

THE RELATIVE ACTIVITY OF MOUSE-EARED (*Myotis* spp.) AND BROWN
(*Eptesicus* spp.) BATS (Chiroptera: Vespertilionidae) IN FIVE HABITAT TYPES
AROUND SPRING MEADOW LAKE

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ABSTRACT

The number of habitat types that bats can efficiently exploit may be limited by bat morphology (mass, wingspan, wing area, wing shape) and echolocation calls. Analysis of these characteristics can be used to predict which habitats bats are most likely to use. Slower, more maneuverable bats such as *Myotis* spp. should be able to exploit cluttered habitats in which prey densities are high, whereas larger, faster bats such as *Eptesicus fuscus* should be less able to use cluttered habitats due to an inability to maneuver efficiently in such habitats. I surveyed bats belonging to two genera, *Myotis* and *Eptesicus*, between 29 July and 30 August, 1997 at Spring Meadow Lake, a state recreation area on the western outskirts of Helena, Montana. Five habitat types were monitored for relative bat activity. The habitats were an open field (OP), a canopied area (CA) characterized by *Salix* spp., and three shoreline habitats representing low (SW), medium (ME), and high (TH) vegetation densities. Overall, bats were found to be most active at the shoreline sites of medium vegetation density, with relative abundance at other habitat types decreasing in the following order: SW, TH, CA/OP. *Myotis* spp. activity reflected this same trend. However, *Eptesicus* spp. activity was not significantly associated with any of the habitat types. Both field and canopy sites were virtually devoid of any bat activity. Greatest bat foraging activity (feeding buzz ratio) was associated with the ME habitat type, reflecting the overall relative abundance of bats. There was a significant difference in foraging activity between the ME and OP habitat types, but not between other habitat types for *Myotis* spp. Results are consistent with research showing that some species of *Myotis* favor aquatic habitats over terrestrial habitats. Greatest relative bat activity at shoreline sites of medium vegetation may reflect a cost-benefit "decision" to forage in an area in which the combination of prey density and extent of surrounding clutter enables the greatest net energy gain.

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INTRODUCTION

All of the 14 species of bats known to occur in Montana are insectivorous vespertilionids falling under 7 genera: *Myotis*, *Eptesicus*, *Lasionycteris*, *Lasiurus*, *Corynorhinus*, *Euderma*, and *Antrozous* (Genter and Jurist 1995). The genera *Myotis* and *Eptesicus* include species that are well adapted to the presence of humans. Specifically, *Eptesicus fuscus* and *Myotis lucifugus* are commonly associated with municipal environments. Both of these species are found throughout Montana. *Eptesicus fuscus* is the only bat of its genus in Montana. However, eight species of *Myotis* occur in the state. Two of these species, *Myotis thysanodes* and *Myotis septentrionalis*, have been assigned “species of special concern” status by the Montana Natural Heritage Program (1998) based upon their apparently limited or vulnerable distribution in the state.

During favorable months during which bats are active (usually April or May through September or October), bats such as *Myotis lucifugus* typically segregate into nursery colonies of females and pups and separate, small bachelor colonies of independent males (Nagorsen and Brigham 1993). Nursery colonies in which pups are born and raised are typically located in sites offering hot, stable temperatures (30-55 °C) (Hill and Smith 1984), whereas males tend to prefer cooler areas (Nagorsen and Brigham 1993). The sizes of maternity colonies can vary. In British Columbia, *Eptesicus fuscus* maternity colonies ranging between 50 and 700 bats have been documented. *Myotis lucifugus* colonies comprised of hundreds or thousands of bats have been documented in the same province. Bats are typically more loyal to roosts that are located near a stable source of insect prey (often a water source) (Kunz 1982). This is especially true for maternity roosts in which pups needing a steady supply of nourishment are raised. This correlation between roost location and available prey sources has led researchers to conclude that selection of foraging habitat may depend upon its proximity to the roost (Furlonger et al. 1987). Therefore, the likelihood that a bat will forage in any given

habitat should decrease as its distance from a roost increases. Depending upon the species, summer roosts may be located in any of the following places: caves, cliff crevices, under rocks, culverts, trees, houses and other buildings (typically in attics or under eaves), or even specially designed bat houses (Hill and Smith 1984; Genter and Jurist 1995).

Studies suggest a correlation between bat morphology, associated echolocation calls, and the habitat types that bats (specifically, aerial insectivores) can most efficiently exploit (Aldridge and Rautenbach 1987). Bats with a high aspect ratio (wing span²/wing area), high wingloading (body mass x acceleration due to gravity/wing area), and pointed wingtips are able to fly high and fast, but are less able to maneuver in cluttered habitats characterized by several obstacles such as tree branches. Conversely, bats with low aspect ratios, low wingloading, and more rounded wingtips are slower, yet more capable of flying in cluttered habitats.

Aldridge and Rautenbach (1987) found a significant correlation between these indices of morphology and bats' echolocation call characteristics: the bats capable of fast flight in open areas typically used echolocation calls characterized by lower frequencies and shallow, frequency modulated (FM) sweeps (e.g., Fig. 1), whereas the slower, more maneuverable bats tended to use higher frequency calls with relatively steeper FM sweeps (e.g., Fig. 2). Barclay (1986) also showed that some fast-flying bats of North America are more likely to utilize constant frequency (CF) tails in the latter portions of their calls. Low, CF calls are less subject to atmospheric attenuation and therefore useful for general prey detection over great distances (Simmons and Stein 1980). This advantage is readily apparent for bats that fly fast and cover long distances in a short period of time (Barclay 1986). Long, CF call components also allow the discrimination of moving prey against stationary backgrounds (Simmons et al. 1978). Similarly, FM calls, although more easily attenuated, are also useful in discerning precise location details of both insects and surrounding clutter, but in more close-range situations

(Simmons and Stein 1980). Several bats (e.g., *Eptesicus fuscus*) actually combine FM and CF components in their search calls, which allow them to detect prey while simultaneously monitoring surrounding clutter (Simmons et al. 1978). Also, several bats use multiple harmonics in their calls, presumably to effectively increase the bandwidth of the FM component (Simmons and Stein 1980). Although distinctive echolocation call characteristics are often associated with particular morphologies, they are nevertheless variable (Bell 1982) and likely do not confine some bat species to foraging in particular habitat types (Aldridge and Rautenbach 1987; Kalko and Schnitzler 1993).

Echolocation calls can vary in many features including frequency, duration, shape, and multiple harmonics (Waters et al. 1995; Parsons et al. 1997). Several species of bats possess much variability in call design (Thomas et al. 1987). For example, Thomas et al. (1987) found that the lowest frequency of calls of *Eptesicus fuscus* varied by as much as 8 kHz with duration anywhere between 2 and 10 seconds. Not only can the echolocation calls of bats belonging to the same species vary, but calls used by a single individual may also vary depending upon either the bat's environment or the stage of prey pursuit in which the bat is engaged (Barclay 1986; Kalko and Schnitzler 1993). Bats typically use a progressive sequence of calls during their pursuit of prey (Griffin et al. 1960; Simmons et al. 1979). This pursuit has been divided into four stages: search, approach, tracking, and terminal, comprising a "basic pursuit strategy" (Simmons et al. 1979) characteristic of several fast-flying bats.

As bats progress through their basic pursuit strategy, calls typically become higher in frequency, shorter in duration, more FM, and more rapidly emitted (Barclay 1986; Kalko and Schnitzler 1993). These alterations in echolocation are likely a response to the changing characteristics of reflected sounds as bats approach objects of interest (Barclay 1986). Although calls become increasingly higher in frequency as bats locate and pursue prey, frequency decreases in the terminal phase. Britton et al. (1997) summarized some possible explanations for this decrease in frequency: it may be an

unavoidable effect that high repetition rates have on throat muscles, it may increase the bandwidth of terminal FM calls (thus increasing the range of detailed perception), or it may allow the bat to project its calls over longer distances (this may have evolved as a means of informing relatives about the location of suitable prey).

The terminal phase of pursuit is characterized by a rapid repetition of short, FM (virtually no CF) calls and has been referred to as a “feeding buzz” (Griffin et al. 1960) due to its characteristic sound (when processed by an ultrasound detector) and the fact that detection of a terminal phase indicates that a bat has attempted to capture its prey. Feeding buzzes have been quantified by several researchers as a relative index of foraging activity in various habitat types (e.g., Fenton and Bell 1979; Thomas 1988; Brigham et al. 1997).

It is important to understand the phenomenon of “pulse-echo overlap” (Kalko and Schnitzler 1993) in order to understand why bats need to reduce the duration of emitted sounds as their distance to targets decreases. Recent research has shown that the overlap of an emitted sound wave and its returning echo can interfere with a bat’s interpretation of the reflected sound (e.g., Waters et al. 1995; Parsons et al. 1997). Whether pulse-echo overlap occurs depends upon the duration of the emitted call, the time interval between calls, and the distance between a bat and an object (Kalko and Schnitzler 1993; Britton et al. 1997). As bats approach objects, the potential for pulse-echo overlap increases. Bats can reduce this overlap by emitting calls of shorter duration. Shorter calls do not travel as far as longer calls, but they are typically used in closer proximity to objects, anyway. However, their distance can be increased if they are emitted at lower frequencies (Waters et al. 1995).

