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The influence of reproduction on foraging  
behaviour and diet of big brown bats  
(Eptesicus fuscus) in southeastern Alberta

by

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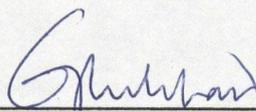
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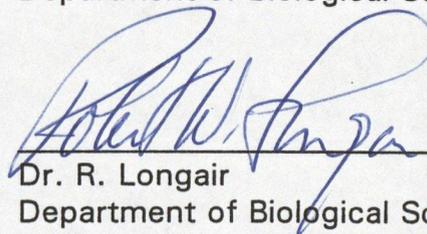
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The influence of reproduction on foraging behaviour and diet of big brown bats (Eptesicus fuscus) in southeastern Alberta" submitted by Lisa C. Wilkinson in partial fulfilment of the requirements for the degree of Master of Science.



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## ABSTRACT

During reproduction, energetic and nutritional demands escalate for female mammals, and can result in foraging behaviour and diet that differ from that of males. An investigation into intersexual feeding habits of big brown bats (Eptesicus fuscus) revealed different feeding strategies. Female bats exhibited site fidelity and appeared to dominate the most profitable feeding site close to the colonies, probably through territorial behaviour. Both sexes probably fed opportunistically, having relatively similar diets, although females may be selective when prey are abundant. The currency for which females foraged may not simply be energy; long foraging times indicated that they may have been trying to meet other dietary requirements, such as calcium, which is critical to support the large juvenile skeleton. Males foraged for similar lengths of time as females, likely due to the lower quality habitat in which they often foraged. Temperature had a strong influence on foraging time and behaviour, more so for males than females.

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## CHAPTER 1. General Introduction

### INTRODUCTION

Foraging behaviour and diet are influenced by a complex array of intrinsic and extrinsic factors. Intrinsic factors, such as age and sex, as well as morphological characteristics, can have profound effects on feeding, both in terms of dietary requirements and foraging abilities (age: Sullivan 1988, Weathers and Sullivan 1991; sex: Belovsky 1978, Clutton-Brock *et al.* 1982).

Obtaining dietary requirements is constrained by, and must be balanced with, other activities, such as territory defence, predator avoidance, mate attraction, and nest building (Krebs 1973; Davies 1977a; Stephens and Krebs 1986). Certain times of the life cycle may alter the required complement of energy and nutrients, thereby influencing diet and foraging behaviour. Specific activities associated with these times may constrain, or compete with, food acquisition. For example, energy and nutrient demands escalate for female mammals during pregnancy and lactation (Gittleman and Thompson 1988). These demands can be especially difficult to fulfil for those species lacking biparental care of young. Thus, reproduction presents an interesting opportunity to evaluate currencies and constraints, and how they influence foraging strategies.

To understand the dietary demands of reproduction, it is instructive to compare females to nonreproductive individuals. Males do not always experience similar reproductive demands as females, particularly if males do not contribute parental care, compete for mates, or engage in mating displays. Intersexual differences in foraging have often been neglected, and deserve more attention. This is the case for foraging studies of insectivorous bats. The paucity of this comparative information is largely a result of the difficulty associated with studying male bats, which are typically solitary, even in otherwise colonial species (Barbour and Davis 1969). Female feeding habits have been well documented, particularly in relation to reproduction and the effects of changing energetic and nutritional demands throughout pregnancy and lactation (e.g. Racey and Swift 1985; Barclay 1989; Rydell 1989). The limitations of echolocation and the restriction to one type of prey, insects, may make fulfilment of dietary demands challenging for female insectivorous bats.

Flight also imposes constraints not experienced by other mammals. A prerequisite for flight is a suitably developed skeleton, apparently necessitating that female bats nurse their young until they are within, on average, 91.2% of adult skeletal size, and 70.9% of adult mass (Barclay 1994). This is considerably larger than other small mammals, which are typically weaned at 37% of adult mass (Millar 1977). For this reason, female bats must supply not only a tremendous amount of energy, but also

calcium, to support the large juvenile skeleton.

Optimal foraging theory has long been the backbone of foraging models, which are based on the premise that animals forage for long-term average-rate maximization of a currency (Stephens and Krebs 1986). Traditionally, net energy gain over a unit of time has been considered as the currency on which maximization is modelled (MacArthur and Pianka 1966; Pulliam 1975; Pyke *et al.* 1977; Werner and Mittelbach 1981; Stephens and Krebs 1986).

Although the focus on energetic intake continues to dominate many investigations of feeding behaviour, models have begun to embrace other currencies, such as essential nutrients. The concept of complementary resources is not new, but has typically been restricted to studies of herbivores (e.g. Freeland and Janzen 1974; Westoby 1974; Dearing and Schall 1992). It addresses the fact that there needs to be a balance of nutrients as well as a minimum amount of energy (Westoby 1977; Rapport 1980). In addition, predator food preferences tend to be partial, not absolute (Pyke *et al.* 1977). It is essential to recognize important currencies to understand diet choice and resultant foraging behaviours.

The currencies for which male and female bats forage may be different, and likely operate under different constraints. There are several factors which may influence diet choice and foraging behaviour in reproductive female bats. The purpose of my study was to identify the

ways in which reproductive demands are manifested in foraging behaviour and diet of female bats. The influence of reproductive demands can best be understood by comparing feeding behaviours between male and female bats. Bat colonies at my study site are unusual in that they contain small populations of males. Initially, I examined various aspects of foraging behaviour, primarily determining foraging locations and length of foraging bouts. After establishing intersexual differences in foraging behaviour, I determined diets of male and female bats, and related dietary differences to foraging differences. Finally, I considered the energetic and nutritional content of prey, and the possible role of calcium in determining feeding behaviour, based on nutritional analysis of prey, and implications from foraging and diet analyses.

## STUDY SPECIES

The big brown bat, Eptesicus fuscus, is ubiquitous throughout most of North and Central America (Barbour and Davis 1969; Kurta and Baker 1990). It is the second largest bat in Alberta, weighing 15-24 g (Barbour and Davis 1969), most typically weighing approximately 20 g (van Zyll de Jong 1985). Females tend to be larger than males, with a significantly longer forearm.

Eptesicus fuscus is a generalist in terms of foraging habitat, and will

sometimes forage at considerable heights, up to 50 m above the ground (Whitaker et al. 1977; Caire et al. 1984). Big browns are known to feed on a variety of insect taxa, although beetles (Coleoptera) are typically a major component of the diet (Black 1972; Freeman 1981; Brigham 1990; Brigham and Saunders 1990; Kurta and Baker 1990).

Little is known about the breeding habits of these bats, although they probably mate in the autumn, prior to entering hibernation (Phillips 1966). Knowledge of hibernation sites is also lacking; some bats overwinter in buildings while others likely exploit caves and abandoned mines, and may travel moderate distances, up to 80 km, to reach these sites (Mills et al. 1975). Some hibernation sites have been identified in central Alberta (Schowalter 1980). Maternity colonies are usually located in buildings (Barbour and Davis 1969), although trees and rock crevices are also used (Brigham 1988).

Big brown bats return to maternity colonies in spring; specific timing is weather dependent. Gestation lasts approximately 60 days, but lasts longer if poor environmental conditions force females to use torpor (Kurta and Baker 1990). In eastern North America, E. fuscus usually produce twins (Barbour and Davis 1969). However, in Alberta, single pups are most common, with twins being produced only 15% of the time (Scholwalter and Gunson 1979). At birth, pups weigh approximately 3 g, which is equivalent to about 20% of a female's postpartum mass (Kurta and Baker 1990).

Females lactate from 32 to 40 days (Kunz 1974), and pups begin to fly before they are fully weaned, at 18 to 35 days of age (Kurta and Baker 1990). Females nurse newly volant pups to supplement their poor foraging success. By the time pups begin flying, their forearm length is comparable to that of adults (Kurta and Baker 1990; Holroyd 1993).

Male insectivorous bats are typically solitary, so little is known about their behaviour. Occasionally, males will roost in maternity colonies (Barbour and Davis 1969). Male E. fuscus are often found in the same areas as females during the summer, and probably use the same hibernation sites. Patterns of prehibernation fat deposition differ between the sexes, beginning one month earlier in females than in males (Pistole 1989). The onset of fat storage coincides with the cessation of lactation for females, and with the completion of spermatogenesis in males, at which time the mating season begins (Pistole 1989).

Hibernation can be a critical time for bats, insufficient fat stores decrease chances of survival, and may be largely responsible for juvenile mortality (Kunz 1987; Brigham 1987; Thomas et al. 1990). Bats with low fat stores may become active for brief periods in an attempt to find food (Brigham 1987). The condition in which bats leave hibernation influences their ability to reproduce; females may abort or resorb fetuses if they are not in adequate physical condition (Racey 1982). This occurrence is exacerbated if the ambient temperature remains cold in spring.

Eptesicus fuscus appears to conform to the general life history pattern of vespertilionid bats, producing many litters over a long time. The longest reported life span is 19 years (eastern North America; Paradiso and Greenhall 1967), and a bat at my study site was at least 18 years old in 1993 (it was banded as an adult in 1976).

## STUDY SITE

The study site was located in and around Medicine Hat, in southeastern Alberta (50°02'N, 110°40'W). The study area (to the farthest limits of radio-telemetry coverage) was approximately 120 km<sup>2</sup>. Medicine Hat is bordered by prairie and agricultural land, with the South Saskatchewan River running through the city, providing riparian habitat (see Figure 1.1). Cottonwoods (Populus sp.) are the dominant tree species along the river and in city parks.

Two maternity colonies of big brown bats were located in the attics of 80 year old red-brick school buildings. The schools are located in a residential area, less than one kilometre apart and approximately one kilometre from the river (see Figure 1.1). The Elm Street School (ESS) contained the largest colony, numbering between 100-120 adults. The attic is large with a variety of roosting locations, ranging from 2-7 m from the floor. The other colony was located in Montreal Street School (MSS) and

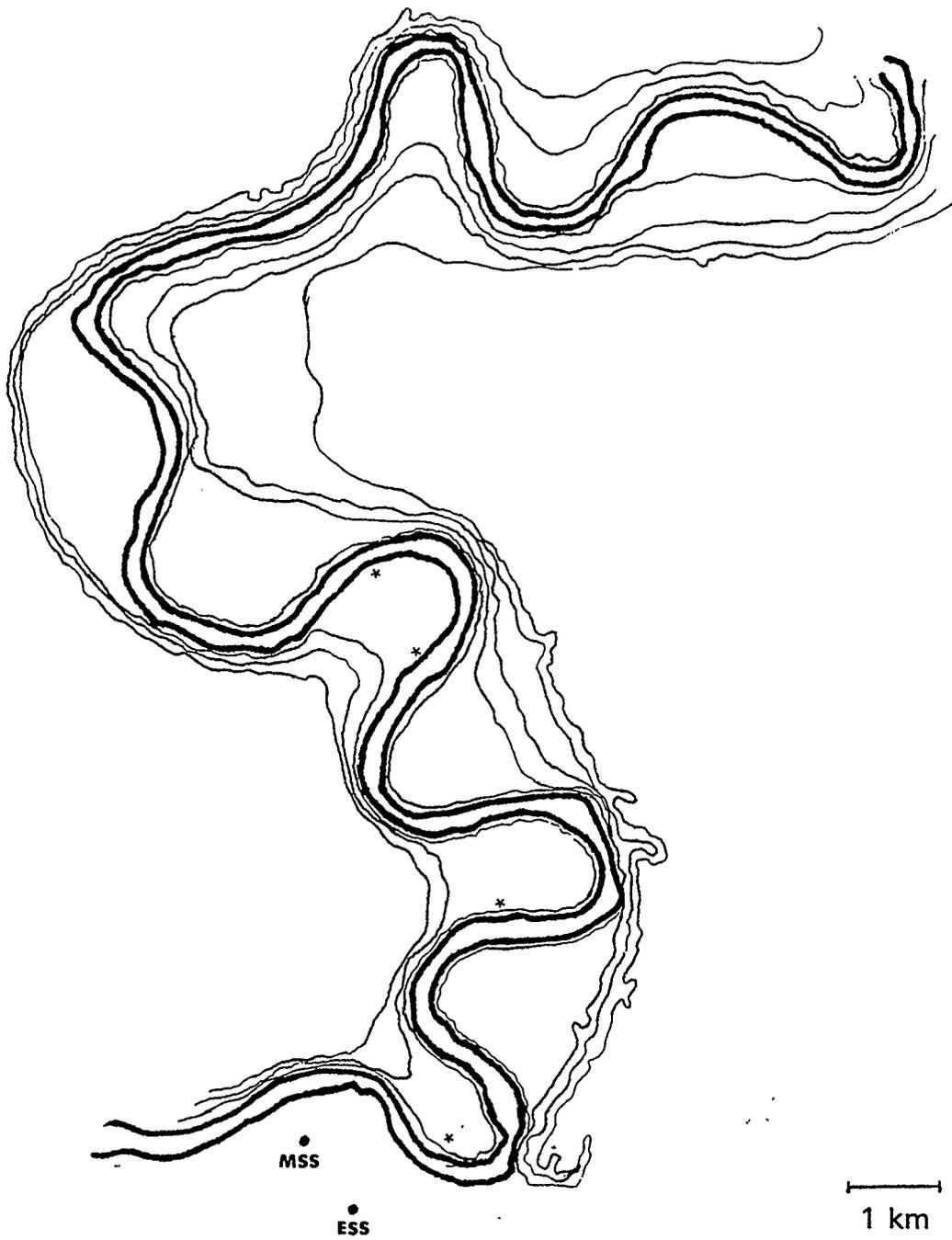


Figure 1.1. Map of study area, Medicine Hat, Alberta.

- Maternity colonies
- \* Insect traps

contained approximately 80 bats. The attic is smaller, with most roosting areas below 4-5 m.

Colonies were composed predominantly of females and their young, with a small population of males in each. Females demonstrate strong fidelity to their colonies, whereas males often roost away from the schools, in houses or cliffs (Hamilton and Barclay 1994). Throughout five years of research at these colonies, only one male was captured at both colony sites, indicating that males, to a lesser extent, also exhibit roost fidelity (Holroyd 1993; Hamilton, pers. comm.; pers. obs.).

Bats typically begin returning to the schools from hibernation sites in early May, depending on the weather. Parturition dates also vary with weather conditions, typically occurring between the second and third weeks of June (Holroyd 1993). Adults begin to use alternative roosts once pups are completely independent, and seem to leave the vicinity entirely.

## GENERAL METHODS

My study was conducted over two years, from June 1 to August 15 in 1992, and from May 10 to August 16 in 1993. Bats were captured with 9 m monofilament mist nets, set 7-8 m in front of roost exits, at a height of 8-9 m. Once removed from the net, bats were placed in cloth bags for a minimum of one hour to allow emptying of the digestive tract. Bats were

sexed and reproductive condition was assessed for females. Pregnancy was indicated by pronounced abdominal swelling, typically on the right side of the animal. Milk expression, by palpation of nipples, was indicative of lactation, while swollen nipples surrounded by worn fur and the inability to express milk indicated postlactation (Racey 1974). Male bats were also classified as being in the periods of pregnancy, lactation or postlactation in accordance with their capture dates. This facilitated intersexual comparisons under similar environmental conditions while taking into account changing reproductive demands of females. Juveniles were distinguished from adults by the incomplete ossification of the metacarpal-phalange epiphyseal joint (Racey 1974).

Each bat was given a unique band combination, using coloured and numbered split-ring bands. Forearm length was measured with vernier calipers to the nearest 0.05 mm, taking three measurements of the right forearm and using the average. Bats were weighed to 0.05 g using an Ohaus model C151 portable electronic balance. Tooth class/wear was recorded as an estimate of age (Christian 1956; Holroyd 1993). Feces were collected from the cloth bags for dietary analysis.

## CHAPTER 2. Foraging Behaviour

### INTRODUCTION

Bats are behaviourally and morphologically adapted to forage effectively in certain habitats. Wing morphology, and to a lesser degree, echolocation call type, have been implicated as the primary characteristics dictating habitat use by foraging bats (Aldridge and Rautenbach 1987; McKenzie and Rolfe 1986). Wing morphology affects manoeuvrability; long narrow wings allow fast flight in open areas, whereas shorter, wider wings permit quick turns in cluttered environments (clutter refers to physical features, such as trees, which reduce the openness of a habitat) (e.g. Norberg and Rayner 1987; Saunders and Barclay 1992). Eptesicus fuscus is considered a "mid-range" bat in terms of wing morphology, although it is most often observed foraging in open habitats (Kurta and Baker 1990; pers. obs.). Echolocation call type influences prey selection (Goldman and Henson 1977; Bell and Fenton 1984; Barclay 1985; Saunders and Barclay 1992) and will be discussed in the following chapter.

While morphology may be the paramount factor determining foraging areas, within this framework other extrinsic factors further influence selection of foraging areas. Prey availability is important (Barclay 1985; Geggie and Fenton 1985; Racey and Swift 1985; Rydell 1989), in addition

to environmental conditions (temperature: Anthony et al. 1981; Grinevitch et al. in press; rainfall: Leonard and Fenton 1983; Fenton et al. 1990). Low prey abundance can lead to territoriality and aggression (Bradbury and Vehrencamp 1976; Swift 1980; Belwood and Fullard 1984; Racey and Swift 1985), putatively resulting in resource and habitat partitioning. Roost availability and location, and even proximity to hibernation sites, can also influence foraging location (Furlonger et al. 1987).

Due to inferences based on ecomorphology, most foraging studies have investigated interspecific habitat use primarily on the basis of clutter, sometimes considering prey availability (e.g. McKenzie and Rolfe 1986; Aldridge and Rautenbach 1987; Saunders and Barclay 1992). One gap remaining in our knowledge is possible differential habitat use by bats of different sexes. The solitary nature of male insectivorous bats has thus far precluded indepth investigation into intersexual differences in foraging habitat or behaviour. Comparing intersexual differences within the same species cannot be limited to examination of clutter, because bats share the same wing morphology and manoeuverability. Only when females are pregnant, and therefore subjected to increased wing loading, are clutter-related differences expected within a species (Brigham et al. 1992; M. Kalcounis, unpubl. data). In addition, most available foraging areas in my study area are virtually devoid of clutter; only scant pockets of trees exist. Thus, the problem of how to discern differential use of foraging areas

invokes the use of a different set of criteria, other than degree of clutter.

