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The Ecology of Prairie-Dwelling Bats in Southeastern Alberta

by

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ABSTRACT

I investigated species composition, and foraging and roosting ecology of bats on the prairies in south-eastern Alberta. Five bat species occur in the area, with *Myotis ciliolabrum*, *Myotis evotis*, and *Eptesicus fuscus* being the most common. My results show that the riparian zone is critical habitat to bats in south-eastern Alberta for both roosting and foraging. Greater than one kilometre from the river, there was virtually no bat activity. Both bat activity and insect abundance along the river and over springs was significantly higher than on the prairies. The majority of the bat activity along the river occurred within the riparian cottonwoods. All bat species roosted in rock crevices in the cliffs or coulees or in sandstone boulders in the river valley. No bats ever roosted in trees. My study suggests that maintenance of foraging habitat for prairie bats is critical to the preservation of prairie bat populations.

ACKNOWLEDGEMENTS

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General Introduction

The North American prairie is one of the largest and most disturbed ecosystems on the continent. Over the last 150 years, greater than 90% of the original habitat has been altered for ranching and agricultural activities (Dorn, 1996). In Alberta, 80% of prairie habitat has been cultivated, and 109, 600 oil and gas well sites have been cleared, along with the associated access routes and pipelines (Adams *et al.*, 1996). Natural prairie ecosystems are very dynamic, naturally adapted to disturbance from fire, wildlife grazing, drought and floods. However, they are not adapted to the continuous and frequent high soil disturbance created by cultivation (Adams *et al.*, 1996). In the past, the grazing pressure created by bison (*Bison bison*) was infrequent, as the nomadic herds would not return to the same area for several years (Adams *et al.*, 1996).

Prairie rivers only occupy approximately 2% of the western grasslands, but they are important wildlife habitat (van Tighem, 1996). Riparian zones contain the majority of trees and large shrubs in the prairies, and these provide important habitat for birds and insects, shelter from the sun for larger mammals and reptiles, and important erosion control (van Tighem, 1996). Riparian zones are also vital in providing for both quality and quantity of water. Like the grasslands, prairie rivers are dynamic, adapted to seasonal flooding, which maintains the riparian vegetation (Rood and Mahoney, 1991), and recharges the water table (van Tighem, 1996). However, many recent studies have shown drastic declines in riparian forests (Bradley *et al*, 1986; Rood and Mahoney, 1990) and increases in soil erosion (Dorn, 1996). Concurrently, 39% of the endangered bird species in Canada are native prairie

species (Holroyd, 1996) many of which to varying respects, are dependent on riparian zones (van Tighem, 1996).

Due to the drastic habitat loss, the last two decades has seen a surge of concern and work to conserve prairie species (Holroyd, 1996). Although bats are not usually considered threatened prairie species, this is largely due to a lack of information. Virtually nothing is known about the biology of prairie bats compared to species living in urban or forested areas (Barclay and Brigham, 1996). In particular, almost nothing is known regarding critical roosting and foraging habitat for bats in the prairies. While bats in forested and urban areas roost in decaying and/or hollow trees (Barclay and Brigham, 1996) and buildings, respectively, such sites are less available in the prairies and bats likely use other roost substrates. As in other habitats, bats in the prairies likely play a key ecological role as the major predators of nocturnal, flying insects (Brigham 1993a), but the extent of their impact is unknown.

As with other prairie dwelling animals, bat populations on the prairies may be negatively affected by human alteration of the natural grassland ecosystem. However, the first step in assessing the status of prairie bat populations is to gain an understanding of the ecology of bats in natural undisturbed habitats. Therefore, I studied prairie bats in a sparsely populated and relatively unaltered prairie area.

The goals of my study were three fold, 1) to investigate the species composition and abundance, life history characteristics, population dynamics, and diet of prairie bats, 2) to assess the foraging ecology and habitat-use of prairie bats, 3) to investigate roosting ecology of prairie bats.

Study Site

My study area was along the South Saskatchewan River and the Red Deer River, in south-eastern Alberta (centred around lat 50°73', long 110°56', Elevation 700m; Fig 1.1). The rivers are two of the major drainage basins in southern Alberta. Sites were located near the towns of Bindloss and Empress, and further south in the Suffield National Wildlife Area (SNWA), which is the easternmost 459 km^2 of Canadian Forces Base (CFB) Suffield (Gummer, 1997). The South Saskatchewan River is the eastern boundary of the SNWA. The SNWA was grazed until 1976, but since then access to the base has been restricted. I worked primarily in the north block of the SNWA, and along the South Saskatchewan River north of the base up to Empress. Sites along the Red Deer River were located near Bindloss and Empress, and further west at Buffalo. The convergence of the two rivers is just east of Empress.

The study area is appropriate to study the natural roosting and foraging behaviour of bats, because this area of Alberta has very low human population density. While much of the area is composed of cattle ranches and agricultural fields, CFB Suffield comprises one of the largest areas of native, protected mixed-grass prairies on the continent (D. Gummer pers. comm.). Along the South Saskatchewan River there is virtually no human development. There are few buildings within two kilometres of the river, and most farms tend to be greater than five kilometres from the river. The Red Deer River valley is more populated, with the population largely centred around the river, with towns such as Bindloss, Empress, and Buffalo adjacent to the river. The study area is near the northern edge of the mixed short-grass prairie (Coupland, 1987), and is semi-arid, receiving 30-35 cm of precipitation annually, and 16-17cm on average from May to August (Environment

Empress

Red Deer River

Bindloss

Buffalo

CFB
Suffield

Saskatchewan
Border

Hwy #1

South
Saskatchewan
River

Hwy 41

0   20   40

km

Medicine Hat
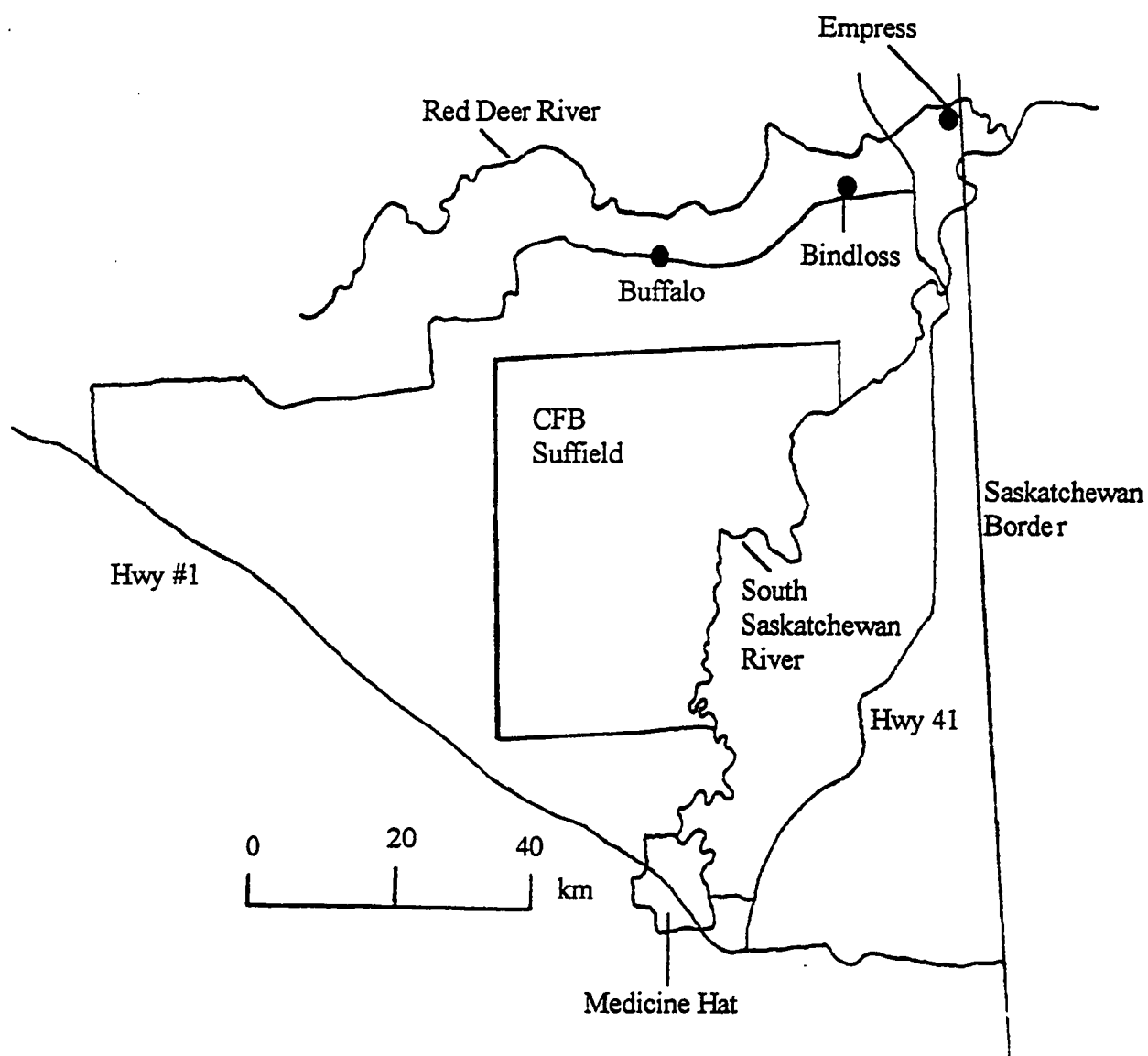
Figure 1.1. Map of study area in south-eastern Alberta

Canada).

I studied within habitats along the rivers and up to five kilometres away from the river valley on the grasslands. In the northern portion of the study area, the river valley of the South Saskatchewan is quite steep, with only a narrow flood plain. The slope and cliffs of the river valley are steep, rising sharply up within 10-500m from the river. There is extensive coulee development (coulees are steep runoff valleys within the cliffs, running perpendicular to the river; Fig 1.2), with lots of side passages, and crevices. The substrate of cliffs and coulees is sandstone, and is easily eroded. There is also ironstone stratification, and patches of bentonite. Vegetation is sparse along this part of the river. Juniper (*Juniperus* spp.), sage (*Artemesia* spp.), prickly pear cactus (*Opuntia polyacantha*), ball cactus (*Coryphantha vivipara*) and wild rose (*Rosa* spp.) and grasses (spear grass-*Stipa comata*; blue grama grass-*Bouteloua gracilis*) are the common species in the coulees. Trees are rare, and tend to exist as scattered clumps of riparian "forest" along the water's edge. Patches of cottonwoods in groups of 5-45 trees are the dominant feature. The cottonwoods are likely *Populus deltoides* based on leaf structure and distribution, but as three cottonwoods species can occur in the area, and the fact that the three species can hybridize (Stettler *et al.*, 1996), I cannot make positive identification. Chokecherry (*Prunus virginiana*) and willow (*Salix* spp.) are also present as undergrowth. Forest patches are disjunct, often with several kilometres between adjacent patches.

The Red Deer River and much of the southern end of South Saskatchewan River study area (southern portion of Suffield National Wildlife Area), has very different slope development and glacial erosion patterns to that described above. Both have extensive flood plains up to 12 km wide. The area lacks the extensive and steep cliff and coulee
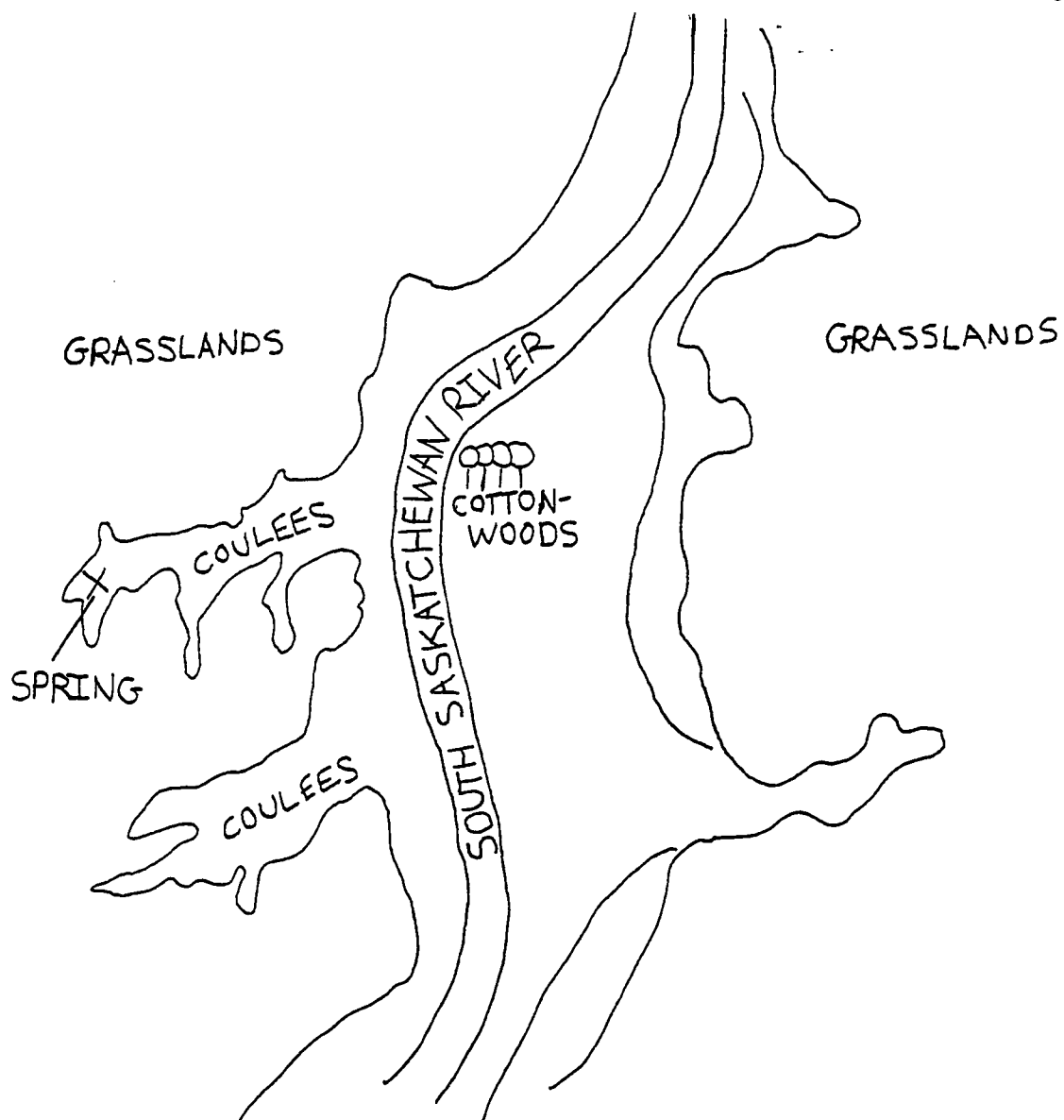
Figure 1.2. Schematic of study area along the South Saskatchewan River

development. The river valley rises gradually, and the slope has been eroded smooth and flat. Vegetation is more abundant. At the Red Deer River, extensive riparian cottonwood forests exist, extending for several kilometres along the river and up to half a kilometre back from it. The southern area along the South Saskatchewan River also has large cottonwood riparian forests, and expanses of willow and shrub undergrowth. The cottonwood forests are not as dense and large as along the Red Deer River, but contained >150 trees and covered an area at least 100*20 m.

I also studied at three natural springs near the South Saskatchewan River. These springs dry up over the course of the summer, with some going completely dry by mid-summer. Two springs were in the SNWA, in areas isolated from cattle. Vegetation grew in and around the water, and both had water depth greater than 1m at the beginning of the summer. Both springs were at the top of a coulee, in natural runoff passages. The other spring was on grazed land, with no vegetation around the water's edge, and was 0.8km from the top of the coulees. Cattle were only present in the area infrequently.

Chapter 2. Natural History, Species Composition and Diet of Prairie-Dwelling Bats in South-Eastern Alberta.

INTRODUCTION

Compared with that of other ecosystems in western North America, little is known about the bat fauna on the prairies. Across the whole ecosystem, aside from a few anecdotal observations, only six studies have been conducted (Tuttle and Heaney, 1974; Farney and Jones, 1980; Schowalter and Allen, 1981; Saunders and Barclay, 1992; McNalley and Barclay, 1995; Bogan *et al.*,1996). In south-eastern Alberta, prior to this study, only two surveys had been performed. The first was a brief survey at Dinosaur Provincial Park (Schowalter and Allen, 1981) and the second was a month long survey of the Suffield National Wildlife Area (McNalley and Barclay, 1995). My study was in part prompted by the results of the latter study. Six species were caught, and bats were more abundant than previously thought (McNalley and Barclay, 1995). The two most common species were the western small-footed bat (*Myotis ciliolabrum*), and the western long-eared bat (*Myotis evotis*). These two species accounted for 50.6% and 32.9% of captures, respectively. Smaller numbers of little brown bats (*Myotis lucifugus*), big brown bats (*Eptesicus fuscus*), and hoary bats (*Lasiurus cinereus*), plus one long-legged bat (*Myotis volans*), were also caught.

Myotis ciliolabrum is one of the smallest bats in North America, with forearm length averaging 32.2mm and mass 4.9g (van Zyll de Jong, 1985). The western small-footed bat is restricted to western North America, in arid badland and prairie habitats, ranging from southern Canada to central Mexico (van Zyll de Jong 1985; Barclay 1993). It is on the Blue

List in Alberta and British Columbia (Anonymous 1991; Holroyd *et al.*, 1994). The Blue

List classification means species are at risk, but the threat is less immediate than those on the

Red List (Anonymous, 1996). Species which are vulnerable, but for which information is

limited are also in this category. Most information about this species is based on anecdotal

observations. This species usually roosts in rock crevices (van Zyll de Jong, 1985). *M.*

ciliolabrum has a diverse diet, feeding on Lepidoptera, Diptera, Coleoptera, and Trichoptera

(Jones *et al.*, 1973; Woodsworth, 1981; Warner, 1985).

Myotis evotis is a small bat, with average forearm length 38.6mm and mass 6.8g (van

Zyll de Jong, 1985). This species has a similar range to that of *M. ciliolabrum* and is

present only in western North America from southern Canada to Mexico. The western

long-eared bat occurs in a variety of habitats from dry shrub to forested areas (Manning and

Jones, 1989). *M. evotis* is a gleaner (Faure and Barclay, 1992), but also can also aerial hawk

for insects. Individuals roost in a variety of habitats: trees, tree stumps, rock crevices (van

Zyll de Jong, 1985; Vonhof and Barclay, 1997). Lepidoptera and some Coleoptera are

commonly found in the diet of *M. evotis* (van Zyll de Jong, 1985; Barclay, 1991).

Myotis lucifugus and *E. fuscus* are two of the most abundant bat species in North

America, ranging across most of Canada, the United States, and Mexico (van Zyll de Jong,

1985). They are commonly found living in buildings (van Zyll de Jong, 1985), or use trees

in forested areas (Kalcounis and Hecker, 1996; Vonhof, 1996; Vonhof and Barclay, 1996).

Both hibernate and are aerial hawkers (van Zyll de Jong, 1985). *M. lucifugus* is a smaller

species, with forearm length averaging 37.0mm and mass 7.9g (van Zyll de Jong, 1985).

The diet is diverse, consisting of a range of smaller insects including Diptera,

Ephemeroptera, Lepidoptera, Trichoptera, and Coleoptera, with aquatic insects

predominating. *E. fuscus* is larger, with average forearm length 47.4mm, and mass 17.9g (van Zyll de Jong, 1985). Big brown bats appear to favour Coleoptera, which is usually dominant in their diet, but this bat also eats Lepidoptera, Diptera, and Hemiptera.

