selected on the basis that it was large enough to encompass the detection ability of an acoustic system, and that it was protected from livestock and vehicle travel.

To compare differential habitat use, each habitat examined must be sampled simultaneously to prevent pseudoreplication. Multiple nights of sampling provide an assessment of the level of temporal variation within and among habitats. To determine if bats exhibited greater use of a particular habitat, 1 replicate of each habitat type was simultaneously sampled passively for 3–5 consecutive nights to account for potential nightly temporal variation. Each habitat was sampled continuously from before sunset to after sunrise.

For this study, we define "site" as any single location, and "replicate" as a group of 4 sites, 1 from each habitat type. Although we would have preferred to sample all 3 replicates (12 sites) simultaneously, because of logistics and equipment limitations replicates were sampled in succession. Moving from one replicate to the next, all habitat types were sampled 2–4 times per month between June and October, and 1 or 2 times per month during the winter months when both bat activity and species composition were reduced. Sampling all 4 habitats simultaneously throughout the seasons allowed for a rigorous comparison of habitat use. Sampling intensity during seasonal migration periods was increased to enhance the possibility of detecting species that might occupy the area for a short period of time during the year. Any detected seasonal change in habitat use and activity levels also may reflect seasonal changes in prey availability across habitats.

Many of the previous investigations of resource partitioning by bats have failed to clearly state assumptions before data collection. Biases and limitations of research equipment and methods should be addressed during the design phase of such studies (Hayes 2000; Sherwin et al. 2000), resulting in a more rigorous, accurate, and justified comparison of habitat use. We assumed that all habitats were equally accessible to all bats, proper replication was obtained by sampling 1 site of each habitat type simultaneously for multiple nights across seasons, all bats were randomly distributed vertically, any particular species was equally detectable from each habitat type, and all acoustic equipment had an equal ability of detecting bat echolocation calls. Conclusions obtained from our study apply directly to this particular local mosaic of riparian habitats, and inferences to other areas should be made with caution.

Equipment failure was common in the initial phase of data collection and it became apparent that the number of successive nights of simultaneous sampling from all 4 habitats would be limited. To determine if sampling devices functioned properly throughout a night, each night before sunset and again the following day after sunrise we verified the recording of sound by one of us rubbing our fingers together in front of the detector's transducer and generating ultrasonic noise. If the passive acoustic system in any 1 of the 4 habitats failed to function properly from sunset to sunrise on any given night, then the data from all 4 habitats for that night have been omitted from data summaries and statistical analyses to meet the stringent requirements of the experimental design. From a total of 54 nights of acoustic sampling, there were 24 individual nights of simultaneous data collection from all 4 habitats, including 2 instances of 3 successive simultaneous full nights of data collection from all 4 habitats, and 8 instances of 2 successive simultaneous full nights of data collection from all 4 habitats.

Anabat II bat detectors and Zero-crossings Analysis Interface Modules (Titley Electronics, Ballina, New South Wales, Australia) linked to laptop computers were used to acoustically detect free-flying bats. Echolocation sequences of bats were recorded directly to the hard drive of laptop computers using Anabat6 software. Sites were surveyed passively (researcher absent) throughout the entire night using a passive monitoring system described by O'Farrell (1998). Passive monitoring systems were set up each evening before sunset and taken down each morning after sunrise. All detectors were set at the same sensitivity level.

Data analysis.—Methods for monitoring and determining identity of species followed those of O'Farrell et al. (1999). A sequence is defined as a series of individual vocalizations (calls > 0.5 ms) and containing more than 2 individual calls produced by a single bat as it passes within range of a detector (O'Farrell and Gannon 1999; Sherwin et al. 2000; Thomas 1988). Sequences that were unidentifiable because of either poor quality or lack of distinctive characteristics were left unidentified.

To determine relative activity at a site it is necessary to quantify the number of sequences recorded. A simple counting of total recorded files containing 1 or more sequences tends to improperly estimate activity levels (Kalcounis et al. 1999), because it does not take into account multiple sequences within a file of different individuals of a single species (underestimation) or multiple files of sequences that may result from a single individual in a short amount of time (overestimation). A less-biased assessment of relative activity levels within and across habitats can be developed using an Activity Index approach (Miller 2001). This method determines relative activity at a site by counting the number of 1-min intervals, as indicated by a recorded file, within a given time period (e.g., an entire night) in which a particular species is active. A species is considered present during a 1-min block of time regardless of the number of sequences within a file, or the number files for that species within the 1-min interval (Miller 2001).

