

UNIVERSITY OF CALGARY

The behaviour, diet and morphology of the little brown bat (*Myotis lucifugus*) near the
northern extent of its range in Yukon Canada.

By

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ABSTRACT

I investigated how nocturnal mammals, specifically little brown bats (*Myotis lucifugus*), adjust their foraging behaviour and diet in northern areas where there is a short reproductive season, low temperatures and short nights. In Watson Lake, Yukon (60°06' N, 128°46' W), *M. lucifugus* remained nocturnal throughout the summer, despite considerable variation in temperature and night length. Individuals did not use open-field habitat except when emerging from or returning to the maternity roost. *Myotis lucifugus* used habitats not commonly used in more southern latitudes, specifically the forest interior. Unlike more southern populations, *M. lucifugus* in Watson Lake foraged extensively on non-volant prey, specifically spiders, particularly when temperatures and flying insect abundance were low. *Myotis lucifugus* in the north was more adapted to foraging in cluttered environments and possibly gleaning insects from vegetation than those in a southern location (Calgary, Alberta, Canada; 51°05'N, 114°05'W) because they were significantly smaller and had smaller wings.

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DEDICATION

To Giuseppe and Teresa Talerico

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CHAPTER ONE

GENERAL INTRODUCTION

Few studies have focused on the behaviour of northern (subarctic and arctic) nocturnal mammals. These animals, which live at the northern extent of their species' range, are of interest because they live in an environment of seasonal temperature and light extremes. In the north, animals generally experience lower temperatures and a greater range of hours of sunlight than more southern populations. In the winter, darkness can last up to 24 hours and in the summer the sun may not go below the horizon. The absence of night during the summer months is especially intriguing in regards to nocturnal animals. How do nocturnal animals meet their energy demands in the land of the midnight sun? Do they change their behaviour as the nights get shorter? Do they become diurnal? The goal of my study was to address some of these questions, and specifically how lower temperatures, a short reproductive season, and changes in night length influence the behaviour and diet of northern nocturnal mammals.

High latitude environments are challenging for animals because of the severity and unpredictability of the weather, the wide seasonal differences between winter and summer, the annual variability in weather, the short growing season, as well as variations in food availability (Downes, 1965; Underwood, 1975). To survive and reproduce, organisms must be able to tolerate a wide range of climatic conditions experienced over their life times. Broad tolerances allow these organisms to be less restricted in their habitat use and typically they have a greater geographical range than organisms with less tolerance (Stevens, 1989). Density and richness of organisms at high latitudes tends to be lower than at low latitudes where animals tend to have a narrower range of tolerances (Altringham, 1996; Parker *et al.*, 1997; Stevens, 1989). In response to these environmental extremes, animals reaching the edge of their distributional range may exhibit more behavioural plasticity than near the centre of their distribution (Case *et al.*, 2005; Holt and Keitt, 2005; Holt *et al.*, 2005).

Northern animals can cope with climatic stresses through behavioural, physiological and morphological means. During periods of cool temperatures, northern animals can conserve heat and energy by reducing their activity and remaining in well insulated nests, roosts or dens (Chappell, 1980; Prestrud, 1991). To increase heat absorption, they can bask in the sun, huddle with other individuals, enter a curled posture, and choose warmer habitats to live and forage in (Danks, 2004; Prestrud, 1991). Many animals have the ability to emerge and be active at much lower temperatures than more temperate conspecifics (Danks, 2004). Some species of insects are able to survive in cold, dry habitats by having freezing tolerance and desiccation resistance (Danks, 2004). Some mammals, such as bats, can save energy by actively lowering their metabolism and body temperature by entering torpor (Barclay *et al.*, 2001).

Northern birds and mammals can also adapt to cooler temperatures by regulating their thermal conductance. They tend to have more insulation through hair, fur, feathers, and/or fat than southern birds and mammals in order to retain heat (Prestrud, 1991; Underwood, 1975). Body mass is predicted to be greater for species of birds and mammals at higher latitudes or in colder environments than species at lower latitudes or in warmer climates (Bergmann's rule; Bergmann, 1847; Blackburn *et al.*, 1999). Larger body mass is advantageous at high latitudes because larger birds and mammals expend less energy in thermoregulation due to a lower surface-to-volume ratio (Burnett, 1983; McNab, 1971). This allows more energy to be directed towards other activities such as reproduction and growth (Solick, 2004). However, recent studies on mammals have challenged Bergmann's rule (e.g. Ashton *et al.*, 2000; Meiri and Davan, 2003; Meiri *et al.*, 2007). An organism in a cold environment can also reduce its heat loss by decreasing the surface area of its extremities. Allen's rule predicts that body extremities (i.e. wings, feet, and ears) should be smaller and/or shorter in endothermic animals of cooler climates than warmer climates (Allen 1877).

In addition to climatic challenges, northern animals also face extreme changes in light cycles throughout the year. The number of hours of darkness varies with latitude over the seasons, becoming more extreme with increasing latitude. During the winter,

north of the Arctic Circle, the sun does not go above the horizon and darkness persists. In the summer months, the sun does not go below the horizon, resulting in continuous daylight. Long summer days may be beneficial to diurnal animals because they have an increased period of time to forage and replenish energy deficits from the winter and also meet energy demands of reproduction in the summer. For nocturnal animals, however, the summer months bring added challenges because there is a decrease or absence of their dark activity period. Short nights impose a short foraging period on nocturnal animals and thus it may be difficult for them to meet their energy requirements, especially for reproductive individuals that have increased energy demands.

The short summer, relatively cool summer temperatures and limited periods of darkness may result in lower reproductive rates or higher mortality rates of nocturnal mammals at the northern edge of their distributional range. Females may not be capable of replenishing their energy deficits from the previous winter, meeting the high energy demands of the summer (which may include pregnancy and lactation), and preparing for the following winter, all in a span of a few months that coincide with the least amount of daily darkness. Likewise, young-of-the-year may be stressed to obtain enough energy for growth and energy reserves for the following winter, during cool late summer and early fall evenings.

Northern animals can adapt to the short reproductive season by emerging early in the spring, and choosing a warm environment to have their young (e.g. south facing aspects). Some northern insects are also able to develop more rapidly (e.g. some mosquitoes and black flies) or extend juvenile growth period over several seasons (Danks, 2004).

How nocturnal animals cope with changes in light intensity over the summer may be explained by considering why they are nocturnal. Two primary explanations have been proposed as to why. During the day there may be an increased risk of predation and/or increased competition from diurnal animals. Many nocturnal and diurnal predators depend on vision and thus may be more efficient at capturing prey during the day or on brighter nights (Brigham and Barclay, 1992; Bender *et al.*, 1996; Clarke, 1983; Kramer and Birney, 2001). Nocturnal animals may be more susceptible to being

captured during the light hours when they are not protected by the cover of darkness (Speakman, 1991). Nocturnal animals may also avoid exploitative or interference competition for scarce resources (Birch, 1957; Case and Gilpin, 1974) from diurnal animals in similar niches (e.g. tree swallows) by foraging during the night (Speakman *et al.*, 2000). If predation risk is a northern nocturnal animal's primary concern, then in the absence of a dark foraging period (i.e. mid summer), the animal will be active during peak prey activity times, even if during the daytime hours, because predation risk is equalized over the 24-hour period (Speakman *et al.*, 2000). The behaviour and activity patterns of the animal would mimic the behaviour and activity patterns of its prey. If nocturnal animals are active at night to avoid competition with diurnal animals, then they should be most active when diurnal competitors are not (Speakman *et al.*, 2000).

Previous Studies

I know of three studies examining the behaviour of nocturnal mammals north of the 60th parallel. In southern Yukon, Canada (61°N), deer mice (*Peromyscus maniculatus*) changed their activity patterns over the summer season (Gilbert *et al.*, 1985). In June, they emerged later than in September, but always returned at 07:00 throughout the summer; the length of foraging periods increased by four hours from June to September. In northern Sweden (65°N) (Rydell, 1989a) and Norway (69°N) (Speakman *et al.*, 2000), the northern bat (*Eptesicus nilssoni*) foraged in the 'daylight' during the summer, but only when the sun was at its lowest (22:00 to 02:30 in Sweden and 22:00 to 02:00 in Norway) and never during the day. During daylight 'nocturnal' foraging, northern bats avoided open areas when feeding at 5-15 m, and foraged in groups at 50 m or more above the vegetation (Rydell, 1989a). Unlike in southern populations, northern bats avoided foraging over lakes (Rydell, 1989a). Bat activity was highly correlated with ambient light levels, suggesting that predation risk varies with light level (Speakman *et al.*, 2000).

Although there are relatively few studies on how nocturnal mammals behave during the summer at high latitudes, many studies have examined how a variety of nocturnal animals are influenced by changes in moonlight. During the full moon, when nights are the brightest, small nocturnal rodents forage for less time or do not emerge at

all (Bowers, 1988; Clarke, 1983; Kotler *et al.*, 1991; Kramer and Birney, 2001; Topping *et al.*, 1999). They avoid more exposed, open habitats on bright nights and instead forage in more protected, covered habitats such as forest interiors (Bowers, 1988; Gilbert and Boutin, 1991; Kotler *et al.*, 1991; Price *et al.*, 1984). Some mammals were more selective in their food choice when in exposed habitats, taking only high quality items on brighter nights (Bowers, 1988; Kotler *et al.*, 1991). These changes in behaviour with increased moonlight illumination have been attributed to the increased threat of predation by nocturnal predators (Bowers, 1988; Clarke, 1983; Kotler *et al.*, 1991; Topping *et al.*, 1999).

Study Organism

I chose bats (Chiroptera) as my study organism because they are exclusively nocturnal (Duverge *et al.*, 2000; Rydell and Speakman, 1995) and their behaviours are relatively easy to study, unlike many nocturnal animals. Bat activity can be passively monitored using ultrasonic detectors and consequently many locations can be monitored on the same night. A large sample size is also possible because during the summer, female bats of many species aggregate in roosts to form maternity colonies. Emergence and return of bats at the maternity colony is easily observed. Bats can also be captured in mist nets.

Research Objectives and Predictions

The primary objective of my study was to determine how nocturnal mammals, specifically bats, adjust their foraging behaviour in northern areas where there is a short reproductive season, low temperatures and short nights. I examined: (1) timing of emergence and return, (2) foraging habitat, (3) diet, and (4) insect abundance and distribution.

I hypothesized that the short reproductive season, low temperatures and short nights limit the foraging opportunities of northern bats. Therefore, the amount of energy collected during the ‘dark’ hours would be reduced, compared to bats at lower latitudes (Speakman, 1991). I thus expected that to cope with potential energy deficits, bats at high latitudes must modify their foraging behaviour. I predicted that during mid-summer, when nights are the shortest, bats emerge from the maternity roost before sunset and

return after sunrise. Second, I predicted that bats shift their foraging habitats with changes in light intensity over the summer. Specifically, during periods of high light intensity (e.g. around the solstice), I predicted that foraging bats avoid open areas, such as open fields and lakes, and instead forage in shaded areas such as forest edges and in the forest interior. Third, I predicted that bats forage at lower ambient temperatures than in more southern locations. Lastly, I predicted that bat foraging behaviour and diet vary according to temperature and with the invertebrates available in foraging habitats. Specifically, during periods of low temperatures, I predicted that bats forage more on non-flying invertebrates such as spiders. If bats obtain some prey via gleaning then I predicted that the wing morphology differs from that in southern populations.

Site Description

I conducted research with an assistant and volunteers from 7 May to 20 August 2006 in the south-eastern Yukon, in the vicinity of Watson Lake ($60^{\circ} 06' N$, $128^{\circ} 46' W$) (Fig. 1.1). Because both the lake and town are named Watson Lake, I refer to the lake as Watson Lake and the town as the town of Watson Lake. Watson Lake is in the Liard Basin ecoregion within the Boreal Cordillera Ecozone (Scudder, 1997). It is located below the treeline, in the scattered permafrost zone at an elevation of 680 m (Scudder, 1997; Rawn *et al.*, 2001). Watson Lake has an area of 15.4 km^2 and is surrounded primarily by boreal forest, dominated by lodgepole pine (*Pinus contorta*). Other tree species include: *Picea glauca*, *Picea mariana*, *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera* (Scudder, 1997). Developed and open areas around the lake include: the Watson Lake airport on the north shore, residential housing along the northeast shore, the town of Watson Lake to the southeast, and a campground and forestry clear-cuts to the south. Numerous small waterbodies and watercourses exist in the area.

I based the majority of my study around the Watson Lake airport on the north shore of Watson Lake because a maternity colony of little brown bats (*Myotis lucifugus*) roosts in the airport terminal tower during the summer. The Watson Lake airport building is located between the Robert Campbell Highway and Watson Lake. It is completely surrounded by open area (parking lot, runway) in all directions for at least 130 m. Other than three conifers immediately beside the building, the area surrounding the building is

devoid of woody vegetation (> 0.2 m tall). A chain link fence runs around the entire active airport site. During my study, Watson Lake airport was active primarily during the day for smaller aircraft to land. Although it remained open, the airport was rarely used at night except when there was a medical emergency. The runway was only lit when aircraft were landing at night. Flood lights on the south side of the airport tower were on during the night to illuminate the parking lot. Radar is not used at this airport. The airport has a weather station where hourly weather measurements such as cloud cover, temperature, relative humidity and wind speed are made by airport staff. Other buildings such as a fire hall, two air hangers and a bed and breakfast are also located on the airport site.

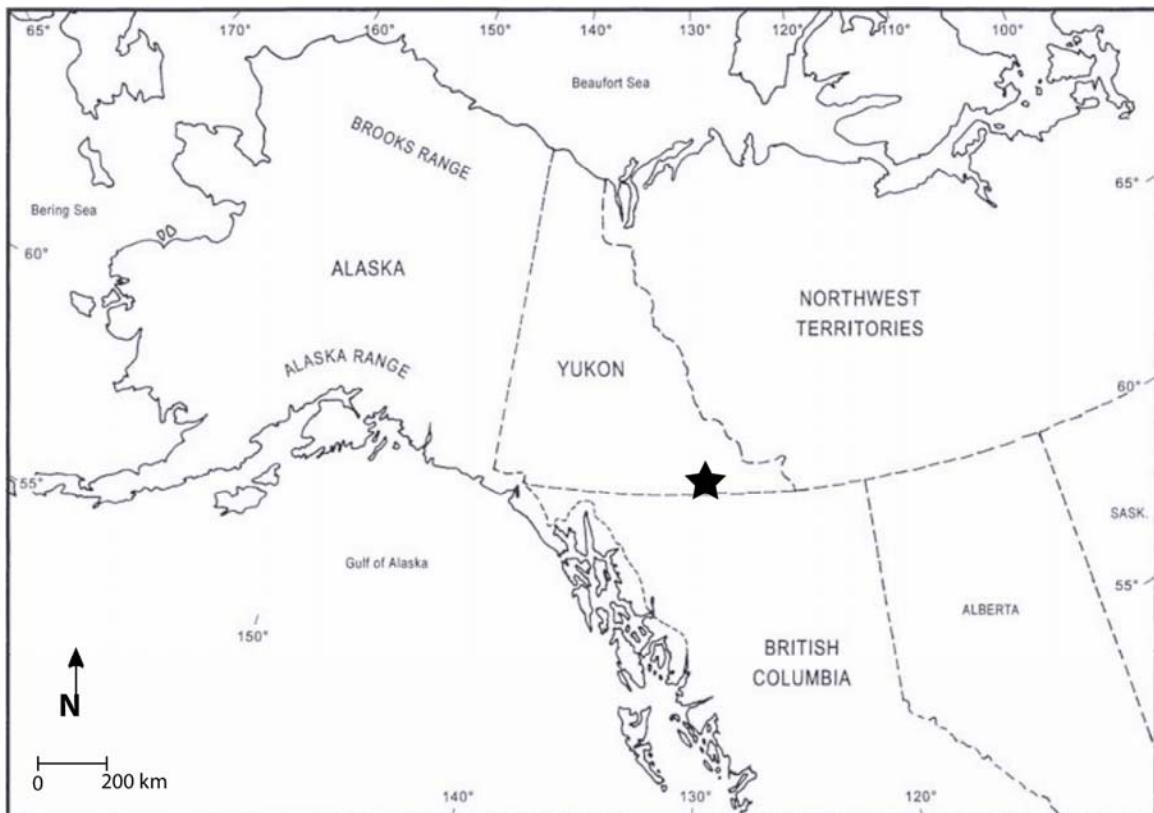


Figure 1.1: Geographic reference map of Yukon (modified from Scudder, 1997). The star indicates the location of my study site, Watson Lake, Yukon.

The area surrounding and within the airport is made up of a number of different habitat types. Extensive human use in the area has created a number of patches of forest and open fields, as well as many forest corridors. Water bodies and courses within the immediate area include Watson Lake, an inlet of Watson Lake, and Watson Creek. For my study, I identified six habitat types in which I assessed bat activity: 1) flowing water, 2) forest corridor, 3) forest edge, 4) forest interior, 5) open field, and 6) standing water. I identified four sites of each habitat type that were at least 180 m apart, for a total of 24 sites (Fig. 1.2). I defined each habitat type as follows:

- 1) flowing water was a water course, with flowing water, that was 5 to 15 m wide and ≥ 200 m long. Woody and herbaceous vegetation may be present along the shoreline but vegetation did not completely enclose the water course with a canopy.
- 2) forest corridor was a linear feature without trees through the forest and was ≥ 50 m long and 2 to 15 m wide (e.g. old road or trail). The forest corridor habitat had forest (tree height > 3 m) on each side of it for ≥ 30 m. The forest corridor was not enclosed by overhanging vegetation.
- 3) forest edge was the interface between an area of forest (tree height > 3 m) and an open field. Forest edge sites were ≥ 60 m long. They had forest on one side that extended ≥ 50 m from the edge, and open field on the other side that extended ≥ 100 m.
- 4) forest interior was an area that had forest in all directions for at least 30 m. Forest was defined as an area densely populated with woody vegetation (height > 3 m). Forest interior sites were situated at least 50 m from any body of standing water.
- 5) open field was cleared land devoid of woody vegetation (height > 0.2 m) in all directions for at least 30 m. All sites were ≥ 150 m from Watson Lake or other bodies of standing water and > 50 m away from a building (not including small storage sheds).
- 6) standing water was a non-flowing body of water ≥ 25 m long and ≥ 10 m wide. Woody and herbaceous vegetation may be present along the shoreline but vegetation did not completely enclose the water body with a canopy. Standing water sites were ≥ 15 m away from forest edge.