The final species present in the area, the hoary bat, is one of the largest species in Canada, with average forearm length of 56.0mm and mass of 26.7g (van Zyll de Jong, 1985). This species ranges across all of North and Central America. It is a migratory bat, coming north for the summers to reproduce. Many studies have found that individuals feed primarily on Lepidoptera (van Zyll de Jong, 1985), but larger Coleoptera and Odonata have also been found in the diet (Barclay, 1985).

The bat community of south-eastern Alberta offers an excellent opportunity to learn more about two poorly studied species, and the ecology of prairie-dwelling populations in general. Little is known about *M. evotis* and *M. ciliolabrum*, and these species are abundant and easily captured in my study area. *M. lucifugus* and *E. fuscus* are probably the best studied bat species in North America, but the information has been collected principally from urban populations in eastern North America (Fenton and Barclay, 1980; Kurta and Baker, 1990), which may not reflect the ecology and behaviour of prairie populations in areas where roosting in buildings is not possible. My goal in this chapter is to present some basic biology and life history characteristics such as species composition, parturition dates, sex ratio composition, and the diet of prairie bats in south-eastern Alberta. These characteristics are important aspects of any organism's ecology, and are the basis for understanding the bat populations in the area. Such information provides the framework for the main research I conducted on foraging and roosting ecology, and any future research in the area.

METHODS

Bat Captures

I carried out field surveys of bats in 1996-1997. I was present in the area from 10 June - 20 August in 1996, and from 15 May - 15 August in 1997. I captured bats with mist nets. Nets were raised 1-3m above the ground, which likely influenced the species of bats I could capture. Bats that forage low to the ground, such as *M. ciliolabrum*, *M. evotis*, and *M. lucifugus*, will have had a higher probability of capture than *E. fuscus* or *L. cinereus* which tend to fly higher (van Zyll de Jong, 1985). I placed mist nets between trees, over springs, and in narrow areas in the coulees with high surrounding slopes which acted to funnel bats into the nets.

I measured forearm length and mass, and determined the sex, and age, and reproductive condition of each individual I captured. I also looked for ectoparasites on each individual. I measured forearm length to 0.1mm with calipers and mass to 0.1g using a Sartorius electronic balance (model PT 600). Before making mass measurements, I held bats for an hour to allow them to digest their food. I assessed individuals as adult or juvenile: bats were classified as juveniles (young of the year) by the presence of cartilaginous ephiphyseal plates of the fourth metacarpel (Anthony, 1988). I classified reproductive condition of females as non-reproductive, pregnant (by palpation of the lower abdomen), lactating (enlarged nipples with a patch of bare skin surrounding the nipple), and post-lactating (nipples appear dry and dark with a bare patch of skin surrounding the nipple; Racey, 1988).

Fecal Analysis

I analyzed feces to determine diet of bats captured in the study area. The validity of fecal analysis as a technique to determine bat diet has been questioned by several authors (Rabinowitz and Tuttle, 1982; Robinson and Stebbings, 1993). Less digestable, hard-bodied insects such as coleopterans and hemipterans have a greater probability to be overestimated, while soft-bodied insects are more digestable, and may be underestimated. However, Kunz and Whitaker (1983) showed in blind experiments that diet proportions for the various orders could be estimated with a high degree of accuracy from fecal analysis. They suggested that pooling and averaging results of analysis may cancel individual errors. Alternative methods such as analysis of stomach contents, is destructive as the animals must be killed. For this study, I believe fecal analysis is a useful tool to estimate what bats eat in my study area. Observer bias was eliminated in this study as I performed all the fecal analysis myself.

I collected feces from bats along the South Saskatchewan river in 1996 and 1997. In the analysis, I included feces collected from bats caught along the Red Deer River at Dinosaur Provincial Park (85 km west of the main study area) in 1997. The habitat in Dinosaur Provincial Park is similar to the South Saskatchewan River, and the species composition is nearly identical. I let feces air dry for at least two weeks. When possible, I softened five fecal pellets from each individual with ethanol, teased them apart, and analyzed them under a dissecting scope to identify insect fragments. I visually determined the relative proportion of each insect group in each fecal pellet. I identified insect fragments to Order, except for Diptera, which were identified to Family. I arcsine transformed diet proportions, and performed a t-test comparing diet proportions of each insect taxa between early summer

and late summer to determine if diet changed over the summer. I also calculated dietary diversity using Levin's diet diversity index (Levin, 1968):

1) $B = 1/\sum p^2_j$

2) $B_a = (B-1)/(n-1)$

Where B= Levin's measure of niche breadth; p=fraction of item in diet; n= number of food categories in diet of all bats (number of insect taxa eaten), and B_a= Levin's dietary diversity index. A value of B_a=1 represents high diet diversity, while B_a=0 is low diet diversity.

RESULTS

Species Composition, and Natural History

I caught a total of 207 bats of six species during the study: the western small-footed bat (*M. ciliolabrum*), western long-eared bat (*M. evotis*), little brown bat (*M. lucifugus*), big brown bat (*Eptesicus fuscus*), and hoary bat (*Lasiurus cinereus*) were the most common (Table 2.1). I caught a single silver hair bat *(Lasionycteris noctivagans)*. My results were similar to the 1995 survey. The most abundant species was *M. ciliolabrum*; over the two summers, 87 (42.0%) individuals were captured, 50 (62.5%) females and 37 (42.5%) males. *M. evotis* and *E. fuscus* were also common, with 61 (29.5%) and 38 (18.4%) individuals captured, respectively. Both *M. lucifugus* and *L. cinereus* were relatively uncommon with 14 (6.8%) and 6 (2.9%) caught, respectively.

I caught similar numbers of both sexes for all species over the two years, except for *M. ciliolabrum* in which a higher proportion of females were captured (Table 2.1). The same pattern was demonstrated as well in 1995. Juvenile bats made up 15-40% of bats

Table 2.1 Number of individuals by sex and age caught over three years along the South Saskatchewan River, Alberta (1995 data is from McNalley and Barclay, 1995).

Species/Sex/Age	Year			
	1995	1996	1997	Total
M. ciliolabrum				
Adult female	23	13	28	64
Adult male	19	5	15	39
Juvenile female	0	2	7	9
Juvenile male	1	4	13	18
M. evotis				
Adult female	16	6	7	29
Adult male	12	6	15	33
Juvenile female	0	3	2	5
Juvenile male	0	3	6	9
M. lucifugus				
Adult female	1	3	4	8
Adult male	3	0	2	5
Juvenile female	0	1	0	1
Juvenile male	0	3	0	3
E. fuscus				
Adult female	2	4	6	12
Adult male	4	1	9	14
Juvenile female	0	1	4	5
Juvenile male	0	8	4	12
L. cinereus				
Adult female	2	1	1	4
Adult male	0	0	2	2
Juvenile female	1	1	0	2
Juvenile male	1	1	0	2
Total	85	66	125	276

captured for each species. *Lasiurus cinereus* and *E. fuscus* had the largest proportion of juveniles captured at 40.0% and 38.6%, respectively. For the three *Myotis* species, juveniles made up 15-22% of each species. The majority of adult females were reproductive. In the cases where I could positively identify reproductive state, only 9 of 76 females (11.8%) were non-reproductive. With the small *Myotis* bats, determination of reproductive state can be difficult, especially in the early stages of pregnancy. Only when bats are in late stages of pregnancy and obviously "bulging" is classification accurate. In late May/early June, all *Myotis* females were classified as "not obviously pregnant" (NOP) and I only used captures after late June to estimate reproductive state.

For all three of the most common species, female bats were significantly larger than males as determined by forearm length of adult bats (Table 2.2). I did not use mass of females to compare the sexes due to mass fluctuation in reproductive females, but I calculated it for adult male bats. For *M. evotis* males, mass averaged (range) 6.7g (5.6g-8.1g; n=33). For *M. ciliolabrum* and *E. fuscus* the mean (range) was, respectively: 4g (3.8-6.2g, n=39), and 17.9g (15.7-20.2g, n=13). Mass almost doubled in pregnant females: I captured several *M. ciliolabrum* greater than 8.0g, and *M. evotis* greater than 9.0g. I also noted significant mass increase in late August as individuals prepared for hibernation: I captured a 33.0g female *E. fuscus* on 16 August.

I identified the first pregnant *Myotis* bats in late June and early July, and I caught pregnant bats until mid-July (Table 2.3). Lactating bats were commonly captured at the same time (mid-July), and until the end of the month. On 23 July, 1996, I tracked a female *M. lucifugus* with a radio-transmitter to a roost in which the bats were visible. At least four

Table. 2.2. Mean (±SE) forearm length for female and male adult bats, and results of t-tests comparing forearm length between sexes

Bat Spp.	Forearm Length				t-value	df	p-value
	Female	N	Male	N			
M. ciliolabrum	32.3mm (0.12)	61	31.4mm (0.15)	36	4.37	95	<0.001
M. evotis	37.7mm (0.28)	29	36.6mm (0.23)	32	3.00	59	0.004
M. lucifugus	37.7mm (0.21)	8	37.3mm (0.22)	5	1.19	11	0.260
E. fuscus	48.1mm (0.43)	12	46.0mm (0.35)	14	3.75	24	0.001

Table 2.3. Dates of earliest capture, latest capture, and the date of the capture of the median bat for the three reproductive conditions of female bats, and juvenile bats for the *Myotis* species, and *E. fuscus*

	Pregnant	Lactating	Post-lactating	Juveniles
M. ciliolabrum				
Earliest	July 5	July 5	July 27	July 27
Median	July 12	July 22	Aug 6	Aug 3
Latest	July 17	July 22	Aug 17	Aug 18
E. fuscus				
Earliest	May 28	July 1	July 31	Aug 1
Median	June 10	July 10	Aug 3	Aug 4
Latest	July 14	July 12	Aug 16	Aug 16
M. evotis				
Earliest	June 29	July 15	July 15	July 27
Median	N/A	N/A	July 20	Aug 4
Latest	July 7	July 23	July 27	Aug 17
M. lucifugus.				
Earliest	July 8	July 22	N/A	Aug 6
Median	N/A	N/A	N/A	N/A
Latest	N/A	July 27	N/A	Aug 17

juveniles were present in the roost. They were pink, with hair just beginning to grow, but their eyes and ears were open. Flying juveniles of all bat species were first caught at the end of July, with numbers increasing into the first two weeks of August, concurrent with captures of post-lactating females. Parturition appears to be slightly earlier in *E. fuscus*, compared with *Myotis* species. I identified pregnant bats as early as late May. Lactating bats were found in early July. Post-lactating bats and juveniles were caught at similar times as for the *Myotis* species.

Adult female and male *M. evotis*, *M. lucifugus* and *E. fuscus* seemed to disappear from the study area when their pups became volant. The last adult of these species was captured on 6 August, with the exception of one post-lactating *E. fuscus* caught in late August. On the other hand, I caught adult *M. ciliolabrum* in the study area throughout August, and they appeared early each spring, dominating the May captures (Table 2.4.). Comparing captures in May versus June, the proportion of *M. ciliolabrum* captured was higher (G=11.47, df=2, p<0.01) in May. High numbers of *M. evotis* and *E. fuscus* did not appear until early June. Hoary bats are resident in the area throughout the summer in small numbers, based on echolocation activity (see Chapter 4). However, they were captured only in late summer, simultaneous with a sharp increase in hoary bat echolocation activity.

I noted the occurrence of ectoparasites on bats in the study area . The most common parasites I found were ear mites (Acari: Trombiculidae). Ear mites often formed large colonies of several hundred individuals on the bats' pinna and tragus, although they ranged from a few individuals, to colonies covering the entire pinna and tragus. They parasitized all bat species except *M. lucifugus*, and hoary bats. *M. ciliolabrum* and *M.*

Table 2.4. Number of bats captured for each species within each month along the South Saskatchewan River. Number of bats captured are separated into adults and juveniles for July and August when the young become volant.

Bat Species	May	June	July		August	
	Adults	Adults	Adults	Juveniles	Adults	Juveniles
M. ciliolabrum	18	21	17	6	5	20
M. evotis	1	17	15	2	1	12
M. lucifugus	1	3	5	0	0	4
E. fuscus	2	7	5	0	6	17
L. cinereus	0	0	1	0	3	2

evotis had similar rates of parasitism, 28.0% (n=82) and 24.6% (n=55) respectively, while *E. fuscus* was lower, with only 8.6% (n=32). A comparison of the number of individuals parasitized between the two *Myotis* species (combined) and *E. fuscus* (with Yates correction) were not quite significant (χ^2=3.81, df=1, p=0.051).

Diet

I found eight insect orders in the diet of bats I sampled. Coleoptera, Lepidoptera, Diptera, and Hemiptera composed the majority of the diet (Figure 2.1). I found small amounts of Neuroptera, Hymenoptera, Ephemeroptera, and Trichoptera, but the combined proportion of these orders formed less than 2% of the diet of any species. *M. ciliolabrum* (n=85) had a reasonably diverse diet. Diptera, and Lepidoptera were dominant in the diet, with smaller proportions of Coleoptera consumed. Levin's diversity index was 0.29.

Myotis evotis (n=65) ate a high proportion of Lepidoptera, with smaller proportions of Coleoptera, and Diptera. Levin's dietary diversity index was 0.28, similar to that of *M. ciliolabrum*. The diet of *M. lucifugus* (n=16) was difficult to determine as the insect fragments were highly masticated. From the identifiable portions the diet was composed of Diptera, Lepidoptera, Coleoptera, and Hemiptera in order of decreasing diet proportions. The rest of the diet was unknown. Levin's diversity diet index was relatively high, at 0.49.

The diet of *E. fuscus* (n=38) was dominated by Coleoptera, with small amounts Lepidoptera, Diptera, and Hemiptera. I identified June beetle (Scarabaeidae) tarsi in at least 9 (23.7%) of the fecal samples analyzed. Levin's diet diversity index was low 0.19. The diet of *Lasiurus cinereus* (n=7) was primarily Lepidoptera, with a small amounts of Coleoptera.
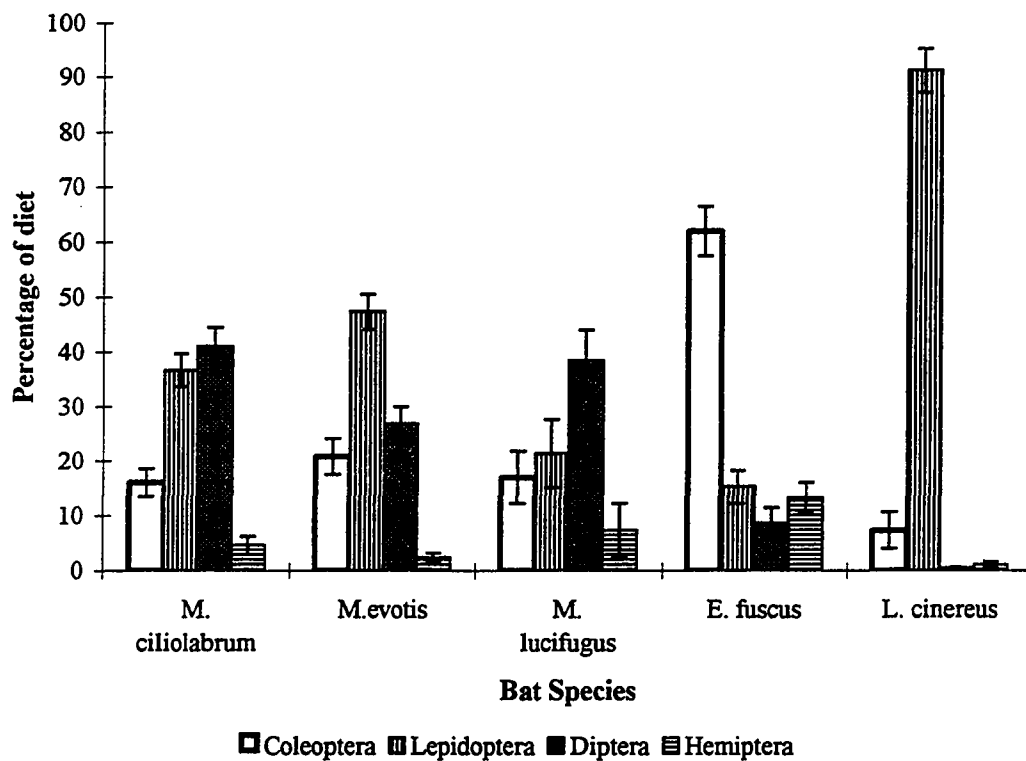
Figure 2.1. The mean percentage (±SE) of the four most common insect orders in the diet of prairie bats in south-eastern Alberta

Levin's diet diversity index for *L. cinereus* was 0.02, reflecting its specialized diet.

Based on wing morphology, I identified Diptera in the diet of bats to Family (Figure 2.2). Four families were identified in the diet: Culicidae/Chaoboridae, Muscidae, Tipulidae, and Chironomidae. I grouped Culicidae and Chaoboridae together because positive Family identification was not possible from wing fragments, as wing venation is very similar (R. Longiar pers. comm.). However, I tentatively identified wing fragments as biting mosquitoes, Family Culicidae, as Chaoboridae usually only occurs in standing water (lakes and ponds; Borror and Delong, 1971; Halat and Lehman, 1996), and I caught many mosquitoes on insect traps along the river (see Chapter 4). For the *Myotis* species, Culicidae/Chaoboridae formed the largest portion of the Diptera in the diet (Figure 2.2). The proportion of the total diet eaten for these families was greatest for *M. ciliolabrum*, followed by *M. lucifugus*, and *M. evotis*. Culicidae/Chaoboridae composed 39.3% and 40.7% of the total Diptera eaten, for *M. ciliolabrum*, and *M. evotis* respectively. I found muscid flies to be relatively common in the diets, while Tipulidae, and Chironomidae were rare.

The diet of bats changed over the course of the summer (Table 2.5a). I performed two-factor ANOVA with bat species and season (early summer = May and June; and late summer = July and August) for each insect taxon (Table 2.5a). There was no significant interaction for any insect taxa. The model was significant for four insect taxa; Coleoptera ($F=31.52$, $df=4$, 199, $p<0.001$); Lepidoptera ($F=16.37$, $df=4$, 199, $p<0.001$); Diptera ($F=11.37$, $df=4$, 199, $p<0.001$); Culicidae/Chaoboridae ($F=8.43$, $df=4$, 199, $p<0.001$). The model was not significant for Muscidae ($F=1.00$, $df=4$, 199, $p>0.25$). Diet differed significantly among species of bats. The proportion of Diptera consumed decreased
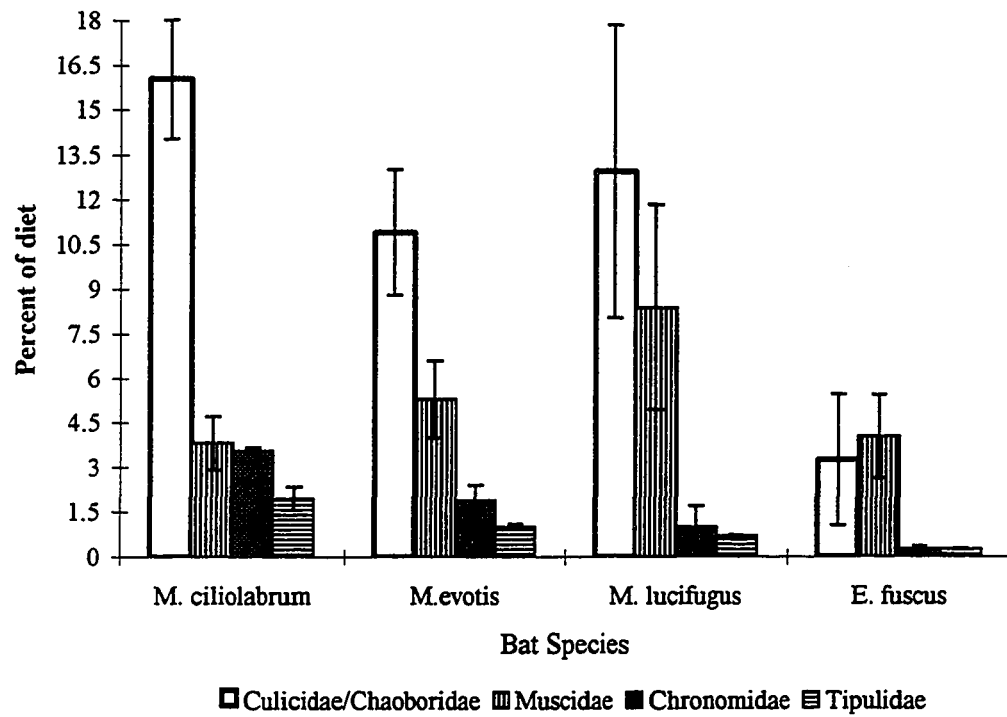
Figure 2.2. Mean percentage (±SE) of Dipteran families in the diet of prairie bats in south-eastern Alberta

Table 2.5. Mean percentage (±SE) of Insect Order/Family found in the diet of prairie bats over the course of the summer (early and late), and results of a two-factor ANOVA comparing species and season along the South Saskatchewan River, Alberta.