Statistical analyses were performed separately for each replicate. Combining data collected from the different replicates into 1 data set per habitat type for statistical analyses of the homogeneity of habitat sites is not appropriate in this case, because sites of the same habitat type were never sampled simultaneously, and to do so would be pseudoreplication (Hurlbert 1984). Habitat use for all species of bats

Table 1.—Percentage of total time of acoustic detection for each bat species. Moapa Valley, Nevada.

Species	Total min of activity	Percent total (%)	Rank
Antrozous pallidus	530	3.14	9
Corynorhinus townsendii[a]	9	0.05	14
Eptesicus fuscus	987	5.84	5
Euderma maculatum	616	3.65	8
Lasiurus blossevillii	665	3.94	6
Lasiurus cinereus[a]	58	0.34	11
Lasiurus xanthinus	3,715	21.98	2
Lasionycteris noctivagans[a,b]	14	0.08	13
Macrotus californicus	273	1.62	10
Myotis californicus	1,737	10.28	3
Myotis thysanodes[a]	8	0.05	14
Myotis yumanensis	653	3.86	7
Nyctinomops macrotis[a,b]	47	0.28	12
Pipistrellus hesperus	6,400	37.87	1
Tadarida brasiliensis	1,186	7.02	4
Total	16,898	100	

[a] Species omitted from analyses because of insufficient data.

[b] Species detected acoustically, but not captured.

Table 2.—Pairwise comparisons of bat activity for all bats combined in replicates 1 ($SE = 86.838$) and 2 ($SE = 50.408$). Significant values are in bold type. Moapa Valley, Nevada.

		Replicate 1		Replicate 2	
Habitat (I)	Habitat (J)	Mean difference (I − J)	*P*	Mean difference (I − J)	*P*
Riparian marsh	Mesquite bosque	−63.13	1.000	−161.43	**0.023**
	Riparian woodland	−461.25	**0.000**	−282.14	**0.000**
	Riparian shrubland	−105.50	1.000	−50.43	1.000
Mesquite bosque	Riparian marsh	63.13	1.000	161.43	**0.023**
	Riparian woodland	−398.13	**0.001**	−120.71	0.149
	Riparian shrubland	−42.38	1.000	111.00	0.225
Riparian woodland	Riparian marsh	461.25	**0.000**	282.14	**0.000**
	Mesquite bosque	398.13	**0.001**	120.71	0.149
	Riparian shrubland	355.75	**0.002**	231.71	**0.001**
Riparian shrubland	Riparian marsh	105.50	1.000	50.43	1.000
	Mesquite bosque	42.38	1.000	−111.00	0.225
	Riparian woodland	−355.75	**0.002**	−231.71	**0.001**

as a single group was investigated by replicate using the chi-square test. Analyses of habitat use for individual species required using the nonparametric Kruskal–Wallis test because of low levels of activity in some habitats. Extremely low levels of activity in December and January (<5 files per site per night) required omitting data collected over these months from statistical analyses. If a significant difference in activity was observed among habitats, multiple pairwise comparisons were adjusted using the sequential Bonferroni test (Sokal and Rohlf 1995; Zar 1999). Chi-square and Kruskal–Wallis tests were performed using an overall alpha level of 0.05 to provide a measure of significance. For multiple pairwise comparison tests, we chose an alpha level of 0.15, which, when divided by the total number of comparisons ($n(n - 1)/2 = 6$), yields an alpha level of 0.025 for each pairwise comparison test.

Results

Fifteen species were identified from the study area (Table 1), all of which were detected acoustically. Thirteen of these species were captured, whereas 2 species, the silver-haired bat (*Lasionycteris noctivagans*) and big free-tailed bat (*Nyctinomops macrotis*), were only detected acoustically. Collectively, 554 bats were captured at trapping or netting locations from a total 313.75 h of effort across 32 nights. Sampling at water sources accounted for 4.3% ($n = 24$) of total captures and 7.5% ($n = 23.5$) of capture effort from 18.8% ($n = 6$) of the nights. Captures from the flyway sampled by routine monthly trapping sessions in riparian woodland site 1 accounted for 60.3% ($n = 334$) of captures and 44.7% ($n = 140.25$) of capture effort from 37.5% ($n = 12$) of the nights. Sampling at an abandoned mine, influenced by a maternity colony of Yuma myotis (*Myotis yumanensis*), contributed 28.9% ($n = 160$) of captures and 0.6% ($n = 2$) of capture effort from 3.1% ($n = 1$) of the nights.