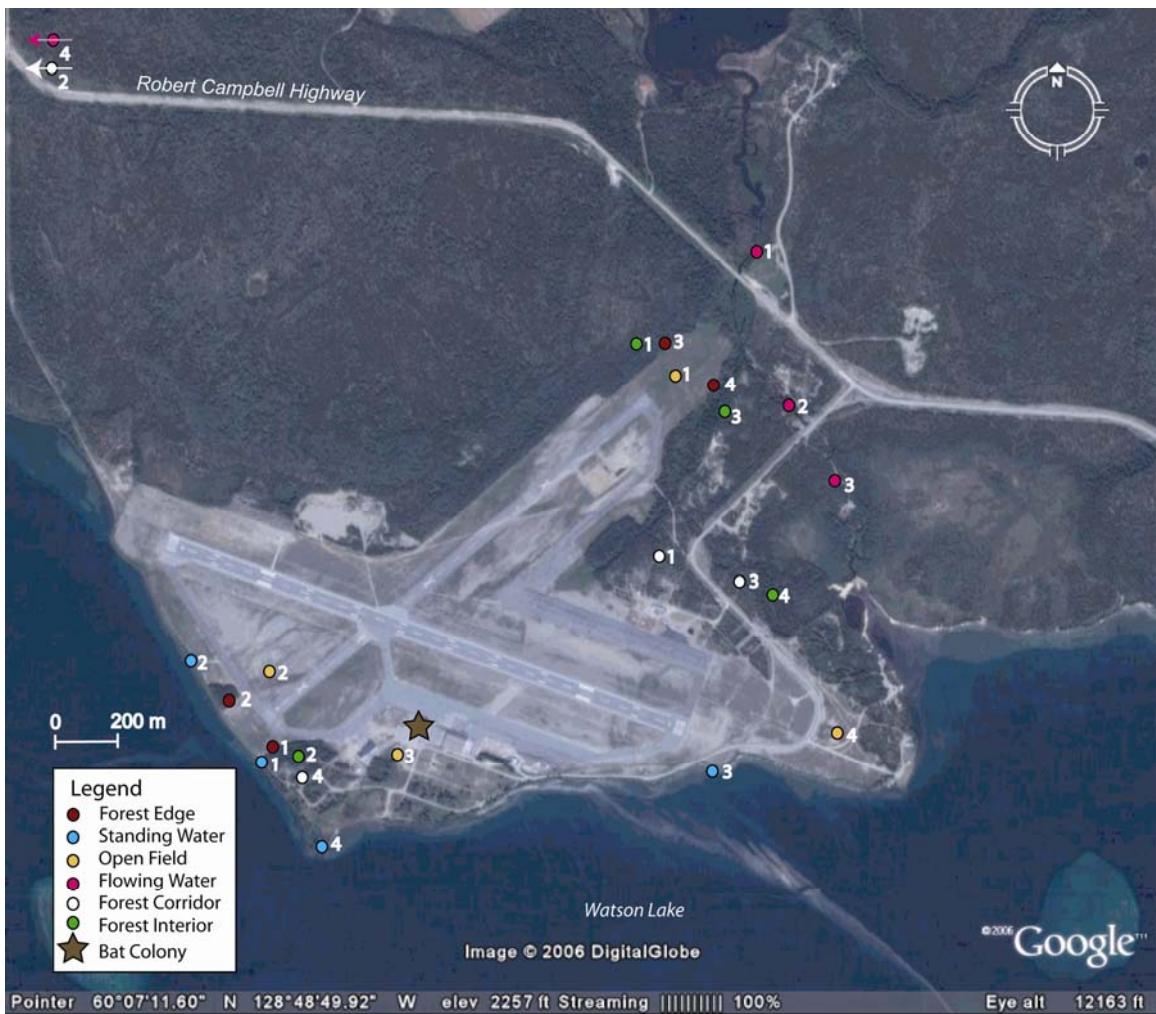


Figure 1.2: Map of Watson Lake airport sampling locations, Watson Lake Yukon (modified from Google Earth by J. Talerico).

Activity at the Watson Lake airport was likely dominated by one maternity colony. I therefore also sampled three other areas that were likely used by different colonies: 1) the town of Watson Lake, 2) Watson Lake campground and 3) Albert Creek bird banding station (Fig. 1.3). I designated one sampling site for each habitat type, when present, at each of the three secondary study areas. I chose these sampling locations based on access (which was limited) and number of buildings in the area. Like the Watson Lake airport, the town of Watson Lake had many buildings, including 430 private dwellings. Albert Creek Bird Banding station and the Watson Lake campground had no permanent buildings within 1 km of each sampling site.



Figure 1.3: Overview map of all sampling locations, Yukon (modified from Google Earth by J. Talerico).

Within the town of Watson Lake, forest corridor, forest interior, and standing water sites were located in Wye Park, a forested area located between Wye Lake and Second Wye Lake, on the east side of the town (Fig. 1.4). Dense residential housing was located east and north of the lakes and country residential homes were located on the shore of Second Wye Lake and to the south and east. Forest edge and open field sites were located on the south side of the Alaska Highway at the TransNorth Helicopter site. I did not want to set-up equipment in exposed sites around town, due to the potential for theft and vandalism. No flowing water, meeting my specifications, was present within the town.

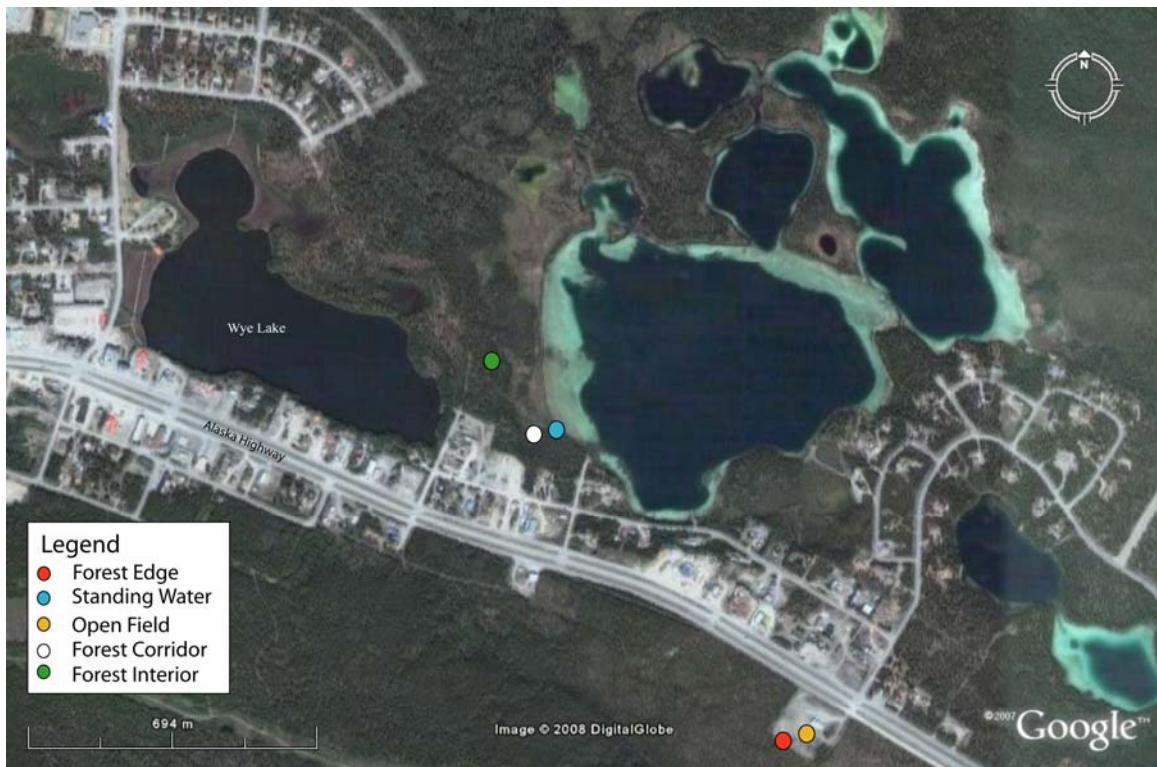


Figure 1.4: Map of town of Watson Lake sampling locations, Yukon (modified from Google Earth by J. Talerico).

The Watson Lake campground was located on the south side of Watson Lake, 3.9 km west of the town centre (Fig. 1.5). The campground area was heavily forested with a few roads leading to campsites, some forest trails for hiking and cross country skiing, and small clearings for camping. No buildings were present within the campground. There were no flowing water, open field, or forest edge sites, meeting my specifications, within the campground. There was a large open area located southwest of the campground, but it was a secure site that I could not gain access to. Two standing water sites were sampled at the Watson Lake campground location, to assess differences between the lake and these smaller bodies of standing water.

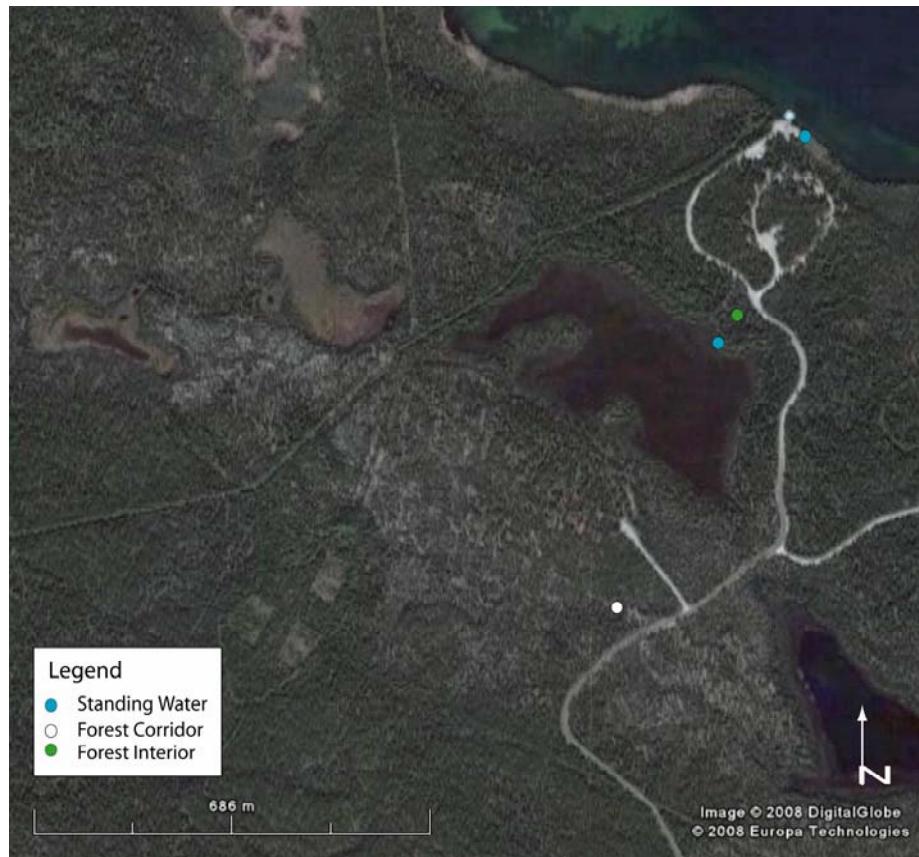


Figure 1.5: Map of Watson Lake campground sampling locations, Yukon (modified from Google Earth by J. Talerico)

Albert Creek bird banding and migration monitoring station was situated along Albert Creek, 15 km west of the town of Watson Lake (Fig. 1.6). The area was mainly composed of regenerating forest and marsh. The area was diverse in habitat types and supported many migratory bird species and individuals (Schonewille and Murphy-Kelly, 2005). All habitat types meeting my specifications were found at Albert Creek bird banding station.

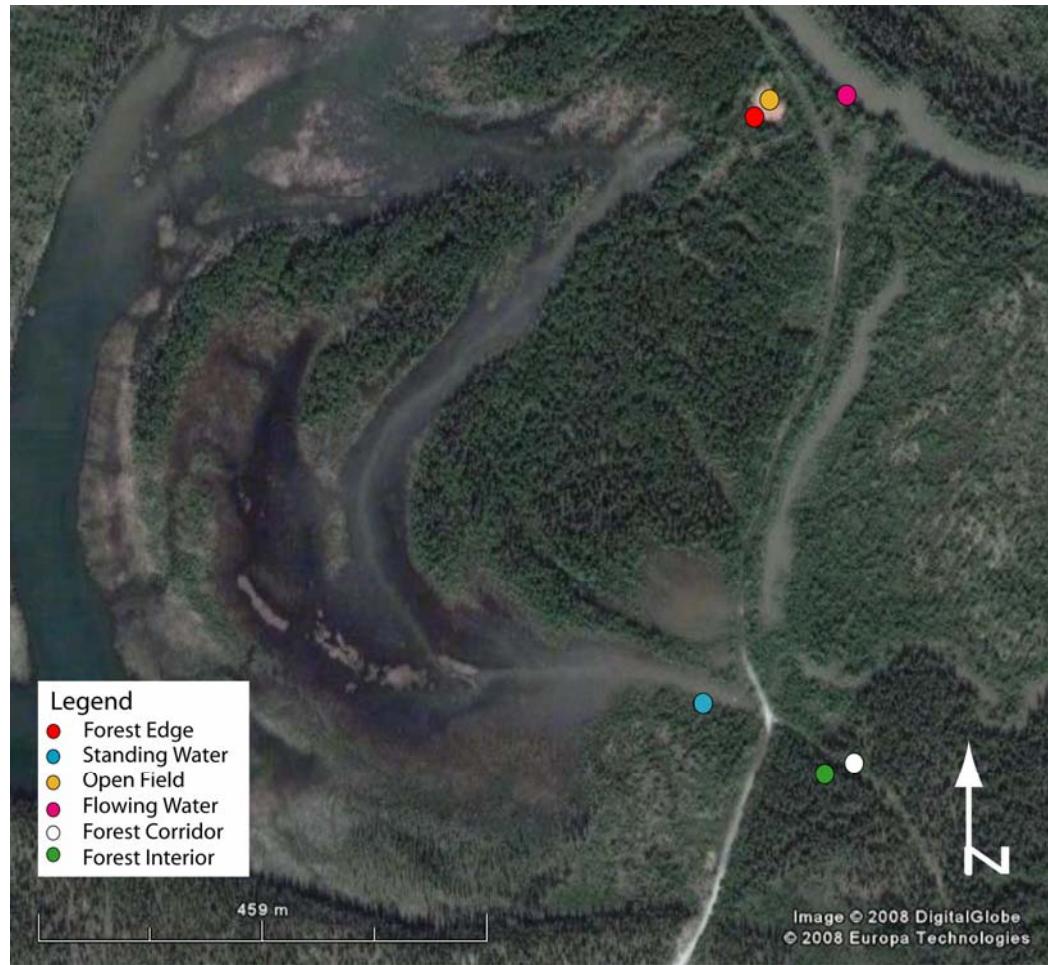


Figure 1.6: Map of Albert Creek sampling locations, Yukon (modified from Google Earth by J. Talerico).

Climate

Watson Lake is located in the Liard Basin climatic region (Scudder, 1997) which has the most days with recorded precipitation in Yukon, mostly in the form of snow (Scudder, 1997). In 2006, the last snowfall in spring was 13 May (14.6 mm). Weather from 2006 is summarized in Table 1.1. Because bats are active at night, all weather measurements are from the night (from time of sunset to sunrise). Precipitation measurements (mm) were made every six hours at the Watson Lake Airport weather station and so nightly precipitation is from 17:00 to 05:00. Daily (24 hour period) minimum and maximum temperatures ($^{\circ}\text{C}$) are in Figure 1.7 (Environment Canada, 2006).

Table 1.1 2006 weather data for Watson Lake Yukon. Night length is defined as the time from sunset to sunrise. Precipitation was measured from 17:00 to 05:00. All measurements were made at the Watson Lake Airport by airport staff.

Month	Temperature ($^{\circ}\text{C}$)		Mean nightly			Total Rainfall (mm)	Total Snowfall (mm)
	Mean Max	Mean Min	Temperature ($^{\circ}\text{C}$)	Relative Humidity	Wind Speed (km/hr)		
May	11.7	0.3	3.8	81.3	3.1	49.2	14.6
June	21.0	7.0	11.5	65.3	4.3	15.2	0.0
July	21.7	9.3	13.0	74.6	3.1	18.6	0.0
August	17.9	7.0	10.3	77.3	4.3	27.4	0.0

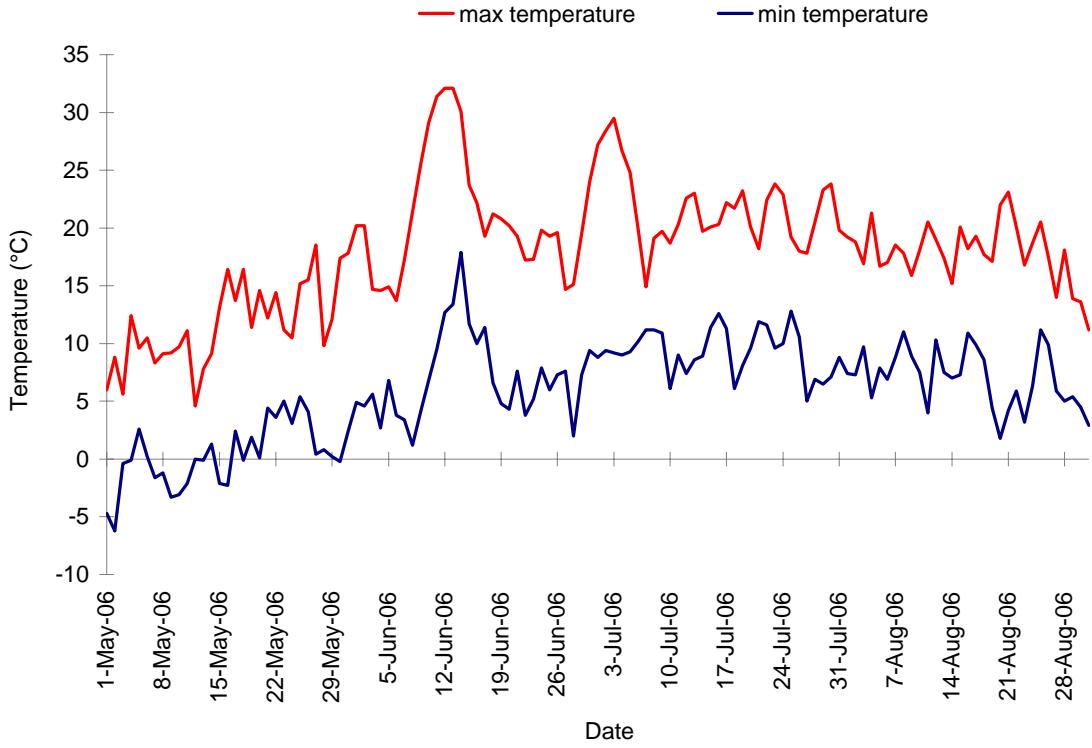


Figure 1.7: Daily minimum and maximum temperatures at the Watson Lake airport in 2006 (Environment Canada, 2006).