The criteria should be based on the ways in which reproductive demands are manifested in male and female bats. For males, these demands are probably minimal. Although males undergo spermatogenesis during the summer (Racey 1982), the energetic costs of this process do not approximate the costs of raising young (Grinevitch *et al.* in press). Male bats also forego foraging more readily than do females, and enter torpor to save energy (Hamilton and Barclay 1994; Grinevitch *et al.* in press). Thus, there is little reason to suspect that male foraging strategy would differ from energy maximization. For females, elevated energy and nutrient demands likely affect foraging behaviour, and may be more pronounced during lactation, because it is an energetically more costly period than pregnancy (Racey 1987). In some bat species, lactating females forage significantly longer than pregnant females in accordance with escalating needs of growing young (*Lasiurus cinereus*, Barclay 1985; *Eptesicus nilssoni*, Rydell 1993). Foraging distances of lactating females have also been reported to decrease (Racey and Swift 1985), because females typically return to the roost, up to several times a night, to nurse young (Swift 1980). It is also possible that dietary demands will influence prey selection, which could consequently influence habitat selection. In contrast, males do not have comparable feeding demands, or similar foraging constraints. Thus, I predicted that male and female *E. fuscus* should exhibit differences in

foraging behaviour.

To investigate possible intersexual differences in foraging, I looked at several aspects of foraging behaviour: time of emergence, amount of time spent foraging, foraging locations, and size of foraging area. I predicted that females would exit the roost earlier than males to maximize foraging time, and to reach the best foraging sites first. I further predicted that female foraging time would be longer than that of males, especially during lactation, and even during post-lactation, when females must increase fat reserves for hibernation. Because of the need to return to the roost to nurse young throughout the night, females would necessarily stay closer to the colony and have smaller foraging areas than males.

## METHODS AND MATERIALS

### Temperature

To understand the possible influence of temperature on prey availability and foraging behaviour, mean ambient temperature at sunset was compared between 1992 and 1993, for June and July combined. In addition, comparisons were made between reproductive stages, between and within years. Temperatures were analysed using ANOVA and Tukey's test.

## Radio-telemetry

Bats of suitable mass (radios should not exceed 5% of the bat's mass; Aldridge and Brigham 1991) were fitted with temperature-sensitive radio transmitters (Holohil Systems Ltd., Woodlawn, Ont., model BD-2T, weighing 0.8 g). The majority of transmitters were placed on bats during lactation because dietary demands are greatest during this time for females, and thus intersexual differences should be most pronounced. I trimmed the fur between the scapulae and used Skinbond<sup>®</sup> (Canadian Howmedica, Guelph, Ont.), a nontoxic surgical adhesive, to attach the transmitter. The battery life of the transmitters was approximately three weeks, although transmitters typically fell off within one to two weeks.

I did not collect foraging data on the night bats were fitted with radios, to allow the bats to adjust to the transmitter (Audet and Fenton 1988). Foraging locations on subsequent nights were established by triangulating radio signals with two Merlin 12 receivers and 5-element Yagi antennas (Custom Electronics, Urbana, IL). On occasions when only one receiver was used, the tracker would change locations regularly to better approximate the location of the bat. Fluctuations in radio signals indicated activity levels, which allowed me to determine whether bats were foraging or night roosting when away from the maternity roost.

Trackers monitored a location where at least one bat was foraging,

although typically more than one bat was within radio range at most locations. Trackers recorded the bat's location as a compass bearing at specific, synchronized times (at least one reading per ten minute period for each bat, but typically every 3-5 min.). Compass bearings were later transferred to maps to triangulate bat foraging locations. Signal strength and amount of fluctuation were also recorded.

On some nights, individuals were followed for their entire foraging bout. On other nights, attempts were made to maximize the number of bats tracked by monitoring a bat for a minimum of one hour, then switching to a new bat at a different location, thereby increasing data on use of foraging habitats. I attempted to locate the same bats at different stages of the night on subsequent evenings. In both of the aforementioned situations, the number of bats tracked was maximized while trying to get at least three or four nights of data on each individual. However, at most locations, trackers were able to monitor more than one bat for the entire night. In addition, cool ambient temperatures in 1993 kept foraging bouts short and bats rarely made more than one foraging trip, such that most bats were tracked during the same time of the night.

### Emergence Time

I recorded the time at which bats exited the roost, and on some

occasions estimated it to within ten minutes based on detection of a bat foraging near the roost. For statistical purposes, emergence was defined as exit time minus sunset time. ANCOVA was used to analyze emergence time, by comparing sexes, years, and their interactions, with a term for individual nested within the aforementioned terms (treated as a random variable). The covariate was log ambient temperature at sunset. I did not include reproductive stage in the analysis because sample size was low for males during the pregnancy period.

#### Foraging Time

I considered the amount of time bats were absent from the roost to be foraging time, unless bats were detected night roosting (based on personal observation, bats in my study area rarely night roosted away from the colony, see Results). To compare foraging time of males and females between the pregnancy and lactation periods, only 1993 data were used, because sample sizes during the pregnancy period in 1992 were too small to include in analysis. Because there was no difference in foraging time between reproductive periods (see Results), data were combined for pregnancy and lactation periods in 1992 and 1993, to compare foraging time between sexes and years. Both of the above analyses were conducted with ANCOVA. A random term for individual was included, and the

covariate was log ambient temperature at sunset. Only when bats foraged were they considered in the above analyses, hence, foraging time was never recorded as zero.

### Foraging Site

Because bats fly so quickly, their specific locations are typically very difficult to locate; triangulation usually resulted in broad foraging areas. As a consequence, attempts to identify foraging areas in terms of microhabitat were unrealistic, more so for males than females because they covered more area and flew out of tracking range more often.

To get a general indication of how males and females were using potential foraging habitat in the vicinity of the colonies, I categorized areas as river valley, city, and prairie (field and prairie outlying the river valley). The locations of foraging bats were classified into one of the three habitats, and the time spent in each habitat was calculated as a proportion of the amount of time they were tracked. This comparison was useful to indicate habitat preferences within the vicinity of the colonies only. ANOVA and Tukey's test were used to compare habitat use between sexes and years.

### Foraging Time "Away"

When bats flew out of telemetry range they were considered to be "away" (versus "tracked"). This is an important distinction because bats could invariably be located anywhere along the river valley within a several kilometre stretch. Once bats flew out of range they were foraging over field and prairie, or were flying in the river valley in excess of 13 km from the roost.

The proportion of time bats were "away" while foraging was calculated per night as a percentage of the entire time they were foraging. "Away" times were calculated for males and females within pregnancy and lactation periods in 1993, because telemetry coverage was not as extensive during the previous field season. ANCOVA was used to analyse "away" time, with comparisons by sex, reproductive period, and their interaction, with a random term for individual. The covariate was log ambient temperature at sunset.

### Foraging Area

Areas were drawn as minimum convex polygons (Audet 1990; Wilkinson 1992), based on foraging location points identified through telemetry. While a bat was tracked, location points were made every 5-10

minutes, most often being made within five minute periods. Areas were analysed using ANCOVA, with comparisons by sex. Covariates included foraging (tracking) time and log ambient temperature at sunset.

### Light Tagging

Chemiluminescent light tags (American Cyanamid Company, Charlotte, NC.; weighing 0.15 g) were used to gain more precise information on foraging locations in relation to the river and shore, and the height at which bats were foraging. Light tags emit light for approximately two hours and are visible from at least 30 m away. Light tags were attached with Skinbond<sup>®</sup> to the ventral surface of the bat. Tagging was carried out on two occasions, once with pregnant females and once with nonreproductive females. It was not possible to light tag lactating individuals because bats were generally captured as they returned from foraging and had to be kept until the following night to be released with light tags. Bats were released in front of the school from which they were captured. When light tagging was conducted, numerous observers were positioned along the river to record sightings. The information gathered included approximate height at which the bats were flying and location relative to the river and shore.

## Night Roosting

I recorded when bats night roosted away from the maternity colony. Steadiness of the telemetry signal indicated when bats were not in flight. The signal had to be steady for a minimum of 10 min. before it was interpreted as night roosting, because fluctuations in the signal are often subtle.

## RESULTS

### Temperature

Ambient temperature at sunset was significantly lower in 1993 than in 1992 ( $df=1,121$ ,  $F=7.68$ ,  $P<0.01$ ; Figure 2.1). Further, there were significant differences between mean ambient temperature at sunset between reproductive stages. Mean ambient temperature at sunset during the lactation period in 1992 was significantly greater than mean ambient temperature at sunset during pregnancy in 1993 ( $df=3,119$ ,  $F=2.83$ ,  $P<0.05$ ; Figure 2.2).

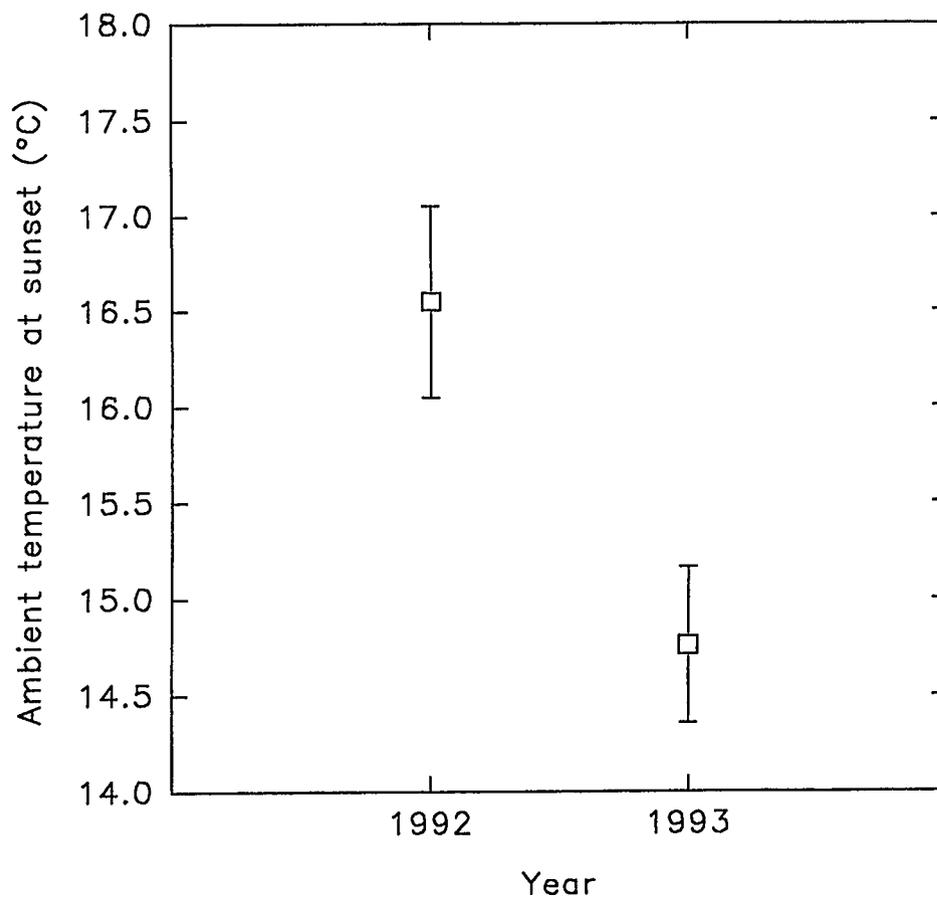


Figure 2.1. Mean ambient temperature at sunset, for the combined months of June and July, in 1992 and 1993. Temperatures were significantly warmer in 1992 than in 1993 ( $P < 0.01$ ).

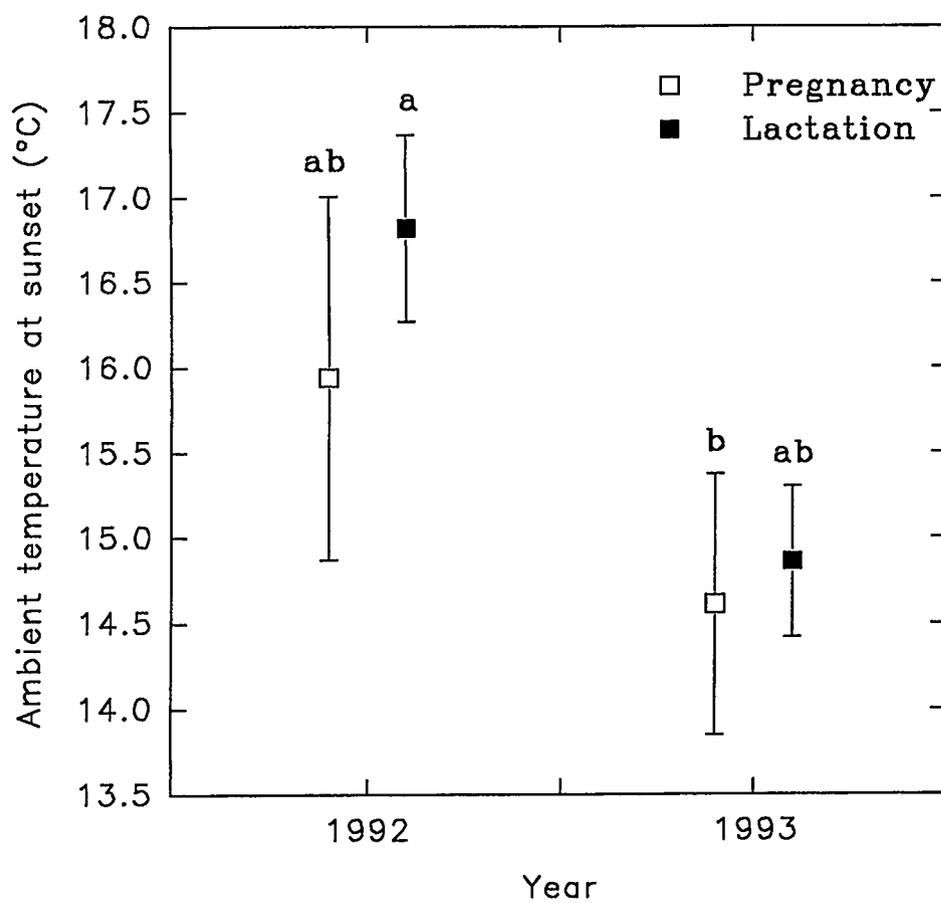


Figure 2.2. Mean ambient temperature at sunset for the reproductive periods of pregnancy and lactation, in 1992 and 1993. Means with the same letter are not significantly different ( $P < 0.05$ ).

## Emergence Time

Observations were made on 35 bats, for a total of 128 observations, over both years. Mean exit time was 73.4 min. after sunset for all bats, and temperature did not significantly influence emergence time. There were no significant differences in emergence time between sexes or years ( $P > 0.05$ ) (Figure 2.3). Significant variation existed in emergence time between individuals ( $df = 31, 93$ ,  $F = 5.34$ ,  $P < 0.001$ ).

## Foraging Time

Ambient temperature at sunset significantly influenced foraging time; lower temperatures were associated with shorter foraging times in both within year (1993;  $df = 1, 31$ ,  $F = 31.88$ ,  $P < 0.001$ ) and between year ( $df = 1, 66$ ,  $F = 31.88$ ,  $P < 0.001$ ) analyses. For all foraging time analyses, means were least square adjusted according to temperature.

Twenty-two bats, with 68 observations, were used in the analysis of 1993 foraging times. During the pregnancy and lactation periods of 1993, mean foraging time was 168.2 min. There were no significant differences in foraging time between sexes or reproductive periods, although there was a trend for females to forage longer than males (Figure 2.4). There was significant variation between individuals ( $df = 18, 31$ ,  $F = 5.54$ ,  $P < 0.001$ ).

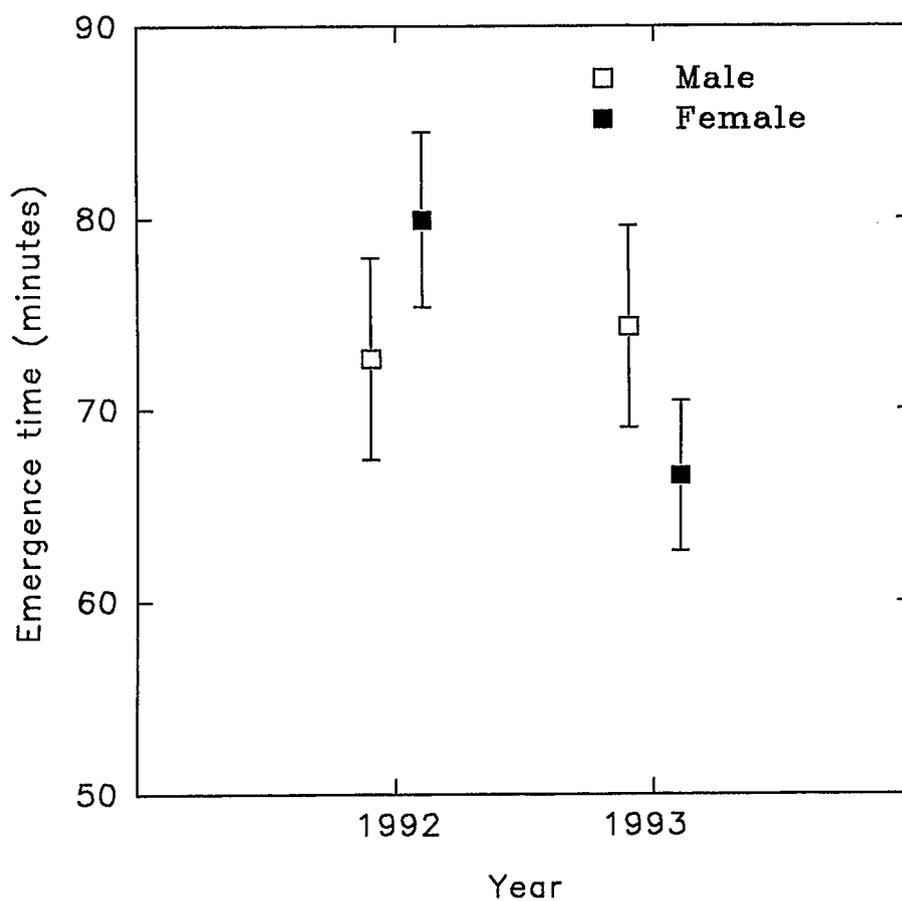


Figure 2.3. Mean emergence time of male and female *Eptesicus fuscus* in 1992 and 1993, across all reproductive periods. There were no significant differences in emergence times between sexes or years ( $P > 0.05$ ).