A total of 25,369 files (each containing at least 1 call sequence) were recorded from the passive acoustic systems within the portion of the study addressing habitat use. Of these files, 94.6% were identifiable to species, whereas the remaining 5.4% were too fragmentary or of poor quality to be identified to species level. All unidentified files were excluded from analyses. Application of the Activity Index yielded 16,898 min of bat activity. Relative abundance of each species, based on total minutes of activity from all habitats combined, revealed that the western pipistrelle (*Pipistrellus hesperus*) and the western yellow bat (*Lasiurus xanthinus*) were the most frequent species encountered and together accounted for nearly 60% of all bat activity (Table 1).

In replicates 1 and 2 there was a significant difference in activity among the 4 habitat types for all species combined (replicate 1, $\chi^2 = 18.680$, $d.f. = 3$, $P < 0.001$; replicate 2, $\chi^2 = 20.072$, $d.f. = 3$, $P < 0.001$). Within replicate 1, pairwise comparisons identified bat activity in the riparian woodland habitat as being significantly greater than all other habitats. Similarly, replicate 2 identified significantly greater activity in the riparian woodland habitat, as well as showing that the mesquite bosque had significantly more activity than the riparian marsh (Table 2). Although similar activity patterns were observed in replicate 3, no statistical significance was detected in activity levels ($\chi^2 = 3.686$, $d.f. = 3$, $P = 0.297$). Across all replicates, more than half of all bat activity occurred in riparian woodland (51%, $n = 8{,}614$ min), with intermediate–low levels in mesquite bosques (19.5%, $n = 3{,}292$ min) and riparian shrubland (18.9%, $n = 3{,}189$ min), and the lowest level in riparian marsh (10.7%, $n = 1{,}803$ min).

Individual species comparisons of habitat use produced similar results, and at the selected alpha level statistical significance varied by replicate (Table 3). Based on separate pairwise comparisons, several species demonstrated distinct use of certain habitat types (Table 4). Four species (*L. noctivagans*, hoary bat [*Lasiurus cinereus*], fringed myotis [*Myotis thysanodes*], and *N. macrotis*) were only encountered in the study area for short periods of time (Table 1) coinciding with spring or autumn migration periods. Riparian woodlands accounted for 93.1% ($n = 54$ min) of activity of *L. cinereus* and 44.7% ($n = 21$ min) of activity of *N. macrotis*. Insufficient data were obtained for these species to include them in statistical analyses. Although known to be a year-round resident and occasionally active during winter months, *C. townsendii* was rarely detected acoustically. Insufficient data for this species also negated statistical analysis.

DISCUSSION

More than one-half (51%) of all bat activity was detected in riparian woodland habitat, which represents less than 1% of all riparian habitat in the study area. This concurs with Rogers et al. (2006), who found that bat activity in riparian forest was significantly greater than in 3 of 4 other habitat types studied. Similarly, Sherwin et al. (2000) found that use by 3 of 4 bat guilds was significantly higher in cottonwood forests than in 2 of 3 other riparian habitat types. Care should be exercised when interpreting total bat or guild activity within each habitat because it will be cryptically related to the densities of individual species. For example, in our study 87.9% of pallid bat (*Antrozous pallidus*) activity was detected in riparian woodland habitat. If the density of *A. pallidus* was much greater than that of other species, this would be reflected in the increased detection of bats as a single group in riparian woodland habitat. Acoustic equipment cannot provide an estimation of density, but only an estimate of the proportion of time a species spends in each habitat. However, assuming that individuals of the same species will exhibit similar habitat use, the proportion of time spent by each species in each habitat is not necessarily dependent on density. Thus, an examination of the proportion of time a species occupies each habitat is indicative, minimally, of the rank order of use of each habitat.