Sunrise and Sunset

The time between sunset and sunrise varies greatly at 60° N. In May, the time between sunset and sunrise is approximately seven hours. This decreases to a minimum at summer solstice (21 June) of approximately 4.75 hours and then increases again into late August with approximately 8.5 hours (Figs. 1.8a and 1.8b). The short period of darkness is further reduced in midsummer by the increased duration of civil twilight. Civil twilight is the time after sunset and before sunrise when the centre of the sun is less than 6° below the horizon. During this period, terrestrial objects can be distinguished because it is essentially not ‘dark’. In Watson Lake, the centre of the sun does not go 6° below the horizon from 9 June to 3 July and so civil twilight persists (Figs. 1.8a and 1.8b).

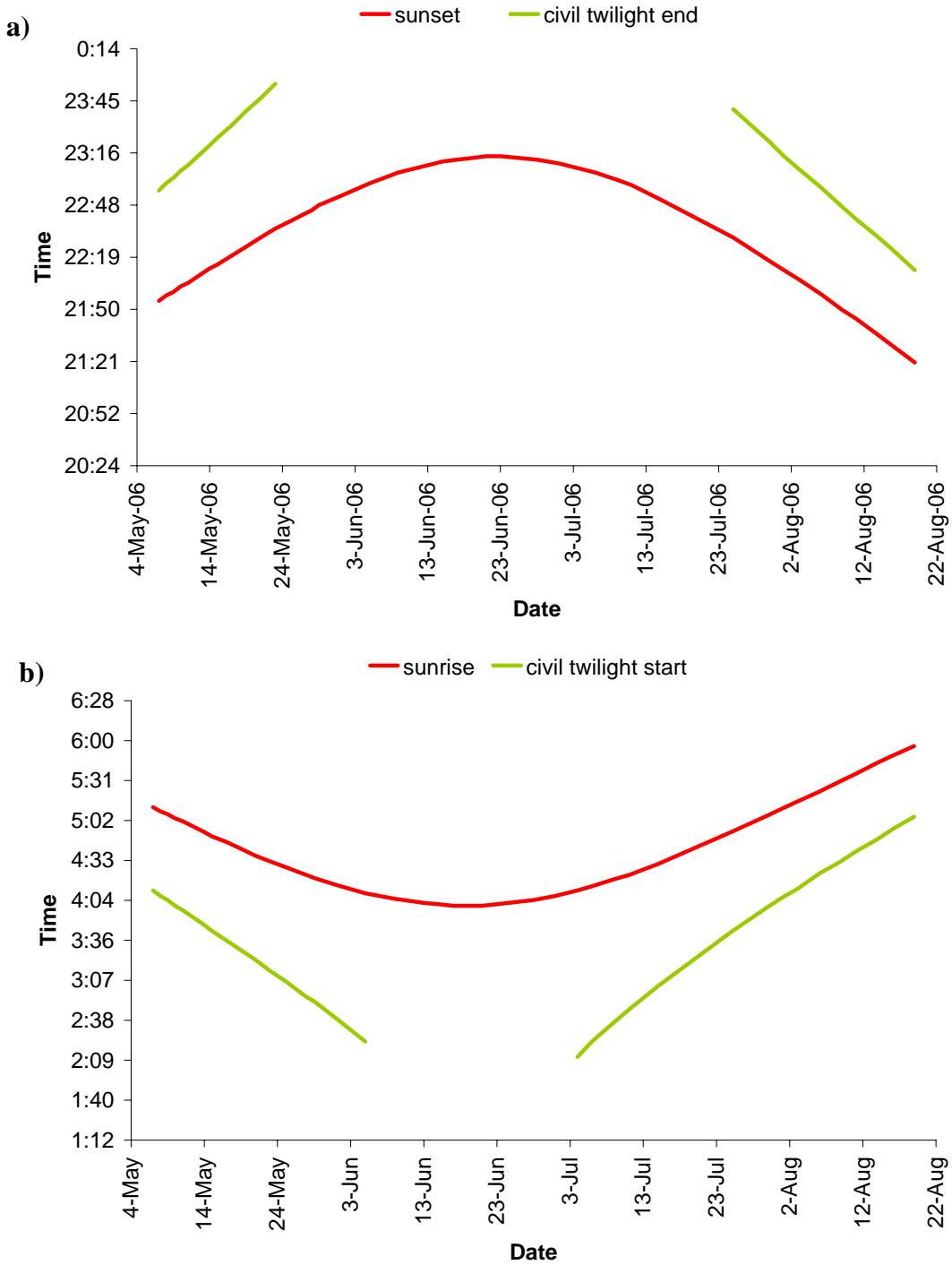


Figure 1.8: Time of sunset and end of civil twilight (a) and time of sunrise and start of civil twilight (b) in Watson Lake Yukon, 2006 (National Research Council Canada. 2006).

Study Species

Myotis lucifugus (little brown bat, Vespertilionidae) is a ubiquitous species that inhabits most of North America. It ranges from Mexico to northern Canada and Alaska and has been documented as far north as Minto, Alaska ($65^{\circ} 42'N$, $148^{\circ} 49'W$) and Dawson City Yukon ($64^{\circ} 4'N$, $139^{\circ} 20'W$; Parker, 1996). This species has a large altitudinal range, from sea level (Nagorsen and Brigham, 1993) to 2769 meters above sea level (C. Lausen and J. Talerico unpublished data). *Myotis lucifugus* is the most prevalent bat species in Yukon; only one other species (*M. septentrionalis*) has been captured (Lausen *et al.*, 2008; Jung *et al.* 2006) although others likely exist (Slough and Jung, *in press*). Six subspecies of *M. lucifugus* exist (Fenton and Barclay, 1980) with *M. l. lucifugus* occurring in my study area.

Myotis lucifugus is well-studied near the core of its range (e.g. Anthony and Kunz, 1977; Anthony *et al.*, 1981, Belwood and Fenton, 1976; Cagle and Cockrum 1943) but poorly near the edge of their range (e.g. Parker, 1996; Whitaker and Lawhead, 1992). It uses a variety of environments, including the northern boreal forest, arid grasslands, ponderosa pine (*Pinus ponderosa*) forests and the humid coastal forest (Barcaly and Fenton, 1980; Nagorsen and Brigham, 1993). Like many other northern-latitude bats, there is sexual segregation in this species (e.g. Barclay, 1991; Jung *et al.*, 1999). During the summer, females live together in maternity colonies where they give birth to one young each. Males and non-reproductive females typically roost alone or in small colonies. Maternity colonies are often found in hollow trees or in man-made structures such as buildings. During the winter months, male and female *M. lucifugus* hibernate in caves and abandoned mines which can be up to 50 to 800 km from their summer roost (Fenton, 1969; Nagorsen and Brigham, 1993). In Yukon, it is not known where bats spend the winter. It has been hypothesized that because of the lack of known caves and cold ambient temperature in the winter, they may hibernate in coastal Alaska or the karst topography of western Northwest Territories (B. Slough and T. Jung, pers. comm.)

Myotis lucifugus is an aerial insectivore, but is also capable of gleaning (Ratcliffe and Dawson, 2003). It emerges at dusk to feed and typically has two foraging bouts before dawn, separated by a period of night roosting (Anthony *et al.*, 1981). It typically forages over water and is occasionally captured or detected along forest corridors (Barclay, 1991; Broders *et al.*, 2003, 2004; Buchler, 1976; Fenton *et al.*, 1980; Fenton and Bell, 1979; Jung *et al.*, 1999; Parker *et al.* 1997; Saunders and Barclay, 1992; von Frenckell and Barclay, 1987). Activity within the forest interior is uncommon (Barclay, 1991). *Myotis lucifugus* forages 1-4 m above the ground when foraging along the margins of lakes and streams (Fenton and Bell, 1979), and 0.5-2 m above the surface of calm water (Barclay, 1991; Fenton and Bell, 1979). Individuals are opportunistic hunters that capture and consume free-flying insects (Fenton and Bell, 1979; Nagorsen and Brigham, 1993) and non volant insects on the water's surface (Fenton and Bell, 1979). Although opportunistic, they feed heavily on aquatic invertebrates such as caddisflies (Trichoptera), and midges (Diptera: Chironomidae) (Belwood and Fenton, 1976; Fenton and Bell, 1979; Nagorsen and Brigham, 1993; Whitaker and Lawhead, 1992). They also eat other flies (Diptera), smaller beetles (Coleoptera), moths (Lepidoptera) and hoppers (Homoptera; Whitaker and Lawhead, 1992). In central Alaska, limited sampling by Whitaker and Lawhead (1992), suggested that *M. lucifugus* ate primarily moths and spiders, indicating that they were gleaning at least some of the time.

A maternity colony of approximately 100 to 150 *M. lucifugus* roosts on the north shore of Watson Lake, in the control tower of the Watson Lake Airport (Fig. 1.9). Bats roost within the walls of the control tower and consequently cannot be observed while roosting. Another maternity colony of approximately 60 *M. lucifugus* roosts in the attic of Hougens Department store, in the town of Watson Lake (Fig. 1.10). Typically, bats arrive in late April and depart in mid-September (T. Jung, pers. comm.).

The Thesis

In this thesis I examine the behaviour, diet and morphology of *M. lucifugus* near the northern extent of its range in southeastern Yukon, Canada. In Chapter Two, I investigate characteristics and emergence behaviour of the maternity colony in the Watson Lake airport. In Chapter Three I examine how the behaviour and diet of *M. lucifugus* changes throughout the summer season in Watson Lake. Specifically, I examine when the bats are active, what habitats the bats forage in and what the bats eat. I then correlate these changes in bat behaviour and diet to changes in season and insect diversity and abundance over the summer. In Chapter Four, I compare the morphology of little brown bats in the Yukon to that of southern conspecifics. I examine differences in mass, forearm length, wing loading and aspect ratio, and the relationships to foraging behaviour. In Chapter Five, I summarize my research findings.



Figure 1.9: Watson Lake airport, Yukon Canada. The maternity colony of *M. lucifugus* is located in the control tower (photo by J. Talerico).



Figure 1.10: Hougen's Department Store, Watson Lake, Yukon, Canada. The maternity colony of *M. lucifugus* is located in the attic (photo by J. Talerico).

CHAPTER TWO

CHARACTERISTICS AND EMERGENCE BEHAVIOUR OF THE MATERNITY COLONY IN THE WATSON LAKE AIRPORT

Introduction

Bats are one of the most diverse mammalian orders (Altringham, 1996). They occupy an extensive range of habitats and possess diverse ecological adaptations. However, regardless of distribution, behaviour, or foraging habits, bats are almost exclusively nocturnal (Duverge *et al.*, 2000; Rydell and Speakman, 1995). Departure from and return to day roosts is typically correlated with the timing of sunset and sunrise (Erkert, 1978; reviewed in Erkert, 1982; Issac and Marimuthu, 1993; Lee and McCracken, 2001; Marimuthu, 1984). Body condition, reproductive status, temperature, precipitation, cloud cover and wind speed can all influence the timing of emergence, but ultimately the onset of emergence is controlled by light levels (Erkert, 1978; Erkert, 1982; Shiel and Fairley, 1999). Light levels provide cues as to when activity should commence (Erkert, 1982). Emergence at lower light intensities reduces the risk of predation from diurnal birds of prey and vision-dependent nocturnal animals (Speakman, 1991).

Correlating emergence and return with the timing of sunset and sunrise could severely restrict the foraging time available for bats at high latitudes, during mid-summer. A short, cool, summer season, combined with restricted foraging periods, could prevent bats from meeting their energy demands, especially during pregnancy and lactation. Energy deficits could result in lower reproductive rates and higher over-winter mortality. Bats at high latitudes may therefore balance the costs (risk of predation) and benefits (increased foraging period) differently than more southern populations to achieve maximum fitness.

In this chapter, I focus on the characteristics and behaviour of a colony of little brown bats in north-western Canada, near the edge of the species range. Specifically, I assess the reproductive timing and success of female *M. lucifugus* and how they may be influenced by the northern environment. I also describe how changes in night length and light intensity influence the timing of emergence and return over the summer. I predict that to meet demands during mid-summer, when nights are the shortest, bats emerge from the maternity roost before sunset and return after sunrise.

Methods

Bat Capture

I captured bats using mist nets of various lengths (2.6 to 18 m). I placed mist nets in a variety of locations including: around two maternity colonies (Watson Lake Airport and Hougens Department store), near water bodies (Watson Lake, beaver ponds), and across narrow forest trails and access roads. Upon capture, I immediately placed bats in individual cloth bags for one hour so they could empty their digestive system and an accurate mass could be obtained. I documented the species, sex, age, and reproductive condition of all captured bats. Juveniles were distinguished from adults by the degree of epiphyseal fusion of the fourth metacarpal joint (Anthony, 1988). I classified female reproductive condition as: non-reproductive (furred, unswollen nipples), pregnant (recognized by palpation of the abdomen), lactating (swollen nipples), or post-lactating (bare unswollen nipples) (Racey, 1988). Males were classified as non-scrotal (testes not descended) or scrotal (testes descended).

I determined body size by measuring mass and forearm length. I measured the mass of each bat, to the nearest 0.1 g, using a calibrated digital scale. I used calipers to measure the length of the right forearm of each bat to the nearest 0.01 mm. The average of three forearm measurements was used to reduce error. I also measured ear length (from the base to the tip of the ear) using a ruler, to the nearest 0.5 mm. The average of three ear-length measurements was used to reduce measurement error.

Bat Emergence and Return

From 7 May through 19 August 2006, an assistant and I recorded the time of emergence and return (to the nearest minute) of bats at the Watson Lake airport. Bats emerged through two main exits via gaps in the siding at the north-east and north-west peaks of the airport roof (Figs. 2.1 and 2.2). Three nights each week, we sat outside the two primary exits from 45 minutes before sunset until 20 minutes after sunrise. My assistant observed from the roof, approximately 3 m from the north-west exit where bats were observed without difficulty. Due to different lighting conditions, I observed from 10 m beneath the north-east exit so that I could silhouette the bats against the twilight sky. We tried to remain stationary and quiet throughout the observation periods. We used Pettersson D-100 bat detectors (Pettersson Elektronik AB, Uppsala Sweden) to help with observations, although light intensity allowed visual observations at all times. Hourly measurements were made of temperature, precipitation, cloud cover, and wind speed at the Watson Lake airport weather station.

To determine whether bats were flying during the day, I set-up four AnaBat II bat detectors with AnaBat CF Storage ZCAIM units (Titley Electronics, Ballina, New South Wales, Australia) in weather-proof plastic containers outside the roost during the day on two occasions. Each detector was set at a division ratio of 16 and a sensitivity of 8 and was mounted on a tripod one meter off the ground. I measured light intensity every 10 minutes, in the open-field habitat using a HOBO data logger (Onset Computer Corporation, MA, USA).

Statistical Analyses

I statistically analyzed emergence and return data using JMP IN statistical software (version 7.0.1). I divided the summer season in two ways for analyses: 1) by light season (early, middle and late) and 2) by reproductive season (pregnant and lactating/volant juvenile). I omitted the first six nights of emergence counts (7 May to 14 May) from analyses as my field assistant and I were not completely familiar with the colony during this time. Light seasons were based on civil twilight. Early (15 May to 6 June) and late (4 July to 19 August) in the summer, civil twilight ended each night and started the following morning. During the middle of the summer (7 June to 3 July) civil

twilight persisted over the entire night. The general timing of reproductive condition was based on data from bats captured at Watson Lake. The pregnancy period was from the beginning of May until 13 July and the lactation/volant young period was from 14 July to 19 August. To analyze emergence, I used the timing of emergence of the fifth bat and the median bat. The fifth bat was a better representation of the onset of emergence than the first few bats which were often outliers, emerging considerably earlier than the rest of the colony. The median bat emergence time is a good representation of the general timing of emergence at the airport colony because it reduces the effects of early and late flyers (Kunz and Anthony, 1996). For return to the maternity colony, I used the timing of the median bat and fifth-last bat (four bats prior to the last bat observed).

I conducted analyses of variance (ANOVA) for emergence (fifth and median bat), return (median bat and fifth last), and length of the activity period (first bat emerge to last bat return) with light season or reproduction season as the main effect. I also conducted an ANOVA on light intensity at emergence (fifth bat and median bat) and at return (median and fifth bat) over the light seasons. The early season was excluded from the return light-intensity analysis due to insufficient data. I used Tukey's highly significant difference (HSD) test to make post-hoc pairwise comparisons. I tested model residuals for normality using the goodness of fit, Shapiro-Wilk W test and log or square-root transformed the data if necessary. A W value of > 0.85 indicated that the assumption of normality was satisfied. I also did regression analyses to identify if there was a relationship between: 1) night length and the duration of time bats were away from the roost and 2) the temperature and the number of bats emerging. I used $\alpha = 0.05$ and report means \pm SE.

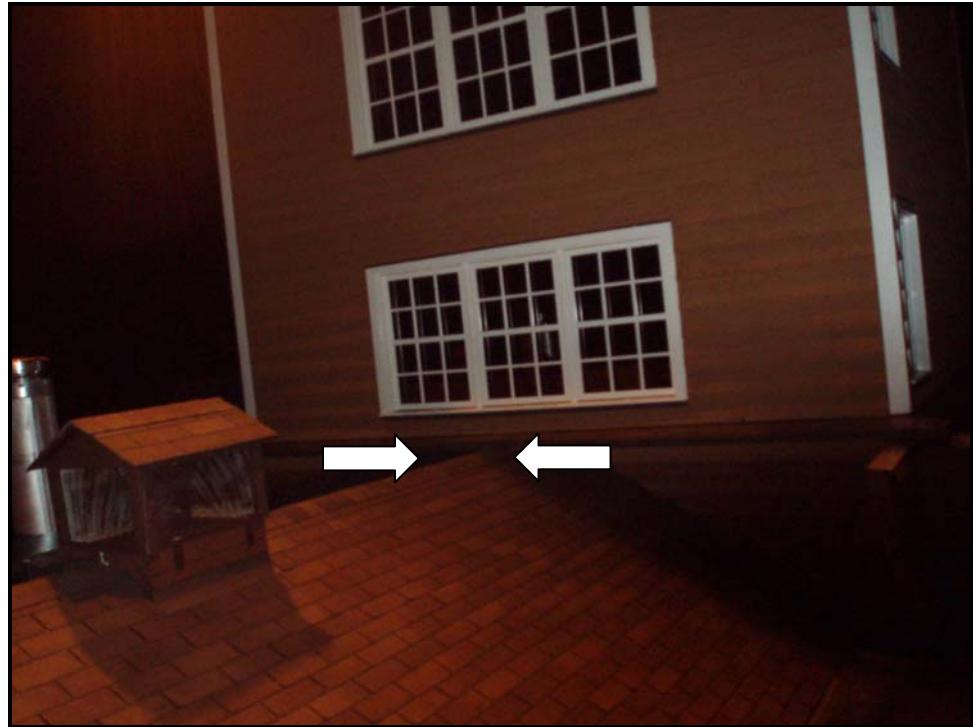


Figure 2.1: Bat exit locations (denoted by the white arrows) on the north-west side of the airport tower, Watson Lake Yukon (photo by J. Talerico).