Species/Season	Coleoptera	Lepidoptera	Total Diptera	Family Culicidae/ Chaoboridae	Family Muscidae
M. ciliolabrum					
Early (n=37)	25.7(±4.8)	29.6(±4.2)	42.2(±5.1)	22.1(±3.3)	3.9(±1.4)
Late (n=48)	8.6(±1.9)	42.1(±4.2)	39.6(±4.8)	11.3(±2.7)	3.7(±1.2)
M. evotis					
Early (n=25)	31.0(±6.8)	37.9(±4.5)	30.8(±5.0)	15.9(±4.0)	5.2(±1.7)
Late (n=40)	14.5(±3.0)	53.3(±4.2)	24.3(±4.2)	7.8(±2.2)	5.3(±1.9)
M. lucifugus					
Early (n=4)	41.5(±9.4)	10.0(±7.1)	47.5(±10.5)	23.8(±14.3)	1.0(±1.0)
Late (n=12)	8.9(±3.0)	25.2(±7.8)	35.4(±6.7)	9.3(±4.5)	10.8(±4.4)
E. fuscus					
Early (n=9)	68.4(±12.0)	7.7(±4.4)	13.9(±8.7)	11.6(±8.8)	1.9(±0.8)
Late (n=29)	60.1(±4.7)	17.7(±3.6)	7.1(±2.5)	0.7(±0.6)	4.7(±1.8)
Total Species					
Early (n=75)	33.4(±3.9)	28.7(±2.9)	35.4(±3.4)	18.9(±2.4)	4.0(±0.90)
Late (n=129)	22.0(±2.4)	38.5(±2.6)	27.2(±2.6)	7.6(±1.3)	5.1(±0.94)
*Anova Factors					
Species	F=35.65, df=3, p<0.001	F=17.52, df=3, p<0.001	F=14.54, df=3, p<0.001	F=5.58, df=3, p=0.001	-----
Season	F=19.12, df=1, p<0.001	F=12.92, df=1, p<0.001	NS	F=16.99, df=1, p<0.001	-----

*Results of a two-factor ANOVA comparing the proportion of each insect taxa consumed by bats.

Table 2.5b). Mean insect biomass (mg) of insect Orders/Family (±SE) captured on insect traps over the course of the summer; Early summer (May and June), Late Summer (July and August), along the South Saskatchewan River.

Season	Coleoptera	Lepidoptera	Total Diptera	Family Culicidae/Chaoboridae	Family Muscoidae
Early (n=76)	0.80 (0.38)	5.10 (2.03)	3.64 (0.75)	0.60 (0.11)	0.44 (0.20)
Late (n=162)	0.30 (0.07)	1.49 (0.65)	1.85 (0.22)	0.10 (0.03)	0.33 (0.09)
	*p=0.028	*p=0.002	*NS	*p<0.001	*NS

*Results of t-test comparing mean biomass of each insect taxa between seasons.

from early summer to late summer, but not significantly so. A significantly higher

proportion of Coleoptera and Culicidae/Chaoboridae was consumed in early summer

compared with late summer. A significantly lower proportion of Lepidoptera was consumed

in early summer compared with late summer (Table 2.5a).

Total mean insect biomass also changed over the course of the summer (Table 2.5b).

The biomass of total Diptera species decreased from early to late summer, but not

significantly (t=1.02, df=283, p=0.31). However, the mean biomass of

Culicidae/Chaoboridae was significantly higher in early summer (t=6.42, df=283, p<0.001).

The mean biomass of Coleoptera and Lepidoptera were also significantly higher in early

summer (t=2.21, df=283, p=0.028 and t=3.08, df=283, p=0.002, respectively). The higher

proportions of Lepidoptera in early summer is contrary to the change in dietary proportions,

but use of passive sticky traps likely biased sampling against larger Lepidoptera which were

frequently seen in July and August. Small, weak fliers such as dipterans have the best

probability of capture, and thus the mean dipteran biomass from trapping is likely a fairly

accurate representation of true availability.

DISCUSSION

Species Composition, and Natural History

The species composition of the bat fauna of south-eastern Alberta is similar to other

northern North American arid habitats. *Myotis ciliolabrum*, *M. evotis* and *E. fuscus* are

common inhabitants of these areas (Fenton *et al.*, 1980; Schowalter and Allen, 1981;

Holroyd *et al*, 1994; Bogan *et al.*, 1996). In badland habitats, *M. ciliolabrum* is often the

most abundant species (Farney and Jones; 1980, Schowalter and Allen, 1981; Bogan *et al*,

1996). The low number of *M. lucifugus* in my study area is unusual, because the species is abundant and widespread, inhabiting most of the continent (Nagorsen and Brigham, 1993). However, similar results were obtained in the badlands of South Dakota, where *M. lucifugus* was rare, or absent (Farney and Jones, 1980; Bogan *et al.*,1996). In my study area there is little standing water and few trees. This could influence the abundance of *M. lucifugus* in the area as this species favours foraging within and around trees (Whitaker *et al.*, 1977), and over standing water (Anthony and Kunz, 1977; Barclay, 1991). Hoary bats were uncommon in my study. The low capture rate is likely a fairly representative picture of the number of hoaries present, rather than a bias against capture using low nets. Hoaries are usually present in low densities as they are solitary (van Zyll de Jong, 1985), and appear to defend feeding areas from other bats (Barclay, 1985).

South-eastern Alberta appears to be good habitat for both sexes of bats, as well as good breeding habitat. Juveniles made up a substantial proportion (15-40%) of the captures. Both *E. fuscus*, and *L. cinereus* are high fliers, typically flying above the 3m at which nets were set, and the high proportion of juveniles captured may reflect the less adept flight of juveniles. For all species the proportion of females which were reproductive was high compared with results from dry interior British Columbia, where 42-62% of females were non-reproductive (Holroyd *et al.*, 1994). The number is also high considering many yearling female bats are non-reproductive (Kunz, 1974a).

The equal sex ratio in all but *M. ciliolabrum* is notable as several authors have noted segregation of female and male bats in different areas (Fenton *et al.*, 1980; Barclay, 1991; Grindal *et al.*, 1992). The insect abundance on the prairies appears to be sufficient to support both males and females despite the high energy demands during lactation (Kurta and

Bell, 1989). Interestingly, in Badlands National Monument in South Dakota, two studies found >75% bias towards males for the most abundant species, especially for *M. ciliolabrum* (Farney and Jones, 1980; Bogan *et al.* 1996). These results are contrary to the dominance of females in my study area. The reasons for the low number of females captured in the latter two studies is unclear, as the authors netted bats in several different habitats, which included springs and cottonwood trees which are likely good foraging areas (see Chapter 4; Farney and Jones, 1980; Bogan *et al.*, 1996).

A trend for larger females than males has been noted in vespertilionid bats, especially in forearm (Williams and Findley, 1979). Larger female *E. fuscus* has been noted by several authors (Myer, 1978; Williams and Findley, 1979), but this study is one of the first to report significantly larger forearm length for western small-footed bats. Many reasons have been suggested for larger females in general, including the need for females to be larger to compensate for the greater wing loading during pregnancy, and greater fat reserves to handle the stress of reproduction (Williams and Findley, 1979).

Parturition dates for *Myotis* species in my study area are similar to other surveys in arid habitats (Davis and Barbour, 1970; Tuttle and Heaney, 1974; Bogan *et al.*, 1996), and central Alberta (Schowalter *et al.*, 1979). *Myotis* females appear to give birth within the first two weeks of July, with the majority of the population giving birth between the first and second week of July. Juvenile bats become volant and females wean their young in late July-early August. Based on these dates, the two-and-a-half to three-week general *Myotis* development time from birth to volancy, found in studies of *M. lucifugus* (O'Farrell and Studier, 1973), appears to hold for both *M. ciliolabrum* and *M. evotis*. The parturition dates for *E. fuscus* appear to be a couple of weeks behind eastern populations (Kunz,

1974b), and urban populations in south-eastern Alberta, in which births occur around mid-June (Hamilton, 1996). Few *E. fuscus* were captured between mid-June and mid-July, but based on the first juvenile captures, females likely give birth in early July. Juvenile big brown bats are flying by 3 weeks, but do not seem to venture far from their roosts until older than 25 days (Hamilton, 1996). The first juvenile *E. fuscus* were not captured in my study until late July.

Adult *M. evotis*, *M. lucifugus*, and *E. fuscus* appear to leave the study area earlier than juveniles do, perhaps to begin migration to winter hibernacula while juveniles remain in the study area, at least until mid-August. The same pattern has been reported for *M. lucifugus* maternity colonies in buildings (O'Farrell and Studier, 1975; Schowalter *et al.*, 1979). The adults may leave early to avoid competition with juveniles for declining food resources (Kunz, 1974a; Racey, 1988), or to get to mating sites in hibernacula (Schowalter, 1980).

I caught *M. ciliolabrum* in larger numbers early in the season, and adults were caught throughout August. Based on this, I suggest that *M. ciliolabrum* may hibernate in the area. I found a couple of deep crevices (>30m) which could be potential hibernacula. *M. ciliolabrum* has been found hibernating near its northern range limit in British Columbia, at similar latitudes to my study area (Nagorsen *et al.*, 1993), and just south in Montana (Swenson, 1970).

L. cinereus was only captured in late summer, when hoary bat numbers were higher in the area based on echolocation monitoring (see Chapter 4). The increased numbers were likely due both to the presence of flying juveniles and to individuals which were migrating south through the area to wintering grounds (Findley and Jones, 1964).

In my study area, ear mites were the most common ectoparasite. Both *M. ciliolabrum* and *M. evotis* are parasitized on the ears by chiggers *Leptotrombidium myotis* (Jones *et al*, 1973; Manning and Jones, 1989). The rates of parasitism found in this study are much higher than for other reported populations for *M. ciliolabrum* and *M. evotis*. Most authors have reported specimens of *M. ciliolabrum* and *M. evotis* to be free of ectoparasites or very low rates of parasitism (<5%) (Krutzsch, 1955; Jones *et al*, 1973; Dooley *et al.*, 1976; Manning and Jones, 1989), suggesting that the relatively solitary habits of these species may reduce rates of parasitism. However, *M. evotis* and *M. ciliolabrum* roost in compact and narrow crevices in the prairies (see Chapter 3), and it is possible that the tight chambers may bring bats into greater contact with feces, and roost walls (Scott and Duszynski, 1997). As many ectoparasites exist and reproduce entirely within roosts or on bats (Marshall, 1982), this may facilitate parasite transmission.

Diet

Little is known about the diet of the western small-footed bat. In the few samples analyzed in other studies, *M. ciliolabrum* had a diverse diet, feeding primarily on Lepidoptera, Diptera, and Coleoptera (Jones *et al*, 1973; Woodsworth, 1981; Warner, 1985). Shima (1996, unpublished data) analyzed feces from southern Alberta and found that *M. ciliolabrum* consumed much higher proportions of Hemiptera, Hymenoptera, and Neuroptera than I found in my study. Lepidoptera composed the greatest diet component, with proportions similar to my study. In Shima's (1996) analysis, the diet also consisted of approximately 10% Diptera and 10% Coleoptera. Based on insect availability (see Chapter 4), my study area in south-east Alberta appears to have a nocturnal, flying insect fauna

dominated by Dipterans, which is reflected in the diet of *M. ciliolabrum*. From wing morphology, *M. ciliolabrum* should be a generalist forager, as it has a with low aspect ratio and wing loading (Norberg and Rayner, 1987; Shima, 1996). *M. ciliolabrum* consistently takes both Coleoptera and Lepidoptera (Woodsworth, 1981; Warner, 1985; my study), indicating that individuals can handle both soft and hard-bodied prey items. In the Okanagan Valley in British Columbia, western small-footed bats also ate a large proportion of Trichoptera, but this is likely a reflection of prey availability (Woodsworth, 1981).

Lepidoptera was the major diet component of *M. evotis*. Lepidoptera have been found to be a major diet component of this species in several studies (Whitaker *et al.*, 1977; Warner, 1985; Barclay, 1991). The long-eared bat is a gleaner, picking non-volant insects off vegetation (Faure and Barclay, 1992). Observations of long-eared bats support the idea that gleaning may be an important foraging strategy to this bat in my study area. Individuals appear to spend the majority of their time within and around the trees in the riparian zone (B. Chruszcz, pers. comm.). Coleoptera and Diptera were also consumed in relatively high proportions, but as *M. evotis* can employ both gleaning and aerial hawking foraging strategies (Faure and Barclay, 1992), some diet diversity is not surprising.

The diet of *M. lucifugus* is diverse throughout its range. Similar to most studies, I found that Lepidoptera and Dipterans (especially Chironomidae) are important prey items of this species (Belwood and Fenton, 1976; Anthony and Kunz, 1977; Whitaker et al. 1977; Griffith and Gates, 1985; Warner, 1985; Barclay, 1991). Coleoptera and Trichoptera have also been found in the diet in other areas, with varying amounts consumed, but they are usually lesser dietary components than Lepidoptera and Diptera (Buchler, 1976; Whitaker *et al.*, 1977; Warner, 1985).

My study agrees with most other analyses of *E. fuscus* diet which show beetles are the most important prey items (Whitaker, 1972; Griffith and Gates, 1985; Warner, 1985; Brigham and Saunders, 1990; Whitaker, 1995; Hamilton, 1998). *Eptesicus fuscus* has been termed a beetle strategist (Black, 1972), but Brigham and Saunders (1990) consider it an inappropriate label as *E. fuscus* clearly can catch and consume other prey. Instead, *E. fuscus* appears to favour Coleopterans as prey items when available. June beetles (Scarabidae) are frequently noted in the diet of big brown bats (Whitaker, 1972; Whitaker *et al.*,1977; Whitaker, 1995; my study). Lepidoptera and Hemiptera commonly form a small proportion in the diet of *E. fuscus* in other studies (Whitaker, 1972; Whitaker *et al.*, 1977; Griffith and Gates, 1985).

Most other authors agree that Lepidopterans are important prey items for *L. cinereus* (Black, 1972; Whitaker, 1972; Barclay, 1985; Warner, 1985). Black (1974) suggested that moths may be one of the most predictable food items due to their abundance, size, and diversity. The echolocation frequency used by hoary bats is quite low, and larger insects have a greater probability of being detected at greater ranges than do small insects (Barclay, 1985). Barclay (1985), however suggested that *L. cinereus* forages not selectively on larger moths, but opportunistically on larger insects, as larger Coleoptera, and Odonata have also been reported in the diet in other areas.

Mosquitoes are often minor diet components in the diet of bats (Anthony and Kunz, 1977; Whitaker *et al.*, 1977), but are not generally believed to be an important food source. In high latitude populations (>64° N), bats consume mosquitoes relatively frequently (Rydell, 1989; Whitaker and Lawhead, 1992). In May and June, mosquitoes were the most abundant insect caught on insect traps on cold nights in my study (see Chapter 4). The high

proportion of mosquitoes in the diet of bats caught in May and June in my study area is likely a reflection of insect availability. The declining consumption of mosquitoes towards mid-summer paralleled the decreasing relative abundance caught on insect traps. Similarly, Barclay (1985) found the consumption of chironimids by *Lasioncyteris noctivagans* corresponded with abundance.

The diet of the bats in my study area changed as the summer progressed. Diptera and Coleoptera were consumed in greater proportions earlier in the summer. Diptera are often the most abundant insect group in cold ambient temperatures (Rydell, 1989). Consumption of Lepidoptera increased over the summer. Studies which have looked at temporal variation across the summer noticed a similar change in diet composition (Anthony and Kunz, 1977; Warner, 1985). Insect abundance is greatest towards mid-summer when females are lactating (Anthony and Kunz, 1977; Racey, 1985). In particular, Lepidoptera abundance peaks in July (Black, 1974). Decreasing amounts of Diptera and Coleoptera in bats' diets likely occur due to greater overall abundance and diversity of other insects.

Summary

The bat community along the South Saskatchewan River in south-eastern Alberta is fairly diverse, with five species occurring in the area throughout the summer. *Myotis ciliolabrum* is the most abundant species, followed by *M. evotis* and *E. fuscus*. *M. lucifugus* and *L. cinereus* are uncommon. Similar numbers of male and female bats are found in the area, except for *M. ciliolabrum* in which females are more common. Females give birth in the first two weeks of July, and juveniles begin flying at the end of July. The prairie appears to be good breeding habitat as most of the females in the population are reproductive. The

diet of bats in the area is dominated by Diptera, Coleoptera, and Lepidoptera and dietary proportions change over the course of the summer, and appear to parallel changes in insect availability.

The basic biology and life history characteristics presented in this chapter set up the background for the following chapters looking at the foraging and roosting ecology of bats in my study area. Knowing the species present, relative abundance, timing of reproduction, and the diet of bat provides a framework in which to interpret results.

CHAPTER 3. Roost Selection and Roosting Behaviour of Prairie Bats in South-Eastern Alberta.

INTRODUCTION

Bats spend over half their lives subjected to the selective pressures of their roost environment (Kunz, 1982). Due to the importance of the roost environment, a great deal of recent research has investigated factors influencing roost selection, particularly in forested areas. On the prairies, where bats roost is unknown, let alone the factors influencing selection of roosts. Roosting habitat may be limiting to prairie bats (Barclay, 1993; Brigham, 1993b). The paucity of trees, buildings and other complex vertical structures in the area likely restricts the roosting opportunity of most bats to crevice roosts in steep sides of the river valleys and the coulees. Elsewhere, in natural populations in their range, *M. lucifugus, M. evotis*, and *E. fuscus* all use trees as roosts (Brigham, 1991; Kalcounis and Hecker, 1995; Vonhof, 1996; Vonhof and Barclay, 1996; Crampton and Barclay, 1998; Kalcounis and Brigham, 1998). The small cottonwood (*Populus* spp.) riparian forests along prairie rivers likely offer limited roosting opportunities in the appropriate tree size and decay categories (Vonhof and Barclay, 1996). Bats select for large decayed trees, and low canopy closure (Brigham, 1991; Vonhof and Barclay, 1996).