Although every species was detected at least once in all 4 habitat types, obvious biases in habitat use were observed (Figs. 1 and 2). Although some species (e.g., western red bat, [*Lasiurus blossevillii*], *Ma. californicus*, and Brazilian free-tailed bat [*Tadarida brasiliensis*]) were equally common in all habitats, other species exhibited a clear dominant use of a particular habitat type (e.g., *A. pallidus*, big brown bat [*Eptesicus fuscus*], and *L. xanthinus*). Ground cover in the riparian woodland habitat is relatively sparse, composed mainly of grasses and small shrubs. This structure may be conducive to *A. pallidus*, which routinely forages on ground-dwelling prey (Hermanson and O'Shea 1983), and may offer insight into why it was detected 87.9% of the time in this habitat. Although Kurta and Baker (1990) suggested that *E. fuscus* is a habitat generalist, they also implied that when found in the arid southwest of North America it is often restricted to forested highlands. We found that *E. fuscus* demonstrated considerable use of riparian woodland habitat over other habitats, which perhaps mimics some characteristics of montane habitats where it is more commonly found. The spotted bat (*Euderma maculatum*) was routinely detected over riparian marshes and used this habitat more than any other species, which coincides with observations from Rabe et al. (1998), who observed this species foraging over open meadows. *L. xanthinus* roosts primarily in palm trees (Higginbotham et al. 2000), which likely accounts for the large portion of time that it was detected in riparian woodland habitat. California myotis (*Myotis californicus*) spent more than 50% of the time in mesquite bosque habitat, which correlates with foraging observations in other studies (Simpson 1993). *M. yumanensis* is commonly found foraging low over moderate to large bodies of water. Although examination of our data suggests substantial use of riparian woodland, 38% of activity of *M. yumanensis* occurred at riparian woodland site 3, which was within approximately 70 m of a large pool. *T. brasiliensis* did not concentrate activity in any particular habitat type, which may reflect the ability of this species to forage at least 270 m above the ground, and thus often out of the range of ground-based acoustic detection (Griffin and Thompson 1982).

A qualitative assessment of habitat use for select species from the study area is summarized as follows. Riparian marsh—All species except 1 (*E. maculatum*) spent less than 17% of their time in riparian marsh habitat. Mesquite bosque—*E. maculatum* and *My. californicus* spent more time in mesquite bosque habitat than the other habitats combined. Mesquite bosque was rarely used by *A. pallidus*, *E. fuscus*, and *L. xanthinus*. Riparian woodland—*A. pallidus*, *E. fuscus*, *L. xanthinus*, and *M. yumanensis* spent more time in riparian woodland habitat than the other habitats combined. All species, except *E. maculatum* (<1%), spent at least 24% of their time in riparian woodland. Riparian shrubland—*L. blossevillii*, *Ma. californicus*, and *T. brasiliensis* spent at least 27% of their time

TABLE 3.—Results from chi-square tests of comparisons of habitat use by individual bat species. Probability levels for significant differences are in bold type. Moapa Valley, Nevada.

Species	Replicate	χ^2	*d.f.*	*P*
Antrozous pallidus	1	20.461	3	**0.000**
	2	7.451	3	0.059
	3	2.867	3	0.413
Eptesicus fuscus	1	11.736	3	**0.008**
	2	1.915	3	0.590
	3	3.583	3	0.310
Euderma maculatum	1	11.030	3	**0.012**
	2	17.269	3	**0.001**
	3	5.329	3	0.149
Lasiurus blossevillii	1	6.057	3	0.109
	2	5.593	3	0.133
	3	10.955	3	**0.012**
L. xanthinus	1	19.729	3	**0.000**
	2	11.189	3	**0.011**
	3	7.617	3	0.055
Macrotis californicus	1	0.295	3	0.961
	2	4.363	3	0.225
	3	2.796	3	0.424
Myotis californicus	1	6.114	3	0.106
	2	17.652	3	**0.001**
	3	8.384	3	**0.039**
Myotis yumanensis	1	15.716	3	**0.001**
	2	5.747	3	0.125
	3	4.011	3	0.260
Pipistrellus hesperus	1	10.680	3	**0.013**
	2	7.022	3	0.071
	3	1.839	3	0.607
Tadarida brasiliensis	1	3.446	3	0.328
	2	2.705	3	0.439
	3	1.020	3	0.796

TABLE 4.—Summarized statistics[a] (*P*-values only) from individual pairwise comparisons for each bat species. Significant values are in bold type. Moapa Valley, Nevada.