Figure 2.2: Bat emerging from the north-east exit location of the airport tower, Watson Lake, Yukon (photo by K. Melton).

Results

Size and chronology of the airport maternity colony

Bats were already present at the Watson Lake maternity colony on 7 May, when we made our first emergence observations. At this time, there was still snow on the ground, the lake was frozen and there was no foliage on the trees. Bat presence was observed by airport staff until 18 September. The size of the Watson Lake airport maternity colony varied over the summer in 2006 (Fig. 2.3). The number of bats emerging ranged from 17 adults (28 May) to 196 adults (9 June). It is likely that during the summer some of the bats did not return to the airport colony each night and were instead roosting in one or more alternative roosts. We also observed 5 bats (3 juveniles and 2 adult females) roosting outside on the walls near the airport terminal entrance on three nights. Throughout the summer, my field assistant and I looked for bats in the two adjacent buildings but no bats were observed emerging from or returning to these buildings. We did not find any natural roost sites in the area. Residents living along the shoreline of Watson Lake reported that little brown bats occasionally roosted under the eaves of their log homes.

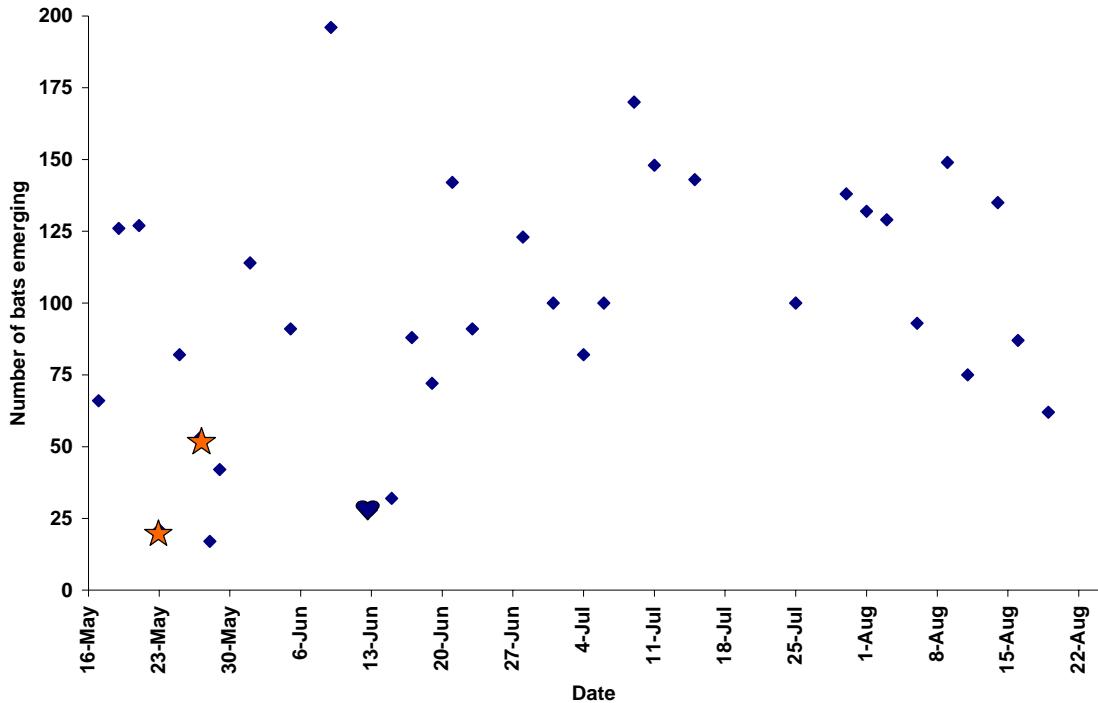


Figure 2.3: Number of bats emerging from the Watson Lake airport colony in 2006. Stars indicate nights with > 5 mm of rainfall, and the heart represents when runway lights were on and emergency vehicles arrived during emergence.

Based on my capture data at the colony, the majority of the adult bats in the Watson Lake airport colony were female (66 adult females: 8 adult males). I only mist-netted at the colony on four nights because I did not want to disturb the bats and cause them to re-locate. Only one of the four capture nights was in the middle of the summer. Bats were not accessible while roosting. Due to the limited number of capture nights at the colony during the middle of the summer, I base reproductive success (the proportion of females reproducing) of the colony on captures on 16 July. Reproductive success of the female bats at the airport colony was low (32 %, n = 47). Only 15 of the 47 female bats I captured were reproductive (4 pregnant and 11 lactating), 30 were non-reproductive and 2 were of unknown reproductive condition. A low reproductive rate (33 %, n= 24) was also found for female bats that I captured around the airport site, that were

most likely roosting at the airport. Reproductive rate at the airport maternity colony was significantly lower than found at the colony in 2005 (Jung *et al.* unpublished data; $\chi^2 = 16.89$, df = 1, p < 0.0001) and at the Hougens Department Store colony in 2006 ($\chi^2 = 33.83$, df = 1, p < 0.0001). In 2005, the airport colony had a reproductive rate of 63 % (n = 64) and in 2006 Hougens Department Store colony had a reproductive rate of 74 % (n = 96).

Few males were captured at either site in either year. At the airport colony in 2006, 8 of the 74 bats captured were male. Two were in the early stages of scrotal development and 6 were non-scrotal. In 2005, three non-scrotal males were captured (n = 66 bats). Around the airport site, only one male (non-scrotal) was captured (n = 25) and at Hougens Department Store, three non-scrotal males were captured (n = 102).

Stages of female reproduction were extended and overlapped in Watson Lake. I captured noticeably pregnant females from 30 May until 2 August. Lactating females were captured as early as 14 July and volant juveniles on 2 August. Both the airport colony and Hougens Department Store colony were primarily made up of juveniles by mid-August (85 %, n = 20 and 83 %, n = 6, respectively), indicating that females had left the colonies and were likely no longer nursing their pups at this time.

Emergence Behaviour

At the airport colony, bats departed singly. Prior to and during the emergence period, we could hear bats vocalizing and scratching the siding at the exit points. When bats emerged, they often circled the airport tower and flew towards the two conifers located on the north side of the airport terminal. They then flew a few times around the conifers and north-east side of the airport roof, often passing near the north-east entrance. Occasionally, bats hung in the conifers or on the side of the airport terminal before departing for the night. While the bats were circling the conifers, I often detected feeding buzzes (rapid series of echolocation calls). Bats continued to circle the conifers and north-east side of the roost until there were more than five bats and then they would all suddenly depart together.

Throughout the summer, most of the bats took the same route when departing the airport roost (Fig. 2.4). They flew west, approximately two meters off the ground, close to the side of the airport terminal until they reached the chain link fence. The bats flew close to the fence, approximately 1.5 m above the ground, until just before they reached the fire station. At this point, they flew approximately 30 m across a small road into the forest. Once in the forest they dispersed to other locations. On three occasions, we observed bats flying north across the open runway, twice at 10 m above the ground and once less than 0.5 m from the ground. We rarely observed bats on the south side of the airport, around the parking lot, where numerous lights were on throughout the night.



Figure 2.4: General route taken by the bats at the Watson Lake airport maternity colony after emergence. Note the solid line denotes the pathway of the bats and the black dashed line is the chain link fence (modified from Google Earth by J. Talerico).

Bats returned to the airport colony via the same route they used during emergence, but also from the east. When traveling from the east, beside the old airport hanger, the bats flew approximately one meter off the ground, close to the hanger's outside wall. They then flew over the tarmac, typically less than 0.5 m from the ground, until they reached the conifers at the airport terminal. Once in the vicinity of the airport terminal, returning bats circled the trees and tower a few times before entering the roost via the exit locations. I often detected feeding buzzes during this time. Bats that returned the latest often went directly into the roost and did not circle the trees and tower. During mid-summer, when the light intensity was high, bats circled low around the conifers many times, then swooped towards the northeast exit, circled around the trees again and then eventually went into the roost. No predators were ever observed directly at the airport roost at emergence or return, but a great grey owl (*Strix nebulosa*) was observed on two occasions (16 and 19 June) around the airport site.

The pattern of emergence and return was noticeably different around solstice compared to early and late in the summer. Early and late in the summer, there were clear emergence and return periods with a break in between (e.g. 1 June 2006; Fig. 2.5a). We observed little or no activity at the roost during the middle of the night. Near solstice, there was considerable overlap between emergence and return (e.g. 21 June 2006; Fig. 2.5b).

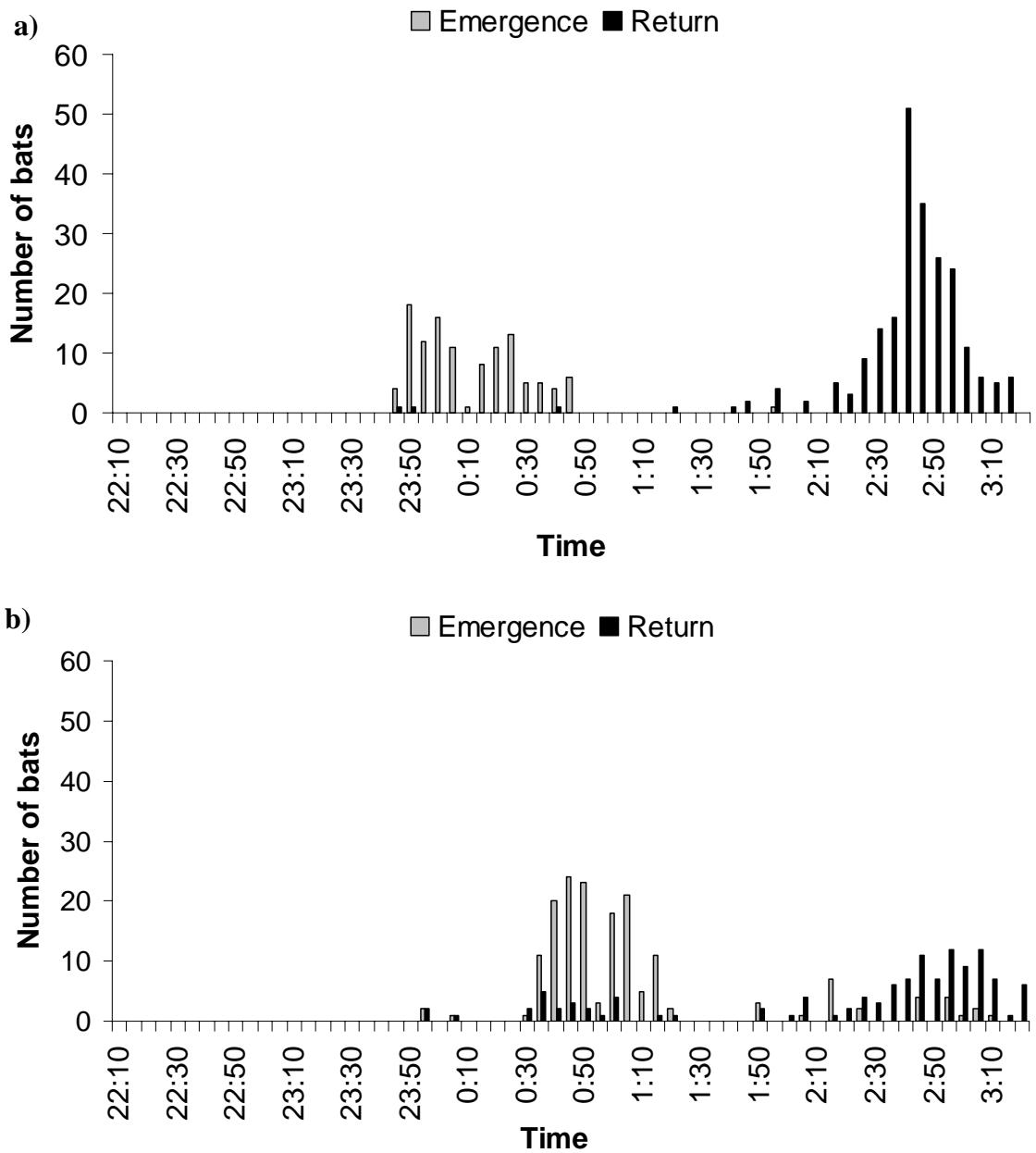


Figure 2.5: Emergence and return of bats on 1 June 2006 (a) and 21 June 2006 (b) at the Watson Lake airport colony.

Environmental factors and bat emergence

A number of environmental factors influenced the emergence of bats at the airport colony, specifically heavy rain and the presence of running emergency vehicles. On two nights (23 and 27 May), there was more than 5 mm of rain and few bats emerged (Fig. 2.3). Similarly, few bats emerged on 13 June after the arrival of an ambulance and an airplane, during a medical evacuation (23:50 to 0:03). Both emergency vehicles were running with their lights on, while parked directly in front of the maternity colony at the airport. The runway lights were also on. Prior to the arrival of the emergency vehicles, bats departed as normal, but after the vehicles arrival, few bats emerged. I excluded all three of these nights from analyses. Bats emerged during nights with light rain (< 3 mm). I thus included all nights with low precipitation in analyses ($n = 9$). No emergence counts were done on nights with blowing snow. However, on 12 May, 14.6 mm of snow fell and bats were still observed flying by airport staff.

Bats began emerging (fifth bat) over a range of temperatures (2.7 °C to 17.9 °C) from mid-May to mid August (Fig. 2.6). On the majority of nights that emergence was observed, the temperature at emergence was > 5 °C. During these nights, there was no influence of temperature on the number of bats emerging ($r^2 = 0.074$, $p = 0.13$). However, on the two nights that it was < 5 °C, few bats emerged, indicating that the threshold temperature for bat emergence may be approximately 5 °C. However, sample size was small for nights below 5 °C and both nights occurred during the early season when colony size was small.

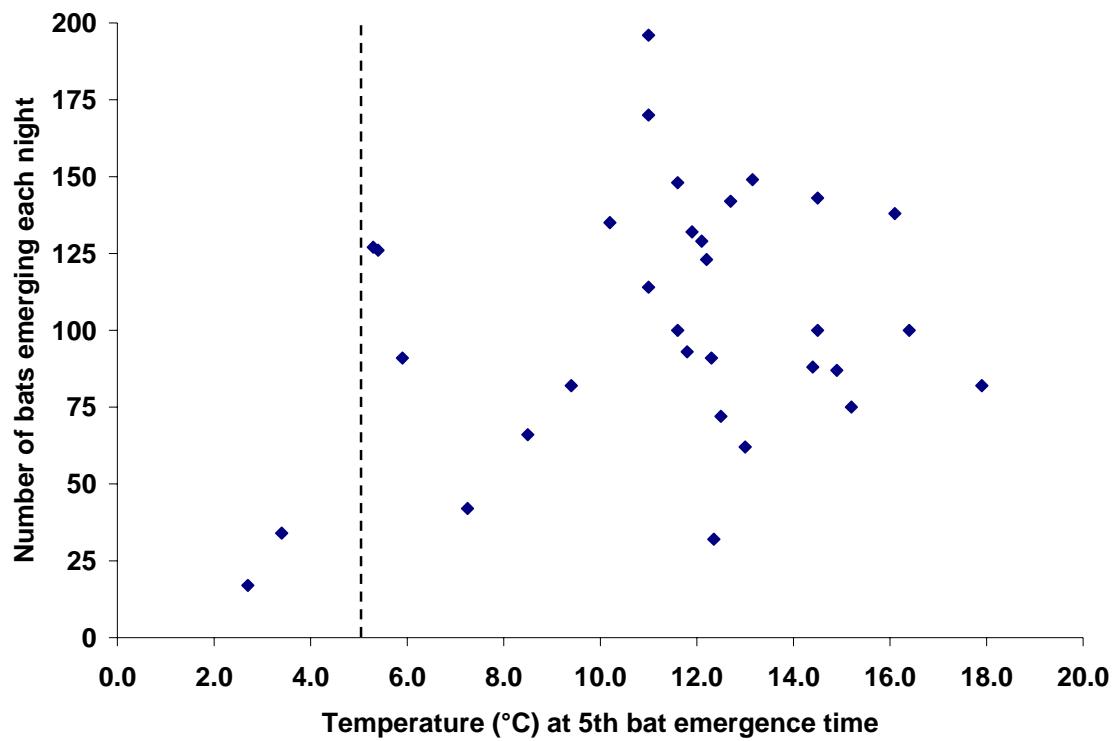


Figure 2.6: Number of bats emerging from the Watson Lake airport maternity colony in 2006 and temperature ($^{\circ}\text{C}$) at 5th bat emergence. Note: the vertical, dashed line shows the possible threshold temperature for bat emergence in Watson Lake.

Timing of emergence and return

Bats remained nocturnal throughout the summer in Watson Lake. They consistently emerged from the maternity roost after sunset (Fig. 2.7a) and returned before sunrise (Fig. 2.7b). On only one occasion did bats ($n = 2$) emerge before sunset (15 May) and that was by a maximum of four minutes. No bats were detected during the day.

The duration that bats were out of the roost (first bat emerge to last bat return) was positively correlated with the duration of the night ($r^2 = 0.93$, $p < 0.0001$; Fig. 2.8). Bats were out longer, relative to night length, when nights were longer. Over the summer, the time of sunset varied by 114 minutes (21:21 to 23:15) and the onset of bat emergence varied by 121 minutes (22:03 to 0:04). Likewise, the timing of sunrise varied by 108 minutes (4:01 to 5:49) and the return of the last bat varied by 131 minutes (3:04 to 5:15). Length of the activity period varied significantly ($F_{3,19} = 72.24$, $p < 0.001$) with both light and reproductive seasons ($F_{2,2} = 5.08$, $p = 0.017$; $F_{1,1} = 91.94$, $p < 0.001$, respectively). Bats were away from the airport maternity roost significantly longer in late summer (330 minutes \pm 23.42; 4 July to 19 August; $n = 11$) compared to mid-summer (214 minutes \pm 23.42; 7 June to 3 July; $n = 9$). In early summer, bats were away from the roost for 236 minutes \pm 43.18 (15 May to 6 June; $n = 3$). Bats were away from the roost significantly longer during the lactation/volant juvenile period than during the pregnancy period.