Due to the potential variability of echolocation, it is likely not a limiting factor affecting habitat use (Aldridge and Rautenbach 1987). Thus, researchers have reasoned that foraging efficiency in certain habitat types should first depend upon flight capabilities and secondarily depend upon echolocation call characteristics (Aldridge and

Rautenbach 1987). The studies conducted by Aldridge and Rautenbach, among others (e.g., Kalcounis and Brigham 1995), linking morphology to habitat suitability have led researchers to predict relative bat activity in given habitat types based upon bat species' physical suitability to these habitats. However, these predictions are not always accurate due to other factors that contribute to the use of foraging habitat (Brigham et al. 1992). For example, a major ecological factor affecting habitat use is the availability of suitable prey.

Both Saunders and Barclay (1992) and Aldridge (1986) suggest that a bat's morphology is more important in determining which prey are effectively available than in determining which habitat types a bat can utilize. Therefore, habitat associations may be more the result of foraging in response to locations of suitable prey than in response to habitat type (Saunders and Barclay 1992). For example, *Eptesicus fuscus* may often fly high (Nagorsen and Brigham 1993) because available prey tend to fly high. Similarly, some *Myotis* species (e.g., *Myotis yumanensis*) may often fly low over water (Brigham et al. 1992) because available prey are associated with water surfaces. In such cases, effective prey availability would be determined by morphology and echolocation, but links between morphology and habitat use would not be as direct as Aldridge and Rautenbach's (1987) results suggest. Questions concerning the influence of prey availability over habitat selection have been included in several studies (e.g., von Frenckell and Barclay 1987; Brigham et al. 1992; Kalcounis and Brigham 1995; Ekman and DeJong 1996).

Although it is possible that bats select prey according to taxon, most evidence suggests that prey size (more importantly, surface area) is the determining factor affecting prey selection (Belwood and Fenton 1976; Anthony and Kunz 1977; Barclay 1985; Aldridge and Rautenbach 1987). Based upon studies on *Lasiurus cinereus*, Barclay (1986) concluded that there is not enough evidence to support the hypothesis that bats select prey according to taxon. Barclay and Brigham (1994) even found evidence

that refutes the idea of taxon selection, although they conceded that bats may recognize different types of insects by their flight patterns (a possibility that would support Black's (1972) idea that certain bats exhibit different "tastes").

Anthony and Kunz (1977) concluded that *Myotis lucifugus*, a representative of small, maneuverable species, is restricted to preying upon insects ranging in body lengths between 3 and 10 mm. They based this range on data from fecal analyses and postulated that a bat's echolocation call characteristics in conjunction with logistics concerning the bat's body size determine the size range of suitable prey. They suggested that the wavelength (inversely proportional to frequency) of echolocation calls used by *Myotis lucifugus* restricts potential prey to a size range greater than a minimum detectable size. Any insect smaller than this minimum size, 3 mm, should be difficult to detect by calls with wavelengths that are longer than 3 mm. The higher frequencies used by smaller bats should therefore necessitate preying upon smaller insects.

Although there should be no maximum size that a small bat's echolocation cannot detect at close range, Anthony and Kunz (1977) postulated that the maximum size of suitable prey would be determined by the bat's ability to capture and overcome larger insects. They concluded that, for *Myotis lucifugus*, the energy costs of capturing insects larger than 10 mm would outweigh the energy gained by eating these larger insects. On the same line of argument, larger bats should be able to prey upon a range of insects falling between larger minimum and maximum boundaries than those for smaller bats (Barclay 1985). Therefore, small insects favored by small bats should not be major prey items for larger bats such as *Lasiurus cinereus*, which feed almost exclusively on large insects. Evidence supporting this niche differentiation was provided by Whitaker (1972) in a study comparing *Lasiurus borealis*, a larger bat, to *Myotis lucifugus*. Although both species preferred to eat Lepidoptera, *Myotis lucifugus* preyed upon smaller moths than did *Lasiurus borealis*.

Despite several examples of prey selection being limited by insect size, some studies have shown that larger bats are able to detect smaller prey than one might predict based upon their echolocation frequencies. For example, Waters et al. (1995) found that *Nyctalus leisleri*, a fast-flying bat weighing 11-20 g, fed predominantly upon Diptera with body lengths averaging 11 mm. Waters et al. suggested that the wavelength of the calls, with an average frequency of ca. 26.5 kHz (search phase), used by these bats does not restrict them from detecting small prey, disputing the hypothesis that low echolocation frequency eliminates small insects from a large bat's potential detectable prey. Waters et al. explained that large bats may be able to detect small insects more easily if the flight behavior of these insects effectively increases their detectable surface area.

The perpendicular orientation of the wings of flying insects effectively increases their surface area. Sound reflected from perpendicularly oriented wings is called a "glint" (Kalko and Schnitzler 1993). Long, shallow FM bat calls are best suited to detecting these glints. Waters et al. (1995) suggested that the low frequency of the calls used by larger bats such as *Nyctalus leisleri* is necessary in order for small insects to be detected outside a zone of pulse-echo overlap. Since small prey reflect fewer sound waves, more robust calls (i.e., lower frequency and/or CF) may be better suited to detecting these prey over longer distances. Increased detection distances should allow more time for less maneuverable species to catch prey, regardless of prey size. Also, some seemingly ponderous bats may actually be flexible enough to alter their behavior (i.e., by flying more slowly) in order to catch these smaller insects (Rydell and Yalden 1997).

Waters et al. (1995) suggested that the abundance of small prey in the diets of some relatively large bats likely reflects an abundance of suitable prey and therefore the use of opportunistic foraging behavior. However, there are likely other factors affecting these bats' selection of small prey. The niche of bat species such as *Nyctalus leisleri* is

quite complex. It is therefore difficult to generalize about limitations upon some bats' foraging capabilities. Overall, the fact that *Nyctalus leisleri*, a large bat, is able to capture small prey provides evidence that, although morphology and echolocation are associated (Aldridge and Rautenbach 1987), associations between morphology and prey selection may be more difficult to predict.

It is likely that other large bats (e.g., *Lasiurus cinereus*) select large prey due to surface area rather than taxon (Barclay 1986). For example, the large surface area of moth wings makes them more available than other taxa containing small-winged insects of similar body sizes, but smaller total surface areas. Barclay noted that ease of detection facilitated by larger surface areas is more important to large, fast-flying bats because they need to detect their prey over longer distances. Therefore, although it may seem that large bats such as *Lasiurus cinereus* select prey according to taxon, it is more likely that they select the most easily detected prey (those with large surface areas), which happen to belong to only a few insect orders. Although Waters et al. (1995) showed that, in some cases, environmental factors (often unidentified) may prevent large bats from foraging upon larger insects, a seemingly more energetically favorable choice than smaller insects, the idea that glints increase the effective surface area of small insects and thus makes them more detectable by *Nyctalus leisleri* provides further support in favor of the large role that effective surface area plays in determining prey selection by large bats.

Several bat genera include small species that are able to select prey from a wide variety of insect orders, thus exhibiting opportunistic foraging behavior (Fenton 1982). For example, several studies have concluded that most members of *Myotis* spp. tend to be generalists (e.g., Anthony and Kunz 1977; Brigham et al. 1992). In one such study, Anthony and Kunz (1977) found that *Myotis lucifugus* was able to feed on insects from the following orders: Diptera, Coleoptera, Lepidoptera, Trichoptera, Ephemeroptera, Neuroptera, Homoptera, and Hymenoptera, with selection of Diptera occurring most often. However, Whitaker (1972) found that Lepidoptera, not Diptera, were favored by

Myotis lucifugus in Indiana. *Myotis yumanensis* is another small bat with varying prey preferences. Brigham et al. (1992) found that this species selected prey predominantly from any of four orders: Trichoptera, Diptera, Coleoptera, and Lepidoptera, based on availability during a season.

Most researchers have concluded that small bats which are able to exploit a wide variety of insect prey will feed opportunistically on whatever is most abundant on any given night (Anthony and Kunz 1977; Brigham et al. 1992; Arlettaz 1996). Although small bats seem to be generalists, increasing prey availability tends to result in more selectivity by the bats (Brigham et al. 1992). Anthony and Kunz (1977) speculated that bats presented with many, similar-sized prey options may select those that are most easily detected (i.e., hard-bodied beetles) or others that exhibit unique morphology indicating the presence of something favorable to these bat (i.e., *Myotis lucifugus* preference for mayflies over moths). Hence, taxon selection by small bats might occur secondarily to selection based upon size (surface area).