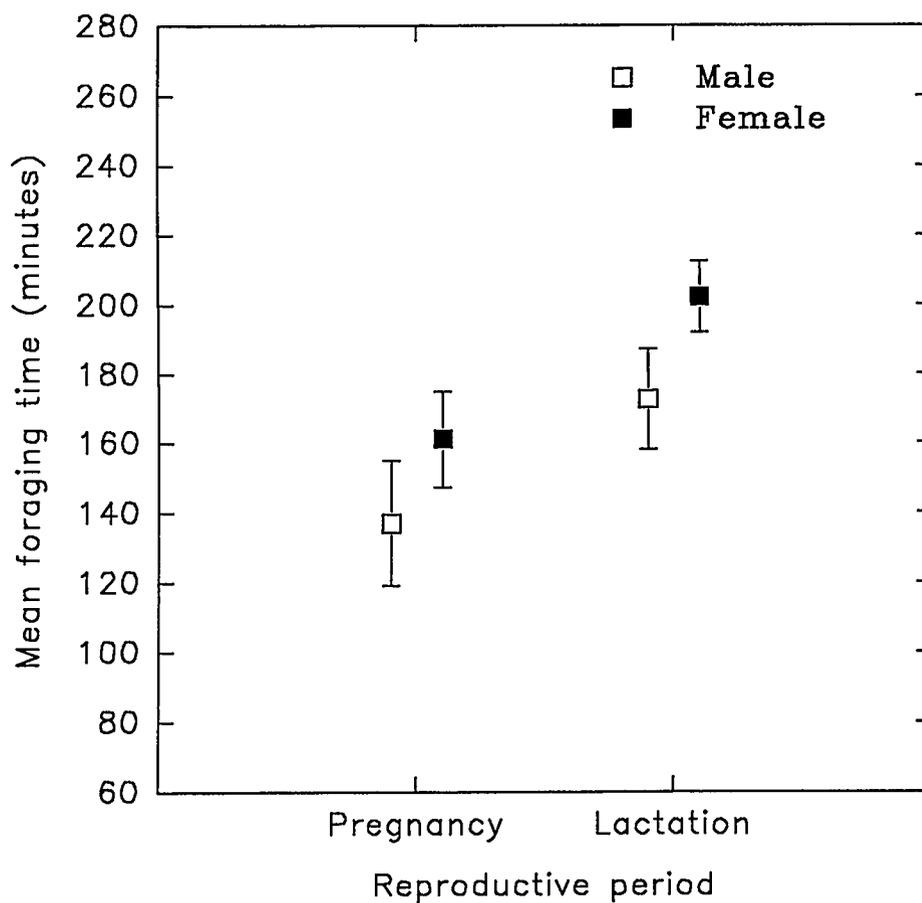


Figure 2.4. Mean foraging time of male and female *Eptesicus fuscus* during the reproductive periods of pregnancy and lactation in 1993. There were no significant differences ( $P > 0.05$ ).

In the comparison of foraging time during 1992 and 1993, data from 31 bats were used, with 98 observations. Foraging time in 1992 (mean = 215.8 min.) was significantly longer than in 1993 (mean = 152.1 min.;  $df = 1, 33.9$ ,  $F = 5.23$ ,  $P < 0.05$ ; Figure 2.5). There was no significant difference in foraging time between sexes (Figure 2.5). There was a trend towards short foraging times among males in 1993. There was significant variation in foraging time between individuals ( $df = 27, 66$ ,  $F = 31.88$ ,  $P < 0.001$ ).

#### Foraging Site

Thirty-eight bats were included in the habitat analysis, with 96 observations. There were no significant differences between sexes or years in habitat use. Bats of both sexes foraged significantly more often in the river valley than in the city or prairie, when they were within tracking range ( $df = 2, 91$ ,  $F = 385.33$ ,  $P < 0.001$ ; Figure 2.6).

#### Foraging Time "Away"

Tracking data for 25 bats, with a total of 75 observations, were used in "away" time analysis. Ambient temperature did not significantly influence "away" time. Male bats spent a significantly greater percent of foraging

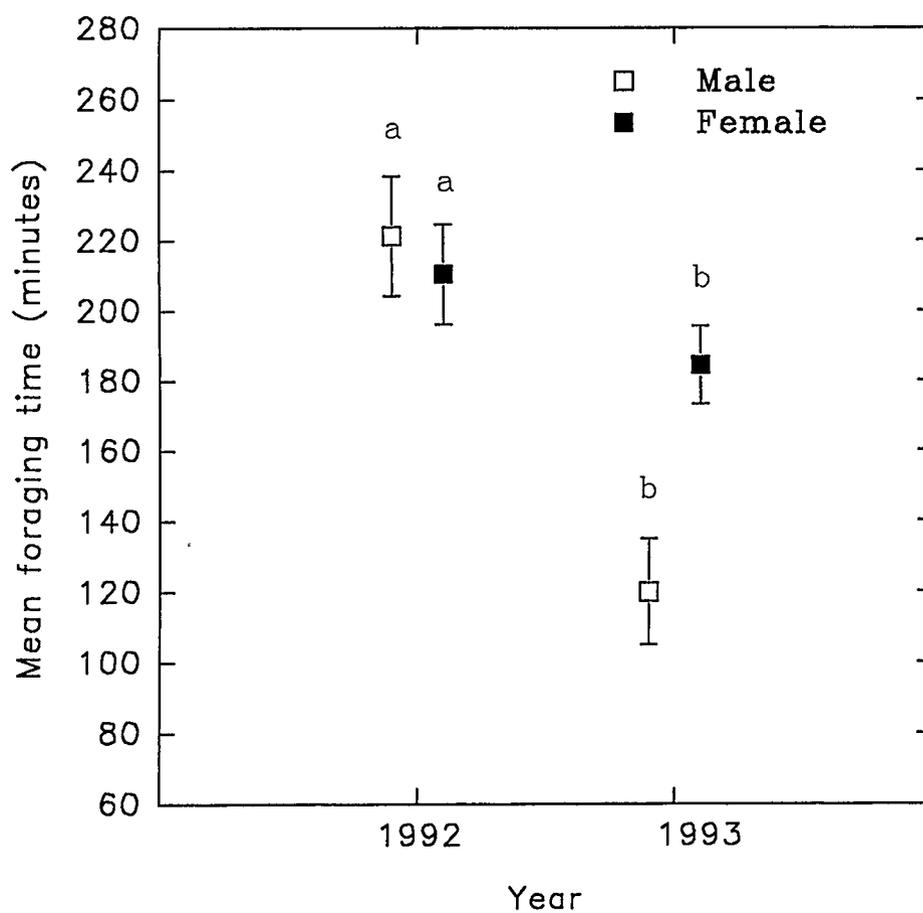


Figure 2.5. Mean foraging time of male and female *Eptesicus fuscus*, during the lactation and pregnancy periods of 1992 and 1993. Means followed by the same letter are not significantly different ( $P < 0.05$ ).

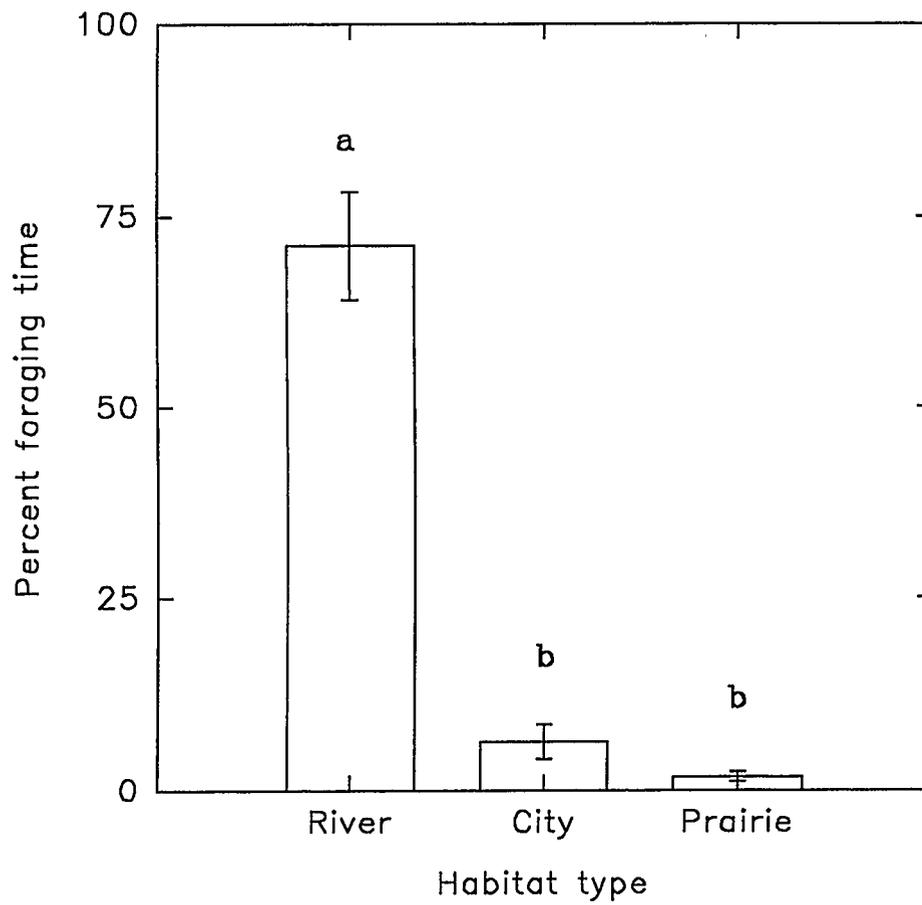


Figure 2.6. Percent of foraging time spent in different habitats (river valley, city and prairie), while within tracking range, of male and female Eptesicus fuscus in 1992 and 1993.

time "away" (mean = 48.0%) than did females (mean = 17.62%;  $df = 1,34.2$ ,  $F = 4.98$ ,  $P < 0.05$ ; Figure 2.7). There were no significant differences between reproductive periods, although there was a trend towards lower "away" times during the lactation period, especially among females. There was significant variation between individuals in "away" time ( $df = 21,50$ ,  $F = 2.16$ ,  $P < 0.05$ ).

### Foraging Area

Only a small number of tracking nights yielded enough reliable "pinpoint" locations to permit calculations of foraging area. One foraging night from five individuals of each sex, during the lactation period, was used. In addition, only foraging times in excess of 60 min. and less than 180 min. were used.

Male bats had significantly larger foraging areas than did females ( $df = 1,6$ ,  $F = 15.56$ ,  $P < 0.001$ ; Figure 2.8). Ambient temperature at sunset did not significantly influence foraging area. The interaction between foraging (tracking) time and sex was significant ( $df = 1,6$ ,  $F = 21.77$ ,  $P < 0.01$ ). Slope for male area (versus foraging time) was significantly different from zero ( $P < 0.01$ ) with a positive slope, whereas the slope for female foraging area did not differ significantly from zero. Thus, as foraging time increased, a male's foraging area increased, whereas females stayed

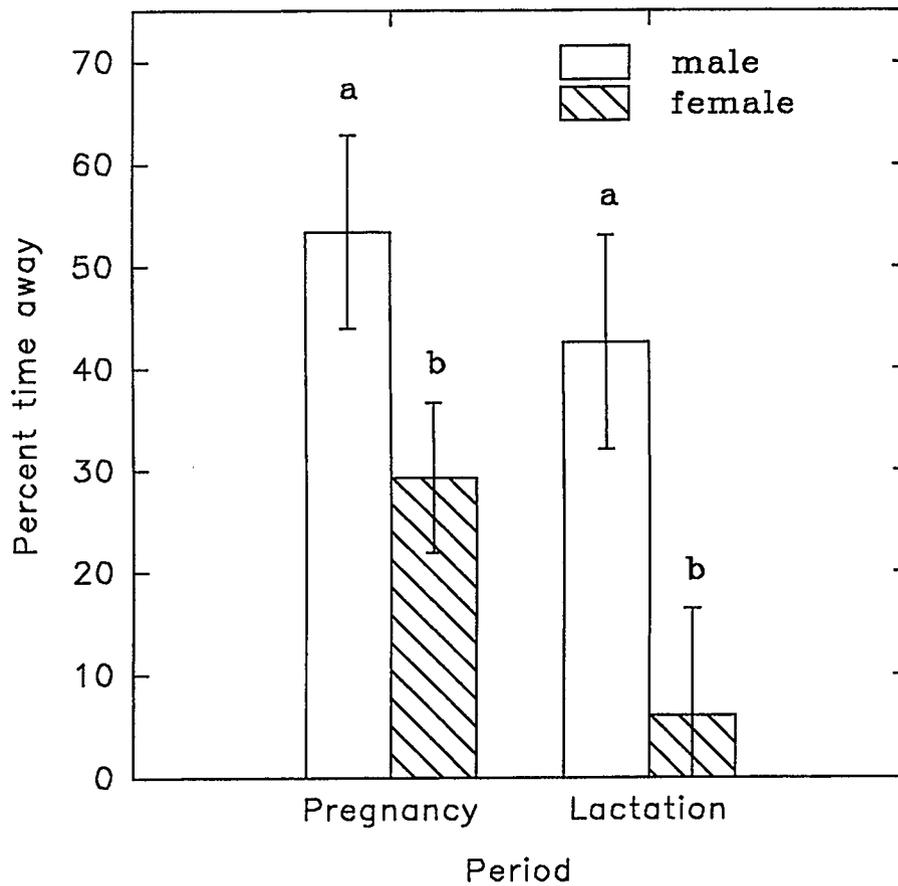


Figure 2.7. Percent of foraging time male and female Eptesicus fuscus spent "away", during the reproductive periods of pregnancy and lactation in 1993. Bars with the same letter are not significantly different ( $P < 0.05$ ).

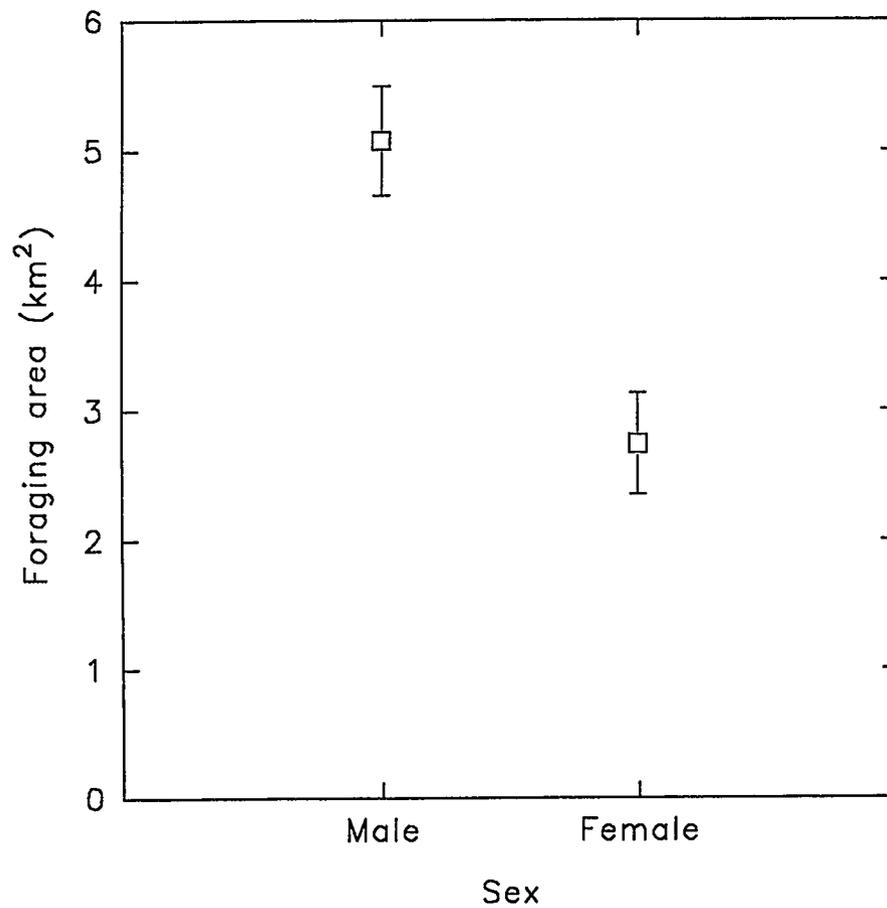


Figure 2.8. Mean foraging area of male and female *Eptesicus fuscus* during the lactation period in 1993. Male foraging area was significantly larger ( $P < 0.01$ ).

within a foraging area of relatively constant size over time.

### Light Tagging

Eight pregnant females were light tagged on June 17, 1993, and five nonreproductive females were light tagged on August 8, 1993. The large size of the available foraging area made observation of light tagged bats difficult, although two pregnant individuals and one nonreproductive individual were sighted. Observation times were between two to four minutes per bat. The pregnant bats were observed foraging over vegetation along the shore of the South Saskatchewan River, approximately 1-2 m above the ground. These bats were also seen over the river, flying 6-7 m above the river. The nonreproductive individual was observed over the river, foraging approximately 10 m above the water.