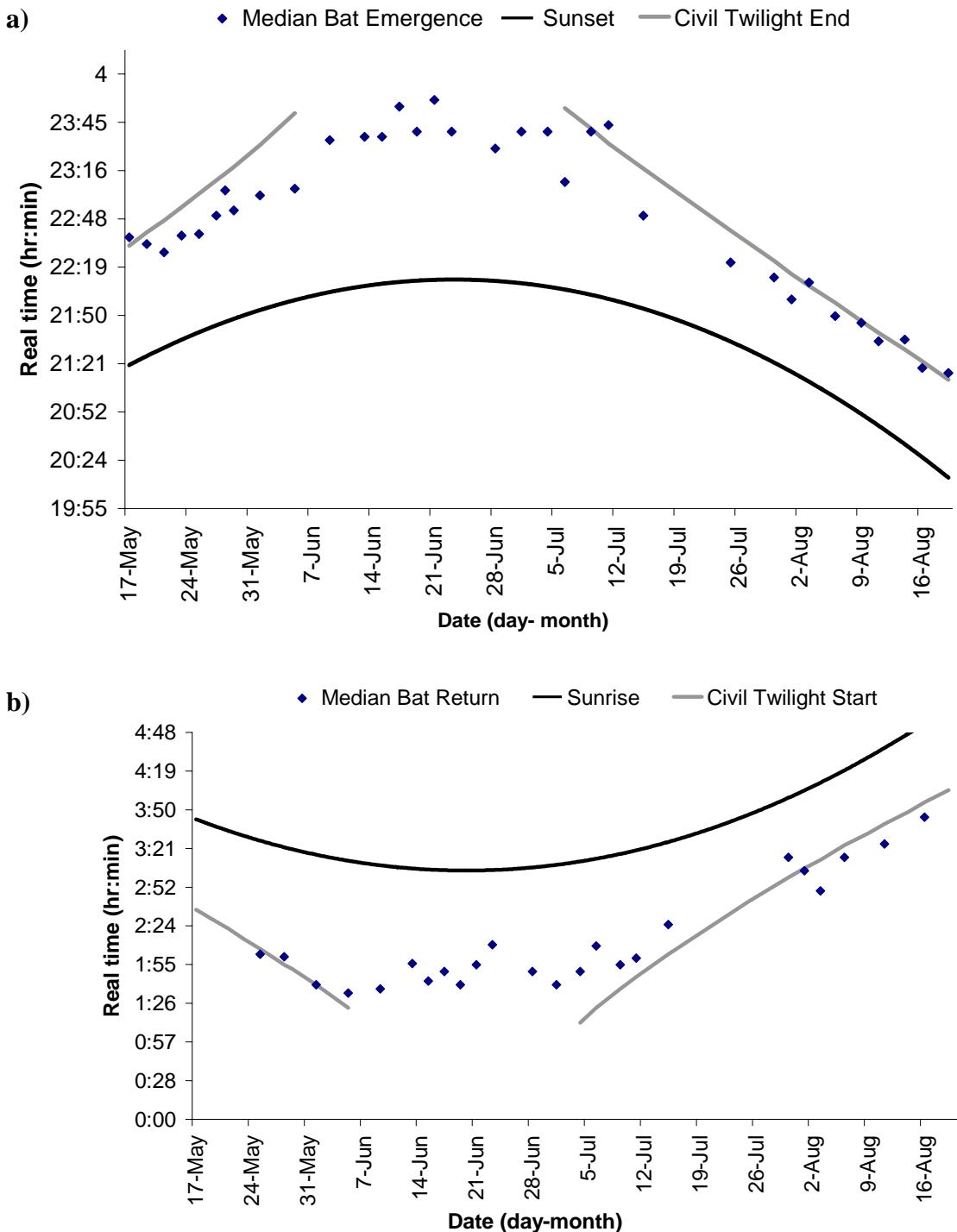


Figure 2.7: Time of median bat emergence (a) and median bat return (b) to the Watson Lake airport maternity colony, Yukon in 2006. Dark solid line denotes sunset (a) and sunrise (b) and grey solid line denotes end of civil twilight (a) and start of civil twilight (b).

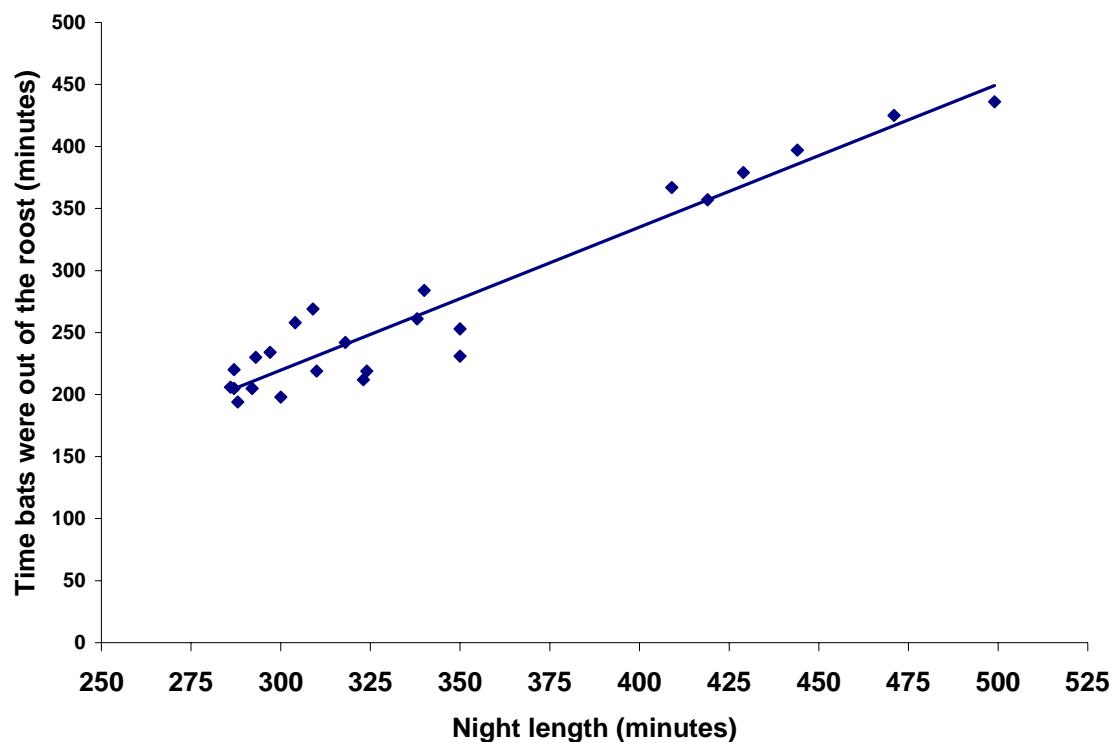


Figure 2.8: Duration of the bat activity period (time between first bat and last bat) and night length (time between sunset and sunrise) at the Watson Lake airport maternity colony, Yukon in 2006.
($y = 1.15x - 126.31$)

Emergence of bats from the maternity colony

Early and late in the summer, the median bat emergence time corresponded closely to the end of civil twilight (Fig. 2.7b). During mid-summer, when civil twilight persisted over the entire night, the median bat emerged significantly later in relation to sunset ($F_{2,29} = 8.84, p = 0.001$; Fig. 2.9). The light intensity (lumens/m²) when the median bat emerged was significantly less late in the summer than in early or mid-summer ($F_{2,19} = 10.35, p = 0.0009$; Fig. 2.10). The time after sunset and light intensity (lumens/m²) at which the fifth bat emerged were not significantly different over the three light seasons ($F_{2,29} = 2.37, p = 0.11$ and $F_{2,19} = 2.98, p = 0.07$, respectively). When dividing the summer by reproductive timing, the median and fifth bat both emerged significantly later, relative to sunset, during the pregnancy period than during the lactation/volant young period ($F_{1,30} = 20.01, p = 0.0001$; $F_{1,30} = 8.48, p = 0.0067$, respectively).

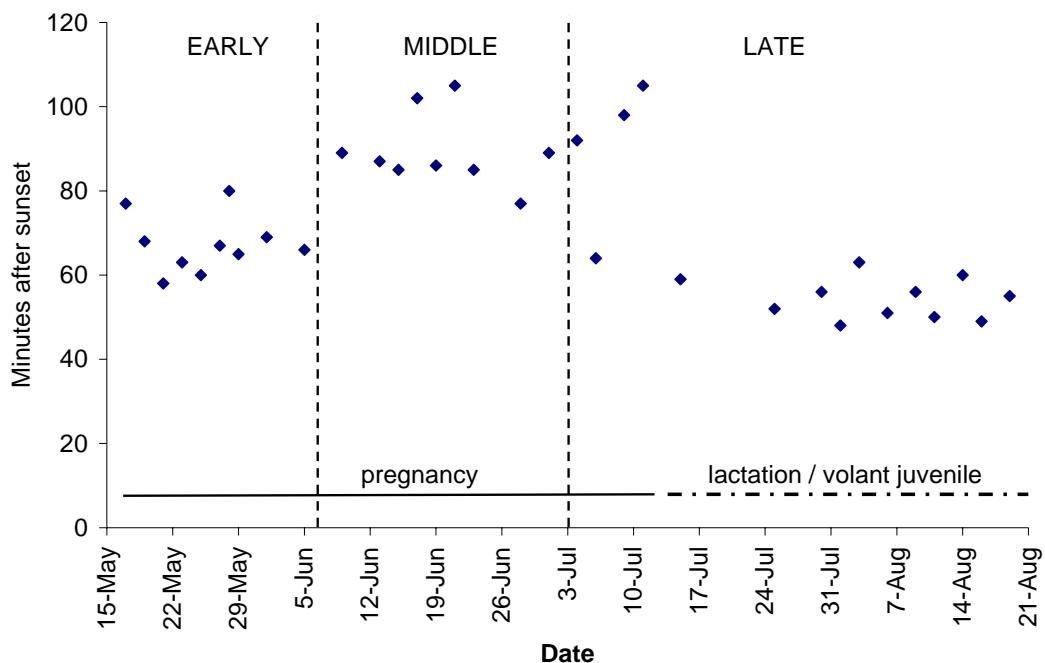


Figure 2.9: Minutes after sunset that the median bat emerged from the Watson Lake airport maternity colony, Yukon in 2006.

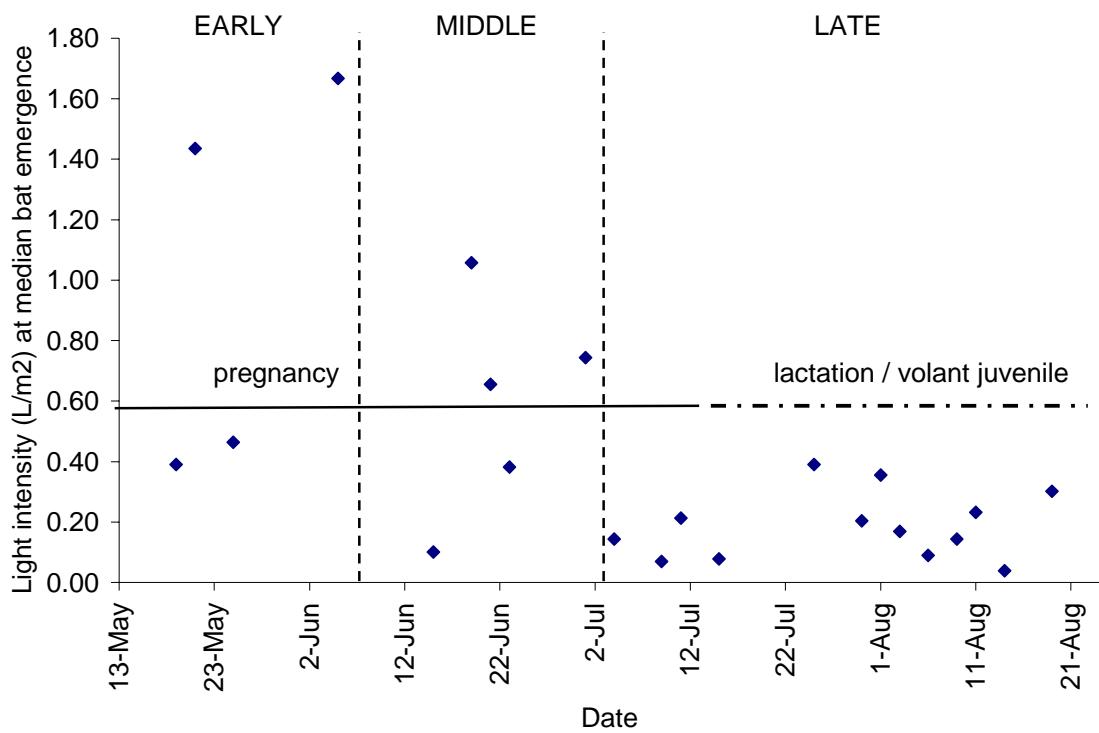


Figure 2.10: Light intensity (lumens/m²) at median bat emergence at the Watson Lake airport colony, Yukon in 2006.

Return of bats to the maternity colony

As with emergence, the time that the median bat returned to the roost mirrored the time that civil twilight started (Fig. 2.9). The median and last bat both returned to the roost significantly earlier, relative to sunrise, early in the summer than during late summer ($F_{2,21} = 4.34$, $p = 0.027$ and $F_{2,21} = 4.63$, $p = 0.022$; Fig. 2.11). Light intensity (lumens/m²) when the fifth-last bat returned to the roost did not vary significantly ($F_{1,12} = 3.05$, $p = 0.11$), but the light intensity when the median bat returned to the roost was significantly greater in the middle season than in the late summer ($F_{1,12} = 6.33$, $p = 0.03$). The early season was excluded from light intensity analysis due to small sample size ($n = 4$). Reproductive stage did not have a significant effect on the fifth-last or median bat return time to the maternity roost ($F_{1,22} = 1.18$, $p = 0.29$ and $F_{1,22} = 3.79$, $p = 0.06$, respectively).

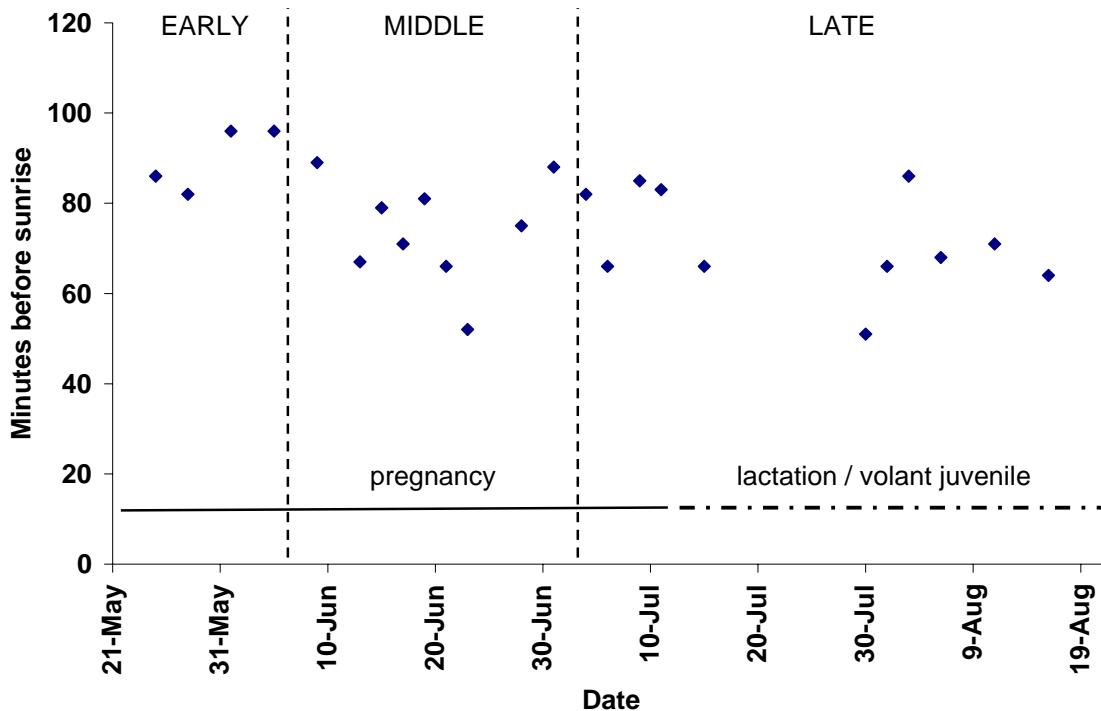


Figure 2.11: Minutes before sunrise that the median bat returned to the Watson Lake airport maternity colony, Yukon in 2006.

Discussion

Reproductive chronology

The time period that *M. lucifugus* occupied the airport colony in Watson Lake was similar to that at a site in New Hampshire (late April/beginning of May until mid September; Kunz and Anthony, 1996). In this study, however, the stages of reproduction were more overlapped and gestation was longer, than those reported for southern conspecifics. Female little brown bats in Yukon were pregnant for approximately one month longer (parturition: mid July to early August) than reported in southern Alberta (J. Coleman unpublished data), British Columbia (Herd and Fenton, 1983), New Hampshire (Kunz and Anthony, 1996), New York (Buchler, 1980) and Quebec (Henry *et al.*, 2002) (parturition: mid to late June). As a result, pups in Yukon became volant nearly one month later than in southern populations. None of the previous studies reported a substantial overlap in reproductive stages. In Northwest Territories, however, pregnant little brown bats ($n = 2$) have been captured in late July (Lausen, 2006), indicating that prolonged gestation and overlapping reproductive stages may be common north of 60° .

The long gestation period and overlapping reproductive stages in northern Canada may be a result of lower spring and summer temperatures (Lewis, 1993; Racey and Swift, 1981; Rydell, 1991). It is likely that bats at the northern edge of their range need to enter torpor during the spring and summer more often than southern conspecifics do, to reduce energy demands. Maintaining a warm body temperature is a significant energetic expense for bats because they are vulnerable to heat loss due to their small size, large lungs and naked wing membranes (Neuweiler, 2000). Behavioural and physiological compensation may be the best way to meet increased energy demands of pregnancy and lactation because of their inability to store large amounts of fat (Reynolds and Kunz, 2000). However, torpor can have fitness costs for reproducing female bats (Grinevitch *et al.*, 1995). Torpor can prolong gestation, slow fetal growth and decrease milk production, thus delaying pup maturation (Racey and Swift, 1981). Variation in the amount of torpor used by female bats in Watson Lake may explain the reduced synchrony of parturition (Lewis, 1993). Females that used torpor more often due to lower body condition, poor foraging success or cooler roost conditions, likely had longer

pregnancies. Timing of parturition also may have been abnormally late in 2006. Mean temperatures were lower and precipitation was greater than the long term average, especially in May (Table 2.1). Increased precipitation and lower temperatures during early summer can delay parturition (Grindal *et al.*, 1992; Lewis, 1993; Racey and Swift, 1981; Rydell, 1989b).