Based upon studies involving both large and small bats, one might conclude that most insectivorous Vespertilionids select prey from what is effectively available to them and are therefore, largely opportunistic. Hence, surface area seems more important than taxon when it comes to prey selection by aerial insectivores. Whereas small bats utilizing high, FM calls can afford to select prey from swarms of various small-bodied insects (Barclay 1985), larger bats, using lower, shallower FM calls may be limited to preying upon relatively solitary insects with larger surface areas (not simply longer body lengths). Therefore, at least in the case of *Lasiurus cinereus*, larger bats may seem to exhibit more selective prey choice simply because only certain insect orders (e.g., Lepidoptera) include volant insects sporting surface areas large enough to be efficiently detected and captured by fast bats utilizing low-frequency echolocation calls. Of course, the limitations upon prey selection are not black and white, as Waters et al. (1995) showed. Some assumptions about available prey limitations are inapplicable to some species such as

Nyctalus leisleri. This large bat may actually benefit from swarms of small insects (the assumed domain of small bats) because swarms provide a greater potential for the detection of glints (Waters et al. 1995).

Habitat selection is likely influenced by the three major factors: morphology, echolocation, and the availability of suitable prey (Aldridge and Rautenbach 1987; Brigham et al. 1992). Bats likely select foraging habitats in which they can energetically benefit. Therefore, habitat selection will ultimately be the result of a cost-benefit analysis (which may include factors such as predation that are not discussed in this paper) instinctively performed by each bat (Ekman and DeJong 1996). For example, Brigham et al. (1997) found that, if prey availability is constant, then small bats will avoid clutter in favor of more open areas, thus avoiding unnecessary maneuvering through clutter and concomitant energy loss. Although morphology and echolocation used by both fast and slow bats likely affect the niches that they can exploit, wide variations in these traits probably allow a certain amount of flexibility in bats' foraging habitat selection (Hart et al. 1993). Since bats likely forage where the most suitable prey are available, understanding of the habitat associations of insects is necessary for an understanding of habitat selection by their predators.

Hart et al. (1993) noted that aquatic habitats harbor a significant source of flying insects. In a study of the inland dispersal of Trichoptera and Ephemeroptera, Kovats et al. (1996) found that greater concentrations of insects remained localized at the shores of both a river and a lake when compared to terrestrial areas away from the water. Hart et al. (1993) hypothesized that the high concentrations of aquatic flying insects near water may explain the association of *Lasiurus borealis* with aquatic areas. Other genera may also prefer aquatic habitats on similar grounds. Aquatic species are included in many of the insect orders favored as prey by *Myotis* spp. (e.g., Coleoptera, Diptera, Ephemeroptera, and Trichoptera). Thomas (1988) found that 64.4 percent of insects found over water sites were also small-bodied and thus of suitable size for *Myotis* spp.

Kovats et al. (1996) also found that larger Trichoptera were able to disperse farther, likely resulting in smaller insects remaining at shoreline areas. This large percentage of suitable-sized prey near water likely explains the high affinity for water exhibited by some species of *Myotis* (Furlonger et al. 1987; Brigham et al. 1992).

In terrestrial habitats, measurements of the abundance of volant insects in cluttered versus open areas support the idea that a greater abundance of these insects is associated with more cluttered habitats (Lewis 1970; Peng et al. 1992; Kalcounis and Brigham 1995). However, Ekman and DeJong (1996) measured greater insect abundance in open, rather than cluttered sites. Despite the disparity between these studies, several researchers have found that the density of insects is usually greater in more cluttered habitats (e.g., Lewis 1970; Aldridge and Rautenbach 1987). Neither Kalcounis and Brigham (1995) nor Ekman and DeJong (1996) measured insect abundance at cluttered versus open aquatic sites. Therefore, one can only infer from these studies that cluttered shores resemble cluttered forests and open shores resemble open fields in terms of insect abundance. Such an inference is supported by a more direct study focusing on the distribution of Dipteran larvae at lakes in which higher numbers of larvae were correlated with shallow water, dense emergent vegetation, and dense shoreline vegetation (Callahan and Morris 1987).

An understanding of morphology, echolocation ability, and prey availability may allow researchers to predict which habitats bats are most likely to use (Aldridge 1986; Aldridge and Rautenbach 1987). The primary objective of this study was to determine habitat associations of bats at Spring Meadow Lake in Helena, Montana and to determine whether observed activity could have been predicted based upon analysis of the morphology and echolocation calls utilized by the dominant genera in the area. A secondary objective was to determine which habitat types were used the most by foraging bats based upon the number of feeding buzzes detected (Fenton and Bell 1979; Thomas 1988; Brigham et al. 1997).

METHODS

Study Area

I surveyed thirty sites within Helena between 12 August and 14 September, 1997 to assess local bat distribution and to aid in choosing a primary study site. These preliminary surveys lasted twenty minutes and were conducted within two hours after dusk. Bats were detected at fifty percent of the preliminary survey sites, with *Eptesicus* and *Myotis* being the predominant genera represented. Based upon the abundance of bats at aquatic sites, I chose Spring Meadow Lake as the site of my focal study.

Spring Meadow Lake was originally a gravel pit run by the Helena Sand and Gravel Company from 1927 to 1964 (Montana Department of Fish, Wildlife and Parks: Spring Meadow Nature Trail Brochure; no date). The area was purchased by the state in 1981 and has since been available to the public as a state park. The lake (area \cong 6 ha) is fed by groundwater, which seeps up through sand and gravel. Ten Mile Creek runs near the lake. Willows (*Salix* spp.) compose most shoreline vegetation, although there are also several large cottonwoods (*Populus* spp.). Future plans for the area include the development of a nature complex through remodeling of the old Powder Co. buildings to the south of the lake (Fig. 3).

Spring Meadow Lake is an ideal site for bat study because there has been an established presence of bats for several years (D. Genter, pers. comm.) and the area includes several habitat types within close proximity of one another. The lake is within an easily accessible, state-managed recreation area that is popular among anglers, swimmers, boaters, and birders during summer months. Management has resulted in three degrees of vegetation density about the shoreline: the swimming area has virtually no vegetation, the picnic area is "well-groomed" with patches of vegetation interspersed between shoreline picnic tables, and a "wild" area on the eastern side of the lake is most heavily vegetated with small footpaths leading through brush to sporadic shoreline

openings (Fig. 3). The state has reported that as many as six species of bats may use the area, but *Myotis lucifugus* and *Eptesicus fuscus* are the two species most likely to be present (Montana Department of Fish, Wildlife and Parks: Spring Meadow Nature Trail Brochure; no date). One might expect this because these two species are quite adaptable to human presence and consequently quite likely to be found in municipal environments (Kunz 1982).

Field Surveys

Potential survey sites around Spring Meadow Lake were classified into five habitat types (Fig. 3). Three of these habitat types are located along the shores of the lake. Shoreline sites were chosen based upon accessibility and the presence of a vegetation-free “window” from which I could record bat echolocation. The extent of vegetation at each shoreline site was used to classify it under a habitat type. I surveyed along 10 meter transects parallel to the shoreline to estimate the degree of vegetation at each site. For the purposes of this study, everything above knee height (ca. 0.46 meters) was considered as vegetation. The shoreline vegetation surveys provided an index to the relative amount of total vegetation in each of these three habitat types.

The five habitat types represent a mix of shoreline and non-shoreline areas. The swimming area (SW) is located along the shores of the northwestern end of the lake and consists mostly of bare sand and virtually no vegetation. The medium vegetation area (ME) is located along the western and southern shores of the lake (but also includes sites at the northern end of the lake) and consists mostly of patches of shrubs and trees interspersed with relatively open patches of bare ground. The sites in this category are “well-groomed,” associated with picnic tables and mowed grass. The final shoreline habitat type consists of thick vegetation (including shrubs and trees). Sites in the thick area (TH) are characterized by vegetation that extends several meters perpendicular to the shore, resulting in a less-managed “wild” area. Sites representing the TH habitat type are

located on the eastern side of the lake, both sides of a peninsula jutting from the south, and the shores of a small, connected pond on the southeastern end of the lake. TH sites tend to be located around more sheltered areas of the lake, which harbor more emergent vegetation. The two non-shoreline habitat types, an adjacent field (OP) and a canopied area (CA), both of which belong to Spring Meadow Lake State Park, are located east and south of the lake, respectively. The former is characterized by tall grasses and some shrubs, while the latter is comprised mostly of willows (*Salix* spp.) greater than ca. 1.5 meters tall.

Ten survey sites from each habitat type were randomly selected to give a total of 50 sites. To monitor relative bat activity at each site, I used an Anabat II ultrasonic bat detector (Titley Electronics, Ballina, Australia) connected to a sound-activated tape recorder (Tandy Corporation, Fort Worth, Texas) via a cable (Thomas 1988). The detector was set at a sensitivity level of 5 and a division ratio of 16; a built-in calibration tone of 40 kHz was recorded at the beginning and end of each survey block in order to compensate for tape speed variations during later data analyses (Fenton and Bell 1981). During each survey, the detector was held between ground and waist level and pointed toward the water (perpendicular to the shore) at shoreline sites or toward the center of the habitat type for CA and OP sites. Surveys were conducted during a 160 minute period which began circa 176 minutes after sunset on each night (sunset times obtained from the U.S. Naval Observatory, January 1998). This survey period was chosen based on logistic constraints and emergent times recorded elsewhere (Fenton and Bell 1979; Fenton et al. 1980). Five survey blocks of 20 minutes each with 15 minute intervals between each survey block constituted each 160 minute survey. I visited a randomly chosen site from each habitat type on each of ten nights between 29 July and 30 August 1997. Thus, by summer's end, each habitat type had been represented a total of two times during each survey block. I recorded the following weather variables at the beginning and end of each survey period: percent cloud cover, wind speed (modified Beaufort scale) and

direction, and temperature (°C). Precipitation was not measured as surveys were aborted at the advent of rain due to sensitivity of the equipment.