Species	Replicate	Site	Riparian marsh	Mesquite bosque	Riparian woodland	Riparian shrubland
Antrozous pallidus	1	Riparian marsh		1.000	**0.001**	1.000
		Mesquite bosque	1.000		**0.001**	1.000
		Riparian woodland	**0.001**	**0.001**		**0.002**
		Riparian shrubland	1.000	1.000	**0.002**	
Eptesicus fuscus	1	Riparian marsh		1.000	**0.021**	1.000
		Mesquite bosque	1.000		0.037	1.000
		Riparian woodland	**0.021**	0.037		0.092
		Riparian shrubland	1.000	1.000	0.092	
Euderma maculatum	1	Riparian marsh		1.000	0.258	0.966
		Mesquite bosque	1.000		0.370	1.000
		Riparian woodland	0.258	0.370		1.000
		Riparian shrubland	0.966	1.000	1.000	
	2	Riparian marsh		**0.002**	1.000	1.000
		Mesquite bosque	**0.002**		**0.000**	**0.001**
		Riparian woodland	1.000	**0.000**		1.000
		Riparian shrubland	1.000	**0.001**	1.000	
Lasiurus blossevillii	3	Riparian marsh		0.644	0.847	1.000
		Mesquite bosque	0.644		1.000	1.000
		Riparian woodland	0.847	1.000		1.000
		Riparian shrubland	1.000	1.000	1.000	
L. xanthinus	1	Riparian marsh		1.000	**0.000**	1.000
		Mesquite bosque	1.000		**0.000**	1.000
		Riparian woodland	**0.000**	**0.000**		**0.000**
		Riparian shrubland	1.000	1.000	**0.000**	
	2	Riparian marsh		1.000	**0.000**	1.000
		Mesquite bosque	1.000		**0.000**	1.000
		Riparian woodland	**0.000**	**0.000**		**0.000**
		Riparian shrubland	1.000	1.000	**0.000**	
Myotis californicus	2	Riparian marsh		**0.000**	1.000	1.000
		Mesquite bosque	**0.000**		**0.003**	**0.001**
		Riparian woodland	1.000	**0.003**		1.000
		Riparian shrubland	1.000	**0.001**	1.000	
	3	Riparian marsh		0.799	0.126	1.000
		Mesquite bosque	0.799		1.000	0.819
		Riparian woodland	0.126	1.000		0.130
		Riparian shrubland	1.000	0.819	0.130	
M. yumanensis	1	Riparian marsh		1.000	**0.007**	1.000
		Mesquite bosque	1.000		0.151	1.000
		Riparian woodland	**0.007**	0.151		**0.015**
		Riparian shrubland	1.000	1.000	**0.015**	
Pipistrellus hesperus	1	Riparian marsh		1.000	**0.005**	1.000
		Mesquite bosque	1.000		0.043	1.000
		Riparian woodland	**0.005**	0.043		0.080
		Riparian shrubland	1.000	1.000	0.080	

[a] Complete statistical results from the 11 separate pairwise comparisons are available from the 1st author upon request.

in riparian shrubland. *A. pallidus*, *E. maculatum*, *L. xanthinus*, and *My. californicus* appeared to not use this habitat.

Lasiurus cinereus, *L. noctivagans*, *M. thysanodes*, and *N. macrotis* were observed migrating through the study area. Historical documentation of these species in low elevations of southern Nevada is relatively rare. Although *C. townsendii* was rarely detected acoustically or by capture, it was observed on multiple occasions in nearby mines and is a year-round resident of southern Nevada. *C. townsendii* is known to emit low-intensity vocalizations and can be difficult to detect acoustically (O'Farrell and Gannon 1999). This species appears to echolocate with higher intensity than does *Ma. californicus*, which we detected acoustically for 273 min; therefore, we hypothesize that C. *townsendii* may potentially be foraging in habitats other than those studied, within closer proximity to its roosts, or both.