Table 2.1: Weather in Watson Lake, Yukon 2005 and 2006 (Environment Canada, 2008). * LT refers to climate normals (1961-1990)

Month	Mean Max Temperature			Mean Temperature			Mean Minimum Temperature			Total Precipitation		
	2005	2006	LT	2005	2006	LT	2005	2006	LT	2005	2006	LT
April	8.5	7.1	6.1	2.5	0.4	-0.4	-3.5	-6.3	-7.1	10.6	34.2	14.3
May	17.0	11.7	13.3	9.7	6.0	6.9	2.3	0.3	0.5	66.5	87.6	37.5
June	19.6	21	18.9	13.8	14.0	12.5	7.9	7.0	6.1	61.8	32.2	54.1
July	19.3	21.7	21.1	13.6	15.0	14.9	7.9	9.3	8.7	61.8	32.9	60.1
August	19.0	17.9	19.2	12.8	12.5	13.0	6.4	7.0	6.8	31.2	53.3	44.3

Slowed or delayed pup growth may have fitness costs for bats in northern climates because it may reduce the amount of time post-reproductive females and pups have to prepare for hibernation. Pup mortality rates are high during their first hibernation season, compared to subsequent years (Davis, 1966; Sendor and Simon, 2003), thus it is critical that they reach the required size and obtain enough energy reserves before the end of the summer. Early parturition is beneficial because it provides maximum time to prepare for hibernation. However, lower temperatures at higher latitudes delay reproduction and thus early parturition may not be possible. In addition, it may not be feasible to meet the increased energy demands of lactation during the short, mid-summer nights. These conditions may result in lower reproductive rates at high latitudes compared to in more southern populations.

Adaptive variation in the size of pups at parturition may occur among bats in different environments (Fujita, 1986). Greater prenatal investment and giving birth to relatively larger pups may be advantageous in cool northern latitudes. This would be the case if the increased costs of flying with a larger foetus are outweighed by the benefits of not having to warm up small pups who cannot maintain their body temperature (Hollis

and Barclay, 2008). Although I could not measure the size of *M. lucifugus* pups, increased birth size has been reported at high latitudes for this species (Fujita, 1986).

Reproductive rates

The reproductive rate of bats in Watson Lake in 2006 varied from 32 % (airport colony) to 74 % (Hougens Department store colony). These rates are lower than those reported in other *M. lucifugus* colonies in Illinois and Indiana ($\geq 97\%$; Cagle and Cockrum, 1943; Humphrey and Cope, 1976) but are comparable to *M. lucifugus* colonies in British Columbia (57 %, Firman *et al.*, 1995; 47 %, Holroyd *et al.*, 1993). These results are consistent with the idea that the reproductive rate of bats declines with increasing latitude (Barclay *et al.*, 2004). If insect abundance and weather during the early and late season is unfavourable at northern latitudes and body condition is poor, female bats may choose to forego reproduction to maximize lifetime reproductive success, thus reducing the average annual reproductive rate (Barclay *et al.*, 2004; Grindal *et al.*, 1992).

Higher apparent reproductive success at the Hougens Department store colony may have been due to differences in roost conditions and composition of the colony. It is likely that the department store roost was warmer than the airport tower roost because the bats roosted in the attic of the heated department store while at the airport, the bats roosted in the unused tower that was heated only indirectly from the terminal building. It is possible that there were a variety of roost locations with different temperature regimes within the tower thus offering suitable roost conditions not only for reproductive females, who prefer warm roosts (Anthony *et al.*, 1981; Encarnacao *et al.*, 2005; Hamilton and Barclay, 1994) but also for non-reproductive females who prefer cool roosts (Hamilton and Barclay, 1994; Encarnacao *et al.*, 2005). Temperature within the department store attic may have been conducive to reproductive females and young-of-the-year. Non-reproductive females and males, that prefer cooler day roosting conditions, may have roosted in other locations around town. Higher reproductive success and lower prevalence of adult male bats at the department store colony indicates that it may have been exclusively a maternity colony whereas the airport colony may have been a

multiple-use colony. Reproductive rate at the department store may thus have been higher than in the general population.

Reproductive success at the airport colony was significantly lower in 2006 than in 2005. Different weather conditions during early gestation may have caused this. In 2006, mean temperatures were lower and precipitation was higher than the long term average and 2005, especially in May (Table 2.1). Female bats are often in poor body condition after hibernation and thus favourable weather conditions in early summer are critical to successful reproduction. Increased precipitation and lower temperatures during early summer can lower reproductive rates and delay parturition (Grindal *et al.*, 1992; Lewis, 1993; Racey and Swift, 1981; Rydell, 1989b). In Watson Lake, females may have chosen to forego reproduction in 2006 to allocate resources to their own survival and maintenance (Barclay *et al.*, 2004). It is possible that the reproductive rate in 2005 also may have been slightly lower than the ‘normal’ because although temperatures were higher, precipitation in early summer was much higher than the long term average. During years with optimal weather conditions early in the summer, I would expect higher reproductive rates than observed in 2005.

Further studies are needed to examine the reproductive biology and life history of northern bats. Specifically, what is the average length of gestation of female bats in northern populations? What is the average mass of a bat pup at birth? How do the growth rates of northern bat pups compare to those in southern populations? At what age do female bats first reproduce? What are the fat reserves prior to hibernation of both post-reproductive females and young-of-the-year? How do the over-winter-mortality rates and longevities of northern bats compare to more southern populations. I predict that unlike in southern populations (see also Schowalter *et al.*, 1979), female *M. lucifugus* do not reach sexual maturity until their second fall due to the harsher conditions and the short season. I also hypothesize that because of lower reproductive rates, northern bats have a longer life expectancy than individuals in more southern populations.

Bat emergence and return

Emergence behaviour

The emergence and return behaviour of bats at the airport colony suggests that the perceived risk of predation was high in Watson Lake. Throughout the summer, bats regularly departed from the colony area in groups, after circling the tree and north-east side of the roof together. Group departure from the conifers after emergence may have been an anti-predator behaviour (Fenton *et al.*, 1994; Speakman *et al.*, 1995). Clustering may have reduced an individual's probability of being preyed upon while departing the unprotected airport site (selfish-herd phenomenon; Hamilton, 1971).

The bats also consistently flew in the most protected areas when exiting from and returning to the airport roost. When flying in open areas, they flew close to buildings, fences and the ground. These routes were often not the most direct route to their destination. For example, the general emergence route from the airport colony to the forest patch is approximately 220 m. The flight distance to the same forest patch, from the airport colony, over the exposed parking lot, is 145 m. Bats may have taken the longer route beside the linear features to increase their cover against aerial predators (Verboom and Huitema, 1997).

Temperate insectivorous bats are not commonly pursued as prey by nocturnal (e.g. owls) or diurnal (e.g. hawks, falcons and corvids) predators, but predation does occur opportunistically (Baker, 1962, Fenton *et al.*, 1994). Indeed, risk of predation may be significant to bats, even if it is low, due to their slow life histories (Rydell *et al.*, 1996). Maternity roosts are predictable targets for predators, particularly during emergence and return (Baker, 1962; Fenton *et al.*, 1994; Barclay *et al.*, 1982). To reduce predation risk at the colony, bats may alter their behaviour by emerging at lower light intensities (Speakman, 1991).

Although I did not observe any predators directly at the airport roost in 2006, it is possible that the owls in the general area preyed on bats, at least opportunistically. In 2007, I observed a great horned owl (*Bubo virginianus*) preying on a little brown bat that was trapped in a mist net over a beaver pond, in the southern Yukon (unpublished data). The owl attempted to capture the bat (indicated by puncture wounds in the bat) but then

entangled itself in the net. Evidence suggested that the owl also attacked another bat on this occasion because there were numerous other bats trapped in the mist net as well as a large ‘owl sized’ hole. Other potential avian predators may include various species of hawks (Accipitriformes), falcons (Falconidae), corvids (Corvidae), and the osprey (*Pandion haliaetus*).

Emergence and return

Little brown bats in Watson Lake remained nocturnal throughout the summer season, despite large fluctuations in temperature and night length. Contrary to my prediction, the bats consistently emerged from and returned to the airport colony after sunset and before sunrise, respectively. This suggests that light conditions were a major factor influencing the onset of emergence at the northern edge of the range. Based on the behaviour of bats at the roost, it is possible that predation risk was largely responsible for this observation. In mid-summer, the benefits of foraging before sunset and after sunrise, during non-twilight times, may have been outweighed by the risk of predation. The light level and the time at which bats emerged from the colony, varied seasonally. Bats emerged at significantly lower light levels late in the summer compared to in early and mid-summer. They also emerged significantly later, with respect to sunset, during mid-summer, compared to early and late summer. These results partially correspond with the emergence behaviour of little brown bats in New Hampshire (Kunz and Anthony, 1996). The onset of emergence in New Hampshire was later, with respect to sunset, during early and mid-summer compared to late summer.

It appeared that the length of the night in mid-summer provided ‘sufficient’ foraging time for the bats in this study and it was not ‘necessary’ to forage before sunset or after sunrise, like reported for *Eptesicus nilssoni* in northern Sweden (65°) (Rydell, 1989a). In this study, the length of the activity period or the time that the bats were away from the roost (first bat emerge to last bat return) was correlated with night length. In mid-summer, the activity period was restricted to 3.5 hours (± 5 minutes) and thus may have limited the amount of prey bats could consume each night.

Lower ambient temperatures early in the summer may have caused bats to emerge at a significantly higher light illumination than observed in late summer. Aerial insect activity is reduced at lower temperatures (Speakman *et al.*, 2000; Taylor, 1963) and thus waiting to emerge at lower light levels may have been unprofitable in early summer. At that time, bats have low fat reserves and thus entering torpor and not feeding may have posed a greater risk than predation. Bats may have emerged at higher light levels in early summer to meet their energy shortfalls by exploiting insects available at warmer temperatures (Rydell, 1989b; Speakman, 1990). Likewise, they may have returned to the roost earlier due to unprofitable feeding caused by cooler temperatures (Anthony *et al.*, 1981).

The apparent emergence temperature threshold of 5°C may indicate when insect densities were low in Watson Lake and it was more beneficial to enter torpor in the roost, than attempting to forage. Foraging during heavy rain was also likely unprofitable and so emergence ceased or was interrupted. I address insect abundance in Chapter Three. My results are similar to the emergence behaviour of *E. nilssoni* in northern Sweden (65°N, Rydell, 1991). In early summer, bats did not forage at temperatures below 6°C apparently because of lower insect densities. They also did not forage in heavy rain.

The bright light prevailing during the night in mid-summer in southern Yukon may explain why the bats emerged significantly later, with respect to sunset, compared to in early and late summer. Departure at higher light levels increases a bat's chance of being preyed upon by predators (Speakman, 1991). Thus, it is likely that the bats delayed emergence until the optimal light level, where there was a balance between the need to forage and predation risk. The risk of predation by emerging at a higher light level was outweighed by the costs of not feeding. If bats are going meet their energy demands during short nights, then they need to emerge and potentially forage at a higher light illumination than during late summer, when nights were longer and warmer. The increased risk of predation caused by emerging at higher light intensities may have been lowered due to the predator avoidance behaviour displayed by the bats (i.e. circling around the roost, flying close to buildings). They may also be able to reduce predation risk by foraging in more protected habitats (Chapter Three).

Differences in emergence time may also reflect changes in the energy and nutrient demand of the bats. Bats emerged significantly earlier, with respect to sunset, during the lactation/volant young period, than during the pregnancy period. Lactating bats have higher energy and nutrient demands than pregnant bats (Anthony and Kunz, 1977; Barclay 1994; Kunz and Hood, 2000) and thus often emerge earlier (*Lasiorus cinereus*, Barclay, 1989; *Eptesucus serotinus*, Catto *et al.*, 1996; *E. nilssoni* and *Nyctalus leisleri*, Shiel and Fairley, 1999). They also return to the roost between foraging bouts, to suckle their young and so additional time is needed (Anthony *et al.*, 1981; Henry *et al.*, 2002).

Conclusion

The variation in emergence timing of *M. lucifugus* in Watson Lake, Yukon may be influenced by varying light levels, predation risk and changes in energy demand related to reproduction. However, it is unlikely that reproductive stage was the major factor influencing the timing of emergence of *M. lucifugus* at the airport colony. The Watson Lake airport colony had a low reproductive rate in 2006 (33 %) and thus the majority of the colony was not influenced by changes in reproductive condition. Furthermore, for the individuals that were reproducing, parturition was not synchronized and there was substantial overlap in the pregnancy and lactation stages. It is thus likely that the timing of emergence and return was based on a combination of factors, specifically energy demand, predation risk and night length. Bats needed to balance the costs (e.g. risk of predation and not feeding) and benefits (increased foraging period) to survive.

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CHAPTER 3

FORAGING BEHAVIOUR AND DIET OF *MYOTIS LUCIFUGUS* AT THE NORTHERN EXTENT OF ITS RANGE

Introduction

It is tempting to extrapolate the ecology of a species at the extremes of its range from studies done at the core of its range. However, this may not be accurate. Individuals living on the northern periphery of the geographic range in the northern hemisphere, often live in a suboptimal environment compared to southern conspecifics. In the subarctic, they also generally experience lower temperatures and a greater range of hours of sunlight, than more southern populations. Differences in prey availability, predation risk, and competition may also be present. Based on these environmental differences, it seems likely that to survive and successfully reproduce, individuals living on the northern periphery of the species' range may differ in their behaviour compared to more southern populations.

In some respects, the little brown bat (*Myotis lucifugus*) is a good species to examine the behaviour of species at northern latitudes. It has a large geographic range, from Mexico to northern Canada and Alaska (64° 4'N, 139° 20'W; 65° 42'N, 148° 49'W, respectively; Parker, 1996), and from sea level (Nagorsen and Brigham, 1993) to 2769 meters above sea level (C. and J. Talerico unpublished data). Despite its extensive range, many studies used to describe its ecology have been conducted in New Hampshire (42° 42' N, 70° 36' W; e.g. Anthony and Kunz, 1977; Anthony *et al.*, 1981; Kunz and Anthony, 1982) and few studies have been conducted on the northern periphery of its range. Due to the lack of studies, it may be tempting to extrapolate the ecology of little brown bats in the north from more southern studies, despite differences in environment and climate. Although these studies are valuable, it is likely that the ecology differs because *M. lucifugus* in the north experiences a shorter reproductive season, lower temperatures and shorter nights than more southern populations.

Two formal studies, one published, conducted at the northern periphery (Alaska) of *M. lucifugus*' range (Parker, 1996; Whitaker and Lawhead, 1992) indicate that the ecology of *M. lucifugus* in the north differs from that of southern populations. Reproductive female *M. lucifugus* in Alaska were reported to successfully reproduce in areas with lower ambient temperatures than southern conspecifics. Differences in diet were also reported. *Myotis lucifugus* consumed spiders in Alaska, a prey item not reported in southern populations. Exploitation of non-volant prey such as spiders indicates that the foraging behaviour may also differ in northern environments.

My study was conducted to determine if and how the foraging behaviour and diet of little brown bats living in the southern Yukon differs from that of southern conspecifics. As stated in Chapter One, I hypothesized that the short reproductive season, low temperatures and short nights limit the foraging opportunities of northern Canadian bats. Therefore, the amount of energy collected during the 'dark' hours should be reduced, compared to bats at lower latitudes (Speakman, 1991) if they behave as southern individuals. I thus expected that to cope with potential energy deficits, bats at high latitudes must be flexible in their foraging behaviour. I predicted that bats shift their foraging habitats with changes in night length over the summer. Specifically, during periods with short nights and relatively high light intensity (e.g. around the solstice), I predicted that to avoid predation (Chapter 2), foraging bats avoid exposed or open areas, such as open fields and lakes, and instead forage in protected, darker areas such as forest edges and in the forest interior. I also predicted that the foraging behaviour and diet of bats vary according to temperature and with the invertebrates available in foraging habitats. Specifically, during periods of low temperatures, when the density of aerial insects is low, I predicted that bats forage more on non-flying invertebrates such as spiders, like their conspecifics in Alaska.

Methods

Bat Activity - Field Work

From 7 May to 20 August 2006, a field assistant and I measured bat activity from 20:15 to 07:00 each night. I chose the length of the nightly sampling period based on the time of sunset and sunrise on the longest night of the summer sampling season (31 August). I assessed three of the six foraging habitats (see Chapter One) each night due to time and equipment constraints. Combinations of foraging habitats sampled each night were pseudo-random, ensuring that every habitat type was sampled at least twice per week.

I acoustically monitored bat activity at each site using AnaBat II bat detectors (Titley Electronics, Ballina Australia) equipped with AnaBat CF Storage ZCAIM units (Fig. 3.1). Detector units were housed in weather-proof plastic containers mounted on tripods, one meter off the ground. The microphone was aimed 25 degrees up from the ground, through an opening in the container. Each detector was set at a division ratio of 16 and a sensitivity of 8. On each detector case, I placed a HOBO data logger (Onset Computer Corporation, MA, USA) that recorded light intensity every 10 minutes. Hourly measurements were also made of temperature, precipitation, cloud cover, and wind speed at the Watson Lake Airport weather station.

I placed bat detectors in the same location at each site throughout the sampling season and defined how bat detectors would be placed in each habitat type based on the orientation to the maternity roost and human use in the area (e.g. ATV use). In the corridor habitats (flowing water and forest corridor), I placed detectors on the shoreline/forest edge of the corridor with the microphone pointed perpendicular to the shoreline/forest edge. Along forest edge sites I placed bat detectors in the ‘middle’ of the length of edge habitat with the microphone facing out towards the open area. Within the forest interior and open-field habitats, I pointed bat detectors in the direction of the Watson Lake Airport maternity roost. In the standing water habitat I placed bat detectors on the shoreline facing out towards the lake.



Figure 3.1: Example of a bat detector set-up (photo by J. Talerico).

Bat Activity - Analysis

I downloaded all files saved onto the compact flash memory card from the AnaBat CF Storage ZCAIM (Titley Electronics, Ballina Australia) onto a computer using CFCread software program. I counted the number of bat passes and feeding buzzes through a combination of visually examining the frequency-time graphs using Analook software and also listening to each file using AnaMusic software. I defined a bat pass as a minimum of two consecutive calls separated from other calls by at least one second (Thomas and LaVal, 1988), and a feeding buzz as a rapid series of shorter bat echolocation calls (Barclay, 1984; Racey and Swift, 1985). I documented the time of the first bat pass, last bat pass and each feeding buzz for each site, every night. I counted the number and timing of feeding buzzes to determine which habitats the bats were feeding in and which habitats were being used strictly for commuting. As only one species of bat (*Myotis lucifugus*) has been documented in my study area, I did not need to discriminate among different genera of bats. I assumed that all *Myotis* passes were from *M. lucifugus* individuals because: 1) it is the only species documented in my study area (*M. septentrionalis* has been captured 60 km north; Lausen *et al.*, 2008); 2) it was the only

species I captured throughout the 2006 field season ($n = 236$); and 3) all my sites surrounded a *M. lucifugus* maternity colony. Echolocation calls of *Myotis* species have a minimum call frequency generally >35 kHz and moderately steep FM-sweeps.