### Night Roosting

I did not detect any bats night roosting away from the colony in 1993, for either sex. In 1992, there were three occurrences of males night roosting, lasting from 20-40 min. During the postlactation period in 1992, one male was away from a roost in a house (near ESS) for approximately five hours every night it was monitored (n = 4 nights; never within tracking

range). Based on the length of time it was away, I concluded that it was likely night roosting for a portion of the night. Only one female (lactating) was recorded night roosting, and this for was approximately 45 min. during a thunderstorm.

## DISCUSSION

### Emergence Time

The decision of whether or not to forage must necessarily precede the decision of when to emerge. Previous research on E. fuscus in the Medicine Hat colonies indicated that temperature and reproductive period were the primary factors governing the decision to forage, especially for males (Grinevitch et al. in press). In that study, females rarely chose not to forage during pregnancy and lactation, while males frequently did not emerge during the pregnancy period. There was a threshold temperature of approximately 12°C, above which bats of both sexes emerged. However, below this threshold, reproductive females emerged significantly more often than did males (Grinevitch et al. in press). Based on personal observation, females failed to forage when the temperature fell more than 1-2°C below this threshold.

Because temperature appears to be the primary factor influencing

foraging decisions for both sexes in Medicine Hat, it is not surprising that ambient temperature at sunset did not influence emergence time. The threshold temperature is the important factor, and above this temperature, there is no noticeable effect on emergence time. The threshold presumably varies with geographic location in relation to local conditions. Audet and Fenton (1988) also found that reproductive females were always active above 12°C.

However, Swift (1980) showed that emergence activity is not always affected by climatic conditions. This could be due to the fact that Swift's (1980) study was conducted in an area with consistently cool ambient temperatures. It is also likely that the colony under study was exclusively female, containing reproductive individuals which tend to be less risk averse due to reproductive demands (Grinevitch *et al.* in press). Presumably there are threshold temperatures, which vary with location, below which no bats will risk foraging because energetic costs of flight will not likely be covered due to reduced prey densities.

At my study site, males and females exited the roost within the same time period following sunset. This can be explained by two reasons. First, there may be significant advantages to clustering; bats leaving as a group may be less vulnerable to predation and may be able to follow other bats to profitable foraging sites (Kalcounis and Brigham in press). Clustering may also be an artifact of colony size; a large number of individuals attempting to

leave the roost may create a bottleneck (Kalcounis and Brigham in press). Swift (1980) found that emergence rate was proportional to colony size, supporting the clustering theory. Furthermore, there is a peak in insect activity at dusk and dawn (e.g. Morgan and Waddell 1961; Swift 1980), making it advantageous for bats to leave after sunset to exploit the first peak in prey activity. Despite my prediction that reproductive females would leave earlier than males to gain initial access to the best foraging sites, this does not seem to occur because males behave similarly, likely for the aforementioned reasons. The advantages of a particular exit time are the same for both sexes. For females to leave before nonreproductive individuals they would have to exit before dusk, exposing themselves to greater risks (i.e. more vulnerable to predation) and possibly lower prey levels.

### Foraging Time

Temperature significantly influenced foraging time of both sexes; high ambient temperatures led to all night foraging, whereas low temperatures truncated foraging bouts. It appears that above the threshold temperature, bats of both sexes are similarly affected by temperature changes. In Germany, Myotis myotis did not exhibit any difference in foraging time between sexes and reproductive states when the temperature

was above 10°C (Audet 1990). Other studies of foraging time of insectivorous bats have reported that foraging time was not correlated with ambient temperature (Leonard and Fenton 1983; Wai-Ping and Fenton 1989; Rydell 1993). To date, most data on foraging time have come from female bats, which, due to reproductive demands, have a very different agenda than do males. Accordingly, these studies concluded that foraging time was not correlated with ambient temperature.

Using temperature as a covariate may not be revealing the full influence of temperature, because whenever bats were foraging, the temperature was usually a minimum of 12°C. Therefore, the effect of temperatures below the threshold was not taken into account. Consistently cool temperatures could be responsible for decreasing prey abundance and diversity, such that insect availability would still be lower than usual on warmer nights. Long term studies of insect activity in relation to environmental conditions indicate that insect activity and abundance are reduced by cool temperatures, strong winds, and rain (Williams 1961; Taylor 1963). Low insect abundance contributes to short foraging periods in other species (Lasiurus cinereus, Barclay 1985), and there is evidence suggesting that bats may only forage when insect densities surpass a certain threshold (Racey and Swift 1985; Rydell 1989). Temperatures were lower in 1993 than in 1992, and insect abundance probably mirrored this difference. Low prey availability would make long foraging trips unprofitable.

Although there were no differences in foraging time between male and female bats, males in 1993 showed a trend towards abbreviated foraging trips. This trend could be an indirect result of cool temperatures reducing prey abundance. The reproductive demands faced by female bats may force them to forage even in less than optimal conditions, until prey densities become too low to outweigh costs of flight. Bats should forage only when insects are plentiful enough to ensure energetically profitable foraging (Rydell 1989), and males are more risk averse than reproductive females in this regard.

Males do not need to risk foraging under conditions of decreased prey availability as they can conserve energy through torpor (e.g. Audet and Fenton 1988; Grinevitch et al. in press). Males can use torpor to save energy for several nights if necessary. One male bat at my study site remained in torpor for seven consecutive nights. This strategy is rarely employed by females (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. in press), because it increases gestation length, and presumably increases neonatal development time (Racey and Swift 1981). Thus, torpor is used by reproductive females only under extreme circumstances due to its inherent costs, which can result in juveniles becoming independent late in the season, leaving less time for both females and juveniles to build energy reserves for hibernation (Kunz 1987; Thomas et al. 1990).

Among reproductive stages in 1993, there was no intersexual difference between foraging times. This corroborates results from previous research on the Medicine Hat colonies (Grinevitch et al. in press). The only other study to compare foraging times between sexes (although male sample size was small) found similar results, in that there was no difference between sexes in the proportion of time spent foraging (Audet 1990). It appears that as long as temperatures are warm enough to foster adequate insect densities, male bats will forage, but may tend towards shorter trips than females in cool temperatures. The greatest impact of temperature on foraging may be that it affects the decision to forage. Results from Grinevitch et al. (in press) indicated that males forego foraging more often than females; a behaviour which is not evident in foraging time analysis but is highly relevant to foraging behaviour.

This begets the question as to why males frequently forage for as long as reproductive females, despite reduced energetic and nutritional demands. Foraging time is generally considered to be a reflection of daily energy demands (see Aldridge and Brigham 1991), but intuitively, it should also be a function of habitat quality in terms of prey availability.

### Foraging Site

Female bats exhibited a strong preference for foraging along the same

stretch of the South Saskatchewan river, demonstrating site fidelity. Male bats also preferred foraging within the river valley over other available habitats. However, males spent significantly more time "away" from the primary foraging area along the river valley than did females. Greater insect abundance around water has been well documented (e.g. Barclay 1985, 1991; de Jong 1994). Lower insect abundance in the outlying areas where males foraged could account for the length of their foraging bouts, which were comparable to those of females, despite lower energetic demands. It is not immediately clear why males would not forage consistently in the presumed best habitat along the river, although several possibilities could explain this behaviour.

The first, and most likely explanation, is that females exhibit agonistic, and likely territorial, behaviour. Territoriality is the maintenance and defence of an area based on its resources (e.g. Brown 1964; Wolf 1970), and in many cases, territoriality diminishes when resources, such as prey, are abundant (e.g. Carpenter and MacMillen 1976; Schoener 1971). Several bat species follow this pattern of territorial behaviour, and intraspecific aggression has been observed among foraging bats at low insect densities (Belwood and Fullard 1984; Racey and Swift 1985). Big brown bats have been observed in agonistic interactions at my study site (I. Hamilton, pers. comm.) and in other locations (Kurta and Baker 1990; S. Holroyd, pers. comm.; M. Vonhof, pers. comm.), resulting in one bat driving away another

individual. Such altercations have been observed in spotted bats (Euderma maculatum; Leonard and Fenton 1983), and have been considered as putatively territorial in Hawaiian hoary bats (Lasiurus cinereus; Belwood and Fullard 1984), where bats foraged around lights, permitting direct observation of behaviour. Rydell (1986a) observed reproductive female northern bats (E. nilssonii) acting defensively within specific foraging sites, later concluding that females were exhibiting territorial behaviour, having a hierarchy within which older females were dominant (Rydell 1989).

Without direct observation, it is impossible to determine conclusively if female E. fuscus in my study area behave territorially. However, based on circumstantial evidence, it is possible that females are behaving territorially, or are at least exhibiting some degree of defensive behaviour at foraging sites. The cool ambient temperatures of 1993 (when "away" time data were analysed) likely contributed to low insect densities, creating circumstances potentially conducive to territorial behaviour. While competition has been cited as the reason for sympatric species exhibiting resource partitioning (Husar 1976; Swift and Racey 1983), it is unlikely that competition alone is responsible for male use of outlying areas, because of observations of apparent agonistic behaviour. The premise that female big brown bats in my study area are acting territorially is corroborated by the fact that females showed more site fidelity than did males.

The other possible reason for males foraging in outlying areas is based

on a premise which is somewhat of a departure from traditional theories concerning territorial behaviour. It has been suggested that in a population where males are polygynous, and have a strong chance of mating with conspecific females, males may leave the best foraging areas to mates (J. Stamp, pers. comm.). This could be taken further, to embrace kin selection: males may have sired individuals in the population, or have been sired by, or be siblings to, females in the population. Thus, males could benefit from increased inclusive fitness. This could explain the way in which males behave at my study site, often foraging for only part, or none, of the night along the river valley. Unfortunately, little is known about mating habits of insectivorous bats in general, and no genetic analysis has been conducted on the Medicine Hat population to determine parentage of individuals. In the absence of any tangible evidence, this premise must for now remain as conjecture.

The fact that males often fed in distant locations indicates that their foraging areas must be larger than those of females. Even when males stayed within the river valley, their foraging areas were significantly larger than those of females and increased in size with amount of time spent foraging. Female foraging area did not increase with time; a further indication of female site fidelity. Foraging distances of lactating females are constrained by nursing duties, limiting them to relatively close feeding sites (Fullard and Barclay 1980; Racey and Swift 1985). In addition, due to the

time constraints placed on females, it seems reasonable that they would regularly use familiar, reliable and close foraging areas. This is consistent with data from female northern bats (*E. nilssonii*), indicating there was little change in their pattern of habitat selection throughout the reproductive period (Rydell 1986b). Rydell (1989) suggested that knowledge of a foraging location enhances efficiency and as such foraging can be maintained at a low cost. Females from the Medicine Hat colonies certainly exhibited these behaviours.

Comparable male and female foraging time is contrary to traditional expectations which are based on the premise that foraging time is a reflection of daily energy demands (see Aldridge and Brigham 1991). Males, in my study area, may need to forage as long as females because they often frequent what appear to be less optimal foraging sites, thus taking longer to fulfil dietary requirements. It is unlikely that males are consuming excess energy for storage because too great a caloric intake would increase flight costs (Barclay 1989), and jeopardize foraging abilities. Storing fat should be limited to prehibernation. Interestingly, male and female bats at the ESS colony gain mass at similar rates and amounts throughout the summer (S. McNally, pers. comm.). The only difference is that females are usually heavier than males at the start of the season. Considering the caloric drain of lactation, females must be consuming more insects than males, further supporting the argument that males are foraging in lower quality habitat.

Male night roosting while "away" could contribute to long foraging times, but based on my tracking data, I think night roosting was rarely employed. Although it was not always possible to track bats for the duration of their foraging bout, males that were followed for lengthy foraging times rarely night roosted, and did so for only short periods. Thus, it is likely that males foraged for the entire time they were out. The constraint of returning to the roost to nurse pups restricts females; only one female bat night roosted away from the maternity colony. Similarly, Caire *et al.* (1984) found that foraging *E. fuscus* did not rest; and other bat species commonly forage continuously (Barclay 1989; Wai-Ping and Fenton 1989; Krull *et al.* 1991).

It is generally accepted that, for females, foraging activity is constrained and necessarily adjusted to meet changing dietary demands, such that time spent foraging reflects energy demands during reproduction (Barclay 1989; Rydell 1989, 1993). For example, Barclay (1989) found that foraging time increased dramatically for *Lasiurus cinereus* between early lactation and fledging. Foraging time should also reflect changing nutritional demands, which could possibly exert a greater influence than energetic demands (see Chapter 4). The greatest energetic and nutritional demands occur during lactation (e.g. Kunz 1987; Kurta *et al.* 1990). Once pups become independent, females need to recoup nutritional losses from lactation, and build fat reserves for hibernation. Thus, postlactation

continues to be an important, if not critical, time for female bats. Foraging behaviour during postlactation has received little attention. Unfortunately, it was virtually impossible to study postlactating females at my study site because they frequently left the roost and the immediate vicinity.

It appears that big brown bats around Medicine Hat conform to predicted foraging patterns, using similar habitats to those previously reported for this species, while exhibiting flexibility within these areas (Caire *et al.* 1984; Furlonger *et al.* 1987). Females seemed to exploit and monopolize the prime foraging area along the river valley. They foraged in areas that likely supported high prey densities, and returned to familiar, reliable and close sites. Males, although preferring the river valley, were more likely to forage in outlying areas despite presumed lower prey densities. Competition from females, in concert with territorial behaviour, probably caused males to use alternative foraging sites, requiring long foraging times.

I analysed the significance of the differential use of habitats by male and female *E. fuscus* in terms of diet. The relevance of prey choices in relation to reproductive demands, and the nutritional implications of prey consumed, will be explored in the following chapters.

### Chapter 3. Intersexual Differences in Diet

#### INTRODUCTION

Knowledge of foraging behaviour and foraging locations of E. fuscus at my study site revealed some intersexual differences. The significance of these differences may be related to the prey items consumed.

Much work has been conducted on diets of insectivorous bats, primarily using fecal analysis (see Whitaker 1988). As with foraging studies, dietary research has concentrated on interspecific comparisons, resource partitioning, and comparisons between reproductive stages of female bats (e.g. Husar 1976; Swift et al. 1985).

While morphological characteristics predispose bats to be effective foragers in certain types of habitat (McKenzie and Rolfe 1986; Aldridge and Rautenbach 1987; Norberg and Rayner 1987), echolocation call design similarly predisposes bats to detect and catch insects within a certain size range (Nachtigall and Moore 1988; Barclay and Brigham 1991). In addition, jaw structure plays a role in determining the types of prey bats are able to consume, primarily in terms of 'crushing ability', which translates into how well bats can consume beetles and other hard-bodied insects (Freeman 1981). Thus, species with strong jaws, such as E. fuscus, are free from many dietary constraints (Freeman 1981; Fenton 1990).

Limitations of the prey detection system and morphological characteristics set the general parameters delineating prey types available to an individual bat. Within these parameters, other factors determining prey selection may come into effect, including energetic and nutritional content of prey. The focus of most bat dietary studies concerned with quality of prey has been caloric content, using size of prey as an indicator of energetic value (Kunz 1973). Nutritional quality of prey has been virtually ignored, but could well play an important role in an animal's foraging strategy (Pulliam 1975; Belovsky 1978; Rapport 1980). Only recently have mineral components of insects been explored (Studier and Sevick 1992). Defining the diet is the first step to understanding any nutritional significance of prey (this aspect will be more fully explored in Chapter 4), and whether or not bats forage specifically for certain types of insects. Furthermore, the different energetic and nutritional requirements between reproductive females and nonreproductive individuals may be manifested in diet choice (Davies 1977b). Certain types of insects may better satisfy the elevated dietary demands of female bats.

It has been suggested that ecomorphology largely determines foraging habitat, and that diet is a result of foraging location. Alternatively, diet requirements could result in selection of certain foraging habitats. In reality, a combination of morphological characteristics, echolocation abilities, and dietary demands probably influence diet to varying degrees. The degree to

which each of these factors influence diet should be dependent on conditions such as age, sex, and particularly, reproductive state.

Knowledge of both foraging sites and diet can be used to determine whether bats are foraging selectively, by comparing insects found in feces to those trapped in foraging areas (e.g. Furlonger *et al.* 1987; Saunders 1989). Whether bats are selective or opportunistic foragers is a difficult question to answer. The key is being able to accurately measure insect availability, from a bat's perspective. I contend that no trapping methods can do this with assurance; insects traps can only give an approximate picture. Traps are fraught with biases, such as light traps with a bias towards phototactic insects; or sticky traps which can not catch heavy insects. Thus, trap samples should only be used as a rough gauge with which to compare insects in the diet, and results should be interpreted with suitable caution, with this caveat in mind.

Studies are divided on their assessment of bats as selective (Belwood and Fullard 1984; Buchler 1976; Jones 1990; Brack Jr. and LaVal 1985) or opportunistic (Swift and Racey 1983; Swift *et al.* 1985; McAney and Fairley 1989) foragers. Laboratory experimentation indicates that bats are capable of high levels of target discrimination (Simmons *et al.* 1990). However, it is difficult to ascertain the degree to which bats can actually use this ability in natural situations (Barclay and Brigham 1994), where a variety of factors influence foraging decisions, including environmental stochasticity,

competition and to a lesser degree, predation. Echolocation is limited in its ability to discriminate prey; bats detect prey at short ranges, typically 1.5 m or less (Schnitzler *et al.* 1987). Although discrimination abilities could be ameliorated by decreasing flight speed, prey encounter rates would consequently decrease (Barclay and Brigham 1994). The supposition that high prey encounter rates (i.e. large, fast flying bats; Swift *et al.* 1985) can potentially facilitate selective feeding (Pulliam 1975; Charnov 1976) may not hold true for bats due to their short detection range. In addition, unselective feeding should be favoured if handling times, and likely digestibility, are uniformly short for all available prey (Swift *et al.* 1985).