Laboratory Analysis

I used DOS software created specifically for bat call analysis (Corben 1993) to analyze recorded bat passes and identify them to genus. To use this system, the field tapes are played in a simple tape recorder connected to a zero-crossings analysis interface module (ZCAIM) (Titley Electronics, Ballina, Australia). The ZCAIM and software project a time-frequency version of each bat call onto a computer monitor (Simmons et al. 1979). Call shape, frequency, time between calls, and call duration are thus observed on screen while the recorded bat calls are simultaneously heard. Visual characteristics of calls are typically used to identify bat species (Fenton and Bell 1981; Thomas et al. 1987). I used reference calls from the Pacific Northwest Bat Call Library (1998) and calls provided by the Montana Natural Heritage Program (The Nature Conservancy) to assist in the identification of recorded bat passes.

I only identified bats of the genera *Myotis* and *Eptesicus* from recorded passes. Although a bat representing another genus was recorded at least once, the majority of recorded passes belonged to either *Myotis* spp. or *Eptesicus* spp. Due to similarities between echolocation calls of *Myotis* spp. (Thomas et al. 1987) and consequent difficulty in distinguishing species of this genus, I only identified bats to the genus level (Hart et al. 1993). However, only one species belonging to the genus *Eptesicus*, *Eptesicus fuscus*, occurs in Montana (Genter and Jurist 1995). I identified *Myotis* spp. passes based on high frequency (greater than 35 kHz), long FM sweeps with virtually no shallow FM tails, and relatively little time between calls (Thomas et al. 1987). *Myotis* spp. passes also sound quite unique: they often sound like a “tick” (Fenton and Merriam 1983), but may sound more “chirpy” in some cases. As the sound of recorded calls can vary, I relied heavily upon shape and frequencies of calls for identification of *Myotis* spp. Calls

of *Eptesicus fuscus* also look and sound quite distinct. They are usually based at 27 kHz with a shorter FM sweep and a shallow FM tail (Fenton and Bell 1981). These calls sound quite tonal. As frequency can also vary (Thomas et al. 1987), I identified most calls under 35 kHz as belonging to *Eptesicus fuscus* and relied much upon the characteristic tonal sound. Unidentifiable bats were occasionally detected and included as part of a count of total bat passes.

I defined a bat “pass” (Fenton 1970) as a sequence of at least five calls. Although others have defined a pass as consisting of at least two calls (Thomas 1988), I preferred the more stringent criterion of five calls as it improves the reliability of the data. At sites of high bat presence, I required that passes be separated by at least two seconds of space in order to constitute two passes. This criterion led to an obvious underestimation of relative bat activity at some sites because they were frequented by many bats whose overlapping calls led me to define long stretches of activity as “one pass”. Additionally, one bat is capable of providing many passes (Hart et al. 1993; Thomas 1988). It is therefore difficult to tell how many bats are actually present during a survey. To compensate for this, my data analyses focused on the relative bat activity at different habitat types. I also quantified feeding buzzes at the sites (Fenton and Bell 1979). Although one can pick out feeding buzzes on screen, they are more easily identified by their characteristic “zip” sound. Since there are varying degrees of feeding buzz intensity, I only counted the definite buzzes for both *Myotis* spp. and *Eptesicus fuscus*.

Statistical Analysis

All but one of the statistical comparisons were made using one-way analysis of variance (ANOVA) and post-hoc tukey tests when ANOVA’s produced significant results (SPSS 1997). Two preliminary tests addressing sampling assumptions were used to augment the core analyses. First, I pooled the total number of bats (from 10 nights of surveys) during each survey block and then tested whether any survey block had more bat

activity than the others. Secondly, to test for differences in vegetation density between the three shoreline habitat types, I compared the percent of shoreline vegetation in 10 meter line transects measured at each survey site.

Core analyses included three tests. First, to test for habitat associations, I compared the total number of bats at each habitat type over the course of the season; these data were log transformed to standardize variance and meet assumptions of normality. Secondly, to test for different trends in habitat use exhibited by the two genera, I used two-way ANOVA to compare the total number of *Myotis* spp. and *Eptesicus fuscus* passes between habitat types. Since varying echolocation call characteristics (e.g., intensity) cause some species to be more easily detected than others, direct comparisons of relative activity between the genera at each habitat type were not attempted (Vaughn et al. 1997). Finally, I determined a feeding buzz ratio (total buzzes/total passes; see Vaughn et al. 1997) at each site as an index of foraging activity and compared habitat types. Because these data are ratios, they were transformed with the arcsin square root function in order to meet assumptions of normality. Two analyses were used to determine whether foraging activity was positively associated with any habitat type. One analysis used a ratio of total feeding buzzes (*Myotis* spp. and *Eptesicus fuscus*) per site divided by total bat passes. The second analysis used only total *Myotis* spp. feeding buzzes per total *Myotis* spp. passes at each site.

RESULTS

Preliminary Tests

ANOVA revealed no significant difference between the number of bats in each of the five survey blocks ($F = 0.483$, $p = 0.748$). Thus, bat activity was relatively constant during an average of 126 to 226 minutes after dusk.

ANOVA revealed a significant difference in percent vegetation between shoreline habitat types ($F = 9.260$, $p = 0.001$). However, post hoc tests (Tukey HSD) revealed that the percent of vegetation at the swimming area (SW) was significantly lower than that at the thick (TH) and medium (ME) habitat types ($p = 0.036$ and $p = 0.044$, respectively), while the percent of vegetation between these latter two habitat types did not significantly differ ($p = 0.996$; Fig. 4). I attribute this to use of line transects that did not accurately reflect the differences in vegetation thickness perpendicular to the shore and maintain that there is nevertheless an observable difference between sites representing ME and TH habitat types. Also, I subjectively noted that more emergent vegetation existed at TH sites, contributing to a greater amount of vegetation than was measured.

Tests for Relative Activity Between Habitat Types

ANOVA revealed a significant difference in total bat passes between the five habitat types ($F = 35.941$, $p < 0.001$). Post hoc (Tukey HSD) analysis showed a significant difference between all pair-wise habitat comparisons except OP and CA ($p = 0.988$). Overall, relative activity between the habitat types was highest at ME sites, with activity at other habitat types decreasing in the following order: SW, TH, CA/OP (Fig. 5).

ANOVA revealed a significant difference in habitat use by *Myotis* spp. between habitat types, but there was no significant difference in habitat use by *Eptesicus fuscus* between habitat types (Table 1; Fig. 6). Therefore, observed differences in total bat

activity at the five habitat types can likely be attributed to variation in relative *Myotis* spp. activity, which reflected the observed differences for total bats (see above).

For both tests of foraging activity ($\arcsin(\sqrt{\text{buzz ratio}})$), ANOVA revealed a significant difference between sites both for total bats ($F = 8.232$, $p < 0.001$) and *Myotis* spp. alone ($F = 3.237$, $p = 0.020$). No bats were detected feeding at OP sites throughout the study (Figs. 7 and 8). Tukey tests revealed that, when tested alone, *Myotis* spp. foraging activity was significantly different between the OP and ME habitat types, with more activity observed at the ME habitat type (Fig. 8). However, there were no observed differences in *Myotis* spp. foraging activity between other habitat types. Tukey tests comparing total bat foraging activity between habitat types revealed that the most foraging activity was associated with the ME habitat type (Fig. 7). Total foraging activity at the ME habitat type differed significantly from all other habitat types except SW.

DISCUSSION

Bats at Spring Meadow Lake appear to be most active at shoreline sites of medium (ME) vegetation densities. Although total bat activity at CA and OP habitats did not differ, activity at sites decreased in the following order: ME, SW, TH, CA/OP. This trend reflected a similar trend in *Myotis* spp. activity between habitat types. However, activity of *Eptesicus fuscus* did not significantly vary with habitat type. There was a significant difference in *Myotis* spp. foraging activity (buzz ratio) between ME and OP habitat types in favor of ME. However, comparisons between all other habitat types revealed no significant differences in *Myotis* spp. foraging activity. Although no analysis of isolated *Eptesicus fuscus* foraging activity was possible due to insufficient data, inclusion of *Eptesicus fuscus* buzzes in a test of total bat foraging activity resulted in a significant association of greatest foraging activity with the ME habitat type.