Roosting in crevices is a common strategy in arid habitats (Tuttle and Heaney, 1974; Humphey, 1975; Vaughan and O'Shea, 1976; Kunz, 1982; van Zyll de Jong, 1985; Wai-Ping and Fenton, 1989; Lewis, 1996). Rock formations such as ridges, and river valleys are often the major three-dimensional features on the landscape. Most *M. ciliolabrum* roosts have been reported in rock crevices (Quay, 1948; Tuttle and Heaney, 1974). *E. fuscus* has been reported using rock crevices as roosts (Brigham, 1991). *M. evotis* seems particularly

flexible: it roosts in cliff crevices (Manning and Jones, 1989), scree slopes (Caceres, 1998) and tree stumps (Vonhof and Barclay, 1997).

In temperate areas most bat species select sheltered natural roosts such as rock and trees crevices (van Zyll de Jong, 1985) which offer the advantage of microclimatic stability, protection from sunlight and adverse weather and reduced risks of predation (Kunz, 1982). Bat are small mammals with high energy expenditures (McNab, 1982). Selecting roosts which have a stable internal environment reduces energy costs, particularly for reproductive female bats. Temperature may be the single most important factor in determining roost choice for many temperate zone bats (Tuttle and Stevenson, 1982). Bats have the ability to enter torpor, which allows for considerable energy savings over homothermy (Wang and Wolowyk, 1988). However, the use of torpor by pregnant females results in slowed fetal development (Racey and Swift, 1981). In temperate areas, the time available to give birth and fledge young is short, and prolonged pregnancy may result in both females and juveniles unable to store adequate amounts of fat for hibernation, resulting in lower post-hibernation survival (McNab, 1982; Kunz, 1987; Thomas *et al.* 1990).

The colony size of roosting bats also affects the roost microclimate and energy expenditures. Clustering behaviour reduces the exposed surface area, increasing retention of heat, and lowering evapourative water loss (Kunz, 1982). Sociality also appears to play an important role in reducing metabolic requirements (Trune and Slobodchikoff, 1976). Roosting groups of bats have a lower metabolic rate than bats roosting singly. In buildings and man-made structures, many bat species roost in large colonies, often greater than a hundred individuals (van Zyll de Jong, 1985). However, in natural populations, crevice roosting species appear to roost solitarily or in small groups (Tuttle and Heaney, 1974;

Vonhof and Barclay, 1996; Vonhof and Barclay, 1997; Brigham *et al.*, 1997). The size of the roost crevices in trees and rock may limit the colony size in natural populations.

Roost availability and abundance also influences the roosting habits of bats (Kunz, 1982). In man-made structures, many species show high roost fidelity (Fenton and Barclay, 1980; Brigham, 1986; Hamilton and Barclay, 1996). In tree and rock crevice roosting populations, many species demonstrate low roost fidelity, frequently switching roosts (Vaughan and O'Shea, 1976; Lewis, 1996; Vonhof and Barclay, 1996; Brigham *et al.*, 1997). This behaviour occurs throughout the reproductive period, despite the costs to lactating females of having to move non-volant young (Vaughan and O'Shea, 1976; Lewis, 1996; Brigham *et al.*, 1997). Several functions have been proposed for the frequent switching behaviour: 1) to avoid predators which would be attracted to frequently used roosts, 2) to respond to changing microclimatic or structural conditions in the roost, and 3) to avoid large populations of ectoparasites by deserting a roost before eggs or pupae in the roost develop (Lewis 1995;1996). The degree of roost fidelity appears to be related to roost permanency and roost availability (Lewis, 1995). Species which exhibit high roost fidelity use roost structures with greater permanency and lower availability.

There have been few studies on the roosting ecology of bats in arid habitats. In the prairies, mid-summer temperatures can exceed 40°C. Studies suggest that bats select sheltering roosts to avoid the worst heat of the day (Tuttle and Heany, 1974; Vaughan and O'Shea, 1976; Lewis, 1996), or switch to more shaded roosts as the day progresses (Vaughan and Vaughan, 1986). Microclimatic differences between roost crevices and ambient conditions are likely to be critical. The small body size and high surface area-to-volume ratio of bats leads to a high evapourative water loss (Webb *et al.*, 1995). In mid-

June, bats remain in diurnal roosts for greater than 17 hours per day, with no fresh water. In mid-summer pallid bats (*Antrozous pallidus*) roost in deep crevices which buffer the internal temperature to around 30°C (Vaughan and O'Shea, 1976). By using deep crevices, pallid bats can roost near the crevice opening in cooler portions of the day and move toward the back of the crevice during mid-day.

Suitable roosting habitat is critical to bats, especially to reproductive females. The dearth of knowledge about roost habitat in arid areas, and on the prairies in particular, severely limits our understanding of the ecology, critical habitats, and status of prairie bat populations. Focusing on reproductive females, the goal of this part of my research was to investigate where bats roost, and to determine some of the factors influencing roost choice.

METHODS

To locate roosts I attached radio transmitters to female bats captured in mist nets. Female bats were the focus of my study due to the greater energetic demands of pregnancy and lactation (Hamilton and Barclay, 1994). I clipped the hair on the dorsal surface between the shoulders and attached transmitters with Skin-bond surgical glue. I used 0.45g Holohill transmitters (battery life=10 days) on the small *Myotis* bats (3.9 - 10.0g), and 0.75g transmitters (battery life=21 days) on the larger big brown bats (14.1 - 25.0g). Each day for the life of the transmitter battery, I tracked bats to roosts with Merlin 12 receivers (Custom Electronics) with Yagi antennae I watched roosts during emergence at dusk to determine the number of bats in each roost. At each roost, I measured slope, aspect, distance to nearest flat ground above and below the roost, and crevice opening dimensions, and where possible internal roost dimensions. Where appropriate, I log transformed roost dimensions

and compared them with t-tests. Hobo™ data loggers were used to record the temperature in roosts and ambient temperature throughout the day. Temperature probes were inserted to a depth of 10cm in known roosts, and Hobo light data loggers were placed next to the crevice opening to record light intensity throughout the day.

RESULTS

Roost Structural Characteristics

Five *M. ciliolabrum*, 15 *M. evotis*, one *M. lucifugus*, and three *E. fuscus* were tracked successfully to a total of 46 diurnal roosts. In addition, two *M. lucifugus*, and one *E. fuscus* roosts were located by observing bats emerging at dusk. All the bats roosted along the river valley, in crevices in the coulees or sandstone cliffs. Roost were located throughout the summer, and bats were tracked to roosts present on both sides of the river. No radio-tagged bat ever roosted in a tree. Three roost types were located. The first was small crevices in vertical slopes and in cliff faces (slope roosts). The second was in water erosion cracks descending into the ground on relatively flat slopes (ground roosts). The last roost type was in cracks in sandstone boulders (boulder roosts). The slope and ground roosts were in soft sandstone which crumbles very easily, and are likely highly ephemeral, easily eroded by heavy spring rainfall. The boulders were harder, cemented sandstone.

All *M. ciliolabrum* and *M. lucifugus*, but only 2 of 15 radio tagged *M. evotis* females roosted in slope roosts or ground roosts (Table 3.1). Two of the *M. lucifugus* roosts were located in the ceiling of a small cave, but were grouped with the slope roosts in the analysis. For all *Myotis* species, the slope roosts (n=11) in vertical slope faces tended to be located in

Table 3.1. Mean (range) characteristics of sandstone slope crevice roosts for *M. ciliolabrum*, *M. evotis*, *M. lucifugus* and *E. fuscus*, along the South Saskatchewan River, south-eastern Alberta.

Species	Substrate	N	Crevice open dimensions (cm)	Distance to flat ground below(m)	Distance to flat ground above(m)	# of bats emerging
M. ciliolabrum	Slope roost	5	4.5*2.7 (3-7)	2.5 (0.85-4.2)	2.67 (0.75-6.0)	3.2 (2-6)
	Ground roost	4	119.7*158.0 (37-502)	5.5 (3-8)	4.5 (2-7)	2-35 bats
M. evotis	Slope roost	2	29*9 (3-29)	0.9 (0.8-1.0)	1.2	4.5 (2-8)
	Ground roost	2	44.5*36 (21-68)	---	---	5.0 (4-6)
M. lucifugus	Slope roost	4	5.8*7.4 (1.5-19.5)	3.0 (1.5-6.5)	4.5 (*0-11) *2 roosts in ceiling of cave	24.5 (13-41)
Combined *Myotis* species	Slope roost	11	9.4*4.3 (1.5-19.5)	2.4 (0.8-6.5)	3.1 (0-11)	---
	Ground roost	6	94.6*117.3 (21-502)	5.5 (3-8)	4.5(2-7)	---
E. fuscus	Slope roost	5	74.9*3.9 (3-180)	4.4 (1.2-6.5)	5.8 (2-8)	20.0 (5-37)

the middle of the cliff face, with most >1m above flat ground below. The opening dimensions of the slope roosts were small (mean = 9.4cm * 4.3cm) for combined *Myotis* species. Few internal roost measurements could be taken without destroying the roosts, but they appeared to be fairly shallow (10-45cm deep; n=5). The roosts located in ground crevices (n=6) were large, all >1m deep, with lots of small internal cracks and openings for bats to roost in. The crevice openings were relatively large (mean 94.6cm * 117.3cm). One roost was a large tunnel descending >12m into the side of the cliff, and contained a large colony (>35) of *Myotis* bats.

Five of six big brown bat roosts were slope roosts, in crevices in vertical slopes (Table 3.1). Roosts were all well above the ground (mean distance from flat ground below 4.4m, and 5.8m to flat ground above). The roosts were long narrow cracks in the slope face, with narrow opening dimensions (mean = 74.9cm * 3.9cm). Two of the big brown roosts were narrow crevices approximately 50cm deep which penetrated upward into rock overhangs. For all species (*Myotis* as well as *E. fuscus*), the majority of the slope roosts and ground roosts were on south-east facing slopes (Fig 3.1). The distribution of aspects was significantly different from a random distribution (χ^2=32.4, df=3, p<0.001). Data from Hobo-light loggers indicated that south-east facing slopes received direct sunlight just after dawn, and throughout the day, with a sharp drop during late afternoon/early evening (Fig 3.2).

The microenvironment in sandstone slope roosts appears to be more stable than ambient conditions. Roost temperatures from two roosts (one used by a female *M. ciliolabrum*, and the other by a female *E. fuscus*) were taken throughout the day, and compared with ambient temperatures (Fig. 3.3). The fluctuations between maximum and

Figure 3.1. Frequency and the compass direction (slope aspect) of sandstone slope and ground roosts for *Myotis* species and *E. fuscus*, along the South Saskatchewan River.
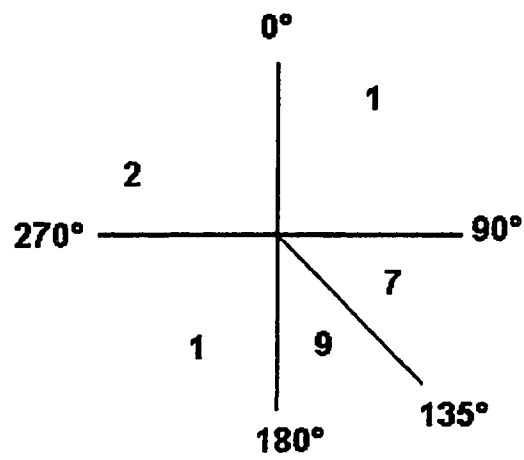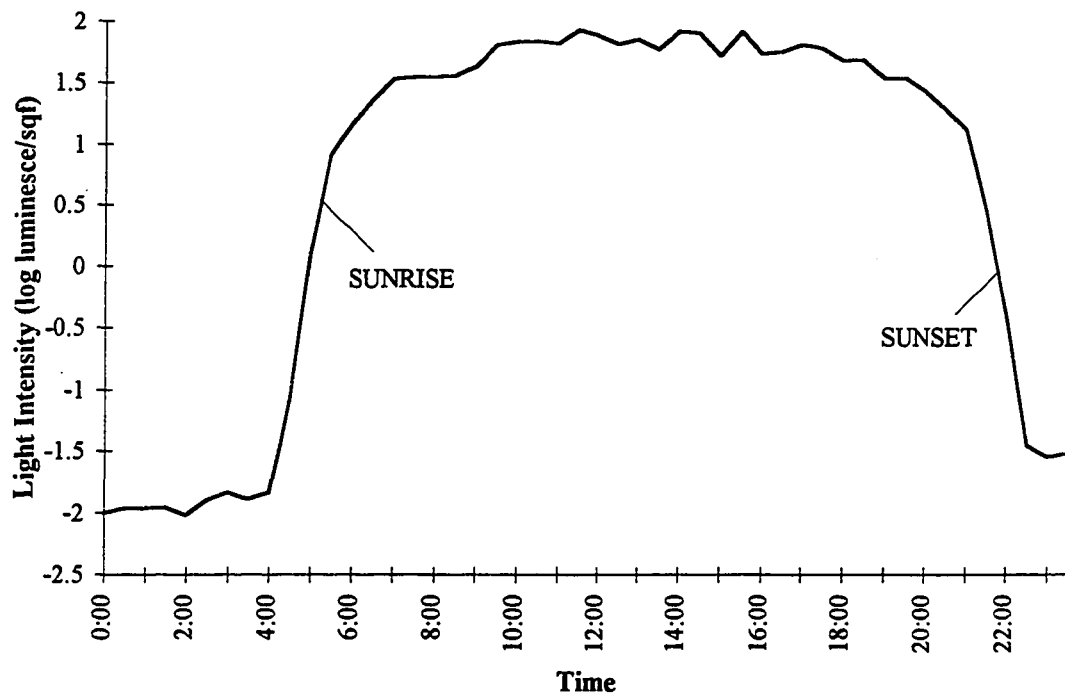
Figure 3.2. Average light intensity (log luminesce/ft^2) per day (n=4 days) hitting a roost crevice on south-east facing slopes.

Fig 3.3a)

Fig 3.3b)

——— Roost Temperature · · · · · · Ambient temperature
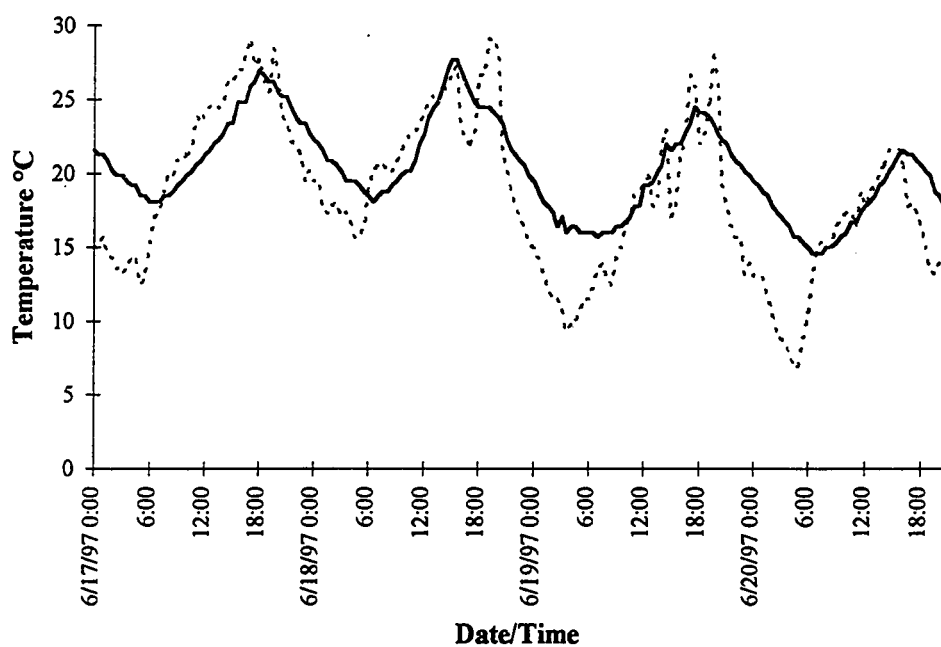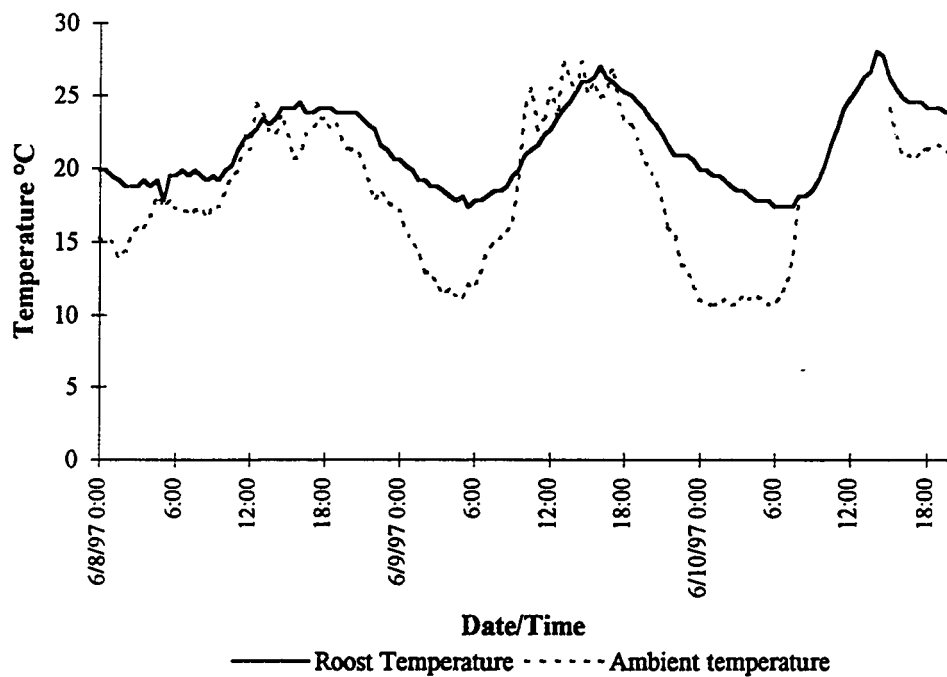
Figure 3.3. Temperature in sandstone slope roosts compared with ambient temperature from a) a roost used by *E. fuscus*, and b) a roost used by *M. ciliolabrum*.

minimum temperatures per day was significantly lower in roosts (mean= 8.7°C) compared with ambient temperature (mean=15.1°C; n=7 days; t=5.99, df=12, p<0.001). In particular roosts were warmer at night. Roosts lose heat at a slower rate than ambient air, and the roosts thus stayed warm over the short summer nights. During the day, roosts warmed up slightly slower than ambient, but reached temperatures similar to daily ambient maxima. These comparisons were performed in June, well before mid-summer. Anecdotal observations of roosts selected in July during extremely hot weather (>35°C) suggested that bats selected roosts which were shaded for most of the day, or deeper roosts, thereby perhaps regulating maximum roost temperature.

The remainder of the *M. evotis* roosts (26 of 30) were located in crevices in sandstone boulders (boulder roosts; Table 3.2). The roosts were long narrow cracks, usually on the top of boulders. Both small and large boulders (range 0.8m-6.2m long) were used, but roosts were low to the ground (mean height 66.0cm; range 22.0cm-155.0cm). The orientation of roost crevices used by pregnant and lactating bats was different. For pregnant bats, 14/15 roosts were narrow horizontal crevices running parallel to the ground (± 20° slope angle; Fig 3.4). For lactating bats, 8/11 roosts were vertical crevices perpendicular to the ground (± 20° slope angle; Fig. 3.5). A χ^2 test comparing the frequency of roost orientation (parallel and perpendicular) between pregnant and lactating bats was significant (χ^2=12.23, df=1, p<0.001). Roost depth was also significantly different between the two reproductive conditions (t=3.44, df=24, p=0.002; Table 3.2). Pregnant roosts were shallow crevices, with relatively large roost chambers. The crevice openings faced sideways. Lactating roosts were deeper vertical crevices, with the opening facing upwards. Roost crevices were long but narrow grooves running through the rock. Lactating roosts were

Table 3.2. Characteristics of boulder roosts of pregnant (P) and lactating (L) *M. evotis* and *E. fuscus* females along the South Saskatchewan River, south-eastern Alberta (Perpend= perpendicular).