If certain insects do possess particularly important qualities to bats, two mechanisms exist by which bats may be able to select prey based on energetic and/or nutritional content. Bats can either forage specifically for certain types of insects, or they can forage (more opportunistically) in specific locations that support certain prey communities. The former method is less plausible because the ability of bats to discern and catch specific prey items in natural settings is questionable (Barclay and Brigham 1994), although these feeding methods are not mutually exclusive.

I predicted, based on elevated energetic and nutritional demands, that female diet would reflect greater selectivity than male diet. Females, especially during lactation, should consume high proportions of certain insects (based on energetic and/or nutritional content), which may result in

lower dietary diversity than males. Overall, I predicted that males would behave opportunistically. I used fecal analysis to reveal dietary differences, and used results of fecal analysis to compare diet to insect trap samples to assess degree of prey selection. Fecal analysis should also reveal changes in prey consumption in concert with changes in reproductive condition.

## METHODS AND MATERIALS

### Fecal Analysis

Feces were air dried for a minimum of five days prior to weighing on a Mettler digital balance. Immediately prior to analysis, fecal pellets were placed in a petri dish with a small amount of 75% ethanol to soften them. Pellets were teased apart under a dissecting microscope and distinguishable insect parts were identified to order and in some cases, family. Insects caught in suction traps (see below) helped serve as a basis for identification. For each fecal sample, I estimated the abundance of each insect taxon present as a percentage of the whole sample based on volume (Kunz and Whitaker 1983). With few exceptions, the number of pellets analysed in each sample ranged from five to 12.

I used a multiple analysis of variance (MANOVA) to compare the abundance of the major insect taxa in the diet (those taxa comprising a

minimum of 10% of the diet) between sexes, reproductive stages, years and their interactions.

For each bat, I calculated the Shannon-Weiner index of diversity based on all insect taxa found in the diet, and used ANOVA to compare sexes, reproductive stages, years, and their interactions.

### Insect Traps

I used suction traps to determine the available insect fauna along the primary foraging corridor, the river valley, during the 1993 field season (Wilkinson 1992). Four locations along the river valley, identified as primary foraging locations through radio-telemetry in 1992, were sampled on a weekly basis (see Figure 1.1). Because it was not always possible to run all traps on the same night, traps were often operated over 2-3 nights, provided temperatures were relatively consistent. Trapping was initiated at sunset, and continued for approximately four hours, or less if the ambient temperature became too cold for foraging (below 10°C; pers. obs.). On nights when the ambient temperature was warm enough to permit bat foraging throughout the night, trap bottles were replaced after four hours and left until sunrise.

Suction traps were equipped with lights, but to obtain an unbiased sample of available prey, I removed lights from most traps. At two

locations, traps with lights were operated simultaneously with traps without lights, placed at least 20 m apart, to determine how light affected the types and numbers of prey caught. Use of lights also augmented the number of insects available for fecal and calcium analyses.

Insects in traps were sorted by order and in some cases, family. Insects were stored in ethanol, and representatives from each taxon were dried and weighed, so that trap catches could be converted into mass. The mass of each insect taxon was calculated as a percent of the mass of the whole sample. Only insects greater than 2.5 mm in length were considered suitable prey for bats (Brigham 1990).

I compared trap catches to fecal samples collected within three days of when the traps were operated. To determine if bats were feeding selectively, a regression line was fitted through data points representing the percentage of each insect taxon (those comprising a minimum of 10% of the diet) found in the feces versus the percentage caught in traps. The regression line was fixed at an intercept of zero to de-emphasize the effect of bats which consumed insect taxa that were infrequently captured, so these points were weighted less heavily (Saunders 1989). If bats were feeding opportunistically, the percentage of each insect taxon in the feces should reflect the percentage in the trap, yielding a slope of one. If there was a significant correlation, the slope of the regression line was tested to determine if it differed from a slope of one.

## RESULTS

### Fecal Analysis

Fecal analyses ( $n = 40$  males;  $n = 57$  females) revealed that eight orders of insects, including four families within Diptera, made up the diet of male and female big brown bats (Table 3.1). Four taxa individually comprised 10% or more of the diet: Coleoptera, Lepidoptera, Chironomidae (Diptera), and Trichoptera. Combined, these taxa accounted for almost 75% of the volume of prey consumed.

There were significant interactions between sex and year ( $df = 4$ ,  $F = 4.41$ ,  $P < 0.005$ ), and between reproductive stage and year ( $df = 8$ ,  $F = 3.85$ ,  $P < 0.001$ ). There was an overall significant difference in the diet (consisting of the four predominant taxa) between sexes in 1992 ( $df = 4$ ,  $F = 5.05$ ,  $P < 0.005$ ), but not in 1993 ( $df = 4$ ,  $F = 0.95$ ,  $P > 0.05$ ). Diet of females also differed significantly between 1992 and 1993 ( $df = 4$ ,  $F = 7.04$ ,  $P < 0.001$ ). There was a significant difference between stages within 1993; diet differed between pregnancy and lactation ( $df = 4$ ,  $F = 14.14$ ,  $P < 0.001$ ), and between lactation and post-lactation ( $df = 4$ ,  $F = 9.16$ ,  $P < 0.001$ ). Multiple comparisons were based on Sidák's multiplicative inequality (Table 3.2).

In 1992, males consumed less Coleoptera and more Chironomidae

Table 3.1. Percent insect taxa in the diet of male and female Eptesicus fuscus, in 1992 and 1993.

Insect Taxa	Male	Female	Male and Female
	Mean Percent $\pm$ SE	Mean Percent $\pm$ SE	Mean Percent $\pm$ SE
Coleoptera	24.40 $\pm$ 4.8	40.4 $\pm$ 5.4	33.45 $\pm$ 3.47
Lepidoptera	21.70 $\pm$ 4.3	14.26 $\pm$ 2.9	17.46 $\pm$ 1.81
Trichoptera	16.53 $\pm$ 3.8	15.89 $\pm$ 3.9	16.16 $\pm$ 1.68
Diptera			
Chironomidae	15.09 $\pm$ 3.5	13.68 $\pm$ 3.3	14.29 $\pm$ 1.48
Muscidae	9.3 $\pm$ 2.7	6.67 $\pm$ 1.7	8.12 $\pm$ 0.84
Culicidae	2.71 $\pm$ 1.0	2.80 $\pm$ 1.5	2.76 $\pm$ 0.29
Tipulidae	2.30 $\pm$ 1.2	1.30 $\pm$ 0.6	1.73 $\pm$ 0.18
Other	1.15 $\pm$ 0.5	0.48 $\pm$ 0.2	0.77 $\pm$ 0.08
Hemiptera	3.66 $\pm$ 1.4	3.41 $\pm$ 1.2	3.52 $\pm$ 0.36
Neuroptera	0.62 $\pm$ 0.4	0.23 $\pm$ 0.1	0.40 $\pm$ 0.04
Hymenoptera	0.21 $\pm$ 0.1	0.27 $\pm$ 0.1	0.24 $\pm$ 0.02
Homoptera	0.39 $\pm$ 0.2	0.1 $\pm$ 0	0.22 $\pm$ 0.02
Unknown	2.33 $\pm$ 1.0	1.06 $\pm$ 0.4	1.61 $\pm$ 0.17

Table 3.2. Contrast statements explaining significant interactions between sex and year, and stage and year, based on diet MANOVA.

	DF	F	P
Male vs Female - 1992	4	5.05	0.0011*
Male vs Female - 1993	4	0.95	0.4382
1992 vs 1993 - Female	4	7.04	0.0001*
1992 vs 1993 - Male	4	1.28	0.2841
Preg. vs Lact. - 1992	4	0.81	0.5227
Preg. vs Post-Lact. - 1992	4	0.91	0.4620
Lact. vs Post-Lact. - 1992	4	1.22	0.3065
Preg. vs Lact. - 1993	4	14.14	0.0001*
Preg. vs Post-Lact. - 1993	4	3.04	0.0213
Lact. vs Post-Lact. - 1993	4	9.16	0.0001*

\* Significant value ( $p < 0.0051$ ), based on Sidák's multiplicative inequality.

than did females, and females in 1992 consumed more Coleoptera and less Chironomidae than did females in 1993. In 1993, bats consumed more Coleoptera during lactation than in the other reproductive periods that year, and chironomids were more abundant in the diet during the pregnancy period than during lactation. Details of these multiple comparisons are in Table 3.3.

There was no significant difference in diet diversity between sexes or years. Diet diversity was significantly greater during the postlactation period than for the other periods ( $df=2,93$ ,  $F=3.10$ ,  $P<0.05$ ; Table 3.4).

### Insect Traps

The number of insects caught in suction traps in 1993 was low, presumably due to cool ambient temperatures. Trap catches increased dramatically during the postlactation period, coinciding with an increase in ambient temperature. Because trap catches from the four locations along the river valley typically contained few individuals, and did not seem to differ in types or relative numbers of insect taxa caught, catches were pooled (Table 3.5). I only used catches from traps without lights because lights attracted a disproportionate number of chironomids (e.g. on one night, at the same location, the trap without a light caught 12 chironomids, and the trap with a light caught 700 chironomids). Only trap samples taken during

Table 3.3. Significant interactions from diet MANOVA, explained by percentages of major insect taxa in the diet of *Eptesicus fuscus*.

Contrast		Insect Taxa			
		Coleoptera	Lepidoptera	Chironomidae	Trichoptera
i) 1992 <sup>†</sup>	male	26.16 <sup>a</sup>	15.94 <sup>a</sup>	11.39 <sup>a</sup>	16.95 <sup>a</sup>
	female	54.65 <sup>b</sup>	8.60 <sup>a</sup>	8.80 <sup>b</sup>	20.12 <sup>a</sup>
ii) female	1992	54.65 <sup>a</sup>	8.60 <sup>a</sup>	8.80 <sup>a</sup>	20.12 <sup>a</sup>
	1993	33.11 <sup>b</sup>	11.28 <sup>a</sup>	17.68 <sup>b</sup>	13.74 <sup>a</sup>
iii) 1993	Pregnancy	9.85 <sup>a</sup>	13.09 <sup>a</sup>	30.97 <sup>a</sup>	22.08 <sup>a</sup>
	Lactation	45.21 <sup>b</sup>	17.98 <sup>a</sup>	5.35 <sup>b</sup>	7.90 <sup>a</sup>

† Means for each insect taxon, within a column and within a section (i, ii, iii), followed by the same letter (a, b) are not significantly different using Sidáks multiplicative inequality measure ( $p < 0.05$ ).

Table 3.4. Diet diversity, using Shannon-Weiner Index of Diversity, for male and female Eptesicus fuscus, within reproductive stages, in 1992 and 1993.

Reproductive Stage	n	Male†	n	Female
Pregnancy	17	0.87 <sup>ax</sup>	17	0.79 <sup>ax</sup>
Lactation	19	0.90 <sup>ax</sup>	31	0.69 <sup>ax</sup>
Post-lactation	5	1.25 <sup>ay</sup>	7	1.03 <sup>ay</sup>

† Means followed by the same letter within a row (a) or within a column (x,y) are not significantly different using Tukey's test ( $p < 0.05$ ).

Table 3.5. Insect taxa found in 1993 trap samples (measured as dry mass), as a percent of the entire sample. Catches represent weekly trap samples, pooled from four locations.

	Percent of Trap Sample				
	Week 1	Week 2	Week 3	Week 4	Week 5
Coleoptera	1.5	3.8	1.7	0	0
Lepidoptera	3.0	0	6.9	36.4	0
Trichoptera	9.2	0	1.7	0	29.2
Diptera					
Chironomidae	55.4	59.6	84.5	45.5	20.8
Muscidae	0	0	0	0	8.3
Culicidae	13.8	25.0	5.1	9.1	37.5
Tipulidae	9.2	7.6	0	0	4.2
Other	1.5	1.9	0	9.0	0
Hemiptera	0	1.9	0	0	0
Neuroptera	0	0	0	0	0
Hymenoptera	1.5	0	0	0	0
Homoptera	4.6	0	0	0	0
Total Mass (g)	0.227	0.112	0.224	0.170	0.035

lactation were used in analysis, due to the large number of corresponding fecal samples. Fecal analysis results from male and female bats were combined because their diets were not significantly different in 1993. Five weekly catches were used for the regression analysis between insects in the diet and insects caught in traps. Catches were from the weeks of June 14, June 21, June 28, July 12, and July 19 (traps were not operated during the week of July 5 due to cool temperature and precipitation).

There were no significant correlations, for the insect taxa tested (Coleoptera, Lepidoptera, Trichoptera, and Chironomidae), between the proportion in the feces and the proportion in the traps over the five sampling dates (Table 3.6).

## DISCUSSION

### Diet Components

The major insect taxa consumed by E. fuscus in my study were similar to those reported in other studies, particularly with regards to the consumption of Coleoptera (Black 1972; Griffith and Gates 1985; Whitaker 1972; Brigham and Saunders 1990). While Coleoptera seem to be universally predominant in the diet of E. fuscus, Hemiptera were the next most common dietary item in studies by Griffith and Gates (1985) and

Table 3.6. Results of regression of proportion of each insect taxon in the feces (by volume) versus the proportion in insect traps (by mass).  $P_{\text{slope}}$  indicates whether a significant correlation exists.

	Slope	$P_{\text{slope}}$
Coleoptera	1.33	ns <sup>†</sup>
Lepidoptera	0.34	ns
Trichoptera	0.42	ns
Chironomidae	0.45	ns

† Not significant ( $p > 0.05$ ).

Whitaker (1972). Lepidoptera were also important in both of the aforementioned studies, although dipterans were conspicuously absent in one case (Griffith and Gates 1985). Dietary differences between geographic areas could simply be a reflection of differences in prey communities, and possibly interspecific competition. The study in which no dipteran remains were found in the feces of E. fuscus found dipterans in the feces of all other bat species examined (Griffith and Gates 1985).

The predominance of beetles in the diet of big brown bats has never been fully explained. While their echolocation calls may predispose them to detecting and consuming prey within a certain size range, this is unlikely to explain the apparent predilection for beetles. It has been suggested that echo strength could be greater from the smooth surface of a beetle carapace, although this likely overlooks the subtleties and complexities of echolocation (Barclay and Brigham 1994). June beetles (Phyllophaga spp.), which are relatively large bodied insects, were commonly consumed by E. fuscus in Medicine Hat, but were never caught in suction traps. Big browns often fly quite high (up to 50m; Phillips 1966) and may therefore be exploiting higher flying insects. Based on the virtual absence of beetles from my insect trap catches, it is possible that some beetles fly relatively high, and are therefore out of trap range. However, light-tagged bats in Medicine Hat were seen foraging 1-2 m above shoreline vegetation as well as high over the river, indicating that they may be flexible in terms of spatial strata.

The conspicuous nature of large beetles, due to size and even flight pattern, likely render them easy targets for bats with appropriate jaw structure, such as E. fuscus (Freeman 1981).

Interspecific competition often results in resource partitioning, and could partially account for E. fuscus's apparent preference for beetles. If other bat species are numerous, competition may result in big brown bats, as fairly generalist foragers, exploiting an otherwise unused spatial stratum. Flying at higher altitudes would avoid much competition because many bats specialize in foraging over water (e.g. Myotis lucifugus; von Frenckell and Barclay 1987), and gleaners take prey from vegetation or from the ground (e.g. Myotis evotis; Faure and Barclay 1992).

Thus, male and female E. fuscus may be consuming large quantities of Coleoptera for similar reasons, related to foraging flexibility and accessibility of Coleoptera. It has been suggested that large insects may provide high energetic returns (e.g. Kunz 1973). However, the handling time required to eliminate the extensive exoskeleton of beetles may reduce the benefit. Furthermore, most insects have a similar energetic content per gram (Cummins and Wuycheck 1971, in Aldridge and Brigham 1991); too much emphasis may be placed on caloric differences between insects that do not differ appreciably in size.

## Intersexual Dietary Differences

Intersexual differences in diet existed in 1992 but not in 1993. The most obvious factor which may have been responsible for this discrepancy is the difference in weather; cooler temperatures in 1993 may have led to a reduction in insect abundance. Further support for the impact of ambient temperature comes from 1994, a dramatically warmer summer (mean minimum temperature in 1994 was 12.6°C, and the mean minimum temperature in 1993 was 10.1°C). Results from 1994 data (from the same maternity colonies) indicate that insect taxa other than the dominant four taxa from my study, such as Hemiptera, were prominent in the diet of E. fuscus (I. Hamilton, unpubl. data).

Low temperatures in 1993 would limit the number of available prey, and would likely necessitate a more opportunistic approach to feeding. This mode of feeding is predicted by optimal foraging theory when prey are scarce (Pulliam 1975; Charnov 1976), and has been observed in field studies (e.g. Davies 1977b). When prey are abundant, predators can afford to be more selective, a strategy apparently employed by female Myotis lucifugus (Anthony and Kunz 1977). Female E. fuscus may thus have been feeding selectively in 1992 when insects were probably more plentiful. Because chironomids were the most abundant insects in trap catches, and beetles one of the least abundant, it could be inferred that females are

selecting beetles, and eating chironomids on more of an opportunistic basis (provided insect trap catches from 1993 are representative of population trends in 1992). Although suction traps are known to catch beetles (Wilkinson 1992), it is possible that they were ineffective in this regard at my study site, due to the large size of many beetle species. Brigham and Saunders (1990) obtained similar results: a predominance of beetles in the diet, with low beetle abundance in traps. Thus, beetles may be under-represented in trap catches, but could still be the object of selective feeding. Low insect availability in 1993 would not have permitted selective feeding, and consequently female diet did not exhibit strong preferences (as indicated by the similarity of male and female diets).