Results indicate that any overall trends in activity by habitat type are likely a result of *Myotis* spp. activity due to the fact that *Eptesicus fuscus* was not significantly associated with any particular habitat type (Fig. 6). However, this lack of significance may also be due to the low number of *Eptesicus fuscus* detections. It is also possible that unidentified bats, not merely *Myotis* spp., contributed to the observed trends in total bat activity, although unidentified passes constituted only a small proportion of total bat passes. Results indicating low use of the CA and OP habitat types by *Myotis* spp. should be expected because neither of these habitats are closely associated with water, a source of flying insects upon which species of *Myotis* predominantly feed. For example, *Myotis lucifugus* and *Myotis yumanensis*, two species of *Myotis* that are known to occur in Montana, have been shown to favor aquatic habitats and the aquatic prey associated with these habitats (Furlonger et al. 1987; Brigham et al. 1992). Since the measured *Myotis* spp. activity was strongly associated with shoreline sites, it is possible that these two

species were among the bat species sampled, although *Myotis lucifugus* is much more likely to be found in municipal settings than *Myotis yumanensis* (Kunz 1982).

Although no measure of insect abundance was included in this study, the greatest abundance of insects likely occurs in the thickest vegetation (TH) around the lake due to the fact that it is the most cluttered (Callahan and Morris 1987; Kalcounis and Brigham 1995). Since bats have been shown to favor areas of high insect concentrations (Hayes 1997), one might expect the most bat activity to be associated with the TH habitat type. However, bats neither foraged most often (buzz ratios) nor spent the most time (passes) in the TH habitat type. It may be that fewer insect prey were located in the TH habitat type when compared to the SW and ME habitat types. Alternatively, bats may forage less often at TH sites (despite potentially greater densities of prey) because increasing clutter effectively decreases the availability of suitable prey. For example, assuming that the greatest abundance of suitable prey is in the TH habitat type, bats may nevertheless be unable to detect this prey at TH sites due to “acoustical complexity” (Brigham et al. 1997) created by confounding clutter (i.e., confusion may result from signals bouncing off of many obstacles other than the target).

Although some “clutter rejection” echolocation strategies (e.g., foraging parallel to vegetation or reducing the duration of calls) allow bats to forage among clutter (Kalko and Schnitzler 1993), some bats may prefer not to forage in such energy-demanding environments. For example, Mackey and Barclay (1989) found that *Myotis lucifugus* preferred to forage over water that lacked emergent vegetation and other sources of echo interference. Mackey and Barclay’s study may also explain why relatively few *Myotis* spp. used the TH habitat type (Fig. 6). It is possible that the significant association of *Myotis* spp. with the ME habitat type is based upon a cost-benefit compromise between foraging where prey is most available and foraging where it takes the least energy to maneuver (Brigham et al. 1997). A similar line of argument may explain differences in activity between SW and ME habitat types. If there were equal numbers of prey in the

SW and ME habitats, for example, then *Myotis* spp. should favor the SW sites due to the opportunity to save energy by avoiding the need to maneuver about clutter (Brigham et al. 1997). However, there are likely more prey in both the ME and TH habitat types compared to the SW habitat type.

The measure of relative foraging activity (feeding buzz ratio) should reflect which habitat types harbor prey that is most easily detected and captured by bats (Vaughan et al. 1997). The use of a ratio should eliminate bias in favor of habitat types with the most relative activity, therefore allowing the test of foraging activity to be independent of total bat passes. The results of total foraging activity reflect total bat activity, which is greatest at the ME habitat type. This result was expected since bats should spend more time at sites at which they can detect and capture more suitable prey. The results for *Myotis* spp. foraging activity suggest that these bats forage equally among sites (omitting OP sites). This lack of significance between sites may be the result of too small a sample size (and thus, relatively high standard errors). However, it is also possible that the results reflect relatively equal numbers of detectable prey at each habitat. If this is the case, then the overall low use of TH sites by *Myotis* spp. may be more a result of the energy demands of flying in clutter than the ability to detect prey in clutter.

Fenton (1990) characterized *Eptesicus fuscus* as a large, fast bat that forages in open areas. Due to its relatively larger body size (and decreased maneuverability), one might expect *Eptesicus fuscus* to be less capable of exploiting the thickly vegetated sites (TH) than *Myotis* spp. (Aldridge and Rautenbach 1987). Although results cannot be used to directly compare the genera, *Myotis* spp. exhibited differential use between habitats, whereas no difference in habitat use was observed for *Eptesicus fuscus*. The relatively few detections of *Eptesicus fuscus* may have contributed to this apparent lack of significant activity among sites. It is possible that relatively few *Eptesicus fuscus* actually use the area, resulting in insufficient data to make comparisons involving habitat use.

Alternatively, *Eptesicus fuscus* may simply not favor any one habitat type. Furlonger et al. (1987) also found no significant differences in use of several habitat types by *Eptesicus fuscus*. Furlonger et al. concluded that *Eptesicus fuscus* is not extensively limited in terms of habitat types that it can utilize. It is possible that the morphology and echolocation calls used by *Eptesicus fuscus* contribute to its ability to use several habitat types. An observed trend for *Eptesicus fuscus* to be most active in ME sites (Fig. 6) likely means that its morphology does not restrict it from utilizing these sites. However, virtually no *Eptesicus fuscus* were detected in TH sites, suggesting that these bats may be less able to utilize thickly vegetated sites. This was also inferred by Fenton (1990), who said that fast bats using long CF calls may be restricted from using cluttered habitats. However, the FM component of *Eptesicus fuscus* calls may confer flexibility upon these bats that is not enjoyed by bats using strictly CF calls.

Another possible cause of no differences in use among habitat types is the flight behavior of *Eptesicus fuscus*. This bat tends to fly high and often above canopy levels, usually greater than 5 m above water (Mackey and Barclay 1989). Such behavior may remove this species from being significantly affected by vegetation densities or other sources of clutter below (Brigham et al. 1997), although clutter can nevertheless interfere with a bat's echolocation even if the bat is not flying within that clutter (Kalko and Schnitzler 1993). Again, as in the case of *Myotis* spp. activity, the trend for *Eptesicus fuscus* to prefer ME sites may reflect a compromise between saving energy (by foraging above less acoustically complex sites) and foraging where suitable prey is most abundant.

Although it is possible to explain these results using morphological and echolocation theory, it would have been difficult to predict these results because I did not know the extent of clutter required to significantly influence bat flight and echolocation nor whether the habitat types at Spring Meadow Lake harbor restrictive vegetation densities. Ignorance of insect densities also makes it difficult to predict which habitat types should be favored by bats. Because morphology may affect bats' ability to capture

prey more so than their ability to maneuver among clutter (e.g., Aldridge 1986; Saunders and Barclay 1992), emphasis upon prey distribution among habitat types may have revealed more about the causes of observed habitat associations. Several alterations in methods would have likely allowed me to make stronger conclusions concerning my results. More samples over the course of a whole summer may have contributed to reduced standard error in the analyses, resulting in more definite conclusions concerning differential site use by *Eptesicus fuscus* total activity and *Myotis* spp. foraging activity.

A measure of insect abundance available to foraging bats would also be beneficial in determining whether prey abundance affects habitat associations at Spring Meadow Lake. Such measurements would either support or refute assumptions that more insects are in more cluttered habitats. One could also measure whether the relative abundance of different insect size classes affects bat activity. One could use sticky traps or other common insect traps such as a Malaise trap to assess insect abundance (Kunz 1988). A different method of measuring vegetation density via line transects would help elucidate the differences between sites. One such method would involve the measurement of several shorter (5 m) transects perpendicular to the shore at each site.

One can tell from the aerial photograph (Fig. 3) that other factors varied along with shoreline vegetation densities. For example, most ME sites are located on the western side of the lake. Such factors as the fact that TH sites should receive sunlight for a longer duration before sunset may influence bat activity. Also, wind direction, which anecdotally came most often from the Southwest, may distribute insects unevenly between TH and ME sites (because insects tend to gather on the leeward sides of vegetation; Lewis 1970). It is therefore possible that confounding variables other than vegetation density influenced the results.

A less subjective and more accurate method of identifying bat calls would improve analysis. Recent advances towards using computers to analyze the characteristics of bat calls sound hopeful because they would eliminate subjectivity due

to human interpretations (Herr et al. 1997). Because characteristics of bat calls within a species can vary geographically, researchers often capture bats within study areas from which reference calls are recorded (e.g., Fenton and Bell 1979). By capturing bats (using mist-nets) and light-tagging bats of known identity, I could have similarly obtained reference calls specific to the study area (Kunz 1988). The use of such reference calls may have contributed to an increased confidence in bat call identification. Capture and light-tagging of bats would also have helped quantify presence of bats at the habitat types, support identification of species using the area, and help determine the spatial distribution of bats at the study area (Brigham et al. 1992).

Although this study provides no specific data on prey availability, energy requirements, and bats' ability to maneuver in the five habitat types, the fact that bat activity was associated with sites of intermediate vegetation density supports the idea that *Myotis* spp. are less likely to use the sites of thickest vegetation, possibly due to morphological and echolocation constraints (Aldridge and Rautenbach 1987). Although some species of *Myotis* are likely capable of maneuvering in TH sites, it might not be energetically favorable to do so (Brigham et al. 1997). Similarly, although it is likely easiest to maneuver at SW sites, the abundance of prey at these sites may not be large enough for bats to attain the greatest net energy gain.