Spp.	Reprod. Cond.	Roost Orientation (relative to ground)	Crevice depth (cm)	Chamber dimensions		Crevice opening dimensions (cm)	Roost Height (cm)
				Length (cm)	Width (cm)		
M. evotis	P	Parallel	3.1	73.0	50.0	44.0 * 3.1	62
	P	Parallel	2.5	38.0	20.5	38.2 * 2.5	56
	P	Parallel	2.2	75.0	21.0	77.0 * 2.2	78
	P	Parallel	3.0	21.0	6.0	6.0 * 3.0	35
	P	Parallel	4.0	200.0	103.0	26.0 * 4.0	110
	P	Parallel	4.0	47.0	33.0	44.0 * 4.0	59
	P	Parallel	2.0	86.0	33.0	18.0 * 2.0	22
	P	Parallel	2.0	95.0	71.0	22.0 * 2.0	52
	P	Parallel	2.0	80.0	35.0	71.0 * 2.0	51
	P	Parallel	4.5	240.0	140.0	28.0 * 4.5	52
	P	Parallel	3.0	38.0	25.0	38.0 * 3.0	26
	P	Parallel	4.0	39.0	18.0	18 * 4	46
	P	Parallel	3.0	57.0	56.0	36 * 3	155
	P	Parallel	3.0	52.0	42.0	23 * 3	85
	P	Perpend.	29.0	45.0	5.5	5.5 * 45.0	42
Mean (±SE)			4.7 (±1.7)	78.4 (±15.9)	44.6 (±9.5)	-----	----
	L	Parallel	1.8	32.0	---	32 * 1.8	112
	L	Parallel	3.0	52.0	50.0	33 * 3	58
	L	Parallel	2.0	95.0	71.0	22 * 2	52
	L	Perpend	11.0	22.0	2.0	2 * 22	37
	L	Perpend	17.0	43.0	3.0	3 * 43	50
	L	Perpend	28.0	28.0	4.0	4 * 28	90
	L	Perpend	15.0	142.0	1.5	1.5 * 142.0	94
	L	Perpend	42.0	223.0	2.5	2.5 * 223.0	103
	L	Perpend	14.8	57.0	1.8	1.8 * 57.0	42
	L	Perpend	24.0	112.0	2.5	2.5 * 112.0	35
	L	Perpend	28.0	65.0	2.0	2.0 * 65.0	113
Mean (±SE)			17.0 (±3.8)	79.0 (±18.3)	14.0 (±7.9)	-----	-----
E. fuscus	P	Parallel	3.0	61.0	34.0	61.0 * 3.0	58
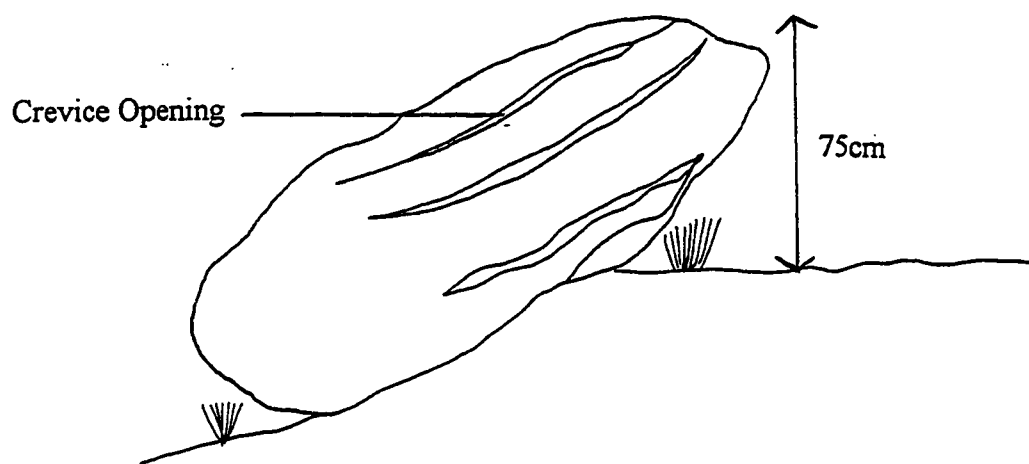
Figure 3.4. Lateral view of a female M. evotis pregnant (parallel) boulder roost.

A)

B)
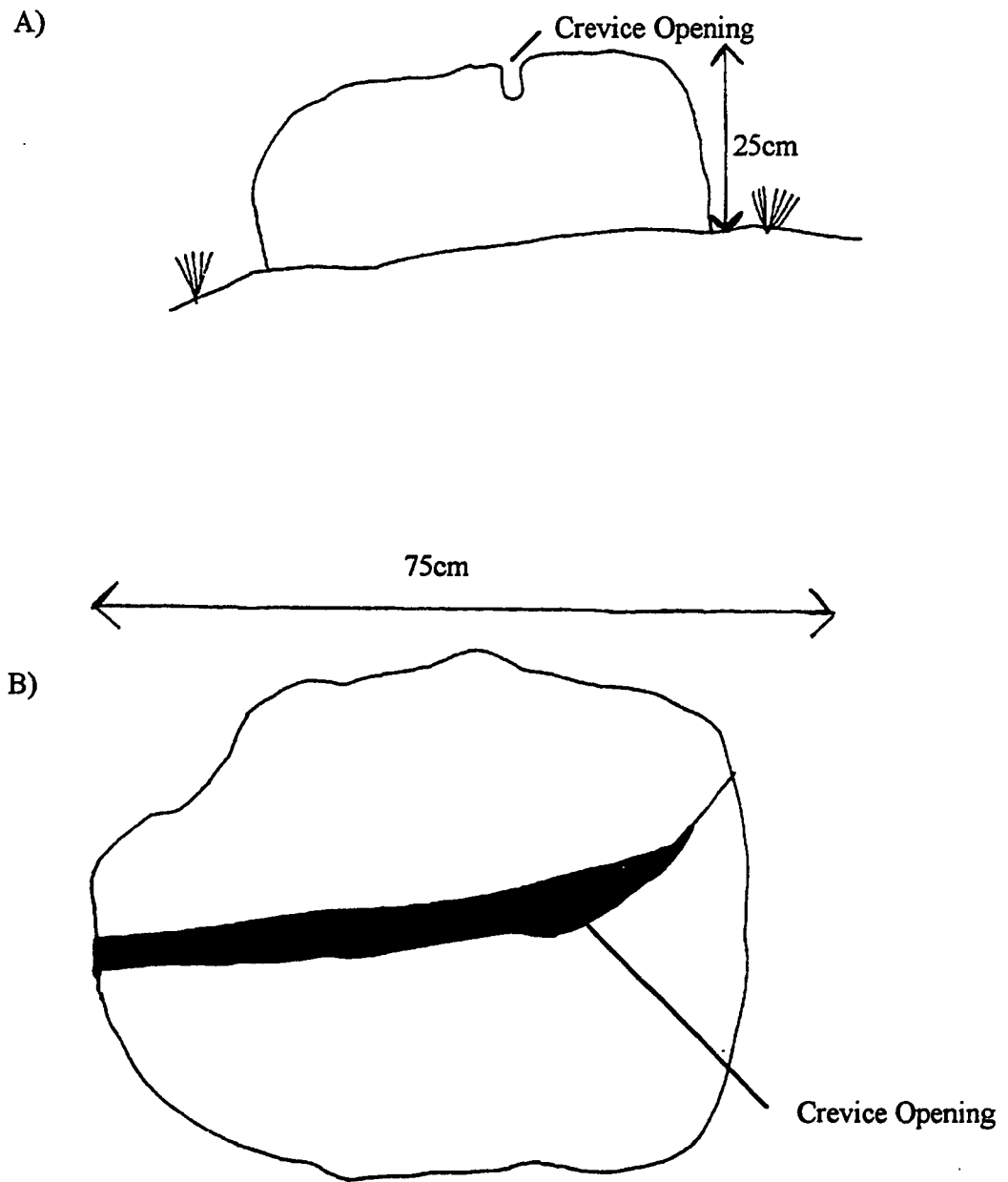
Figure 3.5. A female *M. evotis* vertical (perpendicular) boulder roost; a) lateral view, b) top view

open from above, with no protection from precipitation. For both reproductive conditions

opening dimensions were small (mean = 50.5cm*2.8cm). There was no pattern in the aspect

of the roosts. Approximately half the roosts were on level ground, away from higher slopes,

and thus received direct sunlight for most of the day, while the other half were within the

coulees and were shaded for much of the day. One *E. fuscus* roost was nearly identical to

pregnant *M. evotis* roosts, with a shallow, but large roost chamber, and small opening

dimensions (Table 3.2).

Night Roosting

Bats on the prairies are active all night (see Chapter 4). Radio-tagged *M.*

ciliolabrum, *M. lucifugus*, and *E. fuscus* foraged for several bouts throughout the night,

interrupted by periods of night roosting. Individuals used both their diurnal roosts and caves

as night roosts. Radio-tagged females (n=6) returned to diurnal roosts, and then left again

at least once per night, both during June (pregnancy period) and July (lactation period). I

also found two small caves in which mixed species groups (*M. ciliolabrum*, *M. lucifugus*,

and *E. fuscus*) were observed night roosting together. Individuals hung on the cave ceiling.

The microenvironment in the cave was noticeably warmer, with temperature 2-4°C higher

than ambient on threes nights when bats were present.

Roost Movements and Colony Size

Myotis ciliolabrum roosted in small groups (mean=4.0, range 2-6; n=8). This

excludes one roost, from which >35 and >20 *Myotis* bats exited on two different evenings.

Unlike the rest of the radio-tagged *M. ciliolabrum* (see below), the female tracked to this

roost did not roost any where else (n=6 nights). The colony size of *M. evotis* seemed to depend on the roost substrate. *M. evotis* which roosted in crevices in boulder roosts were usually solitary (n=15). Two individuals roosted together on two occasions. In slope roosts and ground roosts, *M. evotis* formed colonies of 2-8 individuals (mean=5; n=4) individuals. *M. lucifugus* roosted in larger groups (mean=24.5; range= 13-41; n=4), as did *E. fuscus* (mean=19.3; range=5-37; n=6).

Individuals of all bat species moved between roosts, although the time a bat remained in an individual roost varied greatly. *M. ciliolabrum* and *M. evotis* moved the most frequently, remaining in most roosts on average 1.25 days (range 1-3 days; n=30). This excluded one *M. ciliolabrum* female which roosted in a deep inaccessible, and well protected roost for the entire transmitter life (6 days). *M. lucifugus* and *E. fuscus* showed more roost fidelity. Two radio tagged individuals remained in the same roost for the entire time the transmitter remained attached to the bat (5 days and 6 days), and two individuals switched once (mean=3.8 days, range 1-5; n=2 individuals). While prairie bats did not exhibit individual roost fidelity, they remained within a localized area, never moving far between roosts (mean distance between consecutive roosts = 64m, range 2m-400m; n=11). Radio-tagged individuals of all species were captured close to their subsequent roosting areas (<1km from roosts).

DISCUSSION

Roost Structural Characteristics

The cliffs and coulees of the river valley are critical roosting habitat for prairie bats. All bats roosted in sandstone crevices, in the side of slopes or in boulders. On the prairies in

south-eastern Alberta, the river valley is the major three-dimensional feature on the landscape, and it provides the only abundant roosting substrate. No bats ever roosted in the trees in the small riparian forests along the South Saskatchewan River despite apparent crevices. Small crevices in the sandstone and boulders were abundant in the areas where bats roosted, and on a localized scale roosting habitat is likely not limited.

Crevice roosts have the potential to offer reduced risk of predation, protection from sunlight and weather, and microclimatic stability (Kunz, 1982). Predation is not likely a major factor influencing roost selection in the area. Prairie rattle snakes (*Crotalus viridis*), bull snakes (*Pituophis melanoleucus*) and coyotes (*Canis latrans*) are likely the only predators active in the day which would be a threat to torpid roosting bats. Many of the roosts are low to the ground, especially the *M. evotis* boulder roosts. The opening dimensions of crevice roosts are small, however, and this may be a response to predation. It is likely also an important factor in controlling microclimatic stability. Great horned owls (*Bubo virginianus*) are active near roosts around emergence. However, I found bats roosting near the nest of the owls, suggesting that the presence of these predators does not influence roost selection by bats. Most of the crevice roosts offer protection from precipitation and inclement weather. However, the ground roosts and the vertical roosts in boulders used by *M. evotis* during lactation are open to rain. The majority of these two roosts types were found in July or August, and in south-eastern Alberta most of the rain occurs in May and June.

Microclimate stability is probably one of the most important factors roosting bats select for to reduce energy costs. Similar to many studies, slope roosts appear to offer a more stable roosting microenvironment compared with ambient conditions (Tuttle and

Heaney, 1974; Vaughan and O'Shea, 1976; Kunz, 1982; Kalcounis and Brigham, 1998).

Though my data are limited, within sandstone-slope roosts the temperature did not fluctuate

to the same degree as ambient temperature did. At night roosts retain heat and are

substantially warmer than ambient. This has important implications as many bats use their

diurnal roosts as night roosts, and for non-volant young after parturition. Similarly, night

roosts used by other bats are warmer than ambient (Barclay, 1982; Lewis, 1994). Warmer

roosts likely decrease the amount and depth of torpor needed by roosting bats, which is

important to reproductive females for rapid fetal development (Racey and Swift, 1981) and

to young bats, as they are born without fur and thus are likely poor thermoregulators. The

aspect of the majority of the roosts may also be important in controlling roost temperature.

Most slope and ground roosts faced south-east and thus receive direct sunlight early in the

morning. This allows roosts to warm up quickly after dawn, which potentially could

decrease the energy bats need to stay warm. Roosts retain heat into the evening, and bats

can passively warm up before emergence. This thermoregulatory pattern may be important

as several other studies have found roosts with south or south-east aspects (Vaughan and

O'Shea, 1976; Tidemann and Flavel, 1987; Lewis, 1996; Kalcounis and Brigham, 1998).

All bat species used sandstone slope or ground roosts. *E. fuscus* and *M. evotis* also

roosted in crevices in boulders. Only one big brown bat used a boulder roost, while the

majority of the *M. evotis* roosts were in boulders. Although both are in sandstone, the

boulder and slope roosts likely have different heat retention properties, and *M. evotis* may

prefer different microclimatic conditions from the other species. The orientation of the

crevices in boulder roosts used by pregnant and lactating bats was different. The different

roost selection may be due simply to seasonal change. The lactating vertical roosts may be

cooler in July when ambient temperatures are highest. However, another possibility is that the two roost types show different temperature regimes. When ambient temperatures are colder in early summer, the pregnant (parallel) roosts are warmer on average compared with the lactating (perpendicular) roosts (B. Chruszcz pers. comm.). The lactating roosts are warmer at night than the pregnant roosts (B. Chruszcz pers. comm), which would be important for the development of young. Other studies have found similar results. In late spring-early summer, pallid bats (*Antrozous pallidus*) selected roosts with more variable temperature ranges, to take advantage of direct sun warming, and in mid summer bats switch to deeper, more sheltered roosts (Vaughan and O'Shea, 1976; Lewis, 1996).

Roost Movements and Colony Size

Prairie bats demonstrated a frequent roost switching, similar to bats roosting in bats. Roost switch could potentially be caused by the attachment of the transmitters to the bats, but the effect of transmitters on bat activity has not been investigated. *Myotis ciliolabrum* and *M. evotis* appear to select either shallower, less permanent roosts or less protected roosts than *M. lucifugus* or *E. fuscus*. The slope roosts and pregnant (parallel) roosts in boulders are likely ephemeral. Heavy rainfall erodes sandstone slopes and over winter the chinook conditions common on the prairies (freezing, then sudden thaws) likely cracks and alters the narrow cover of pregnant boulder roosts. Tuttle and Heaney (1974) found *M. ciliolabrum* using similar shallow roosts (mean roost depth=6.5cm) in rock crevices in South Dakota. Ground roosts and the lactating (perpendicular) roosts in boulders were open to the elements. Frequent roost switching was demonstrated in these by *M. ciliolabrum* and *M. evotis*. Microclimate is likely more variable in shallow and less protected roosts, and bats

may switch roosts frequently to parallel changing ambient conditions. In slope and ground roosts these species roosted together in small groups. Clustering together in small colonies reduces the exposed surface area and thus likely reduces energy expenditures while roosting. In contrast, past studies found *M. cilolabrum* to roost solitarily (Tuttle and Heaney, 1974). In boulder roosts *M. evotis* seems to prefer to roost solitarily. It is unclear why this occurs, but thermoregulatory properties of boulder roosts are likely important in determining colony size.

Eptesicus fuscus and *M. lucifugus* seemed to select larger, deeper, and more protected cliff crevices which contained larger colonies. The sample size for these species was small, but all the roosts found for these two species appear to be either deeper and/or more protected. No big brown bats and little brown bats were found using ground crevices. The roosts in rock overhangs would be much less susceptible to rainfall erosion. *M. lucifugus* and *E. fuscus* showed more roost fidelity, and larger, sheltering roosts which allow bigger colonies may potentially be a limited resource. While all species exhibited some roost switching, all returned to diurnal roosts within a small localized area along the river. These may represent localized populations which show fidelity on a larger scale.

Although nothing conclusive can be determined as to why bats in natural roosts frequently switch roosts, some of my results have interesting implications. I found relatively high rates of parasitism for *M. ciliolabrum* and *M. evotis* compared with other studies (see Chapter 2). This suggests bats could potentially be switching roosts to avoid greater parasite transmission as eggs and larvae mature in roosts. Roost microclimate may also be important, especially for species which use shallow, less protected roosts. Bats may switch between different roosts depending on the current ambient conditions.

Summary

The coulees and cliffs of the river valley appear to be critical roosting habitat for prairie bats in south-eastern Alberta. All species roosted in the cliffs and coulees. *M. ciliolabrum* and *M. evotis* appear to use shallower, or less protected roosts. *M. lucifugus* and *E. fuscus* used larger and deeper roosts. *M. evotis* roosted in crevices in sandstone boulders. The crevice orientation roosts in boulder roosts differs between pregnant and lactating roosts. Slope roosts appear to show greater microclimate stability compared with ambient conditions. The majority of slope and ground roosts face south-east, which seems to be important in maintaining roost thermoregulatory patterns. Bats appear to remain within localized roosting areas, never moving far between consecutive roosts, which suggests good roosting habitat may be limited along the length of the river.

CHAPTER 4. Foraging Habitat and Activity Patterns of Prairie-Dwelling Bats Along

Riparian Zones, in South-Eastern Alberta.

INTRODUCTION

Bats are the only mammals to have evolved true flight. One of the constraints of

flight is that it is energetically expensive (Speakman and Racey, 1991). This means that

individuals need to have a high consumption rate of prey, and thus should select habitats

with high insect density. This is especially true in northern temperate areas where both

reproduction and preparation for winter hibernation are confined to a few warm summer

months with short nights. Little is known about bats on the prairies in southern Canada, but

as the greatest bat activity usually corresponds to habitats with the greatest insect density

(Racey and Swift, 1985; Rautenbach *et al.*, 1996), the riparian zone may play a significant

role for foraging bats.