Male diet was similar in both years and appeared to demonstrate opportunistic feeding. This is easily explained in 1993 because of presumed low insect availability. In 1992, however, conditions seemed conducive to selective feeding. Differences between male and female diets could be a result of different dietary values of prey consumed (i.e. Coleoptera are more valuable for some nutritional quality), or because males and females foraged in different locations for at least part of the night. The fact that there were no discernible differences in diet between males and females in 1993, when they often foraged in different locations, lends more support to selective feeding by females in 1992. It is unlikely, however, that any bat feeding strategy is predominantly selective; most research points to a more

opportunistic approach (see Fenton 1990). Because of their echolocation systems, selective feeding is probably more difficult for bats than for predators which use other senses for prey detection (Barclay and Brigham 1994, Brigham and Barclay in press). If females do require certain insects to meet dietary requirements, they may attempt to select for them, while feeding opportunistically on other available prey. This approach would help reduce search time (Westoby 1977).

Belwood and Fenton (1976) found that female M. lucifugus fed more selectively than did males, and chose relatively large prey. Their study did not directly compare diet between sexes, but rather compared diet (based on fecal samples) to insect trap catches. Prey choice of females was attributed to increased energetic demands during reproduction, which could be best satisfied by consuming large insects (Kunz 1973). However, chironomids comprised a considerable part of the diet, despite their small size. Due to the abundance and swarming nature of chironomids, they may be readily encountered and captured by foraging bats, in what could be interpreted as opportunistic feeding. In the absence of data on foraging locations in Belwood and Fenton's (1976) study, it remains questionable whether males and females were in fact selecting different prey, or were simply foraging in different places. In addition, it is unclear why males would not also forage to maximize energetic intake, if in fact beetles are a superior source of energy.

Studies of dietary differences between males and females coexisting in the same area are rare. One of the few such studies found that there was no significant difference between males and females, or between pregnant and lactating females (Swift *et al.* 1985). These findings are not entirely dissimilar to my results. Some similarities in diet between the sexes are not unexpected due to shared echolocation call types, dictating the general types and sizes of prey that can be detected. As was suggested by my study, ambient conditions, and consequently prey availability, may be largely responsible for diet choice. Thus, local conditions should play a large role in determining diet (Shiel *et al.* 1991), and could explain lack of dietary differences between males and females.

I found that diet varied significantly between reproductive stages in 1993, most likely reflecting seasonal changes in insect communities. An alternative possibility is that certain insects were more valuable to bats at certain times, but this trend was not detected in 1992, and dietary components were similar for both sexes. Changes in insect assemblages may have been more pronounced in 1993 because of unsuitably low temperatures. Brigham *et al.* (1992) found a similar trend of dietary changes corresponding to seasonal changes in insect availability. Local environmental conditions may be responsible for the degree to which insect communities change throughout the summer.

Increased selectivity should result in obvious preferences for particular

prey; dietary diversity would likely decrease. The absence of intersexual differences in diet diversity further indicates that bats were behaving similarly, and were likely more opportunistic than selective, although the predominance of beetles in the diet of females in 1992 could not be revealed by the index of diversity. Thus, it is important to look at several aspects of diet to fully understand its components. Results from the regression analysis of insect trap catches and fecal samples did not yield conclusive support for either opportunistic or selective feeding. This could well be a function of poor trap catches, confounded by the limitations of suction traps. The only change in dietary diversity was between postlactation and the other reproductive periods, presumably reflecting an overall increase in types of prey available later in the season, although, it has previously been observed that lactation corresponds to a seasonal peak in insect activity (Anthony and Kunz 1977; Barclay 1985; Rydell 1986). Insect trapping success increased dramatically during the postlactation period, and it corresponded to an increase in ambient temperature. Increased dietary diversity during this period could also be driven by bats foraging more widely and thus expanding encounters with different prey. Postlactating females begin to increase both the area and duration of foraging trips until they eventually begin to roost farther away (I. Hamilton, per. comm.; unpub. data), presumably as they move towards hibernation sites. I observed that males also began to leave the roost at the end of the lactation period, probably leaving the vicinity of

the maternity colonies (unpubl. data).

The impact of foraging habitat on diet could potentially be quite dramatic. Despite the differential use of habitat by male and female bats in Medicine Hat, dietary differences were minimal; certainly prey diversity was comparable. Provided diet is a fair reflection of prey availability, it appears that overall, similar types of insects were present in the river valley and in outlying areas. Perhaps the main difference between the two habitats was greater insect abundance along the river (as inferred by other studies). Thus, higher insect densities permit greater foraging efficiency, and possibly selectivity. This may be the premium which female E. fuscus regularly sought and likely defended.

It appears that dietary preferences of E. fuscus, at my study site, are influenced by prey assemblage and availability. Females may have been actively selecting Coleoptera in 1992, but overall, Coleoptera are the most predominant insect taxa in the diet of both sexes. E. fuscus seems to have a natural predilection for beetles, which can easily be explained by extrinsic and intrinsic factors. It is also possible that beetles may be a good source of certain dietary components. The size of the June beetles consumed at my study site may be large enough to possess exceptional caloric value. Beetles are also an excellent source of polyunsaturated fat, which is essential for hibernation, and may be an important consideration in diet selection (see Frank 1992; Brigham, per. comm.). However, if this is the case, beetles

should not be important until closer to hibernation. This preference would therefore not be relevant within the time period over which my study was conducted. If Coleoptera are of particular importance to females, they could possess certain nutritional qualities which females need more than males.

The main impetus behind investigating possible prey selection between sexes is that the escalation of energetic and nutritional demands during reproduction should influence feeding behaviour. While the importance of energy has clearly been addressed, the roles of specific nutrients remain largely in obscurity. The importance, and influence, of nutritional components of prey could be dramatic. Variation in nutritional components of insects could be at least partially responsible for observed intersexual dietary differences.

One nutrient which appears to be of particular importance to female bats, and is in short supply, is calcium (Kwiecinski *et al.* 1987; Studier *et al.* 1991; Barclay 1994). The relevance of calcium to female bats and the role it may play in foraging will be discussed in the next chapter.

## CHAPTER 4. Role of Calcium in Foraging Behaviour and Diet

### INTRODUCTION

Foraging behaviour is influenced by choices that animals must make to satisfy their requirements for energy and nutrients. Traditionally, maximization of net energy intake has been the criterion for modelling foraging strategies (e.g. Charnov 1976; Pyke *et al.* 1977; Vickery 1984; Stephens and Krebs 1986). However, energy acquisition must be in accordance with other needs and considerations, such as predator avoidance, territory defence, and avoidance of toxic secondary plant compounds by herbivores (Krebs 1973; Davies 1977a; Stephens and Krebs 1986). Furthermore, certain periods of the life cycle may impose specific dietary demands which can not be met simply by satisfying energetic requirements (Davies 1977a). This may result in different foraging behaviour from that predicted on the basis of energy demands alone.

With rate of energy intake as the currency of most foraging models, it is assumed that nutrient requirements are satisfied simultaneously. It seems more reasonable to assume, however, that a particular type of prey will not typically contain adequate levels of all required nutrients (Westoby 1977; Belovsky 1978; Rapport 1980; Studier and Sevick 1992). Evidence in support of this has been documented in herbivores; the case of moose

(Alces alces) consuming aquatic vegetation of low energetic content to meet sodium requirements is particularly illustrative of this point (Belovsky 1978).

During reproduction, energy and nutrient demands escalate for female mammals (Gittleman and Thompson 1988). For bats, the role of calcium becomes increasingly important during the reproductive cycle, based on the fact that various microchiropteran species have a large skeletal size at first flight (based on forearm length, which can be up to 95.3% of adult size; Koehler 1991; Barclay 1994). Thus, females not only have a high energy demand, but also a high calcium demand (Barclay 1994).

Birds show a similar trend, fledging at a size comparable to that of adults (Ricklefs 1971). Numerous studies have documented adult insectivorous birds actively selecting calcareous items such as bone and shell fragments (e.g. Mayoh and Zach 1986; Repasky et al. 1991; St. Louis and Breebaart 1991). Turner (1982) found that swallows (Hirundo rustica) could meet their energy requirements consuming insects in one quarter to one sixth the time it took to satisfy calcium demands. Similarly, Seastedt and MacLean (1977) concluded that maximizing the rate of calcium intake was likely the currency, not energy maximization, which governed foraging behaviour of birds with young.

Insectivorous bats are unable to exploit the same inanimate calcium sources as birds due to the limitations of their prey detection systems (e.g. Faure and Barclay 1992). Insectivorous bats are restricted to insects, which

are typically a poor source of calcium (Studier and Sevick 1992), to meet all energetic and nutrient demands. In addition, bats do not have biparental care of young as in many bird species; thus females have to provide the total energy and nutrient supply.

For most female mammals, calcium demand during lactation results in a reduction of skeletal mineral reserves (see Robbins 1983), perhaps more so for bats due to the size of young at weaning. Bone reduction has been demonstrated in little brown bats (Myotis lucifugus) during lactation, while male bats during the same period demonstrated a steady bone accretion (Kwiecinski et al. 1987). Both males and females experience a marked bone loss due to resorption during hibernation, but these mineral reserves are quickly renewed following arousal. Lactation leaves females with lower calcium levels than males prior to hibernation (Kwiecinski et al. 1987).

Maintaining adequate calcium levels is clearly a problem for female bats. When pregnant female big brown bats were fed a diet of June beetles (Phyllophaga rugosa), all caloric and nutrient requirements were adequately met or exceeded, except for calcium, which was one tenth of estimated requirements (Keeler and Studier 1992). Dietary calculations for pregnant E. fuscus indicate they would have to consume two to four times their mass in insects per night to meet calcium demands, yielding 3.5 to 7 times the estimated energy requirements (Barclay 1994). These data indicate that, for insectivorous bats, energy is readily obtainable relative to calcium. A female

bat may therefore select her diet based on calcium content of prey, which varies among insect orders (Studier and Sevick 1992).

Results from fecal analyses indicated that dietary differences existed between reproductive stages in 1993. This could be a reflection of changing insect assemblages across the reproductive season; cool temperatures in 1993 may have made these changes more pronounced than in 1992. Perhaps more important were the dietary differences between females in 1992 and all other bats. These differences could be explained by changing dietary requirements, the fulfilment of which is contingent upon available prey. Diet differences were evident in 1992 when prey abundance was likely greater than in 1993, facilitating more selective feeding. Evaluation of diet in terms of calcium content may reveal possible reasons for diet choice. I predicted that, if any significant differences existed between the calcium content of major insect taxa consumed, Coleoptera would contain the highest amount because it constituted the greatest part of the diet in female *E. fuscus* at my study site. Analyses of insects from Michigan (Studier and Sevick 1992) did not indicate any significant differences in calcium content among insect taxa similar to those in the diet of Medicine Hat bats, although habitat variation could result in different mineral contents between locations. Because calcium content of insects is typically low (Studier and Sevick 1992), I predicted that there may be differences in digestive efficiency between males and females, particularly in

terms of calcium assimilation. Minerals ingested at levels below required amounts are retained with maximal efficiency (Robbins 1983), and thus, female bats should retain proportionally more calcium than males. A feeding study could reveal digestive differences, and I predicted proportionally more calcium would be found in feces from males than in feces from females.

## METHODS AND MATERIALS

### Calcium Content of Prey

Insects caught in suction traps were dried for 48 hours at 40°C, weighed, and digested in sulphuric acid followed by addition of 5 ml of hydrogen peroxide. After digestion was complete, samples were cooled and distilled water was added to dilute to 75 ml. Samples were analysed for calcium content using atomic absorption spectrophotometry (Studier and Sevick 1992). Calcium values, calculated as parts per thousand (ppt or mg/g), were compared by ANOVA and Tukey's test (only insect taxa comprising 10% or more of the diet were included in this analysis).

## Feeding Experiment

To investigate possible differences in digestive assimilation of calcium, I conducted a feeding study in which I compared the amount of calcium in feces relative to the amount of calcium consumed. Feeding trials were run with postlactating and nonreproductive females, and males.

On the night of capture, provided they were returning from foraging, bats were not fed but simply held in cloth bags. Because food can remain in the digestive tract for up to two days, it was necessary to feed bats different insects on alternate nights, and check feces for two days following a meal to collect all related fecal material. Mealworms (*Tenebrio molitor*) and moths were selected due to their palatability and easily recognizable remains in feces. On the first feeding night bats were fed mealworms, followed by moths on the second night, and mealworms on the third night. Mealworms and moths (to be fed to the bats) were weighed, and feces were collected, prior to each feeding. On the fourth night, feces were collected and the bats were released. Only feeding data from the first and second night were used in analyses, because bats were not held long enough to collect all possible feces from the third feeding. Therefore, there were data for two feeding nights for most bats tested, although in some cases I was able to use data from only one feeding night.

I analysed fecal samples under a dissecting microscope to assess the

presence of mealworms or moths. Fecal pellets were separated based on prey content, dried for 48 hours at 40°C, weighed, and analysed for calcium content by atomic absorption spectrophotometry. Similarly, mealworms and moths were dried, weighed, and analysed for calcium content. Calcium concentration (mg/g) was multiplied by dry weight to give amount of calcium in diet and in feces. Amount of calcium in the feces was calculated as a percentage of the calcium in the respective food, yielding percent assimilation.

ANOVA was used to analyse these values, comparing between the three reproductive categories: postlactating females, nonreproductive females, and males. A term for individual within reproductive category was treated as a random variable.

## RESULTS

### Calcium Content of Prey

Results of atomic absorption spectrophotometry showed little variation existed in calcium content of the four taxa tested, Coleoptera, Lepidoptera, Trichoptera, and Chironomidae (Table 4.1). The only significant difference in calcium content was between Trichoptera and Coleoptera ( $df=3,22$ ,  $F=5.9$ ,  $P<0.005$ ). Overall, however, calcium values

Table 4.1. Mean calcium content (ppt) of the four major insect taxa found in the diet of Eptesicus fuscus.

Insect Taxa	Percent in Diet	n <sup>‡</sup>	Mean Calcium Content <sup>†</sup> (ppt)	Standard Error
Coleoptera	33.45	6	3.13 <sup>b</sup>	0.27
Lepidoptera	17.46	11	3.66 <sup>ab</sup>	0.31
Chironomidae	14.29	7	6.57 <sup>ab</sup>	0.50
Trichoptera	16.16	2	8.03 <sup>a</sup>	1.07

† Means followed by the same letter are not significantly different using Tukey's test ( $P < 0.05$ ).

‡ Number of samples tested, each sample consists of one to many individuals (minimum total mass = 0.05g).

were uniformly low, not exceeding 8 ppt.

### Feeding Experiment

The number of male and nonreproductive female bats I was able to catch was small, and not all bats would accept food. Additional bats were tested in 1994 to increase the sample size, although the number of bats successfully fed remained low (postlactating females:  $n = 8$ , nonreproductive females:  $n = 4$ , males:  $n = 5$ ).

The feeding experiment yielded low calcium assimilation values with no significant differences between males, postlactating females and nonreproductive females ( $df = 2, 17$ ,  $F = 0.34$ ,  $P > 0.05$ ; Figure 4.1). There was no significant variation in assimilation values between individuals ( $df = 14, 17$ ,  $F = 0.74$ ,  $P > 0.05$ ).

## DISCUSSION

### Influence of Calcium on Diet

Animals restricted to one prey or food type are more challenged to accommodate special dietary needs than those animals able to exploit a variety of types. The latter is exemplified by herbivores, such as moose

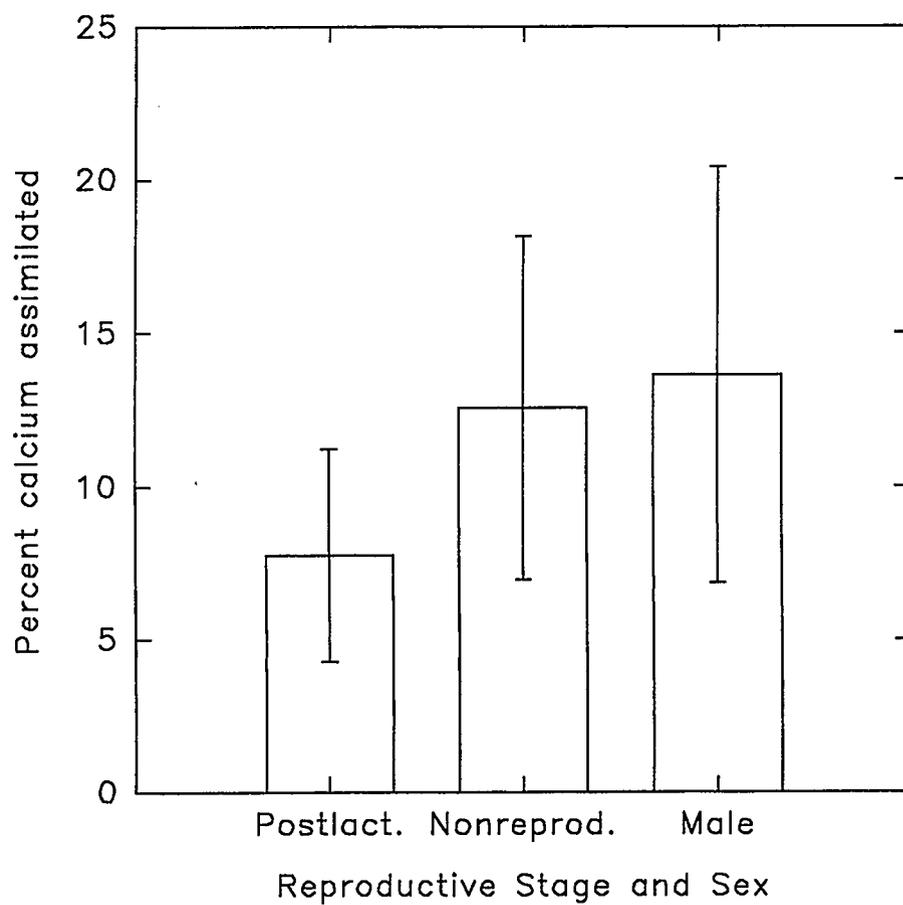


Figure 4.1. Percent calcium assimilated (ppt food/ ppt feces) in postlactating female (n = 8), nonreproductive female (n = 4), and male (n = 5) *Eptesicus fuscus*, from 1993 feeding study.