We found that the distribution of bats was not randomly distributed by habitat in 2 of 3 replicates. Statistical test results interpreting differential use of habitat varied by replicate, suggesting that true replication was not achieved, which can be common in studies of natural systems. Individual species comparisons of habitat use produced similar results, and at the selected alpha level statistical significance varied by replicate. However, biological observations of habitat-use patterns for bats as a group, as well as by individual species, identified clear patterns. Although 8 of the 10 species statistically analyzed demonstrated significant differential use of habitat, none were statistically significant across all 3 replicates. We suggest 2

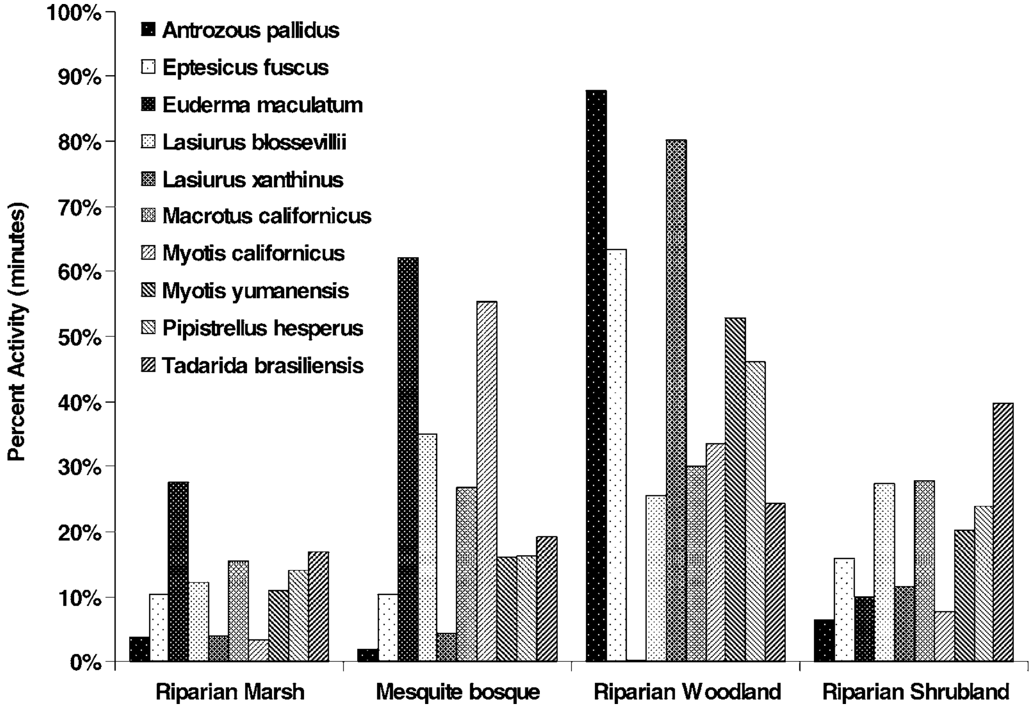

FIG. 1.—Percentage of activity by habitat type for each species from 24 nights between June and November 2000. Moapa Valley, Nevada.

primary reasons for these results: biological significance and statistical significance are not concurrent in this instance, and replicates of at least some of the habitat types were not truly replicates. We determined suitability of habitats as replicates based on obvious characteristics, such as habitat heterogeneity, surface moisture, and similar age class and distribution of vegetation. We suggest that the bats in the study area may be recognizing and selecting other features that pertain more directly to their foraging ability, such as insect type and abundance and perceived background.