Whereas previous studies have measured relative abundance at isolated sites, few seem to focus on measuring relative abundance within sites (i.e., comparing relative abundance about the shores of a given lake versus comparing relative abundance at several different lakes or areas around the lake representing different habitat types.) This study demonstrates that there is a definite presence of bats representing both *Myotis* and *Eptesicus* at Spring Meadow Lake and that spatial partitioning to some extent occurs at the lake. Bats are most likely to be found on the western side of the lake where vegetation density is intermediate compared to other areas of the lake. Virtually no bats use the canopy (CA) and open (OP) areas. Although direct comparisons cannot be made,

it is likely that there is more activity by *Myotis* spp. than *Eptesicus fuscus* at the lake. Although the methods used in this study provide information on relative activity only and not absolute numbers (Thomas and LaVal 1988), capture of bats and light-tagging in future studies may aid researchers in determining population numbers in the area (Barclay and Bell 1988).

This study was the first of such detail to be conducted on the presence of bats at Spring Meadow Lake. Although a maternity roost for *Myotis lucifugus* is likely nearby (Barclay 1984), I was unable to locate one. However, I did find evidence of bat presence at the old Powder Co. buildings to the south of the lake and at the Archie Bray Foundation to the west. If a nearby roost could be located, then future studies concerning feeding habits, reproduction, and actual counts of bats could be conducted (Thomas and LaVal 1988). Future studies at the lake could address the following questions. Does relative bat abundance vary with relative abundance of aquatic insects? Can relative bat activity be correlated to percent of different size classes of insects captured? Which species of bats are truly present at the lake? How large is the population of bats that uses the lake (if a roost is located)? In what capacity do various species of bats respond to different designs and locations of introduced bat-houses? The possibilities for future studies are truly limitless as long as bats continue to use the area. Continued monitoring of the bat population and actual counts in the future may be useful in determining how the proposed development of a nature complex (and remodeling of the old Powder Co. buildings, sites of possible bat roosts) affects the bats that frequent Spring Meadow Lake.

TABLES

Table 1. Results from ANOVA testing for differences in relative activity of *Myotis* spp. and *Eptesicus* spp. between five habitat types at Spring Meadow Lake, Helena, Montana during 29 July - 30 August, 1997.

Variable	df	Mean Square	F	P
Habitat Type	4	5769.265	14.948	<0.001
Bat Genus	1	9564.840	24.783	<0.001
Habitat x Genus	4	3384.515	8.769	<0.001
Residual	90	385.951		

FIGURES

Figure 1. Frequency-time display of an *Eptesicus fuscus* pass recorded at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997. Note frequency (ca. 27 kHz) and shape of calls (short sweep with shallow FM component). The time between calls has been compressed.

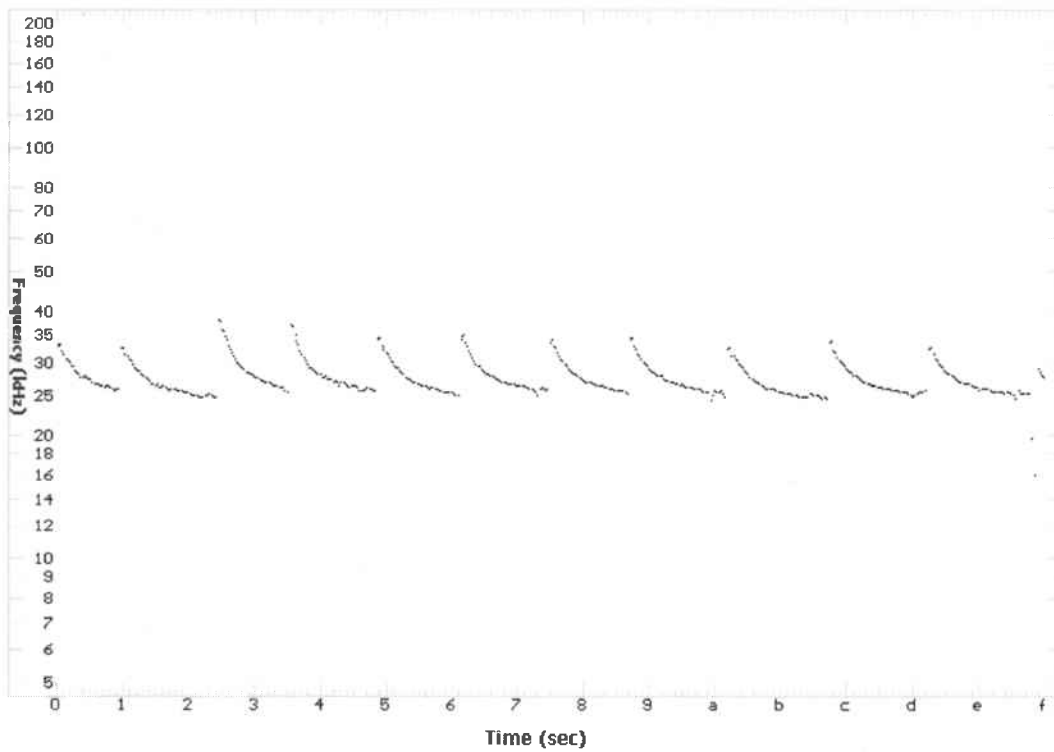
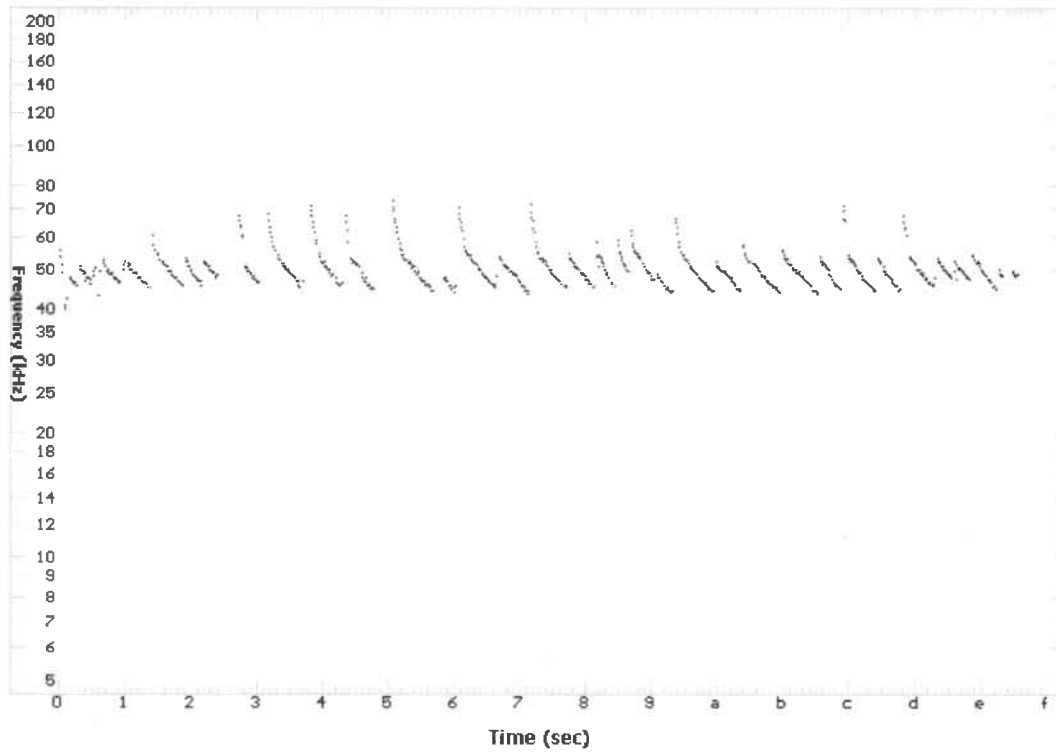


Figure 2. Frequency-time display of a *Myotis* spp. pass recorded at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997. Note frequency (ca. 45 kHz) and shape of calls (steep sweep with no shallow FM component). The time between calls has been compressed.



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Figure 3. Aerial photograph (1995) of the study area, Spring Meadow Lake, Helena, Montana. The study was conducted during 29 July - 30 August, 1997. Shoreline habitat types are located clockwise of labels. (CA = canopied area, OP = open field, SW = swimming area (low shoreline vegetation density), ME = medium shoreline vegetation density, TH = high shoreline vegetation density). Photograph provided by the Montana Department of Transportation.