Studies world-wide have suggested that riparian zones are important in the ecology

of bats in diverse habitats (LaVal *et al.*, 1977; Swift and Racey, 1983; Racey and Swift,

1985; Brigham, 1993b; Rydell *et al.*, 1994; Carmel and Safriel, 1998). In arid habitats,

riparian zones likely play a critical role, sometimes as the only accessible water source (van

Tighem, 1996). Moist habitats along rivers, ponds and springs often have the highest insect

abundance (Barclay, 1985, 1991; Racey and Swift, 1985). The life cycles of many insects

are, at some life stage, tied to water and vegetation (Borror and DeLong, 1971). Bell

(1980) found that riparian forests in the Arizona desert had significantly higher bat activity

than desert or shrub habitat, and many bats forage around trees and smaller shrubs (Racey

and Swift, 1985; Rydell, 1989). In the prairies in south-eastern Alberta, the riparian zone

not only supports the majority of trees and shrubs, but most natural springs are present in runoff valleys in the coulees.

Patches of flying insects tend to be ephemeral resources, both spatially and temporally (Buchler, 1976). Bats are adept at locating and responding opportunistically to insect swarms (Fenton and Morris, 1976; Bell, 1980). Not only have bats adapted to spatial distributions of insects, they have also adopted activity patterns to take advantage of the temporal distribution of insects. Many insects show crepuscular activity patterns, with abundance greatest around dusk and dawn (Lewis and Taylor, 1965) and bat activity usually corresponds, with bimodal or unimodal activity peaks (Swift and Racey, 1983; Racey and Swift, 1985; Maier, 1992).

The purpose of this part of my study was firstly to quantify bat habitat-use and insect abundance on the prairies to answer several questions: 1) Are the riparian zones and springs important to foraging bats? 2) If the river is important, do bats focus their foraging effort around riparian trees? 3) How does the slope topography of the river valley influence bat activity and abundance? Secondly, I wanted to look at the temporal activity patterns displayed by foraging bats to determine the effect time of night has on bat activity?

METHODS

Bat Captures (refer to Chapter 2 for methods)

Echolocation and Foraging Activity

I investigated bat activity using Pettersson ultrasonic detectors. These detectors are tunable and detect ultrasonic frequencies ranging from 10kHz-120kHz, converting them into audible sounds. I assessed big brown bat and hoary bat activity by setting the detector at

25kHz, while *Myotis* species (primarily *M. ciliolabrum*, and *M. evotis*, but *M. lucifugus* is also present) were detected at 40kHz. The three *Myotis* species cannot be recognized separately based on echolocation calls. I distinguished echolocation passes from foraging buzzes. Echolocation passes are a continuous series of echolocation calls used by bats to orient themselves and to navigate when flying. When bats detect and approach insect prey, the pulse duration shortens gradually, and the repetition rate of echolocation calls increases until the they attack the insect (van Zyll de Jong, 1985). The high pulse repetition rate associated with attacks on flying insects are called foraging buzzes (van Zyll de Jong, 1985). I recorded the number of passes and buzzes per unit time.

I monitored echolocation activity over the entire night. I divided the night into three temporal periods: dusk (2.0 hours, starting 30 minutes after sunset), dawn (2.0 hours before sunrise, ending at sunrise), and middle night (the remainder of the night between the dusk and dawn periods). I compared bat foraging activity among six habitats along the South Saskatchewan River: river (along, above or within 15m of the river), coulees (the coulees and cliffs of the river valley extending up to 1km from the river), springs (over and within 5m of standing water), far-prairie (grassland habitat >1km from the top of the coulees), and near-prairie (grassland habitat <1km from the top of the coulees). I further divided river habitat into two sub-categories: treed river (among or within 10m of riparian trees), and untreed river (riparian areas >100m from trees). On calm, windless nights the range of the ultrasonic detectors is approximately 30m (Barclay, pers. comm.). I collected echolocation activity data throughout the night, following a circuit within each period, monitoring two or three habitats at both 25kHz and 40kHz. When collecting echolocation data I remained in

one place for the entire monitoring time in each habitat. I use the term "riparian zone" in this paper to refer to the whole river valley (river and coulees).

To investigate how the steepness of the river valley (large steep coulees vs. flat eroded river valley slopes) effects bat activity and abundance, I monitored two additional habitats. I collected bat-activity data among or within 10m of riparian trees at areas with smooth, flat development of the river valley. Three sites along the Red Deer River composed the Red Deer low-slope habitat (RDR low slopes). Two sites along the South Saskatchewan River, south of the main study area, composed the South Saskatchewan low-slope habitat (SSR low slopes). I compared the activity at these areas with activity from treed river habitat along the South Saskatchewan River, where steep, craggy coulees were present (SSR steep coulees).

Statistical Analysis

I analyzed all data using Systat 5.1 for Windows. I only used activity data from 1997 in the analyses, with one exception because the data were collected differently in 1996 than 1997. For the last question, to determine the role the steepness of the river valleys plays in bat activity, I combined data from 1996 and 1997 for both frequencies due to small sample size for SSR low-slope habitat. For all bat echolocation and foraging activity, I divided the number of passes and buzzes by the time spent monitoring, so the data used in analyzes were passes/minute and buzzes/minute. I analyzed activity data for 40kHz and 25kHz separately. The activity data at 25kHz refers exclusively to big brown bats (*Eptesicus fuscus*). I excluded hoary bat echolocation activity because the foraging style of big brown bats and hoary bats is quite different, and the resulting habitat use is likely

different. I used log (n+1) transformations for passes/minute and buzzes/minute if all data were included in the analysis. A large number of zeros in the data skewed the distribution and resulted in unequal variances between some habitats, so for these comparisons, I divided the data set into two groups: nights with activity, and nights was no bat activity. I log transformed the passes/minute and buzzes/minute on nights with activity. I calculated the proportion of nights with no bat activity for each sampling site within each habitat and period of the night, and arcsine transformed the proportions. All statistical tests used an alpha value to 0.05. In all ANOVA and ANCOVA analyses, I removed non-significant interactions sequentially, starting with higher order interactions. Means are presented with standard error in all figures.

Insect Density and Distribution

I assessed insect abundance using sticky traps. Sticky traps were lengths of PVC piping (37.5cm long*10.5 wide), coated with Tanglefoot insect adhesive. Sticky traps are non-attractive and can easily be used to trap at different heights and in different habitats (Kunz, 1988). I sampled four habitats: river, coulee, near-prairie and springs. I sampled insect abundance over the entire night, in each of the three temporal periods. I placed two replicate insect traps, at heights of 1m and 2m, in each habitat type, in each temporal period. Because the lowest trap was 1m above the ground, the traps sampled aerial insect fauna. I only performed insect trapping on nights when it had not rained for 24 hours prior. I removed insects from each trap and identified them to Order, except for Diptera which I identified to Family where possible. I measured the length of each insect in millimetres. Dipterans less than 2.5mm in length were not identified to family, as diet analysis has found

that *Myotis* bats rarely attack prey less than 3mm in length (Buchler, 1976; Anthony and Kunz, 1977). I calculated total insect biomass using a length-mass conversion employed by Roger *et al.* (1976), and log (n+1) transformed it.

$$W = 0.0305 \, L^{2.62}$$

where   W = mass in milligrams

L = length in millimetres

RESULTS

Bat Captures

I did not catch bats equally in all habitats. I caught 0.79 bats/net-hour in treed riparian areas, compared with 0.44 bats/net-hour within the coulees, and 0.31 bats/net-hour over springs. In a survey of the Suffield National Wildlife area, netting was attempted on the open prairie and no bats were caught (McNalley and Barclay, 1995). Overall, the distribution of captures in my study was not random between the three habitats (χ^2=16.69, df=2, p=0.002; Table 4.1), where expected values were calculated based on the proportion of the total net effort within each habitat. I captured most bats near riparian trees, greater than 60% of each species were captured there. The greatest proportion of any species caught in the trees was 91.7% for *M. evotis*. The species with the greatest proportions of captures in the coulees was *E. fuscus* with 29.7%, nearly twice the proportion of individuals captured there for each of the other species. In the coulees, I captured *E. fuscus* throughout the night, while all but one of the *Myotis* bats were caught around dusk and dawn. Captures were low at springs, due to the low net effort. Netting over springs is highly variable, as

Table 4.1. Number of captures per net hour and percentage of total captures of each species for the three different habitat types where mist-netting was performed along the South Saskatchewan River.

Bat Species	Habitat Captured		
	Treed River	Coulees	Springs
M. ciliolabrum	0.37 (77.0%)	0.21 (17.2%)	0.16 (5.7%)
M. evotis	0.24 (91.7%)	0.04 (6.25%)	0.03 (2.1%)
M. lucifugus	0.06 (76.9%)	0.03 (15.1%)	0.03 (7.7%)
E. fuscus	0.13 (62.2%)	0.16 (29.7%)	0.09 (8.1%)
Total	144	31	10

calm, windless nights are needed for successful netting. Less than 10% of each bat species was captured at springs, although 11.3% of my netting effort occurred there.

The Importance of the Riparian Zone

To determine patterns of habitat use by bats I had to divide the data set, as variances were heteroscedastic between prairie and river habitats. I compared the proportion of nights with no bat activity at each sampling site between five habitat types (river (n=4 sites), coulees (n=4), near prairie (n=5), far prairie (n=5), and springs (n=3)) and the three periods of the night using analysis of variance. Separate analyses looked at 25kHz and 40kHz (Fig 4.1). For the proportion of the nights with no bat activity at 25kHz, the model was significant (F=5.58, df=14,45, p<0.001). Habitat had a significant effect on the proportion of nights with no activity (F=17.56, df=4,45, p<0.001). Both far prairie and near prairie had significantly more nights with no activity than all the other habitats (Tukey post-hoc tests). Also, the far and near prairie were significantly different from each other. Period of the night did not have a significant effect (F=3.04, df=2,45, p=0.058). The overall model was also significant at 40kHz (F=12.44, df=14,45, p<0.001). Habitat (F=39.98, df=4,45, p<0.001) and period (F=3.46, df=2,45, p=0.040) both had a significant effect on the proportion of nights with no bat activity. Tukey post-hoc tests for habitat showed that the far prairie had significantly more nights with no activity than all the other habitats. Near prairie and springs were also significantly different from one another. Based on the lack of bats in the far prairie, I excluded it from all further analysis.

I used analysis of covariance to compare passes/minute on nights with bat activity. Variables in the model were habitat (river, coulees, near prairie, and springs), period,
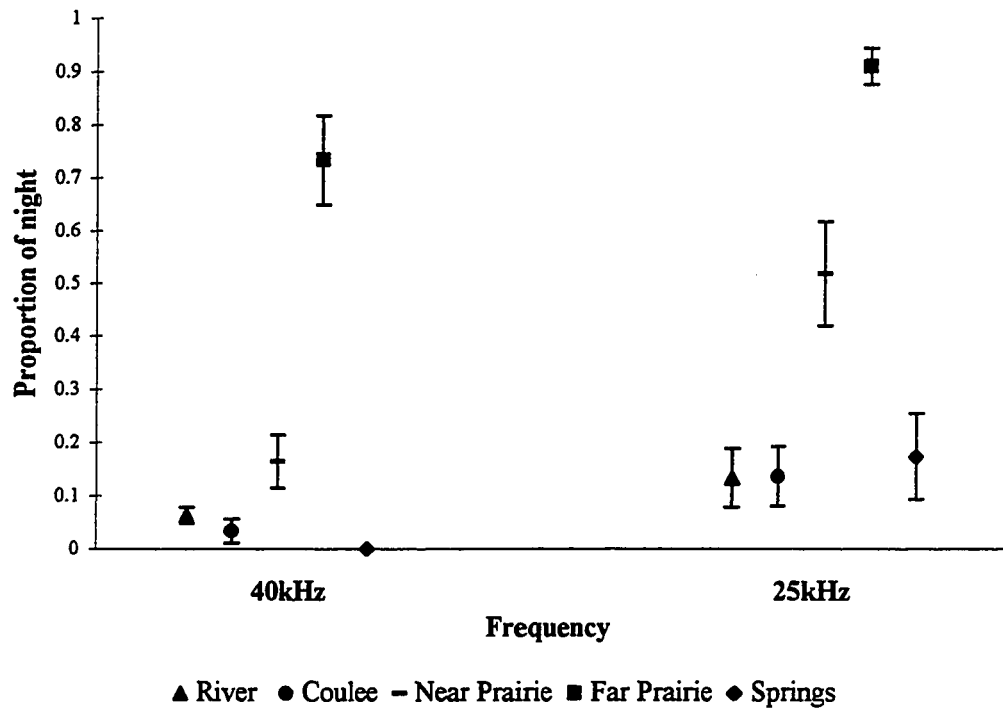
Fig. 4.1. Mean proportion of nights (±SE) with no bat activity along the South Saskatchewan River at 40kHz and 25kHz.

ambient temperature (as a covariate), sampling site (nested within habitat) and interactions.

At 40kHz, all data were included in the analysis (variances were homoscedastic with

removal of far prairie habitat), while at 25kHz only data from nights with activity were

analyzed. At 25kHz, the model was significant (F=3.03, df=17, 198, p<0.001; Fig 4.2).

Habitat had a significant effect on passes/minute (Table 4.2a and Fig. 4.2). Tukey post-hoc

comparisons showed that activity on the near prairie was significantly lower than all other

habitats (Table 4.2b). For sample sizes in all the following ANCOVA's see Table 4.6. The

different sampling sites nested within habitat had a significant effect on bat activity, while

ambient temperature did not (Fig 4.3). The model was also significant for *Myotis* bats at

40kHz (F= 5.22, df=18, 254, p<0.001; Table 4.2a). Passes/minute were significantly

affected by habitat (Fig 4.2). Tukey post-hoc tests revealed that passes/minute on the near

prairie were significantly lower than all other habitats, and there was significantly more

activity at the river than all habitats but springs (Table 4.2c). Ambient temperature had a

significant effect on bat activity (Fig 4.3). Passes/minute did not increase linearly with

temperature, but were greatest between 10-13°C.

I did not statistically analyze buzzes/minute because variances were heteroscedastic,

and removing nights with no bat activity unbalanced the data set. On the near prairie 68%

and 83% of nights had no bat foraging activity at 40kHz and 25kHz, respectively, compared

with 15% and 48% respectively at the river. Although the data were not normal,

buzzes/minute are presented in figure 4.4. with means and standard error which clearly

demonstrates the differences among habitats (Fig. 4.4). The trend for differences between

habitat was similar to that for passes/minute, with buzzes/minute at the river and springs

greater than at the near prairie and coulee.

Table 4.2a). ANCOVA table for passes/minute on nights with bat activity at 25kHz and 40kHz along the South Saskatchewan River. Insignificant interactions have been removed the ANCOVA model.

| Factors | Frequency | | | | | |
| | 25kHz | | | 40kHz | | |
	F	df	p	F	df	p
Habitat	9.31	3	*<0.001	21.86	3	*<0.001
Period	1.73	2	0.181	0.65	2	0.521
Temperature	0.00	1	0.965	6.63	1	*0.011
Sampling site{Habitat}	1.84	11	*0.050	1.70	12	0.067

Table 4.2b). Tukey post-hoc comparisons for habitat type comparing passes/minute at 25kHz.

	River	Coulee	Near Prairie
River	-----		
Coulees	NS	-----	
Near Prairie	*(p=0.001)	*(p=0.009)	-----
Springs	NS	NS	*(p=0.009)

Table 4.2c). Tukey post-hoc comparisons for habitat type comparing passes/minute at 40kHz.

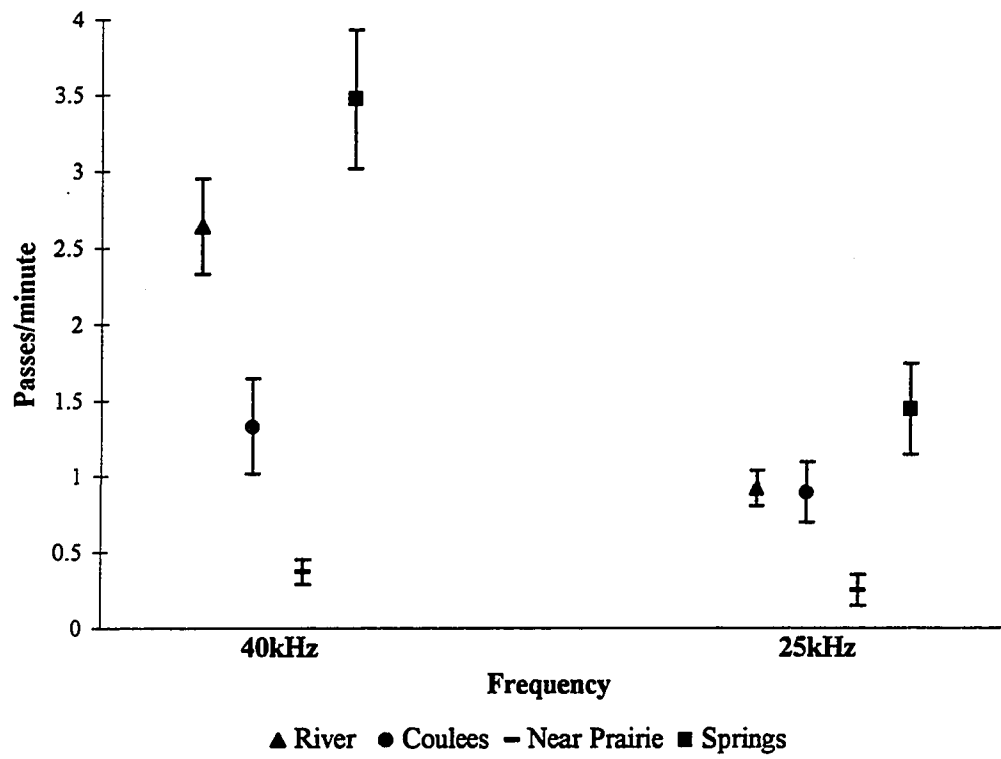|	River	Coulees	Near Prairie
River	-----		
Coulees	*(p=0.005)	-----	
Near Prairie	*(p<0.001)	*(p=0.016)	-----
Springs	NS	*(p<0.001)	*(p<0.001)