(Alces alces), which consume different types of vegetation to meet sodium and energy requirements (Belovsky 1978). In the case of flying foxes (Pteropodidae), which are frugivores, nitrogen may not be a limiting resource for those species which supplement their diet with pollen (Law 1992). Similarly, some fruit bats (Phyllostomidae) are able to supplement protein in their diet by consuming insects (Gardner 1977). Even though complementary resources are often considered to be a constraint on energy acquisition (Pyke et al. 1977; Belovsky 1978; Belovsky et al. 1989), they still provide necessary nutritional options.

If an essential nutrient is scarce relative to energy, foraging behaviour may favour maximization of intake of that nutrient. This is supported by diet patterns of paleotropical fruit bats (Pteropodidae) which, as obligate frugivores, have a diet very low in protein. Thomas (1984) found that bats needed to consume up to 2.5 times their mass in fruit each night to meet protein requirements, while energy requirements would have been met by consuming much less. Similarly, another fruit bat, Artibeus jamaicensis, consumed 40% more food, in terms of energetics, than needed for daily basal metabolism (Morrison 1978). Long foraging distances, which increase flight costs, seem to be the mechanism by which these bats deal with over-ingestion of energy.

In order to forage for a specific nutrient, however, the required nutrient must be readily available or accessible. The calcium content of

insects in Medicine Hat was uniformly low, with levels capable of providing marginal amounts of calcium relative to estimated requirements (Studier and Sevick 1992). Calcium values for insects in my study area were slightly higher (except for Trichoptera, which had considerably higher values) than those reported by Studier and Sevick (1992) in their study of nutrient levels of insects in Michigan (see Appendix 1). Differences in mineral levels in vegetation, water, and soil could account for these differences.

The relative uniformity of calcium levels in the major prey items makes foraging to maximize calcium intake an improbable strategy. Results from the Michigan study corroborate this in that only one order of insects, Plecoptera, could provide sufficient quantities of calcium, with Hemiptera coming close to providing minimal levels (Studier and Sevick 1992). Insects do not provide great enough variation in calcium content to permit selection on that basis.

It is possible that females are over-ingesting energy to fulfil calcium requirements (Barclay 1994). My calculations reveal that lactating female big brown bats are foraging longer, at least in Medicine Hat (207.5 min.) and in the Okanagan (217.2 min.; Brigham 1990), than expected based on energy demands alone (Appendix 2). My estimate of the amount of foraging time lactating females need to meet energetic demands alone was 120-140 min. I based these calculations on estimated energetic requirements, assimilated energy from insects, the number of capture attempts and the

percent of successful captures. The discrepancy between actual foraging times and estimated foraging times could be an artifact of faulty assumptions, particularly in regards to capture attempts and success rates, because sources for these estimates are sketchy.

It is possible, however, that females really are foraging longer than expected to meet nutritional demands, which would support the calcium driven foraging hypothesis. Many other insectivorous bats typically forage for relatively long periods of time during lactation (Swift 1980; Barclay 1989; Wai-Ping and Fenton 1989; Audet 1990; Wilkinson 1992; Rydell 1993), and some frugivorous bats forage longer than expected based on energetic requirements (Morrison 1978; Thomas 1984), which further indicate that energy alone may not be driving foraging strategies. Evidence in support of complementary or mixed diets lends credence to this supposition (Westoby 1977; Belovsky 1978; Rapport 1980).

### Calcium Assimilation

Under both lab (Keeler and Studier 1992) and natural conditions (Studier *et al.* 1991, 1994a,b), calcium levels in feces have been considered as indicators of calcium levels in diets. When fed a diet of June beetles, *E. fuscus* appeared to assimilate calcium with maximal efficiency, as indicated by low fecal calcium levels (Keeler and Studier 1992). Similarly, feces

collected from colonies of E. fuscus showed a similar trend, suggesting maximal calcium assimilation for females (Studier et al. 1991, 1994a). My results indicate that there is no difference in calcium assimilation abilities between sexes and reproductive conditions, despite the calcium drain on lactating females. The calcium assimilation values I obtained are lower than expected; calcium levels in feces from my study bats were considerably higher (by a magnitude of ten) than calcium levels in feces collected from colonies (Studier et al. 1991, 1994a), but it is not uncommon to get different values under artificial circumstances (E. Studier, pers. comm.). Despite these differences, the assimilation values I obtained should remain valid for relative comparisons among bats from my feeding experiment. Furthermore, there is some renal function involved with reabsorption (Robbins 1983), the role of which could be particularly instrumental for calcium assimilation in bats (G. Kwiecinski, pers. comm.). If this is the case, results from fecal analyses may not be an accurate reflection of calcium digestion.

The role of calcium in bat reproduction is clearly important, but much remains to be learned about its acquisition and the physiological mechanisms by which calcium balance is maintained. Bone loss from maternal skeletal reserves is one of the strongest pieces of evidence in support of the hypothesis that bats are calcium stressed. However, a fundamentally important part of the life cycle, hibernation, has been overlooked. During

hibernation there is progressive bone loss, presumably due to mobilization of minerals to help support metabolic demands (Kwiecinski et al. 1987). Following arousal from hibernation bone resorption is arrested and bone tissue is replenished. Temperate insectivorous bats are no exception to this pattern, with both males and females reaching bone densities equal to, or greater than, pre-hibernation levels within 1-2 months following arousal (Kwiecinski et al. 1987). In fact, specific gravity of humeri in females is virtually the same at post-hibernation as at the end of lactation; both of which are similar to post-hibernation levels of males. The apparent ability of bats, of both sexes, to quickly replenish bone tissue seems to have been overlooked. The physiological mechanisms involved with this process are not totally understood, and may operate with smaller amounts of calcium in the diet than present estimates would suggest. In mammals, bone stores are reduced during pregnancy and lactation regardless of the amount of calcium in the diet (see Kwiecinski et al. 1987).

Calcium ingested at levels below required amounts is retained with maximal efficiency (Robbins 1983). Thus, some studies involving nutrient budgets are based on the tenet that low fecal concentrations of a mineral are indicative of maximal assimilation, suggesting that the mineral is deficient in the ingested food (Hungerford et al. 1993; Studier et al. 1994a,b). While this premise is tenable, ecological implications emanating from studies based on this tenet are questionable. Studies which assess

diets as having mineral deficits may in fact be reporting a common condition. Inferring this condition as deleterious may be erroneous; the usual physiological state of an animal, while it may not be ideal, remains the normal condition with which the animal successfully survives. Seldom are animals able, physiologically or behaviourally, to accumulate and store excess nutrients; this is typically not an optimal strategy. Perhaps it would be more accurate to view these mineral deficits as vulnerabilities or limitations; ways in which an animal could be more susceptible to nutritional inadequacies, but do not initially present a tangible stress. The maternal skeleton of bats is clearly challenged (Kwiesinski et al. 1987), yet continues to function successfully.

Nutritional studies may be further confounded by the sources from which requirements are calculated. Captive animals may not behave the same as wild individuals; in fact, assimilation rates may be higher (Barclay et al. 1991; Studier et al. 1988), or lower, as results from my feeding experiment would indicate, in captive situations. Of particular relevance to bats is that the basis for most nutritional requirement estimates come from laboratory rodents (Studier and Sevick 1992), which may not be accurate models. Recent research on nutrient budgets of suckling insectivorous bats (Myotis velifer and Tadarida brasiliensis) indicate that growth requirements for measured nutrients were lower than requirements for rodents (Studier and Kunz in press). Assessments of calcium requirements for bats may be

inaccurate; the implications from this study are that requirement estimates for calcium are excessive.

Thus, inferences regarding calcium deficiencies in bats may not be as dire as presently believed. Bat populations successfully survive and reproduce despite low calcium availability in insects. Granted, if a threshold level of calcium is not reached, a range of consequences could occur.

Dietary calcium deficiency has been documented in captive populations of bats (Buckland-Wright and Pye 1973), with osteoporosis having potentially serious repercussions (Kwiecinski *et al.* 1987). Inadequate calcium in the diet may not only reduce fitness and inhibit females from reproducing, but could hinder juvenile development. Primary mortality of pups occurs over the winter (R. Barclay, unpubl. data), presumably due to their inability to store adequate amounts of fat prior to hibernation (Brigham 1987).

Susceptibility to mortality could be exacerbated by low calcium content of bone, because mineral reserves are drawn upon during hibernation. Thus, in extreme circumstances, pups may not be able to survive the winter, and of those that do, some may not have suitable mineral and energy reserves to successfully reproduce the following spring.

Calcium is clearly an essential nutrient for reproductive female bats, even if requirement estimates are excessive. Bats are challenged by having to satisfy calcium demands from a prey source which, for the most part, has uniformly low calcium concentrations. This likely negates foraging

strategies aimed at selecting prey to maximize calcium intake, although it is possible that females over-ingest energy to meet calcium demands.

Foraging behaviour is a reflection of a complex array of needs and constraints, and as such it can be difficult to isolate the primary driving forces behind feeding strategies. If dietary differences from 1992 female E. fuscus are interpreted as a result of selective feeding, prey chosen may provide the best combination of energy and calcium, in concert with minimal search and handling times. It remains plausible that if prey with high calcium content were available, female bats might exploit those resources.

## CONCLUSIONS

A complex array of factors influence diet choice and foraging behaviour. Many of these factors are common to most animals (e.g. predator avoidance), while other factors are unique. For bats, much of their uniqueness stems from their echolocation systems.

Echolocation call type predisposes bats to detect and catch certain insects, and morphology defines the degree with which bats are able to function well in different levels of clutter. Some argue that bats forage in certain habitats because of ecomorphology, while others argue that availability of suitable prey is largely responsible for habitat choices. These are not mutually exclusive, however, and both of these factors likely operate in concert. As to whether morphology and echolocation impose foraging behaviours which result in a certain diet, or whether specific diet requirements impose foraging behaviours is a moot point. Just as early models of optimal foraging tried to simplify factors influencing feeding strategies, so too does this line of thinking simplify what is clearly a complex foraging system. Broad foraging parameters are dictated by morphology and echolocation abilities, within which other variables influence diet choice and resultant foraging behaviour.

The investigation of dietary considerations can be based on a number of criteria, one of which is the influence of reproductive demands. It is

surprising that many foraging studies have neglected the possible impact of reproduction on diet choice. Studying insectivorous bats provided an ideal opportunity to investigate this point, because of the relatively large calcium demand (at least among mammals) of females. While it appears that calcium is not responsible for diet choices in my study population, it could still play a role influencing the amount of food ingested each night. If insectivorous bats were easy to maintain in captivity, diet choice experiments could be conducted to better define the role of calcium in foraging behaviour of bats. Although results from my study were inconclusive, it is possible that females are better able to assimilate calcium from the diet than are males, under natural conditions.

In summary, female E. fuscus at my study site exhibited a foraging strategy characterised by dominating a profitable feeding site, exhibiting site fidelity, and likely consuming insects on a largely opportunistic basis, with the possible selection of beetles when prey were abundant. The currency for which females foraged may not simply be energy; long foraging times indicated that they may have been trying to meet other dietary requirements. Male diet was, in some respects, similar to that of females, likely reflecting opportunistic foraging behaviour. Male bats showed less site fidelity, spending more time in lower quality habitat than along the river valley. The length of their foraging trips is likely a reflection of needing more time to acquire adequate energy in the lower quality habitats. Male E. fuscus did

not experience similar feeding constraints to females, showing greater flexibility in foraging behaviour. The flexibility shown in diet choice, by both sexes, is necessary when prey are highly susceptible to environmental stochasticity.

There is still much to be learned about foraging strategies of bats; morphological and echolocation variability simply define broad parameters within which other considerations operate, such as the important role of reproductive demands.

## LITERATURE CITED

- Aldridge, H.D.J.N. and R.M. Brigham. 1991. Factors influencing foraging time in two aerial insectivores: the bird Chordeiles minor and the bat Eptesicus fuscus. *Can. J. Zool.* 69: 62-69.
- Aldridge, H.D.J.N. and I.L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* 76: 763-778.
- Anthony, E.L.P. and T.H. Kunz. 1977. Feeding strategies of the little brown bat, Myotis lucifugus, in southern New Hampshire. *Ecology.* 58: 775-786.
- Anthony, E.L.P., M.H. Stack and T.H. Kunz. 1981. Night roosting and the nocturnal time budget of the little brown bat, Myotis lucifugus: effects of reproductive status, prey density, and environmental conditions. *Oecologia.* 51: 151-156.
- Audet, D. 1990. Foraging behaviour and habitat use by a gleaning bat, Myotis myotis (Chiroptera: Vespertilionidae). *J. Mamm.* 71: 420-427.
- Audet, D. and M.B. Fenton. 1988. Heterothermy and the use of torpor by the bat Eptesicus fuscus (Chiroptera: Vespertilionidae): a field study. *Physiol. Zool.* 61: 197-204.
- Barbour, R.W. and W.H. Davis. 1969. *Bats of America*. University Press of Kentucky, Lexington.
- Barclay, R.M.R. 1985. Long-versus short-range foraging strategies of hoary (Lasiurus cinereus) and silver-haired (Lasionycteris noctivagans) bats and the consequences for prey selection. *Can. J. Zool.* 63: 2507-2515.
- Barclay, R.M.R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, Lasiurus cinereus. *Behav. Ecol. Sociobiol.* 24: 31-37.
- Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Animal Ecol.* 60: 165-178.

- Barclay, R.M.R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. *Am. Nat.* 144: 1021-1031.
- Barclay, R.M.R. and R.M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am. Nat.* 137: 693-703.
- Barclay, R.M.R. and R.M. Brigham. 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. *Anim. Behav.* 48: 1013-1021.
- Barclay, R.M.R., M. Dolan and A. Dyck. 1991. The digestive efficiency of insectivorous bats. *Can. J. Zool.* 69: 1853-1856.
- Bell, G.P. and M.B. Fenton. 1984. The use of Doppler-shifted echoes as a flutter detection and clutter rejection system: the echolocation and feeding behaviour of Hipposideres ruber (Chiroptera: Hipposideridae). *Behav. Ecol. Sociobiol.* 15: 109-114.
- Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.* 14: 105-134.
- Belovsky, G.E., M.E. Ritchie and J. Moorehead. 1989. Foraging in complex environments: when prey availability varies over time and space. *Theor. Pop. Biol.* 36: 144-160.
- Belwood, J.J. and M.B. Fenton. 1976. Variation in the diet of Myotis lucifugus (Chiroptera: Vespertilionidae). *Can. J. Zool.* 54: 1674-1678.
- Belwood, J.J. and J.H. Fullard. 1984. Echolocation and foraging behaviour in the Hawaiian hoary bat, Lasiurus cinereus semotus. *Can. J. Zool.* 62: 2113-2120.
- Black, H.L. 1972. Differential exploitation of moths by the bats Eptesicus fuscus and Lasiurus cinereus. *J. Mamm.* 53: 598-601.
- Brack Jr, V. and R.K. LaVal. 1985. Food habits of the Indiana bat in Missouri. *J. Mamm.* 66: 308-315.
- Bradbury, J.W. and S.L. Vehrencamp. 1976. Social organization and foraging in Emballonurid bats. *Behav. Ecol. Sociobiol.* 1: 337-381.

- Brigham, R.M. 1987. The significance of winter activity of the big brown bat (Eptesicus fuscus): the influence of energy reserves. *Can. J. Zool.* 65: 1240-1242.
- Brigham, R.M. 1988. The influence of wing morphology, prey detection system and availability of prey on the foraging strategies of aerial insectivores. Ph.D. Dissertation, York University, North York.
- Brigham, R.M. 1990. Prey selection by Big Brown bats (Eptesicus fuscus) and common Nighthawks (Chordeiles minor). *Am. Midl. Nat.* 124: 73-80.
- Brigham, R.M. and R.M.R. Barclay. 1995. Prey detection by common nighthawks: does vision impose a constraint? *Ecoscience*. In press.
- Brigham, R.M. and M.B. Saunders. 1990. The diet of big brown bats (Eptesicus fuscus) in relation to insect availability in southern Alberta, Canada. *Northwest Sci.* 64: 7-10.
- Brigham, R.M., H.D.J.N. Aldridge and R.L. Mackey. 1992. Variation in habitat use and prey selection by Yuma bats, Myotis yumanensis. *J. Mamm.* 73: 640-645.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.
- Buchler, E.R. 1976. Prey selection by Myotis lucifugus (Chiroptera: Vespertilionidae). *Am. Nat.* 110: 619-628.
- Buckland-Wright, J.C. and J.D. Pye. 1973. Dietary deficiency in fruit bats. *International Zoo Yearbook.* 13: 271-277.
- Caire, W., J.F. Smith and M.A. Royce. 1984. Early foraging behavior of insectivorous bats in western Oklahoma. *J. Mamm.* 65: 319-324.
- Carpenter, F.L. and R.E. MacMillen. 1976. Threshold model of feeding territoriality and test with a Hawaiian Honeycreeper. *Science.* 194: 639-641.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Biol.* 9: 129-136.
- Christian, J.J. 1956. The natural history of a summer aggregation of big brown bat, Eptesicus fuscus fuscus. *Am. Midl. Nat.* 55: 66-95.