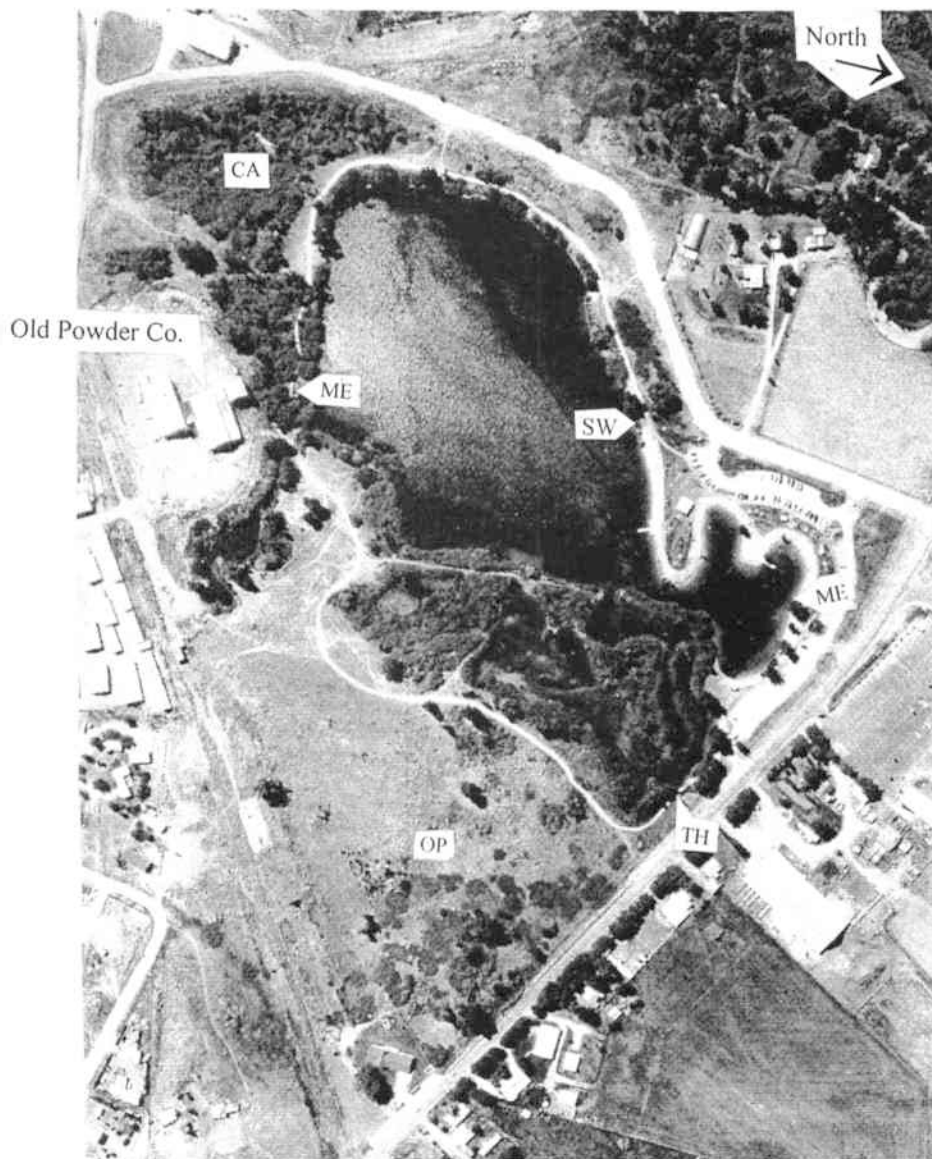


Figure 4. Percent of 10 meter transects covered with vegetation in three shoreline habitat types at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997.

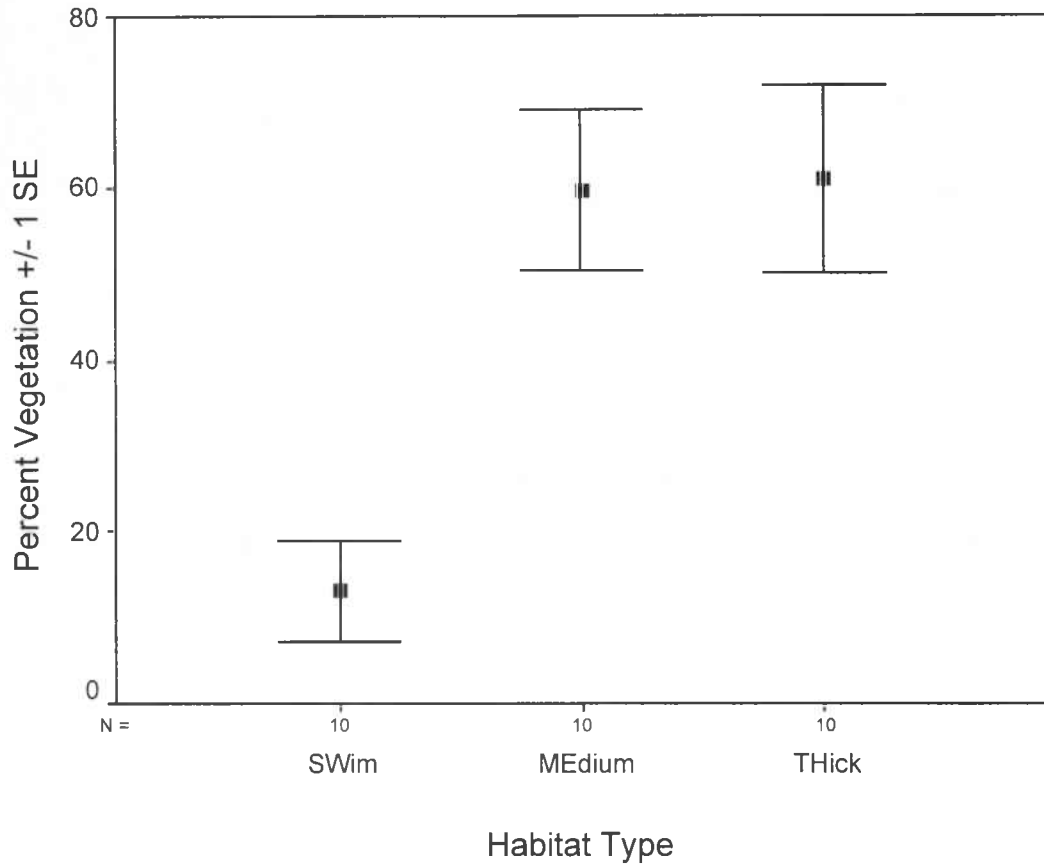


Figure 5. Total bat passes recorded at five habitat types at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997.

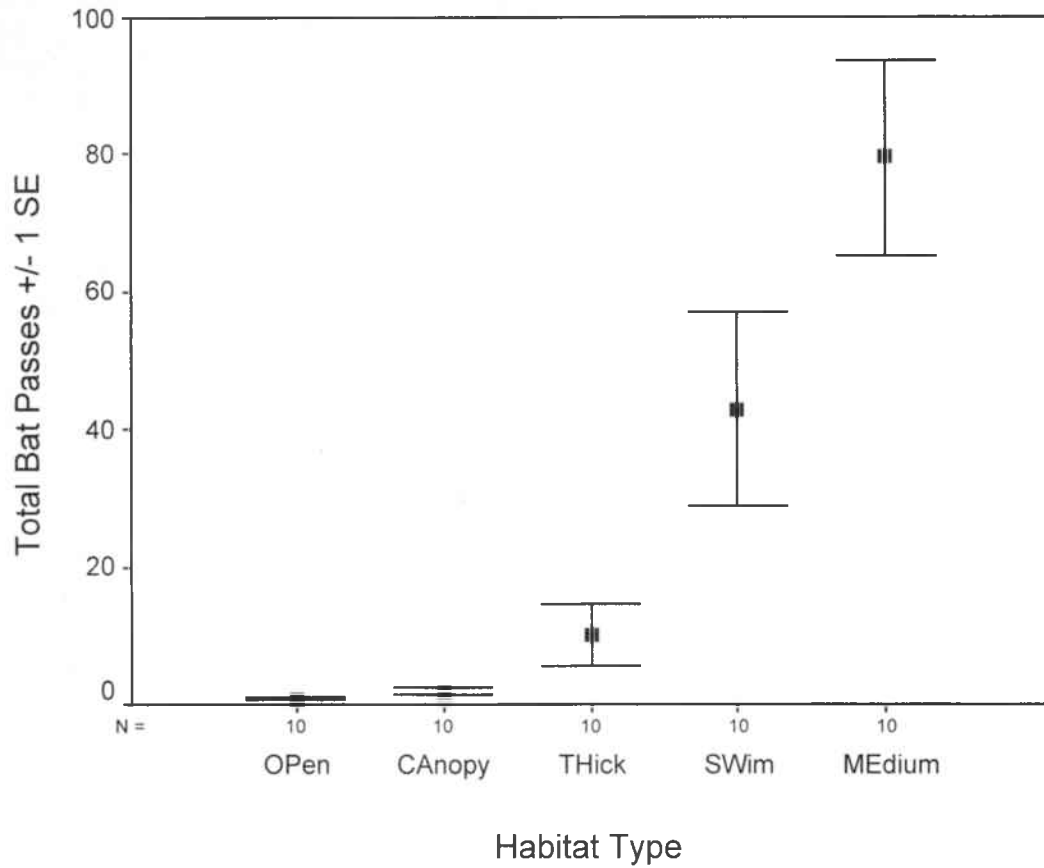


Figure 6. Total recorded passes of *Myotis* spp. and *Eptesicus fuscus* among five habitat types at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997.