Arthropod Survey

Aerial arthropods

I used cylindrical sticky traps to sample airborne invertebrates at each sampling site. Aerial arthropods stick to the surface of the traps upon impact (Kunz, 1988). Sticky traps were made from a piece of 15.1 cm diameter PVC pipe (38 cm long) wrapped with a piece of plastic coated with Tanglefoot® (Fig. 3.2). Plastic sheets coated with Tanglefoot® were removable for ease in trap changes, transport, and analysis. On wooden poles, I mounted sticky traps two and four meters above the ground, approximately one meter apart, at all sampling sites. In aquatic habitats I also placed a trap at water level anchored to the lake or stream bottom and floating on a piece of Styrofoam approximately 1 meter from the water's edge (Fig. 3.3). I chose the heights of the traps to reflect the estimated foraging heights of the bats (Barclay, 1991).

I sampled aerial arthropods from 22 May to 19 August 2006 at three habitat types per night at least three times per week. The three sites sampled each night corresponded to the sites I was acoustically monitoring for bats that night. Sticky traps were set at least 10 meters from the bat detectors to avoid possible interference or bias. Combinations of foraging habitats were pseudo-random ensuring that every habitat type was sampled at least once a week. Length of the sampling period was based on night length and emergence time of the bats at the Watson Lake Airport maternity colony (time from emergence to sunrise, divided into three equal parts).

After each night of sampling for aerial invertebrates, my field assistant and I counted, measured (size categories: < 2 mm, 2.1 -5 mm, 5.1-10 mm, 10.1- 15 mm, and >15.1 mm) and identified (to order, and family for some dipterans) all invertebrates caught in the sticky traps. I removed invertebrates from the sticky traps using tweezers dipped in 70 % ethanol and stored them in 70 % ethanol for future reference.



Figure 3.2: Example of sticky trap. Traps were made from a piece of 15.1 cm diameter PVC pipe (38 cm long) wrapped with a piece of plastic sheet that was coated with Tanglefoot® (photos by J. Talerico).

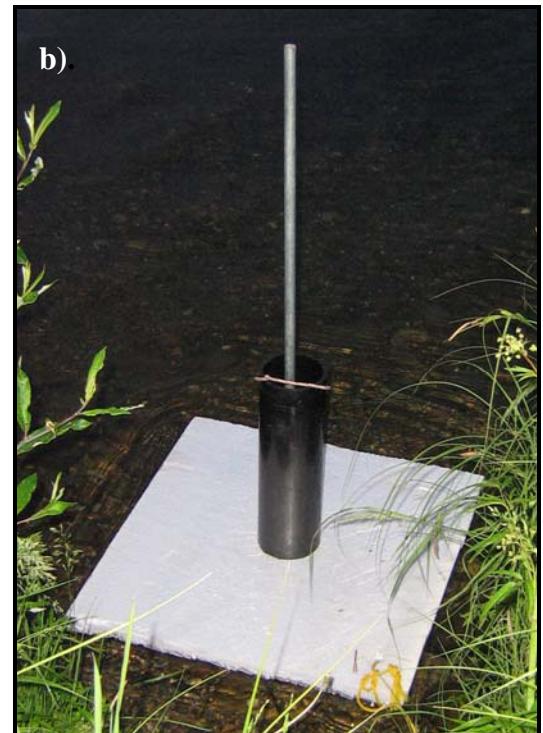


Figure 3.3: Examples of sticky traps a) two and four meters above the ground and b) at water level (photos by J. Talerico).

Arthropods on or among the vegetation

I sampled arthropods flying or crawling among or on the vegetation with a sweep net (30 cm diameter). Sweep net samples were taken on the same nights and at the same sampling sites as aerial insect surveys. I took four sweep net samples at each site. Time of sampling corresponded to sticky trap set-up, first change, second change and take down. I beat the vegetation with the sweep net using 25 rapid strokes in all directions at a variety of heights (ranging from the ground to 3 m). I ensured that different areas of vegetation within the sampling sites were used each night to avoid sampling bias and error. Arthropods collected during sweeping were picked out of the sweep net and deposited in a plastic container containing 70 % ethanol for future analysis. I counted, measured (size categories: < 2 mm, 2.1 -5 mm, 5.1-10 mm, 10.1- 15 mm, and >15.1 mm) and identified (to order, or family for some dipterans) all invertebrates using a dissecting microscope.

Arthropod Biomass

To estimate arthropod biomass, I dried all arthropods collected during sweep net sampling in an oven at 40°C for 24 hours. Arthropods were divided by size class and order (or family for some dipterans) and weighed to the nearest 0.001 g on a Sartorius electronic balance (AG Gottingen, Germany). All arthropods <2 mm were omitted. I estimated the biomass of insects in each sticky trap and sweep net sample using the average individual mass for an order's size class, multiplied by the number of arthropods captured for that order and size class. Dry mass of arthropods captured in sticky traps could not be used because Tanglefoot® was present on all individuals.

Fecal Analyses

Every morning from 23 May to 20 August 2006, my field assistant collected bat fecal pellets from the roof of the Watson Lake Airport around the primary bat exit points. She ensured that the collection areas around the exit points were free of fecal pellets prior to the bats emerging each night, to make certain of the night of deposition. After collection, we dried and stored daily fecal samples in plastic containers until I analyzed pellets for diet.

To identify the arthropod fragments within each fecal pellet, I teased apart individual pellets, softened with 70 % ethanol, under a dissecting microscope (Whitaker, 1988). Identifiable fragments of invertebrates included wings, antennae, legs, claws, tarsi and scales. I used the arthropods I collected with sweep nets to aid with identification and also referred to illustrated keys in Shiel *et al.* (1997) and Whitaker (1988). A potential bias of fecal analysis is that soft-bodied invertebrates such as mayflies (Ephemeroptera) may be under-represented because soft body parts may be destroyed during bat digestion (Whitaker, 1988). I assumed that this potential bias was not a major concern for my study because my insect surveys showed that mayflies were scarce in my study area. In addition, mayfly remains have been documented in *M. lucifugus* fecal pellets (Anthony and Kunz, 1977).

I assigned random identification numbers to each daily fecal sample so that during analysis I was unaware what time period the sample was from. I analyzed three pellets of similar size from each day (264 fecal pellets from 88 days). No fecal pellets were analyzed from 24 May and 9 August because none were deposited by the bats. I estimated the percent volume and percent frequency of non-food items (i.e. bat hair) and prey (to an order level and to a family level for some dipterans) within each pellet. I determined daily diet composition by subtracting the volume of non-food items from the volume of prey items for each pellet and then averaging results from the three daily replicates. Percent frequency is the percent of pellets in which a particular prey type occurred out of the total pellets analyzed.

Statistical analyses

I analyzed data using JMP IN statistical software (version 7.0.1). Model residuals were tested for normality using the goodness of fit, Shapiro-Wilk W test and were log or square-root transformed if necessary. A W value > 0.85 indicated that the assumption of normality was satisfied. I used Tukey's post-hoc test to test all pairwise comparisons for significant results. I used $\alpha = 0.05$ and report means \pm SE.

As in Chapter Two, I divided the summer by light season (early, middle and late) for analyses. Light seasons were based on civil twilight. Early (15 May to 6 June) and late (4 July to 19 August) in the summer, civil twilight ended each night and started the following morning. During the middle of the summer (7 June to 3 July), civil twilight persisted over the entire night.

Bat activity

I conducted repeated measures analyses of variance (ANOVA) for bat activity and feeding activity (number of feeding buzzes/pass/night) recorded at sites around the airport. I tested the effects of habitat, site, and season, as well as the interaction of season by habitat. Site was nested within habitat and was a random effect. I also conducted a non-parametric Kruskal Wallis test on bat activity at the four locations (airport, town, Albert Creek, campground) and an ANOVA on the effect of direction (for the airport sites north or south of the colony) on bat activity.

Arthropod biomass

I conducted repeated measures ANOVA's for the biomass of aerial arthropods (sum of 2 m and 4 m sticky trap biomass per habitat per night) and arthropods flying or crawling on or among the vegetation (sum of 4 sweep net samples per habitat per night). In both models, I tested the effects on arthropod biomass of habitat, site, and season, as well as the interaction of season by habitat. Site was nested within habitat and was a random effect. I also tested the effects of season on Araneae (spider) biomass from the sweep net samples by conducting an ANOVA.

I did not include the 0 m sticky trap data in my analysis because I did not start measuring arthropod biomass at 0 m in the standing and flowing water habitats until 3 July. To determine whether 0 m was an important component of arthropod biomass in

these two water habitats, I performed a repeated measures ANOVA. I tested the effect of trap height (0 m, 2 m, and 4 m), habitat, and site on aerial arthropod biomass. Site was nested within habitat and was a random effect. Season was not included in the model because most of the data were collected in the late season.

Diet

I conducted an ANOVA for the percent volume of Araneae in the diet of bats at the Watson Lake airport colony. I tested the effects of season on percent volume of Araneae consumed.

Results

Bat Activity

Over the summer, I collected 239 detector-nights of bat activity data (177 at the airport and 62 at surrounding locations) with a total of 7742 bat passes (6998 at the airport and 744 at surrounding locations). All passes recorded were *Myotis* passes with a minimum call frequency >35 kHz and moderately steep FM-sweeps. Overall, the bats did not use the open-field habitat (Fig. 3.4). Over 31 sampling nights, a total of only 28 passes and 0 feeding buzzes were recorded in the open-field habitat, and consequently I did not include it in further analysis. Bats were most active in the standing water, forest interior, flowing water, and forest corridor habitats (Fig. 3.4). Forest edges were used to a lesser extent. The feeding rate (number of feeding buzzes/pass/night) within each habitat varied due to differences among sites, but on average standing water had the highest feeding rate (0.05 ± 0.017 feeding buzzes/pass/night), followed by the forest edge (0.03 ± 0.009 feeding buzzes/pass/night), flowing water (0.02 ± 0.01 feeding buzzes/pass/night), forest corridor (0.02 ± 0.007 feeding buzzes/pass/night) and forest interior (0.004 ± 0.002 feeding buzzes/pass/night).

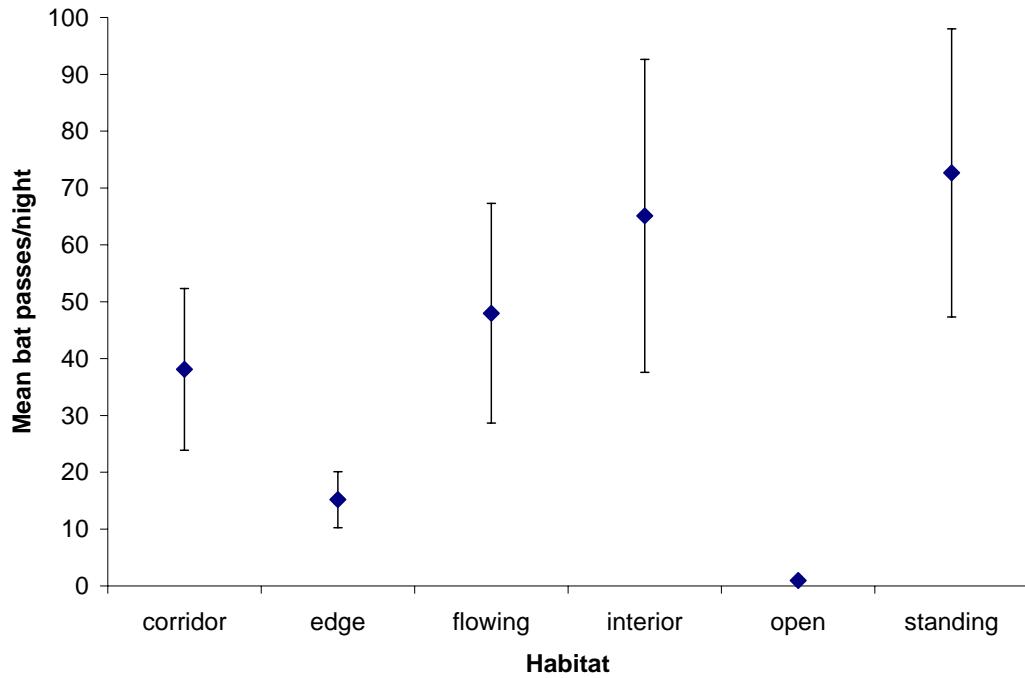


Figure 3.4: Mean (\pm SE) bat passes per night over the summer, in various habitats around the Watson Lake airport in 2006.

The duration and pattern of bat activity differed over the summer around the airport (Fig. 3.5). Bat passes were recorded over 240 minutes (first to last pass) early in the summer, 270 minutes in mid-summer and 480 minutes in late summer. Most activity (>10 passes/30 minutes), however, occurred for 180 minutes in early summer, 180 minutes in mid-summer and 390 minutes in late summer. All first and last bat passes recorded were after sunset and before sunrise, respectively, except on one occasion. On 19 July, two passes (21:45 and 21:47) were recorded before sunset (22:43) in the interior site located between the maternity roost and the lake. Early and late in the summer, when civil twilight ended each night and started the following morning, bat activity exhibited a bimodal pattern. Early in the summer, the first foraging bout or first peak in bat activity was larger than the second. Late in the summer, the two activity periods had relatively the same amount of activity. During mid-summer, when civil twilight persisted over the entire night, only one large peak in activity occurred (Fig. 3.5).

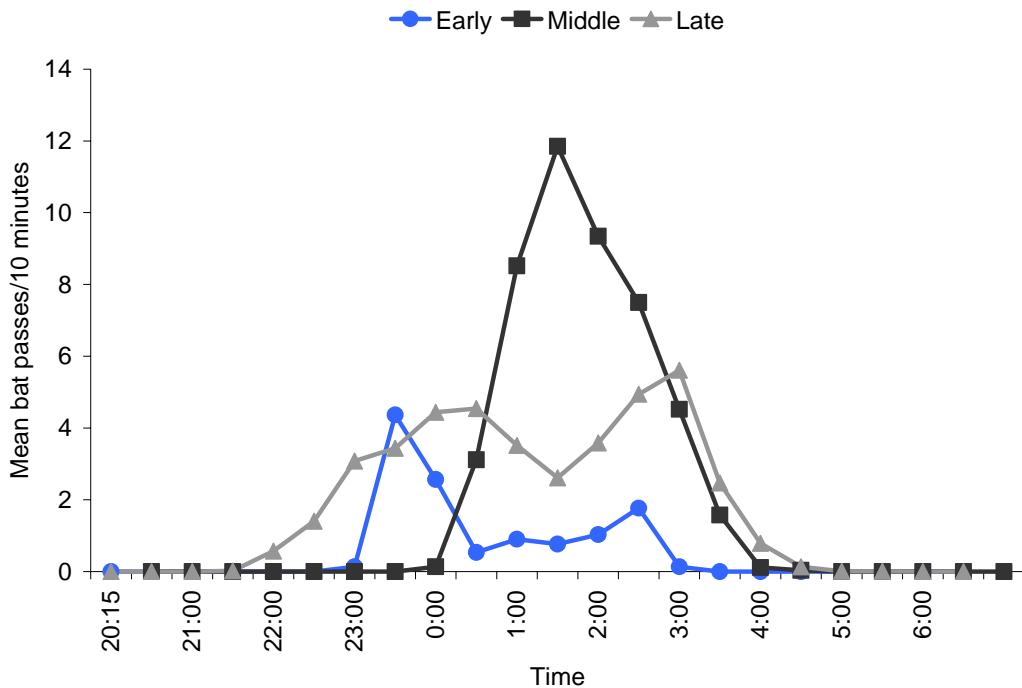


Figure 3.5: Mean bat passes, per 10 minute interval, over the three light seasons at sites located around the Watson Lake airport, Yukon.

Around the Watson Lake airport, bat activity varied significantly ($F_{21, 116} = 2.3, p = 0.001$). Both season and site-within-habitat had a significant effect on bat activity ($F_{2, 116} = 3.57, p = 0.03$ and $F_{15, 116} = 2.38, p = 0.005$, respectively). Activity was significantly lower during early summer compared to mid and late summer (Fig. 3.6). The standing water site located at the beaver pond (standing 4), as well as the forest interior site located between the airport maternity colony and Watson Lake (interior 2), had the highest activity. Overall, habitat did not have a significant effect on bat activity ($F_{4, 116} = 1.81, p = 0.16$). The interaction of habitat and season was not significant ($F_{8, 116} = 0.97, p = 0.46$).

Bat activity also varied significantly with direction from the roost ($F_{1, 144} = 23.16$, $p < 0.0001$). Activity was significantly higher to the south, between the maternity roost and the lake, than to the north of the maternity colony. Within the standing water habitat, bat activity was higher at the beaver pond (standing 4) than the three sites located along the lake (standing 1, 2, and 3; $\chi^2 = 8.61$, $df = 3$, $p = 0.03$), but feeding rate was not significantly different among the standing water sites ($\chi^2 = 5.06$, $df = 3$, $p = 0.17$).

Feeding activity (rate of feeding buzzes/pass/night) also varied significantly around the airport ($F_{29, 116} = 1.89$, $p = 0.009$). Season and habitat did not have a significant effect on feeding activity ($F_{2, 116} = 0.89$, $p = 0.41$, and $F_{4, 116} = 1.11$, $p = 0.38$, respectively), but site-within-habitat did ($F_{15, 116} = 2.81$, $p = 0.0009$; Table 3.1). The standing water site located at the beaver pond (standing 4), which had high bat activity (see above), also had significantly higher feeding activity than three other sites: corridor 3 and 2 and interior 4. The interaction between season and habitat was not significant ($F_{8, 116} = 0.76$, $p = 0.63$).

Using pass data from all four locations (airport, Albert Creek, campground and town), bat activity varied significantly with location ($\chi^2 = 11.92$, $p = 0.008$; Fig. 3.7). The locations near human settlements (airport and town) had higher bat activity than the more remote locations (Albert Creek and campground), and the airport also had higher activity than the town, although not significantly so.

Table 3.1: Mean (\pm SE) feeding rate (feeding buzzes/pass/night) per site within each habitat. Refer to site map (Chapter One) for details of site location.