Fig. 4.2. Mean passes/minute (±SE) at 40kHz and 25kHz compared among habitats along the South Saskatchewan River.
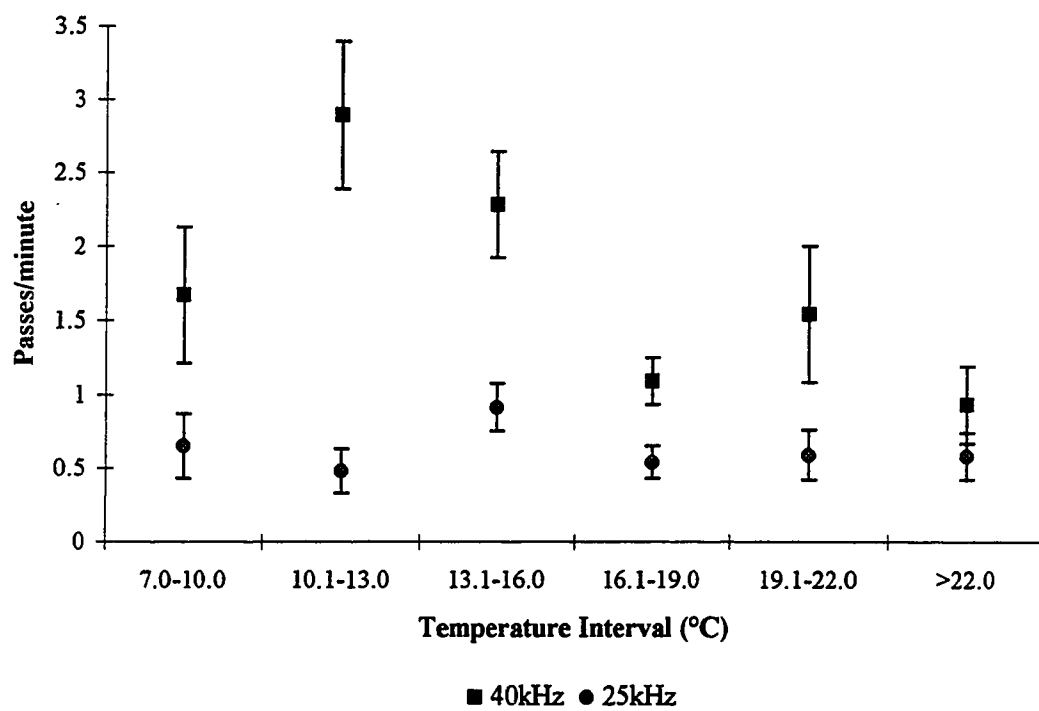
Fig. 4.3. The effect of ambient temperature on mean passes/minute (±SE) at 40kHz and 25kHz.
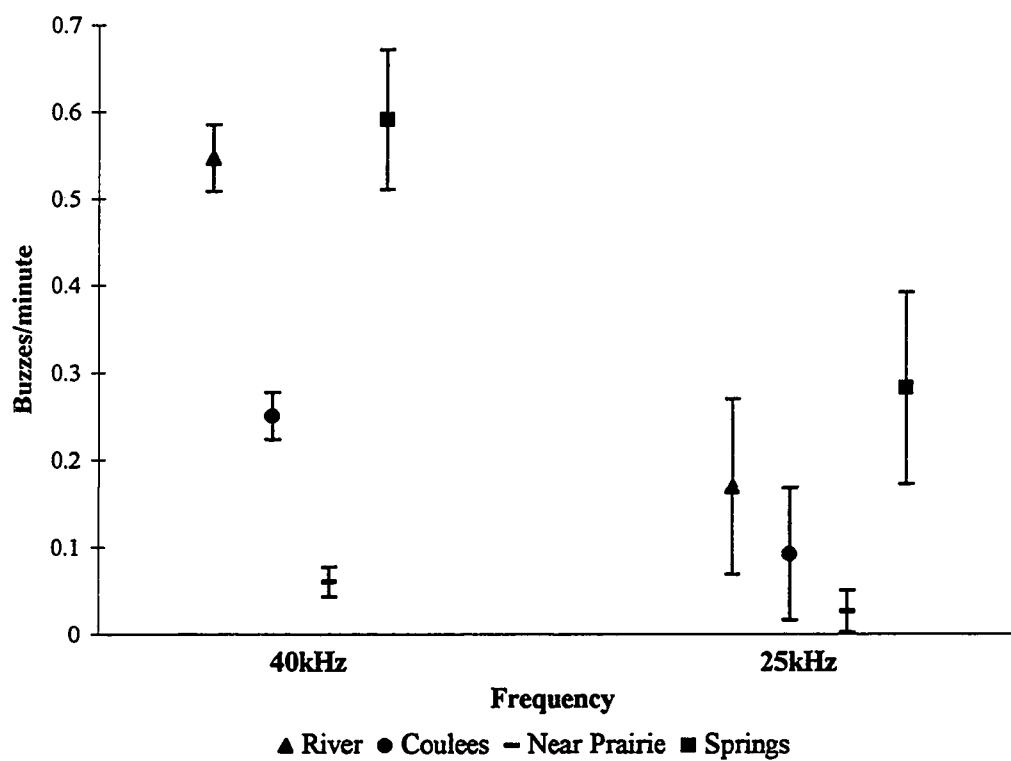
Fig 4.4. Mean buzzes/minute (±SE) at 40kHz and 25kHz compared among habitats along the South Saskatchewan River.

The Role of Riparian Trees

I used a two-factor repeated measures analysis of variance to compared the bat activity and bat foraging activity between treed river, and untreed river areas. Habitat and period of the night were the variables in the model, with sampling site as the repeated measure. At 40kHz, I used all data in the analysis, while only nights with activity were used at 25kHz (before removal of nights with no activity variances were heteroscedastic). For both monitoring frequencies there was no significant effect or interaction with sampling site. Habitat did not significantly affect bat activity at 25kHz for passes/minute (Table 4.3a and Fig 4.5a), but it did have a significant effect for buzzes/minute (Table 4.3b and Fig. 4.5b). At 40kHz, habitat had a significant effect on passes/minute (Table 4.3a and Fig 4.5a). For buzzes/minute at 40kHz, both habitat and period had a significant effect on bat activity. Both passes/minute and buzzes/minute were significantly higher at treed river habitat than untreed river.

Temporal Activity Patterns

Period had a significant effect on bat activity in only two of the above ANOVA's and ANCOVA's looking at bat activity across the whole summer. The lack of a significant effect for period of the night indicated that bats showed similar levels of activity all night long (both *Myotis* species and *E. fuscus*). However, the temporal activity pattern differed depending on the seasons (Fig. 4.6). I divided the summer into two seasons: 1) early summer (May/June), and 2) late summer (July/August). For this comparison, I only used activity from the river and springs, as the majority of activity was found in these habitats. In early summer, bats were most active at dusk and activity decreased throughout the night.

Table 4.3a). Repeated measures ANOVA table for passes/minute for the treed river verses untreed river comparison at 25kHz and 40kHz along the South Saskatchewan River (*=significant).

Factors	Frequency					
	25kHz			40kHz		
	F	df	p	F	df	p
Habitat	14.09	1	0.066	41.86	1	*0.001
Period	10.46	2	0.084	4.09	2	0.076
Sampling site (within subjects)	4.41	3	0.058	0.52	3	0.676

Table 4.3b). Repeated measures ANOVA table for buzzes/minute for the treed river verses untreed river comparison at 25kHz and 40kHz along the South Saskatchewan River (*=significant).

Factors	Frequency					
	25kHz			40kHz		
	F	df	p	F	df	p
Habitat	12.72	1	*0.038	22.33	1	*<0.003
Period	3.00	2	0.192	8.40	2	*0.018
Sampling site (within subjects)	0.03	2	0.969	0.29	3	0.830

Fig 4.5a)

Fig 4.5b)

■ Treed River ● Untreed River
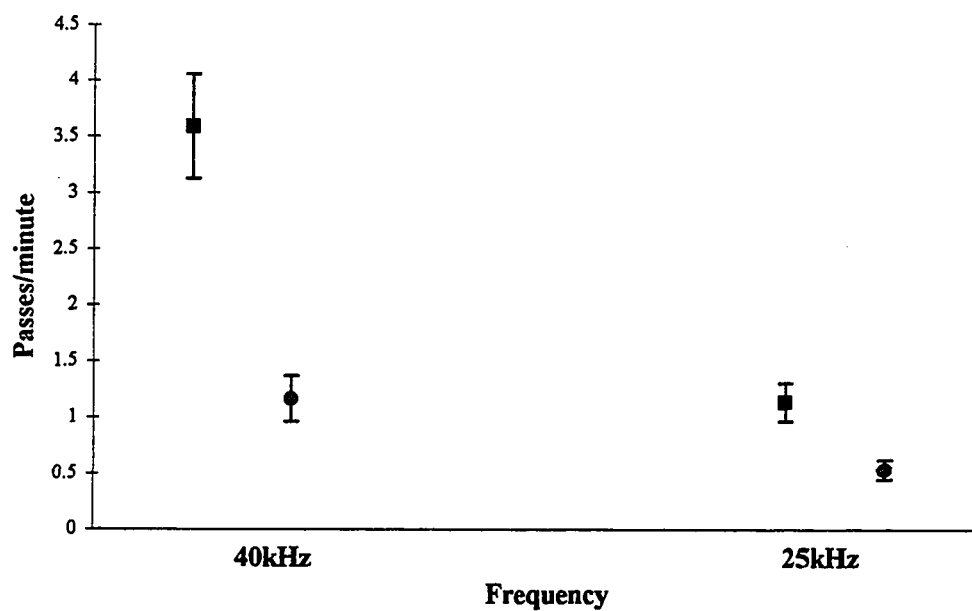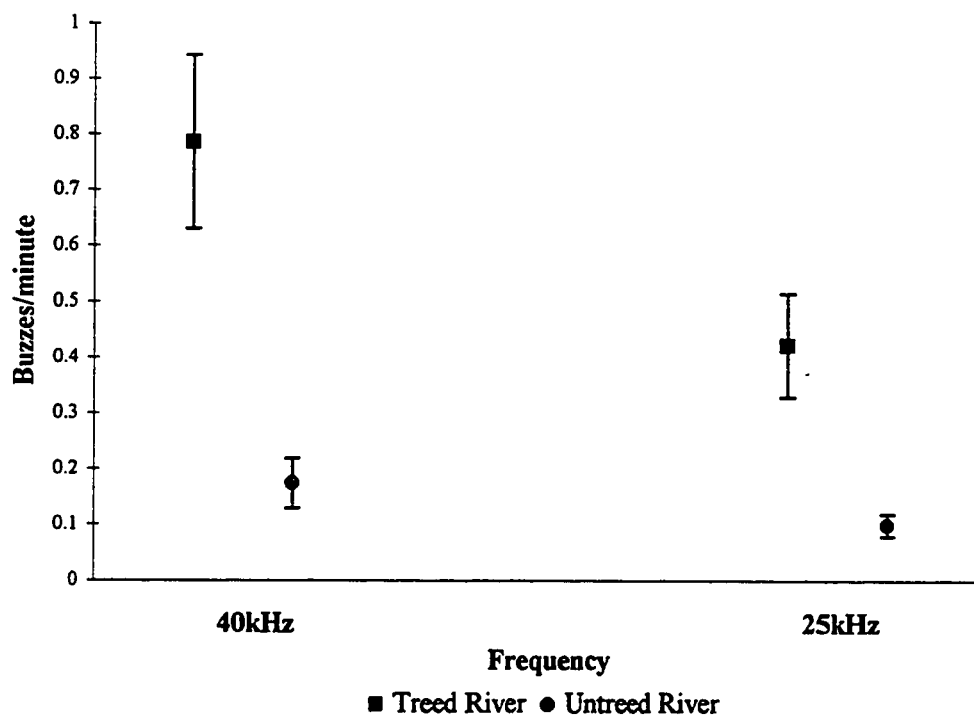
Fig. 4.5. Comparison of mean (±SE) bat activity at 40kHz and 25kHz between treed river and untreed river areas along the South Saskatchewan River, a) passes/minute, b) buzzes/minute.

Fig 4.6a)
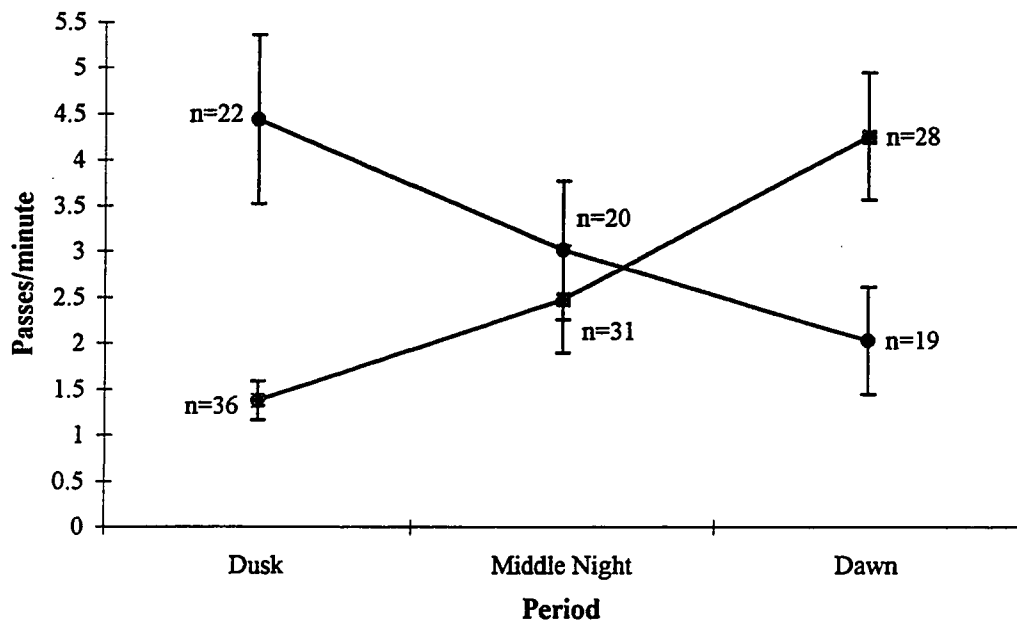
Fig 4.6b)
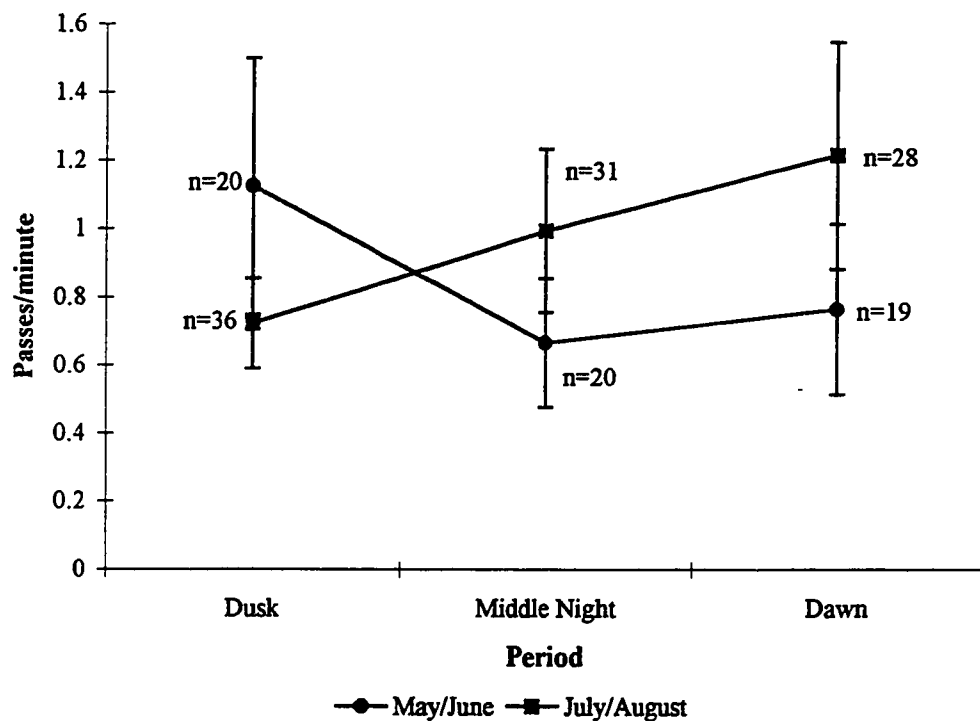
Fig. 4.6. Comparison of mean (±SE) bat activity (by period of the night) between seasons, a) 40kHz, b) 25kHz. Sample size (n) are the total number of monitoring bouts in each period

The reverse pattern occurred in late summer (Fig 4.6). I tested the pattern with analysis of covariance, comparing passes/minute, with period and season as main effects, and ambient temperature as the covariate. At 40kHz, the overall model was significant (F=6.30, df=7, 148, p<0.001). There was a significant interaction between season and period (F=14.25, df=2,148, p<0.001). Passes/minute changed differently over the three temporal periods depending on the season The interaction between season and ambient temperature also had a significant effect on bat activity (F=4.98, df=1,148, p=0.027). At 25kHz, the model was not significant (F=0.631, df=4, 149, p>0.50).

Insect Distribution

I sampled insects to determine if patterns of insect abundance corresponded to bat activity patterns. Insect captures on traps were relatively low (0-45 insects per trap). On average, less than 10 insects were captured per trap. I used analysis of covariance to determine factors influencing total insect biomass. Variables in the model were habitat (river, coulees, near prairie, springs), period, ambient temperature, and sampling site (nested within habitat). The model was significant (F=6.91, df=16, 268, p<0.001). Habitat had a significant effect on insect biomass (Table 4.4 and Fig 4.7). Post-hoc comparison showed that the river and springs had significantly higher insect biomass than the near prairies and the coulees. River and springs were not significantly different. Insect biomass was also significantly affected by sampling site (nested within habitat) and period. Post-hoc comparison for period revealed that the mean total insect biomass in the middle night period (5.31mg) was significantly different from that found in the dusk (18.60mg) or dawn (9.06mg) periods. Temperature also had a significant effect. Insect biomass tended to

Table 4.4. ANCOVA table for insect biomass along the South Saskatchewan River.

Factors	F	df	p
Habitat	20.58	3	*<0.001
Period	8.02	2	*<0.001
Temperature	5.62	1	*0.018
Sampling site{Habitat}	2.72	10	*0.003
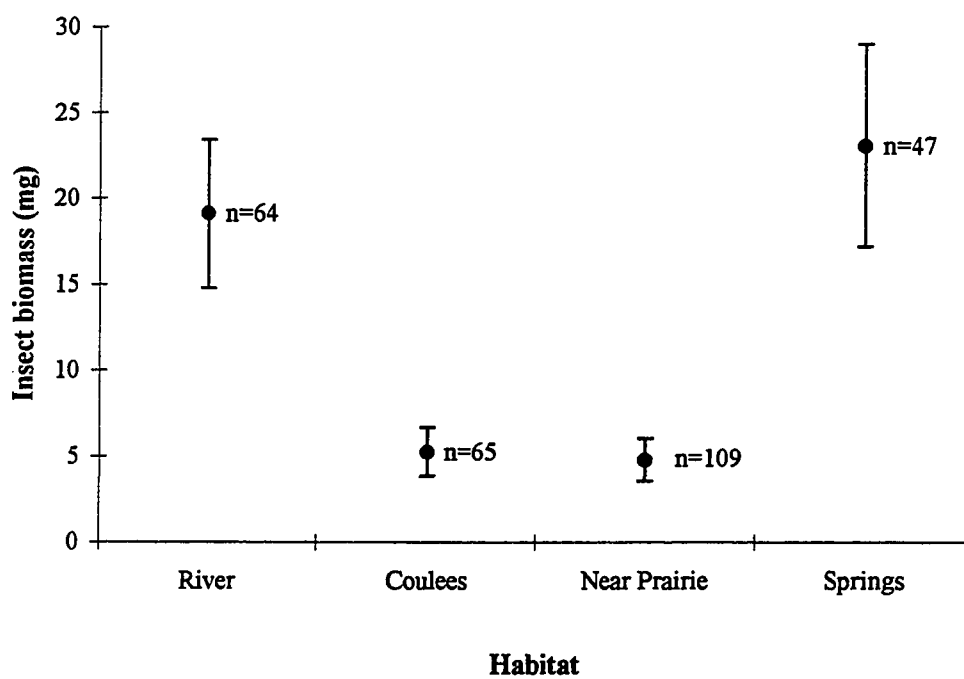
Fig. 4.7. Total mean (±SE) insect biomass (mg) compared between habitats along the South Saskatchewan River. Sample sizes (n) are the total number of traps placed in each habitat.

decrease with decreasing temperature.

The Role of Topography

To determine the effect topography plays in bat abundance, I compared bat activity

in areas with different river-valley topography. Only data from nights with bat activity was

used in the comparison. I compared passes/minute using a four-factor nested analysis of

covariance. Variables in the model were habitat (South Saskatchewan River steep coulees

(SSR steep coulees), South Saskatchewan low coulees (SSR low slopes), Red Deer River

low coulees (RDR low slopes), year, period, ambient temperature, and sampling site (nested

within habitat). For both frequencies, neither year nor ambient temperature had a significant

effect on bat activity. At 25kHz, the model was significant (F=3.81, df=12, 109, p=<0.001;

Fig 4.8) for *E. fuscus* activity. Bat activity was significantly affected by habitat (Table 4.5).