- Clutton-Brock, T.H., F.E. Guinness and S.D. Albon. 1982. Red Deer. Behavior and ecology of two sexes. The University of Chicago Press, Chicago.
- Cummins, K.W. and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Verein. theor. angew. Limnol. 18: 1-158.
- Davies, N.B. 1977a. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46: 37-57.
- Davies, N.B. 1977b. Prey selection and the search strategy of the spotted flycatcher (Muscicapa striata): a field study on optimal foraging. Anim. Behav. 25: 1016-1033.
- Dearing, M.D. and J.J. Schall. 1992. Testing models of optimal diet assembly by the generalist herbivorous lizard Cnemidophorus murinus. Ecology. 73: 845-858.
- de Jong, J. 1994. Distribution patterns and habitat use by bats in relation to landscape heterogeneity, and consequences for conservation. Ph.D. Dissertation, University of Uppsala, Uppsala, Sweden.
- Faure, P.A. and R.M.R. Barclay. 1992. The sensory basis of prey detection by the long-eared bat (Myotis evotis) and the consequences for prey selection. Anim. Behav. 44: 31-40.
- Fenton, M.B. 1990. The foraging behaviour and ecology of animal-eating bats. Can. J. Zool. 68: 411-422.
- Fenton, M.B., C.W. Swanepoel, R.M. Brigham, J. Cebek and M.B.C. Hickey. 1990. Foraging behaviour and prey selection by large slit-faces bats (Nycteris grandis; Chiroptera: Nycteridae). Biotropica. 22: 2-8.
- Frank, C.L. 1992. The influence of dietary fatty acids on hibernation by golden-mantled ground squirrels (Spermophilus lateralis). Physiol. Zool. 65: 906-920.
- Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Am. Nat. 108: 269-289.
- Freeman, P.W. 1981. Correspondence of food habits and morphology in insectivorous bats. J. Mamm. 62: 164-166.

- Fullard, J.H. and R.M.R. Barclay. 1980. Audition in spring species of arctiid moths as a possible response to differential levels of insectivorous bat predation. *Can. J. Zool.* 58: 1745-1750.
- Furlonger, C.L., H.J. Dewar and M.B. Fenton. 1987. Habitat use by foraging insectivorous bats. *Can. J. Zool.* 65: 284-288.
- Gardner, A.L. 1977. Feeding habits. In: *Biology of bats of the new world family Phyllostomatidae. Part II.* (Ed. by R.J. Baker, J.K. Jones Jr. and D.C. Carter). pp. 293-350. Special Publications of the Museum, Texas Tech University, Lubbock.
- Geggie, J.F. and M.B. Fenton. 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool.* 63: 263-267.
- Gittleman, J.L. and S.D. Thompson. 1988. Energy allocation in mammalian reproduction. *Am. Zool.* 28: 863-875.
- Goldman, L.J. and O.W. Henson Jr. 1977. Prey recognition and selection by the constant frequency bat, *Pleronotus p. parnellii*. *Behav. Ecol. Sociobiol.* 2: 411-419.
- Griffith, L.A. and J.E. Gates. 1985. Food habits of cave-dwelling bats in the central Appalachians. *J. Mamm.* 66: 451-460.
- Grinevitch, L., S.L. Holroyd and R.M.R. Barclay. 1995. Sex differences in the use of daily torpor and torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. *J. Zool. Lond.* In press.
- Hamilton, I.M. and R.M.R. Barclay. 1994. Patterns of daily torpor and day roost selection by male and female big brown bats (*Eptesicus fuscus*). 72: 744-749.
- Holroyd, S.L. 1993. Influences of some extrinsic and intrinsic factors on reproduction by big brown bats (*Eptesicus fuscus*) in southeastern Alberta. M.Sc. Thesis, University of Calgary, Calgary.
- Hungerford, B.S., E.H. Studier, E.J. Szuch, G.L. Pace and S. Taylor. 1993. Aspects of caloric, nitrogen and mineral nutrition during growth in nestling eastern bluebirds, *Sialia sialis*. *Comp. Biochem. Physiol.* 106A: 385-389.

- Husar, S.L. 1976. Behavioral character displacement: evidence of food partitioning in insectivorous bats. *J. Mamm.* 57: 331-338.
- Jones, G. 1990. Prey selection by the greater horseshoe bat (Rhinolophus fernmequinum): optimal foraging by echolocation? *J. Anim. Ecol.* 59: 587-602.
- Kalcounis, M.C. and R.M. Brigham. 1995. Impact of predation risk on emergence by little brown bats, Myotis lucifugus (Chiroptera: Vespertilionidae), from a maternity colony. *Ethology*. In press.
- Keeler, J.O. and E.H. Studier. 1992. Nutrition in pregnant big brown bats (Eptesicus fuscus) feeding on June beetles. *J. Mamm.* 73: 426-430.
- Koehler, C.E. 1991. The reproductive ecology of the hoary bat (Lasiurus cinereus) and its relation to litter size variation in vespertilionid bats. M.Sc. Thesis, University of Calgary, Calgary.
- Krebs, J.R. 1973. Analysis of function. In: *Function and evolution in behaviour*. (Ed. by G.P. Baerends, C. Beer and A. Manning). Clarendon Press, Oxford.
- Krull, D., A. Schumm, W. Metzner and G. Neuweiler. 1991. Foraging areas and foraging behaviour in the notch-eared bat, Myotis emarginatus (Vespertilionidae). *Ecol. Sociobiol.* 28: 247-253.
- Kunz, T.H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. *J. Mamm.* 54: 14-32.
- Kunz, T.H. 1974. Reproduction, growth and mortality of the vespertilionid bat, Eptesicus fuscus, in Kansas. *J. Mamm.* 55: 1-13.
- Kunz, T.H. 1987. Post-natal growth and energetics of suckling bats. In: *Recent advances in the study of bats*. (Ed. by M.B. Fenton, P.A. Racey and J.M.V. Raynor). Cambridge University Press, Cambridge.
- Kunz, T.H. and J.O. Whitaker Jr. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. *Can. J. Zool.* 61: 1317-1321.
- Kurta, A., and R.H. Baker. 1990. Eptesicus fuscus. *Mammalian Species*. 356: 1-10.

- Kurta, A., T.H. Kunz and K.A. Nagy. 1990. Energetics and water flux of free-ranging big brown bats (Eptesicus fuscus) during pregnancy and lactation. J. Mamm. 71: 59-65.
- Kwiecinski, G.G., L. Krook and W.A. Wimsatt. 1987. Annual skeletal changes in the little brown bat, Myotis lucifugus lucifugus, with particular reference to pregnancy and lactation. Am. J. Anat. 178: 410-420.
- Law, B.S. 1992. The maintenance nitrogen requirements of the Queensland Blossom bat (Syconycteris australis) on a sugar/pollen diet: is nitrogen a limiting resource? Physiol. Zool. 65: 634-648.
- Leonard, M.L. and M.B. Fenton. 1983. Habitat use by spotted bats (Euderma maculatum, Chiroptera: Vespertilionidae): roosting and foraging behaviour. Can. J. Zool. 61: 1487-1491.
- MacArthur, R.H. and E.R. Pianka. 1966. On the optimal use of a patchy habitat. Am. Nat. 100: 603-609.
- Mayoh, K.R. and R. Zach. 1986. Grit ingestion by nestling tree swallows and house wrens. Can. J. Zool. 64: 2090-2093.
- McAney, C.M. and J.S. Fairley. 1989. Analysis of the diet of the lesser horseshoe bat Rhinolophus hipposideros in the West of Ireland. J. Zool. Lond. 217: 491-498.
- McKenzie, N.L. and J.K. Rolfe. 1986. Structure of bat guilds in the Kimberley Mangroves, Australia. J. Anim. Ecol. 55: 401-420.
- Millar, J.S. 1977. Adaptive features of mammalian reproduction. Evolution. 31: 370-386.
- Mills, R.S., G.W. Barrett and M.P. Farrell. 1975. Population dynamics of the big brown bat (Eptesicus fuscus) in southwestern Ohio. J. Mamm. 56: 591-604.
- Morgan, N.C. and A.B. Waddell. 1961. Diurnal variation in the emergence of some aquatic insects. Trans. Roy. Ent. Soc. London. 113: 123-134.
- Morrison, D.W. 1978. Foraging ecology and energetics of the frugivorous bat Artibeus jamaicensis. Ecology. 59: 716-723.

- Nachtigall, P.E. and P.W.B. Moore. 1988. Animal sonar: process and performance. Plenum Press, New York.
- Norberg, U.M. and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Phil. Trans. Roy. Soc. Lond. B. 316: 335-427.
- Paradiso, J.L. and A.M. Greenhall. 1967. Longevity records for American bats. Am. Midl. Nat. 78: 251-252.
- Phillips, G.L. 1966. Ecology of the big brown bat (Chiroptera: Vespertilionidae) in northeastern Kansas. Am. Nat. 75: 168-198.
- Pistole, D.H. 1989. Sexual differences in the annual lipid cycle of the big brown bat, Eptesicus fuscus. Can. J. Zool. 67: 1891-1894.
- Pulliam, H.R. 1975. Diet optimization with nutrient constraints. Am. Nat. 109: 765-768.
- Pyke, G.H., H.R. Pulliam and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.
- Racey, P.A. 1974. Ageing and assessment of reproductive status of Pipistrelle bats (Pipistrelle pipistrellus). J. Zool. Lond. 173: 264-271.
- Racey, P.A. 1982. Ecology of bat reproduction. In: Ecology of bats. (Ed. by T.H. Kunz). pp. 57-104. Plenum Press Co., New York.
- Racey, P.A. and J.R. Speakman. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Symp. Zool. Soc. Lond. 57: 107-125.
- Racey, P.A. and S.M. Swift. 1985. Feeding ecology of Pipistrellus pipistrellus (Chiroptera: Vespertilionidae) during pregnancy and lactation. J. Anim. Ecol. 54: 205-215.
- Rapport, D.J. 1980. Optimal foraging for complementary resources. Am. Nat. 116: 324-346.
- Repasky, R.R., R.J. Blue and P.D. Doerr. 1991. Laying red-cockaded woodpeckers cache bone fragments. Condor. 93: 458-461.

- Ricklefs, R.E. 1971. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*. 115: 177-210.
- Robbins, C.T. 1983. *Wildlife Feeding and Nutrition*. Academic Press, New York.
- Rydell, J. 1986a. Feeding territoriality in female northern bats, *Eptesicus nilssonii*. *Ethology*. 72: 329-337.
- Rydell, J. 1986b. Foraging and diet of the northern bat *Eptesicus nilssonii* in Sweden. *Holarct. Ecol.* 9: 272-276.
- Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssonii* during pregnancy and lactation. *Oecologia*. 80: 562-565.
- Rydell, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. *J. Mamm.* 74: 503-509.
- St. Louis, V.L. and L. Breebaart. 1991. Calcium supplements in the diet of nestling tree swallows near acid sensitive lakes. *Condor*. 93: 286-294.
- Saunders, M.B. 1989. Resource partitioning between little brown bats (*Myotis lucifugus*) and long-legged bats (*Myotis volans*) in southern Alberta. M.Sc. Thesis, University of Calgary, Calgary.
- Saunders, M.B. and R.M.R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology*. 73: 1335-1345.
- Schnitzler, H.-U., E. Kalko, L. Miller and A. Surlykke. 1987. Hunting and echolocation behaviour of the bat, *Pipistrellus kuhlii*. *J. Comp. Physiol. A*. 161: 267-274.
- Schoener, T.W. 1971. Theory of feeding strategy. *Ann. Rev. Ecol. Syst.* 2: 369-404.
- Schowalter, D.B. 1980. Swarming, reproduction and early hibernation of *Myotis lucifugus* and *M. volans* in Alberta. *J. Mamm.* 61: 350-354.
- Schowalter, D.B. and J.R. Gunson. 1979. Reproductive biology of the big brown bat (*Eptesicus fuscus*) in Alberta. *Can. Field Nat.* 93: 48-54.

- Seastedt, T.R. and S.F. MacLean Jr. 1977. Calcium supplements in the diet of nestling lapland longspurs Calcarius lapponicus near Barrow, Alaska. *Ibis*. 119: 531-533.
- Shiel, C.B., C.M. McAney and J.S. Fairley. 1991. Analysis of the diet of Natterer's bat Myotis nattereri and the common long-eared bat Plecotus auritus in the West of Ireland. *J. Zool. Lond.* 223: 299-305.
- Simmons, J.A., M. Ferragamo, C.F. Moss, S.B. Stevenson and R.A. Altes. 1990. Discrimination of jittered sonar echoes by the echolocating bat, Eptesicus fuscus: the shape of target images in echolocation. *J. Comp. Physiol. A*. 167: 589-616.
- Stephens, D.W. and J.R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton.
- Studier, E.H. and T.H. Kunz. 1995. Nitrogen and mineral accretion in suckling bats, Myotis velifer and Tadarida brasiliensis. *J. Mamm.* In press.
- Studier, E.H. and S.H. Sevick. 1992. Live mass, water content, nitrogen and mineral levels in some insects from south-central lower Michigan. *Comp. Biochem. Physiol.* 103: 579-595.
- Studier, E.H., J.O. Keeler and S.H. Sevick. 1991. Nutrient composition of caterpillars, pupae, cocoons and adults of the eastern tent moth, Malacosoma americanum (Lepidoptera: Lasiocampidae). *Comp. Biochem. Physiol.* 100A: 1041-1043.
- Studier, E.H., E.J. Szuch, T.M. Tompkins and V.W. Cope. 1988. Nutritional budgets in free flying birds: cedar waxwings (Bombycilla cedrorum) feeding on Washington hawthorn fruit (Crataegus phaenopyrum). *Comp. Biochem. Physiol.* 89A: 471-474.
- Studier, E.H., S.H. Sevick, J.O. Keeler and R.A. Schenck. 1994a. Nutrient levels in guano from maternity colonies of big brown bats. *J. Mamm.* 75: 71-83.
- Studier, E.H., S.H. Sevick, D.M. Ridley and D.E. Wilson. 1994b. Mineral and nitrogen concentrations in feces of some neotropical bats. *J. Mamm.* 75: 674-680.
- Sullivan, K.A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. *Ecology*. 69: 118-124.

- Swift, S.M. 1980. Activity patterns of Pipistrelle bats (Pipistrellus pipistrellus) in north-east Scotland. J. Zool. Lond. 190: 285-295.
- Swift, S.M. and P.A. Racey. 1983. Resource partitioning in two species of vespertilionid bat (Chiroptera) occupying the same roost. J. Zool. Lond. 200: 249-259.
- Swift, S.M., P.A. Racey and M.I. Avery. 1985. Feeding ecology of Pipistrellus pipistrellus (Chiroptera: Vespertilionidae) during pregnancy and lactation. J. Anim. Ecol. 54: 217-225.
- Taylor, L.R. 1963. Temperature and insect flight. J. Anim. Ecol. 32: 99-117.
- Thomas, D.W. 1984. Fruit intake and energy budgets of frugivorous bats. Physiol. Zool. 57: 457-467.
- Thomas, D.W., M. Dorais and M.J. Bergeron. 1990. Winter energy budgets and costs of arousals for hibernating little brown bats (Myotis lucifugus). J. Mammal. 71: 474-475.
- Turner, A.K. 1982. Timing of laying by swallows (Hirundo rustica) and sand martins (Riparia riparia). J. Anim. Ecol. 51: 29-46.
- van Zyll de Jong, C.G. 1985. Handbook of Canadian mammals. 2. Bats. Nat. Mus. Nat. Hist., Ottawa. 212pp.
- Vickery, W.L. 1984. Optimal diet models and rodent food consumption. Anim. Behav. 32: 340-348.
- von Frenckell, B. and R.M.R. Barclay. 1987. Bat activity over calm and turbulent water. Can. J. Zool. 65: 219-222.
- Wai-Ping, V. and M.B. Fenton. 1989. Ecology of spotted bat (Euderma maculatum) roosting and foraging behavior. J. Mamm. 70: 617-622.
- Weathers, W.W. and K.A. Sullivan. 1991. Foraging efficiency of parent juncos and their young. Condor. 93: 346-353.
- Werner, E.E. and G.G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. Am. Zool. 21: 813-829.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108: 290-304.

- Westoby, M. 1977. What are the biological bases of varied diets? *Am. Nat.* 111: 627-631.
- Whitaker Jr., J.O. 1972. Food habits of bats from Indiana. *Can. J. Zool.* 50: 877-883.
- Whitaker Jr., J.O. 1988. Food habits analysis of insectivorous bats. In: *Ecological and behavioural methods for the study of bats.* (Ed. by T.H. Kunz). pp.171-189. Smithsonian Institution Press, Washington.
- Whitaker Jr., J.O., C. Maser and L.E. Keller. 1977. Food habits of bats of western Oregon. *Northwest Sci.* 51: 46-55.
- Wilkinson, G.S. 1992. Information transfer at evening bat colonies. *Anim. Behav.* 44: 501-518.
- Williams, C.B. 1961. Studies in the effect of weather conditions on the activity and abundance of insect populations. *Phil. Trans. R. Soc. Lond.* B244: 331-378.
- Wolf, L.L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. *Condor.* 72: 1-14.

APPENDIX 3.1 Calcium content (ppt) of some insects  
from south-central lower Michigan.  
From Studier and Sevick (1992).

Taxa	Calcium content (ppt)	
	Mean	s.e.
Coleoptera	1.050	0.052
Trichoptera	1.793	0.110
Lepidoptera	1.221	0.041
Diptera	1.471	0.114
Chironomidae	0.871	0.062

Requirement estimate for calcium = 4.0-8.0 ppt

(National Research Council. 1978. Nutrient requirements of laboratory animals, No. 10, 3rd edition. National Academy of Sciences, Washington, DC.)

APPENDIX 3.2. Calculations for expected foraging time of lactating female Eptesicus fuscus.

Energetic requirements for a lactating female:

- a) with one pup - 90.2 kJ/day
- b) with two pups - 105 kJ/day (Kunz 1987; Kurta et al. 1990)

Amount of assimilated energy from insects:

6.12 kJ/g (Kurta et al. 1990)

Required wet mass of insects per day:

- a) 14.7 g
- b) 17.2 g

Typical insect wet mass (Trichoptera):

0.0077 g (Brigham 1990)

Feeding capture attempt rate:

18.7 insects/min. (Brigham 1990)

Feeding success rate:

85% (Rydell 1989; Brigham 1990; R. Barclay, pers. comm.)

Expected foraging times:

- a) 120 min.
- b) 140 min.