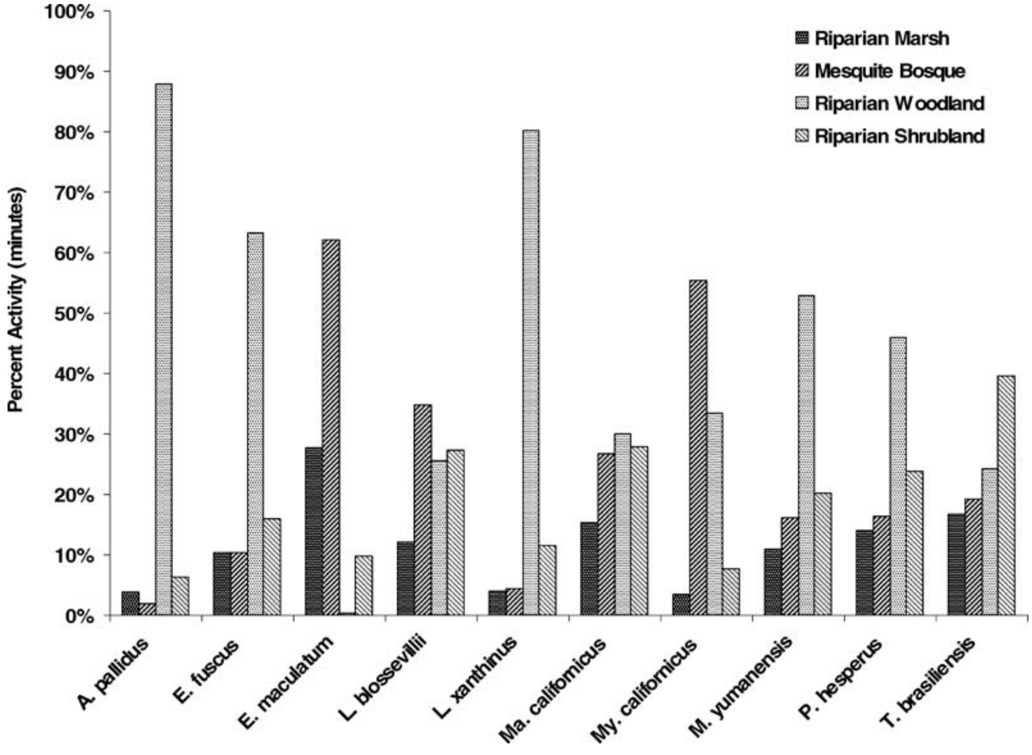

FIG. 2.—Percentage of activity by species for each habitat type from 24 nights between June and November 2000. Full names of bat genera are given in Fig. 1. Moapa Valley, Nevada.

Finally, it is imperative that researchers addressing differential use of habitat by bats adequately address the bias of temporal variation when sampling across replicates. Concurrent sampling at all replicates is necessary if data are to be combined for statistical analysis. To do otherwise is pseudoreplication. With recent advances in Anabat acoustic detection equipment, conducting replicated simultaneous investigations of habitat use patterns of bats is now quite practical.

In our study, 5 of the 15 species of bats acoustically detected were omitted from analyses because of insufficient data. Of the remaining 10 species, only 2 showed no statistically significant difference in habitat use from all 3 replicates studied. Statistical significance is not necessarily equivalent with biological significance, and rejection of null hypotheses is completely dependent upon the significance level chosen. Usually the alpha level used to determine statistical significance is arbitrarily chosen, and biological significance is often not considered in these decisions (Hayes and Steidl 1997; Reed and Blaustein 1997; Steidl et al. 1997). Based on the percentages of time each species spent in each type of habitat (Fig. 2), it appears that even in the absence of statistical significance in some of the analyses, many of the bat species exhibited biologically significant bias in habitat use.

Biological systems can be difficult to model and can be even more troublesome to properly subject to statistical analyses. We found that relatively minor equipment failure prevented collection of data within the strict confines of the statistical design. Although recording bat echolocations directly to a laptop computer was the most efficient method at the time of this study, current advances in some acoustic equipment (e.g., Anabat compact flash storage zero-crossings analysis module) negate the necessity for laptops, power invertors, and large batteries. For future acoustic-based habitat use investigations, we suggest that prospective power analyses be employed to predetermine sample sizes required to detect statistical significance, that biological significance be considered when alpha levels for statistical comparisons are chosen, and that observations suspected to be biologically significant be reported in addition to statistical results.

Fenton (1997) suggested that 2 main factors determine habitat selection by bats: roost availability and prey abundance. The presence of 15 species of bats in the upper Moapa Valley is due likely to the combination of a diversity of riparian habitats and abundant roosting opportunities. Because the California palm groves at the study site are suspected to be nonnative, at least 1 species, *L. xanthinus*, is potentially benefiting from the existence of nonnative habitat at this site. Riparian areas in desert ecosystems offer vital resources for a wide range of wildlife, and may contain several endemic species, yet they are also frequently invaded by livestock grazing and exotic flora and fauna, and are attractive to humans for recreational purposes. Such impacts to riparian habitats need to be assessed more thoroughly to obtain a better understanding of how they affect native wildlife and how best to mitigate negative effects.

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