Tukey post-hoc tests showed that SSR steep coulees were significantly greater than RDR

low slopes, but not from SSR low slopes. Period also had a significant effect. The model

was also significant at 40kHz (F=8.28, df=12, 115, p<0.001; Fig 4.8). *Myotis* bat activity

was significantly affected by habitat (Table 4.5). Tukey post-hoc comparisons showed that

SSR steep coulees had significantly higher activity than either of the areas with low slope

development. The activity at the two low slope areas was not significantly different. Hoary

bat echolocation activity was greater along the Red Deer River (0.182 passes/minute)

compared with the South Saskatchewan River steep coulees (0.121 passes/minute). The

total number of passes in the two habitats were significantly different (χ^2=25.51, df=1,

p<0.001), where expected values were calculated based on the proportion of the total time

Table 4.5. ANCOVA table for passes/minute compared between areas with different river-valley topography at 25kHz and 40kHz (*=significant).

Factors	Frequency					
	25kHz			40kHz		
	F	df	p	F	df	p
Habitat	8.93	2	*<0.001	43.68	2	*<0.001
Period	6.21	2	*0.003	0.26	2	0.773
Year	0.97	1	0.327	1.79	1	0.183
Temperature	0.34	1	0.564	0.33	1	0.567
Sampling site{Habitat}	2.35	6	*0.036	1.56	6	0.165
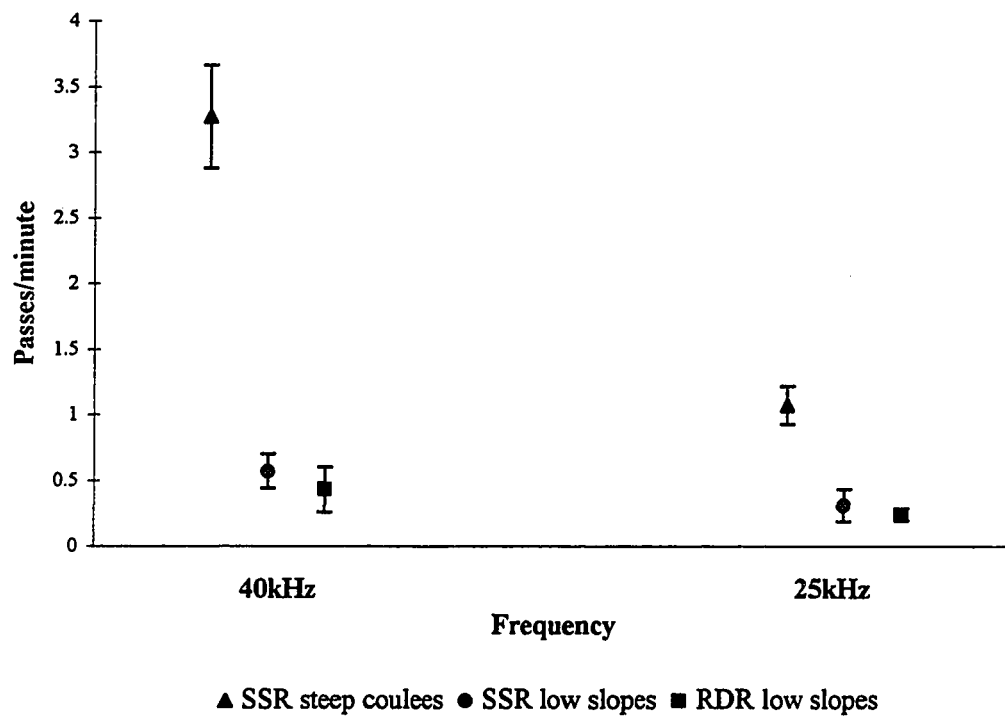
Fig. 4.8. Mean bat passes/minute (±SE) compared between areas with different river-valley slope topography for 40kHz and 25kHz.

Table 4.6 Number of monitoring bouts and total monitoring time for data used in all ANCOVA's for each habitat at both 40kHz and 25kHz along the South Saskatchewan River.

Habitat	Frequency			
	40kHz		25kHz	
	N	Total monitoring time (minutes)	N	Total monitoring time (minutes)
River	120	3863	108	3515
Coulee	62	2075	54	1901
Near Prairie	55	1827	25	965
Springs	36	1434	29	1213
Treed River	73	2544	68	2372
Untreed River	47	1319	40	1143
SSR steep coulees	92	3441	84	3025
SSR low slopes	14	568	13	650
RDR low slopes	25	1401	26	1363

spent monitoring in each habitat. Virtually no buzzes were heard along either low slope areas, so no analysis of buzzes/minute was performed.

DISCUSSION

The Importance of the Riparian Zone

My results suggest that the riparian zone plays a vital role in the foraging ecology of prairie bats in south-eastern Alberta. In the absence of human development, the presence of bats is both dependent upon and centred around the river. Bat activity decreased as distance from the river increased, and greater than a couple kilometres from the river, virtually no bats were heard. On a small localized scale, the movements and habitat-use exhibited along the river on a given night by a foraging bat is related to spatial patterns of insect density. Both bat activity and insect abundance was greatest along the river and over springs. In comparison, bat activity and insect biomass were significantly lower on the grasslands. Wilkinson and Barclay (1997) found similar results in southeastern Alberta near Medicine Hat, tracking foraging big brown bats significantly more often to the river valley than the prairies. The grasslands lack any features to concentrate insects, and insect density is generally low in exposed situations (Racey and Swift, 1985), thus bats are likely only present on the prairies when traveling to springs, or possibly to buildings, rarely stopping to forage.

The situation is very different along the river. The greatest vertical substrate complexity exists along the river (the presence of vegetation and slopes), and high insect abundance is often found near water (Bradbury and Vehremcamp, 1976; Barclay, 1985; Racey and Swift, 1985). The greater insect abundance in this habitat and springs followed expectations, especially as Diptera composed the majority of insect captures, and the larvae

of many Diptera are aquatic (Borror and DeLong, 1971). The river also seemed to boast a high Coleoptera abundance; greater than three times the number of beetles were captured along the river compared with the other habitats.

The river as a whole represents potential foraging habitat, but the majority of bat activity along the river was restricted to scattered trees and small riparian forests. The riparian trees likely provide the greatest potential habitat for insects, supplying shelter from the wind and rain, and habitat for insects to feed and reproduce. Shelter from wind is an important factor influencing the foraging behaviour of bats, by controlling the distribution of insects (Fenton and Morris, 1976; Barclay, 1991). Studies have found that some species rarely forage away from riparian trees (Laval *et al.*, 1977; Racey and Swift, 1985). Riparian forests are especially important to *M. ciliolabrum* and *M. evotis*, based on the combination of echolocation activity, captures, and visual observations. Both *Myotis* species are small, slow, and maneuverable fliers, well suited to cluttered habitats (Norberg and Rayner, 1987) such as amongst riparian trees. Similar to observations by Woodsworth (1981), I observed *M. ciliolabrum* following a foraging "beat" along the margin of the trees. Radio-tagged *M. evotis* in my study area spend almost their entire foraging bout over and within the trees (B. Chruszcz, pers. comm). Elsewhere, *M. evotis* also commonly forages within trees (Barclay, 1991), and as it is a gleaner (Faure and Barclay, 1992), trees likely provide the best foraging substrate to pick up non-volant insects. The insect traps used in this study were passive, and are not effective at capturing larger moths, and beetles. However, among the riparian trees, many Lepidopterans, especially sphinx moths (Lepidoptera: Sphingidae), and June beetles (Coleoptera: Scarabidae) caught in mist nets, suggesting that these insects were abundant there.

My study demonstrated that both the river and springs have high activity of bats. However, springs may be especially critical habitat. I believe that aside from the isolated clusters of riparian trees, springs are one of the few areas on the prairies with consistent concentrations of nocturnal flying insects. In fact, springs may offer a slightly different insect fauna, as bats can trawl insects directly from the water's surface, a foraging strategy commonly used by *M. lucifugus* (Barclay, 1991; van Zyll de Jong, 1985). High bat activity is often closely associated with standing water (Swift and Racey, 1983). Foraging, and especially trawling, may be difficult over the river as the South Saskatchewan has a relatively fast, and strong current. Acoustic detection of prey over turbulent water is more difficult due to ultrasonic background noise created by flowing water, which causes greater clutter and more echoes (von Frenckell and Barclay, 1987).

Springs also likely provide an important source of water for drinking. For the reasons mentioned above, dipping to drink over standing water is likely much easier than over the river. Evapourative water loss likely occurs in prairie bats, especially in the height of summer, as bats remain in roosts >15 hour/day without water, in ambient temperatures which can exceed 35°C. In the arid southwest, bats are commonly captured over water stock tanks, apparently drinking (Chung-MacCoubrey, 1996) Water may be especially important for lactating females. Availability of free water may in fact limit bat abundance in very dry, hot areas (Chung-MacCoubrey, 1996).

The coulees were used by foraging bats to a greater extent than the prairies, but the activity patterns exhibited by *Myotis* species and *E. fuscus* were different. For *Myotis* species the river and springs were the major foraging areas. Bat activity in the coulees at 40kHz (*Myotis* spp.) was far lower than the river and springs. The pattern was different at

25kHz. Activity in the coulees for *E. fuscus* was similar to that along the river. This may represent spatial partitioning of resources as several studies have indicated that bats partition food resources by using different foraging habitats (Woodsworths, 1981; Swift and Racey, 1983). In the coulees, both captures and echolocation activity indicated that big brown bats are frequently present throughout the night, while aside from emergence, and returning to their roosts at dawn, *Myotis* species rarely seem to be present in the coulees. Dead-end side passages with high surrounding walls in the coulees and cliffs may provide shelter from the wind where insects congregate. The use of more open, less cluttered habitats such as the coulees by *E. fuscus* can be explained by the fast, less maneuverable flight of *E. fuscus*, compared with the more maneuverable flight of the *Myotis* species (Norberg and Rayner, 1987).

Temporal Activity Patterns

The pattern of bat activity over the night also appears to mirror the temporal pattern of insect abundance. Along the South Saskatchewan River, bats were active all night. Many species are active throughout the night, emerging for several foraging bouts, interrupted by periods of night roosting (O'Farrell and Bradley, 1970; Bell, 1980; Swift and Racey, 1983; Barclay, 1985; Brigham, 1991). However, typically foraging activity is not equal throughout the night. The greatest activity is usually in the first 2-3 hours after sunset (O'Farrell and Bradley, 1970; Anthony and Kunz, 1977; Bell, 1980; Fenton and Rautenbach, 1986), corresponding with the greatest insect density (Racey and Swift, 1985; Barclay, 1985; Barclay, 1991). Some studies have also shown smaller sunrise activity peaks (O'Shea and Vaughan, 1977; Barclay, 1982; Racey and Swift, 1985; Maier, 1992; Rydell *et al.*,

1994). Bat activity in May and June follows both general pattern of bat activity, and insect abundance. Throughout the summer along the South Saskatchewan, insect biomass is greatest just after sunset, with a second smaller peak towards sunrise. In July and August, the bat activity changes, with activity increasing throughout the night, and peaking towards sunrise. In my study area, reproductive females begin to lactate in early July, and the constraints of lactation may account for the change in bat foraging patterns. Racey and Swift (1985) found that *Pipistrellus pipistrellus* foraged during the dawn insect peak when females were lactating, but not during pregnancy. In July in my study area the first foraging bout at dusk may be short, so females can return to suckle their young, compared with early summer when females are not lactating. To compensate for the short initial foraging bout, females may take greater advantage of the smaller, but temporally predictable insect peak at dawn. Dawn temperature is also higher on average, in July and August, and a high proportion of the bat community appears to emerge again for the sunrise peak.

The Role of Topography

The larger scale distribution of bat populations along prairie rivers seems to depend on topography and the abundance of potential roosting habitat. The topography of the river valley had a significant impact on bat activity and abundance. All bats in my study area roosted in rock crevices within the cliffs and coulees (see Chapter 3) and high bat activity was linked to areas where the river valley is steep and rugged. These areas have plenty of crevices for roosting. The Red Deer River in my study area, and some areas along the South Saskatchewan, have different erosion patterns, with broad flood plains and smooth, low slopes, lacking crevices. Trees, however, are plentiful in these areas. Bat activity in

such areas was low, suggesting that the lack of potential rock roosts limits the presence of bats. Humphrey (1975) suggested that the abundance and distribution of nearctic bats is determined largely by the availability of suitable roosts. The lack of bat activity along the Red Deer River, despite the large cottonwood forests, suggests that cottonwoods do not make good roost trees. The bark on dead, and dying cottonwoods quickly sloughs off (pers. observ.). Interestingly, the pattern of hoary bat activity is reversed. Hoary bats had the highest activity along the Red Deer River. This species is a foliage rooster (van Zyll de Jong, 1985), and the relatively large riparian forests likely provide ample roosting habitat. Along, the South Saskatchewan River, the limited trees almost certainly limits the abundance of *L. cinereus*.

On the prairies in south-eastern Alberta, suitable roosts appear to be prevalent within small areas, but bat populations may have scattered, and potentially disjunct distributions along the length of the river. Dinosaur Provincial Park along the Red Deer River may be another example of a disjunct population. There is high bat activity in the area, and the topography and species composition in the park is similar to my study area (Chruszcz and Holloway, unpublished data). However, the topography of the river valley outside the park on either side is similar to that along the Red Deer River in my study area. At least in the summer months, bats may exist as scattered populations. This may be especially true for the *Myotis* species, which even when foraging do not seem to move greater than a couple of kilometres from their roost area (see Chapter 4).

CHAPTER 5. Conclusions and Conservation Implications

The results of my study emphasize the importance the riparian zone plays in both the roosting and foraging ecology of bats in south-eastern Alberta. The whole river valley is important to bats. The coulees and steep cliffs of the river valley are critical roosting habitat, and to a lesser extent the coulees are used for foraging, especially by *E. fuscus*. The riparian cottonwoods and prairie springs are important foraging habitat as the greatest insect density exists there. Bats appear to be most abundant in steep and craggy areas along the river valley. Within these small localized areas with steep topography, I believe that bats are not roost limited. However, on the broader scale, the distribution of bats along prairie rivers may be disjunct, and potentially roost limited. The summer populations may be isolated from each other. Bats appear to remain within these small areas for the summer, and may return each year. Banded western long-eared bats were recaptured a year later in the same spot along the river where they were first captured (B. Chruszcz pers. comm.). There would be no reason to move to another area several kilometres down the river if roosting and foraging habitat is not limited where they are. If individuals do return to their summer areas, and possibly natal areas, then protection of bat summer roosting habitat is especially critical.

In comparison with areas of the river valley with steep topography, bats appear to be far less abundant in areas with flat, smooth topography. This has favourable implications in terms of conserving bat roosting habitat. The steep badland areas along the river have low human population density as they are not conducive to agriculture or ranching activities. Along the South Saskatchewan, a few ranchers pasture their cattle infrequently within the

coulees, but the cattle can only get down to relatively flat areas which are removed from bat roosts. In contrast, the broad flood plains along the Red Deer River are heavily cultivated, and a lot of cattle ranching is present.

Maintenance of prairie bat populations is also dependent on protection of foraging habitat. The river and riparian trees are critical foraging habitat for prairie bats, and this result has significant implications. Within this semi-arid habitat, trees are so scarce that every tree or small stand of trees is represented on topographical maps. There are a few small groves of trees up on the prairie, in sinkholes, but the majority of the trees are along the river. On the western prairies cottonwoods (*Populus* spp.) are the major and often the only tree species in the ecosystem (Rood and Mahoney, 1991). They are one of the only species able to successfully withstand the extreme conditions: dry, hot summers (reaching >40°C), cold winters (>-30°C), and high winds (Rood and Mahoney, 1991). Within the prairies, riparian areas are recognized as centres of biodiversity for many animal groups such as birds (Savoy, 1991), insects, large mammals and reptiles (Rhodes, 1991), and now bats. For example, up to 75% of bird species along prairie rivers were found to breed exclusively in the riparian forests in southern Alberta (Savoy, 1991). However, several recent studies have raised concern as a reduction of cottonwood density along several rivers in Canada and the United States have been noted after damming (Bradley and Smith, 1986; Rood and Mahoney, 1990, 1991).

Maintenance of cottonwoods depends on periodic flooding (Bradley and Smith, 1986; Rood and Mahoney, 1990). Damming stops or reduces flooding, altering sedimentation patterns and meander rates and lowering the water table. Cottonwoods are phreatophytes, which obtain water directly from the water table and their root systems must

maintain adequate contact with the water table (Rood and Mahoney, 1990). Seedlings are

drought intolerant, but tolerant to flooding. The periodic flooding of prairie rivers raises the

water table, such that seedling root growth can keep up with the drying of the water table

following spring floods. Also cottonwoods are pioneer species, establishing on barren sites.

The size and area of prairie rivers are dynamic, with flooding and flow reduction shifting the

river bed, and creating new point bars and eroding older bars. Age-distribution studies of

riparian cottonwoods along dammed rivers show that there has not been enough

regeneration and reestablishment in the last 20 years to maintain the cottonwood stands

present now (Cordes, 1991). Human agricultural activity also compounds the effect of

dams: cattle trample seeds and graze preferentially on young seedlings, preventing forest

replenishment (Rood and Mahoney, 1990).

My results also suggest that prairie springs are critical foraging habitat for bats.

Since the 1970's the quality and quantity of standing water has declined significantly, largely

due to agricultural expansion (Usher and Johnson, 1993). Preservation of prairie springs

and potholes has received a lot attention in recent years, largely in regard to maintenance of

waterfowl populations. Much of the research has focused on the effects of the

intensification of agriculture, and the associated use of pesticides (Usher and Johnson,

1993). One of the most significant sources of insecticide is the spray program for control of

grasshopper populations (Usher and Johnson, 1993). Runoff or ground water seepage of

insecticide into springs and ponds directly reduces aquatic invertebrate populations, and

food for bats. Studies on insecticide contamination have shown 83-99% decreases in

chironomid larvae biomass, 100% mortality of mayfly nymphs and 90% mortality of

freshwater shrimp (Forsyth, 1993). Herbicides are another concern, as they can affect

invertebrate populations both directly and indirectly. Some herbicides are toxic to invertebrates, interfering with steroid hormone levels and gonad development (Forsyth, 1996). Indirectly, herbicides reduce insect abundance by affecting non-target aquatic vegetation, which is detrimental to aquatic invertebrates that depend upon these plants for food or substrates (Forsyth, 1996). Reductions of 90% in algae productivity has been found with some herbicides (Forsyth, 1993). Along the South Saskatchewan River there is very little agriculture close to the river, but this is not the case in many other agricultural areas, and this study emphasizes the significance of springs and standing water to prairie bats.

My study indicated that in south-eastern Alberta and likely elsewhere in the prairies, river valleys, riparian trees, and prairie springs are important habitat to bats. At present, preservation of bat foraging habitat is critical to the continued presence of prairie bat populations. Currently, the South Saskatchewan River is not dammed in eastern Alberta, but a dam has been proposed in Medicine Hat, downstream of CFB Suffield. In this semi-arid prairie area, trees are naturally scarce, damming the river likely would make the continued regeneration of cottonwood impossible. Evidence is mounting regarding the importance of prairie rivers and riparian trees to wildlife, and hopefully managers will consider this in any future plans to alter prairie riparian habitats.

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