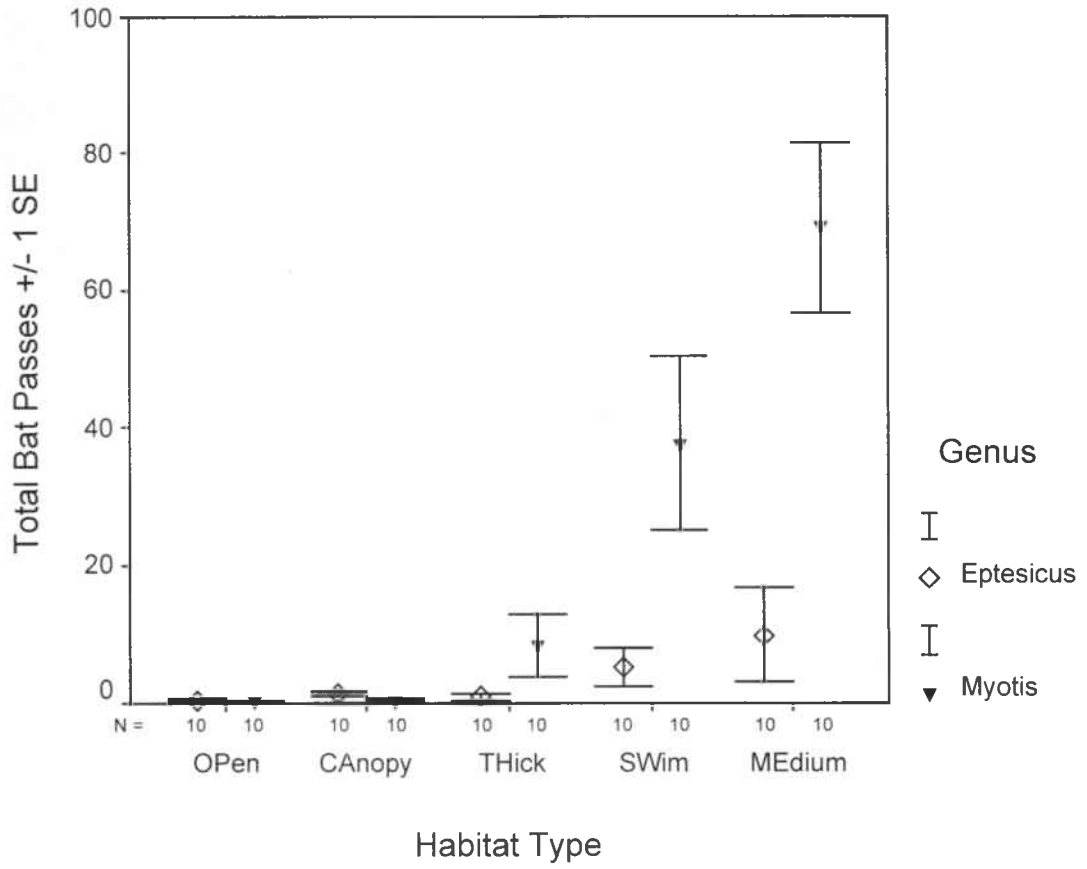


Figure 7. Feeding buzz ratios (feeding buzzes/total passes) for total bats at five habitat types at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997.

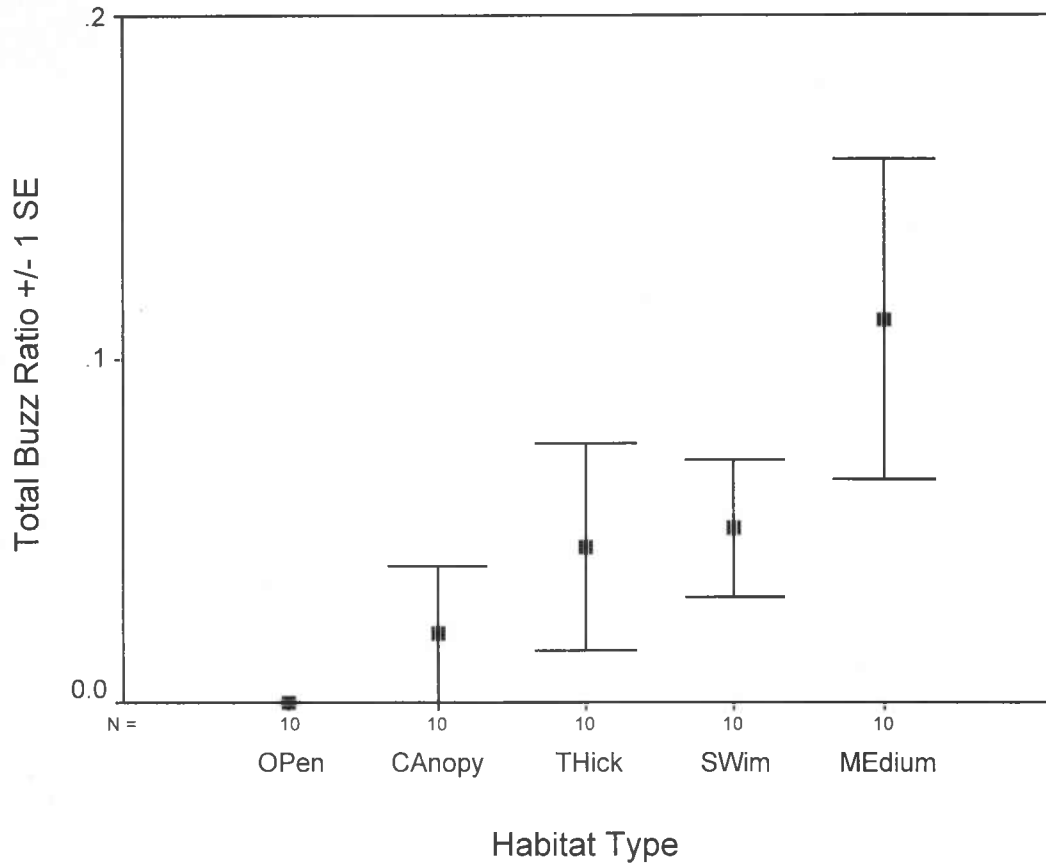
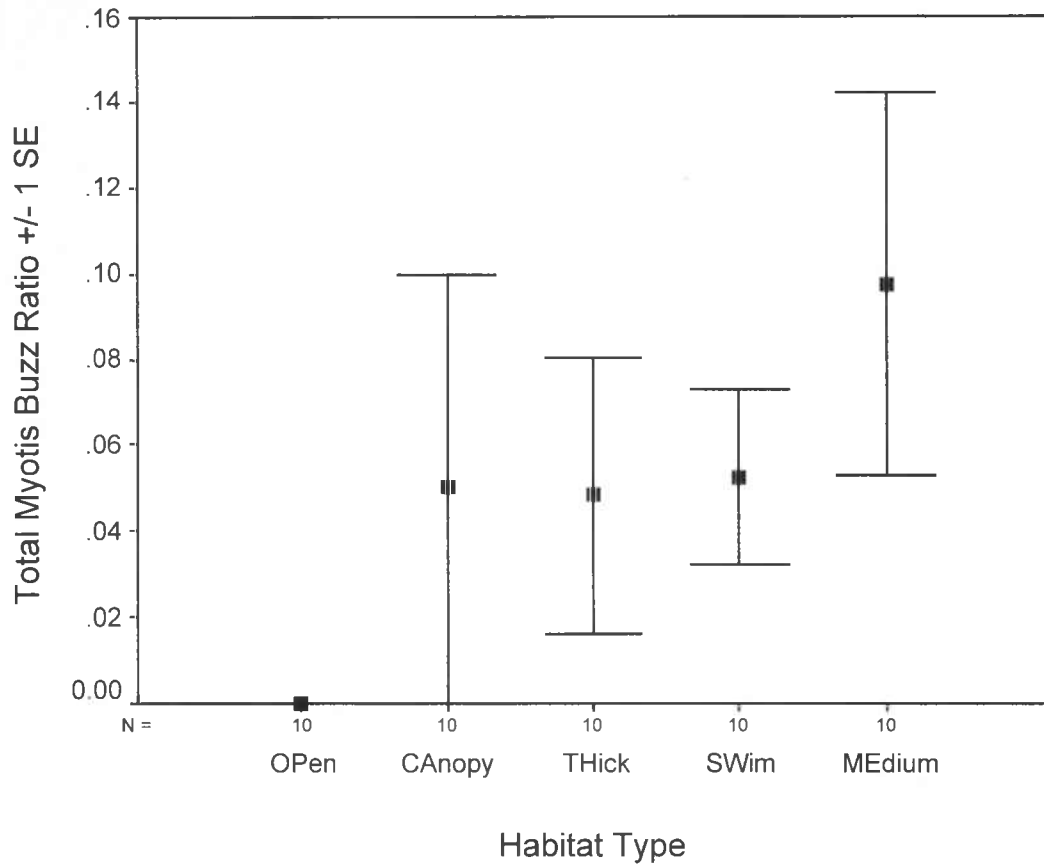


Figure 8. Feeding buzz ratios (feeding buzzes/total passes) for *Myotis* spp. at five habitat types at Spring Meadow Lake, Helena, Montana, 29 July - 30 August, 1997.



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