Forest corridor	Forest interior	Flowing water
1. 0.04 ± 0.02	1. 0.00 ± 0.00	1. 0.03 ± 0.02
2. 0.00 ± 0.00	2. 0.01 ± 0.01	2. 0.06 ± 0.03
3. 0.00 ± 0.00	3. 0.00 ± 0.00	3. 0.00 ± 0.00
4. 0.01 ± 0.01	4. 0.00 ± 0.00	4. 0.01 ± 0.01
Forest edge	Open field	Standing Water
1. 0.05 ± 0.03	1. 0.00 ± 0.00	1. 0.01 ± 0.01
2. 0.04 ± 0.02	2. 0.00 ± 0.00	2. 0.06 ± 0.05
3. 0.02 ± 0.02	3. 0.00 ± 0.00	3. 0.06 ± 0.03
4. 0.01 ± 0.01	4. 0.00 ± 0.00	4. 0.07 ± 0.04

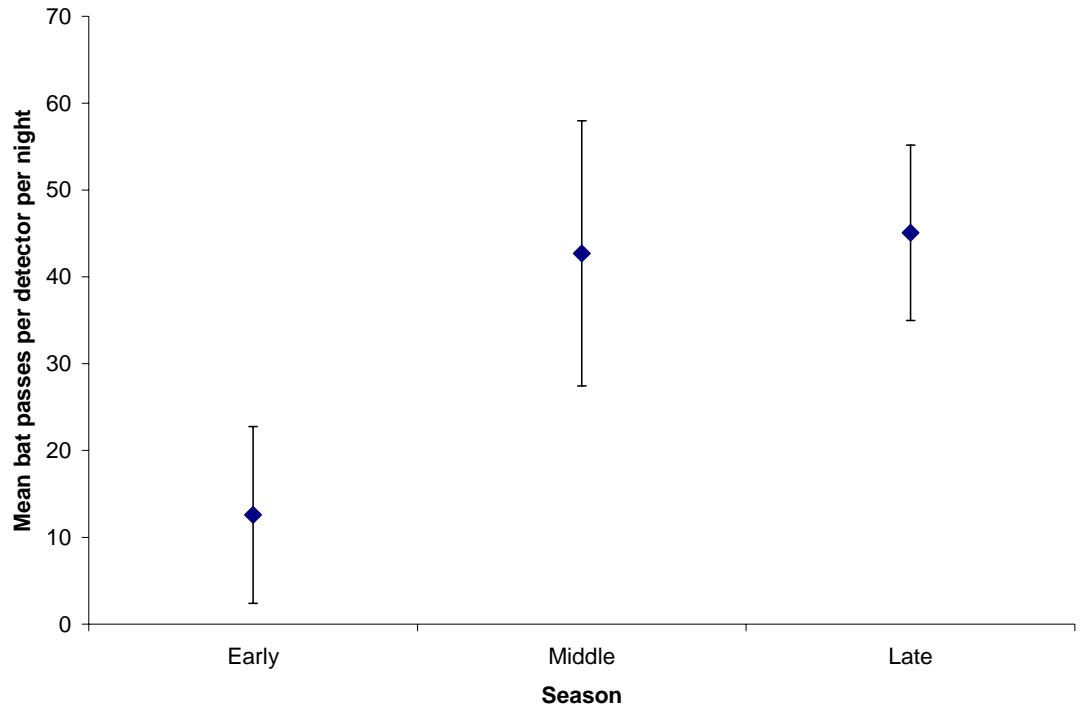


Figure 3.6: Mean (\pm SE) bat passes per detector per night over the three seasons, around the Watson Lake airport in 2006.

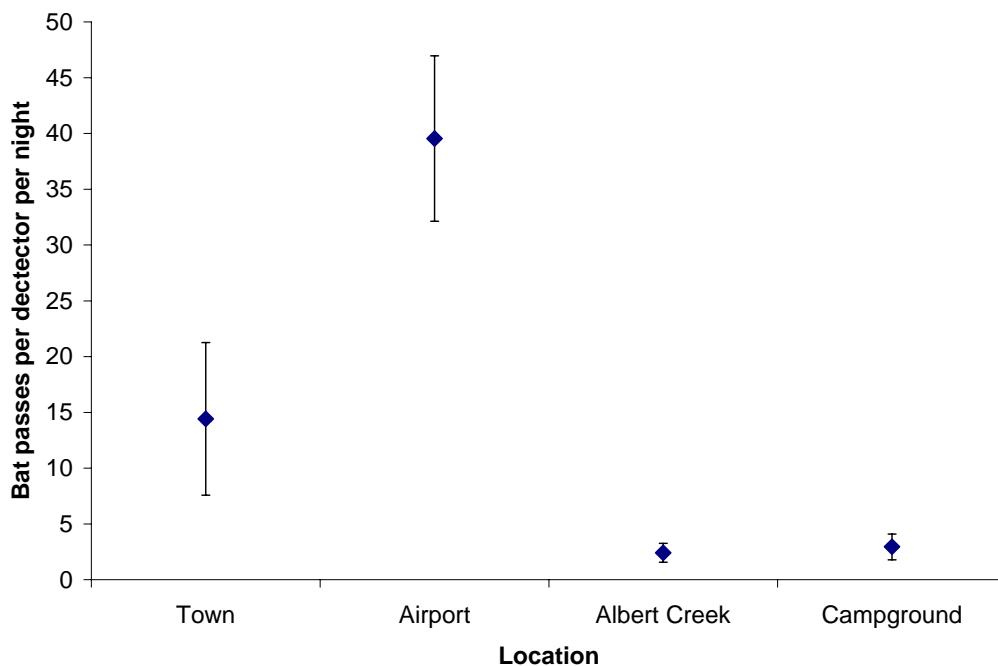


Figure 3.7: Mean (\pm SE) bat passes per detector per night at four areas over the summer in 2006, Watson Lake, Yukon.

Visual observations of bat foraging behaviour

From the end of May to early July, it was possible to make observations of bats foraging around the airport due to the bright light conditions. During this time, we made approximately 30 person-hours of observations. We observed bats in all six habitat types, but the majority of bat activity was concentrated within the standing water and forest interior habitats. Bats were only observed in the open-field habitat adjacent to the roost while departing or returning to the colony. During this time, they flew close to buildings, fences and the ground, and no feeding buzzes were recorded (Chapter Two). A great grey owl (*Strix nebulosa*) was observed in the open-field habitat on two occasions (16 and 19 June), around the airport site. Few observations were made in the flowing water habitat because it was located on the north side of the runway and for convenience reasons the majority of observations were made on the south side of the runway.

Within the forest interior habitat, bats were observed circling among the coniferous and deciduous trees at various heights (1 to 15 m). The majority of passes (~85 %) were at 3 to 10 m above the ground. At the end of May, few feeding buzzes were detected within the forest interior site (e.g. two feeding buzzes in 15 minutes), but around solstice, many feeding buzzes were detected (e.g. 39 feeding buzzes in 10 minutes).

Many spider webs were present within the forest interior during observations.

In the standing water habitat, bats were observed flying in and out of the overhanging vegetation (coniferous and deciduous), along the shoreline at approximately 4 m above the ground. Bats were also observed flying low over the water (< 50 cm). At the lake sites, bats flew along the lake edge, usually 2 to 5 m and no more than 10 m from the shoreline out over the lake. At the beaver pond, bats flew back and forth across the width of the pond (7 to 30 m). While bats skimmed the surface of the water, we recorded many feeding buzzes at both the beaver pond and the lake. Water on the beaver pond was often calmer than the lake. During nights when the lake was rough, no bats were observed foraging over the lake or among the riparian vegetation, but bats were observed foraging over the beaver pond.

Bats were observed flying straight down or across forest corridors at approximately 5 m above the ground. No feeding buzzes were recorded in the forest corridor habitat during observations. Likewise, no feeding buzzes were recorded at the forest edge habitat and bats were observed flying down the forest edge at approximately 5 m.

Arthropods

Aerial arthropods

I caught 13 orders of arthropods (12 orders of insects and 1 order of arachnid) on the sticky traps (2 m and 4 m) over the summer, in the six habitat types. Diptera was the most abundant order (based on mean biomass per night) captured over the entire summer (0.21 g), followed by Lepidoptera (0.097 g) and Hymenoptera (0.0067 g). Number of arthropod orders captured increased throughout the summer (early n = 4, middle n = 8 and late n = 11). Diptera was the most plentiful in early and mid-summer (mean 0.023 g, 0.13 g, respectively), and in late summer Lepidoptera was the most abundant (0.088 g). There was a large hatch of Diptera in the standing water habitat from 6 to 16 June. Some insect orders were captured only in one or a few specific habitat type(s), and others were captured in most habitat types (Table 3.2). The most abundant orders by habitat type over the three seasons are listed in Table 3.3.

Table 3.2: Orders of aerial insects, captured in the sticky traps, found only in specific habitat type(s) and insect orders not found in certain habitat types.

Order	Captured only in
Coleoptera	standing water and flowing water
Ephemeroptera	standing water
Hemiptera	standing water
Neuroptera	forest edge
Orthoptera	open-field
Psocoptera	flowing water

Order	Not captured in
Hymenoptera	forest corridor
Lepidoptera	forest interior
Trichoptera	open-field and forest corridor

Table 3.3: The three most abundant arthropod orders captured in the sticky trap samples in early (15 May to 6 June), middle (7 June to 3 July) and late (4 July to 19 August) summer. Note: number associated with the order is mean biomass (g) per night. n/a denotes that no other orders were captured.

	Early	Middle	Late	
CORRIDOR	(n = 2)		(n = 5)	(n = 6)
Diptera	0.00076	Diptera	0.018	Lepidoptera
n/a	-----	Homoptera	0.00010	Diptera
n/a	-----	Lepidoptera	0.00030	Araneae
EDGE	(n = 3)		(n = 7)	(n = 6)
Diptera	0.00014	Diptera	0.017	Diptera
Hymenoptera	0.000097	Lepidoptera	0.0025	Lepidoptera
n/a	-----	Araneae	0.0012	Trichoptera
FLOWING	(n = 2)		(n = 4)	(n = 7)
Homoptera	0.00025	Diptera	0.015	Trichoptera
n/a	-----	Homoptera	0.0057	Diptera
n/a	-----	Lepidoptera	0.0038	Lepidoptera
INTERIOR	(n = 4)		(n = 5)	(n = 8)
n/a	-----	Diptera	0.027	Diptera
n/a	-----	n/a	-----	Homoptera
n/a	-----	n/a	-----	Hymenoptera
OPEN	(n = 3)		(n = 7)	(n = 7)
Lepidoptera	0.0025	Diptera	0.0034	Lepidoptera
Diptera	0.00041	Homoptera	0.00058	Orthoptera
n/a	-----	Lepidoptera	0.00023	Diptera
STANDING	(n = 4)		(n = 6)	(n = 7)
Diptera	0.021	Diptera	0.049	Lepidoptera
n/a	-----	Trichoptera	0.0047	Trichoptera
n/a	-----	Coleoptera	0.00099	Diptera

Mean aerial arthropod biomass per habitat per night varied significantly ($F_{33, 59} = 3.69$, $p < 0.0001$). The interaction of season with habitat on the aerial arthropod biomass was not significant ($F_{10, 59} = 0.73$, $p = 0.69$). Season had a significant impact on aerial arthropod biomass ($F_{2, 59} = 37.12$, $p < 0.001$). There was significantly less aerial arthropod biomass in early summer compared to mid and late summer (Fig. 3.8). Habitat and site did not have a significant impact on aerial arthropod biomass ($F_{5, 59} = 1.56$, $p = 0.22$ and $F_{16, 59} = 1.22$, $p = 0.28$, respectively). When analyzing only the standing water sites (2 m and 4 m), mean aerial insect biomass did not vary significantly ($F_{3, 13} = 1.08$, $p = 0.39$) across the seasons.

Sticky trap height (0 m, 2 m, and 4 m) had a significant effect on aerial biomass in the standing and flowing water habitats during July and August ($F_{2, 36} = 3.69$, $p = 0.035$). Tukey's post-hoc test could not determine how biomass differed among the three trap heights, but 0 m had a slightly higher least square mean than 2 m and 4 m (Fig. 3.9). Because of this result, I ran the overall aerial biomass model again using 0 m and 2 m data for the water sites, and 2 m and 4 m data for all of the terrestrial sites. This model did not include season because most of the 0 m data were collected in late summer. The overall model explained a significant proportion of the variation in arthropod biomass ($F_{21, 22} = 2.27$, $p = 0.03$). Habitat had a significant effect on aerial biomass in late summer. The standing water habitat had the highest biomass and significantly higher than the forest interior habitat.

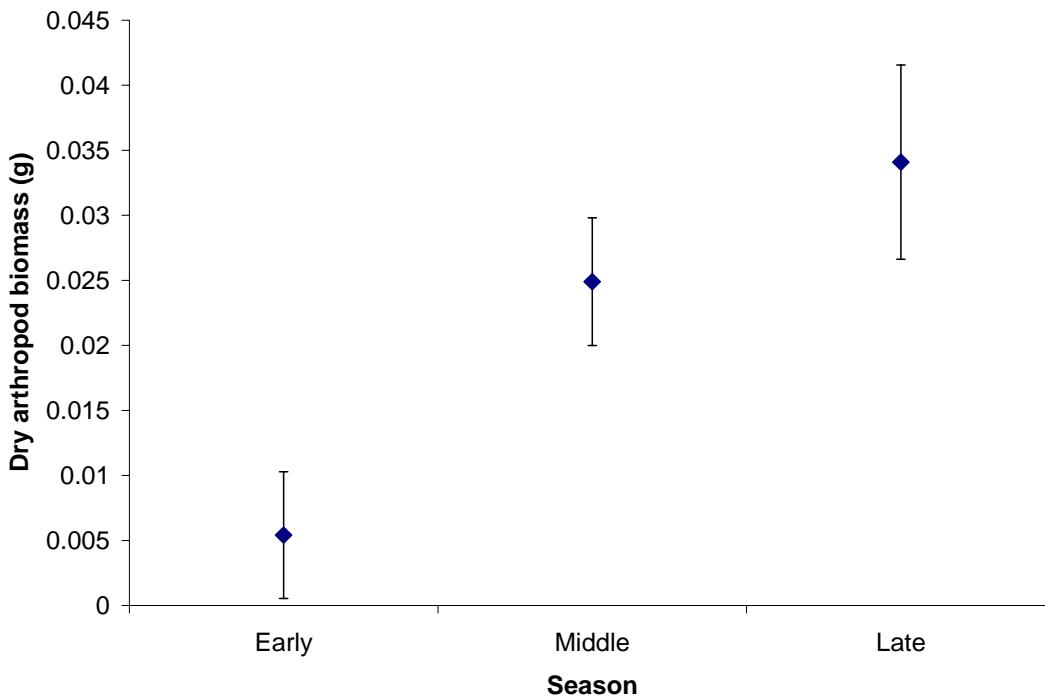


Figure 3.8: Mean (\pm SE) aerial arthropod dry biomass per habitat per night (at 2 m and 4 m) over the summer in 2006, Watson Lake, Yukon.

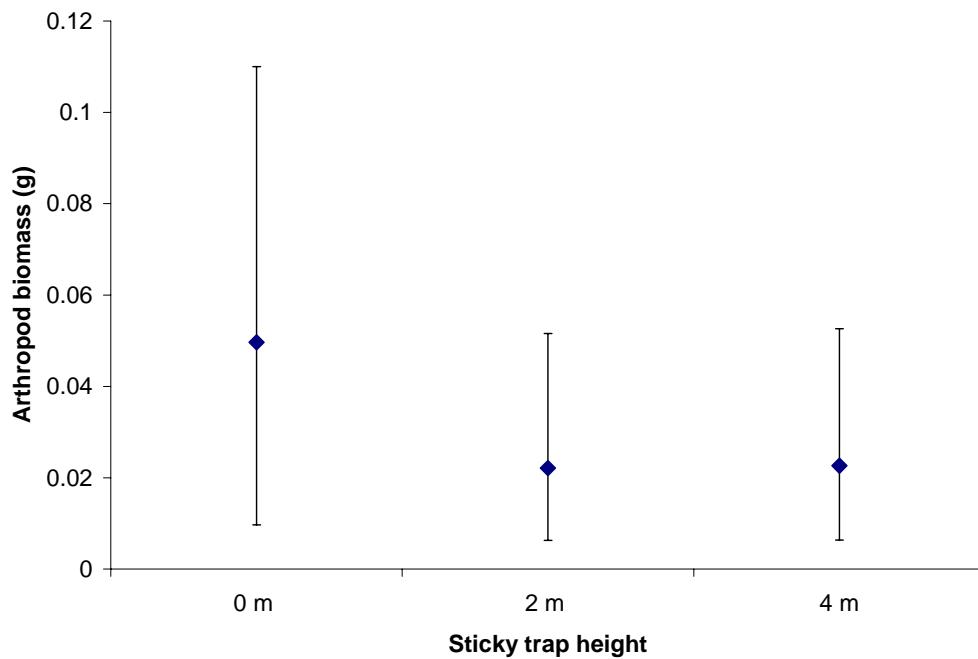


Figure 3.9: Least square means (\pm SE) of aerial arthropod biomass at 0 m, 2 m and 4 m in the flowing water and standing water habitats, Watson Lake, Yukon. Values have been back-transformed for display.

Arthropods on or among the vegetation

I caught 15 orders of arthropods (14 orders of insects and 1 order of arachnid) in the sweep nets over the summer, in the six habitat types. Diptera was the most abundant arthropod order (based on mean dry biomass per night) captured over the entire summer (2.01 g) followed by Araneae (0.58 g) and Coleoptera (0.29 g). The number of arthropod orders captured increased throughout the summer (early n = 9, middle n = 13 and late n = 14). Araneae was the most abundant arthropod in early and late summer (0.11 g and 0.25, respectively) and Diptera was the most plentiful in mid-summer (1.80 g). A large Dipteran hatch (chironomids and other Diptera) occurred from 10 to 22 June in the standing water habitat. These dates are slightly later than observed in the sticky traps (6 to 16 June). Unlike the sticky traps, most arthropod orders were found in every habitat type, with few exceptions (Table 3.4). The most abundant orders by habitat type over the three seasons are listed in Table 3.5. Araneae, Hemiptera and Coleoptera were observed more often in the sweep net samples, while lepidoptera were more common in the sticky traps. Araneae biomass did not vary significantly over the summer ($F_{2, 83} = 1.42$, p = 0.25).

Mean biomass of arthropods flying or crawling on or among the vegetation per habitat per night varied significantly ($F_{33, 53} = 6.73$, p < 0.0001). Season, habitat, site, and the interaction between season and habitat significantly influenced arthropod biomass ($F_{2, 53} = 37.43$, p < 0.0001; $F_{5, 53} = 2.88$, p = 0.04; $F_{16, 53} = 2.77$, p = 0.003; $F_{10, 53} = 2.87$, p = 0.0061, respectively). There was significantly less biomass in early summer than in mid and late summer (Fig. 3.10). Tukey's post-hoc test could not determine how biomass differed among habitats. Standing water 1 had significantly higher arthropod biomass on and among the vegetation than: forest interior 1 and 3, forest edge 4, flowing water 3, open-field 3, and corridor 3. The standing water habitat in mid-summer had significantly higher arthropod biomass than all other habitats, in all seasons, except the open-field habitat in late summer and forest edge habitat in mid-summer.

Table 3.4: Insect orders, captured with a sweep net, that were found only in a specific habitat type and insect orders not found in certain habitat types.

Order	Captured only in
Orthoptera	open-field, forest edge
Thysanoptera	forest edge
Order	Not captured in
Plecoptera	forest interior, open-field
Psocoptera	forest corridor, forest edge, open-field
Trichoptera	forest corridor

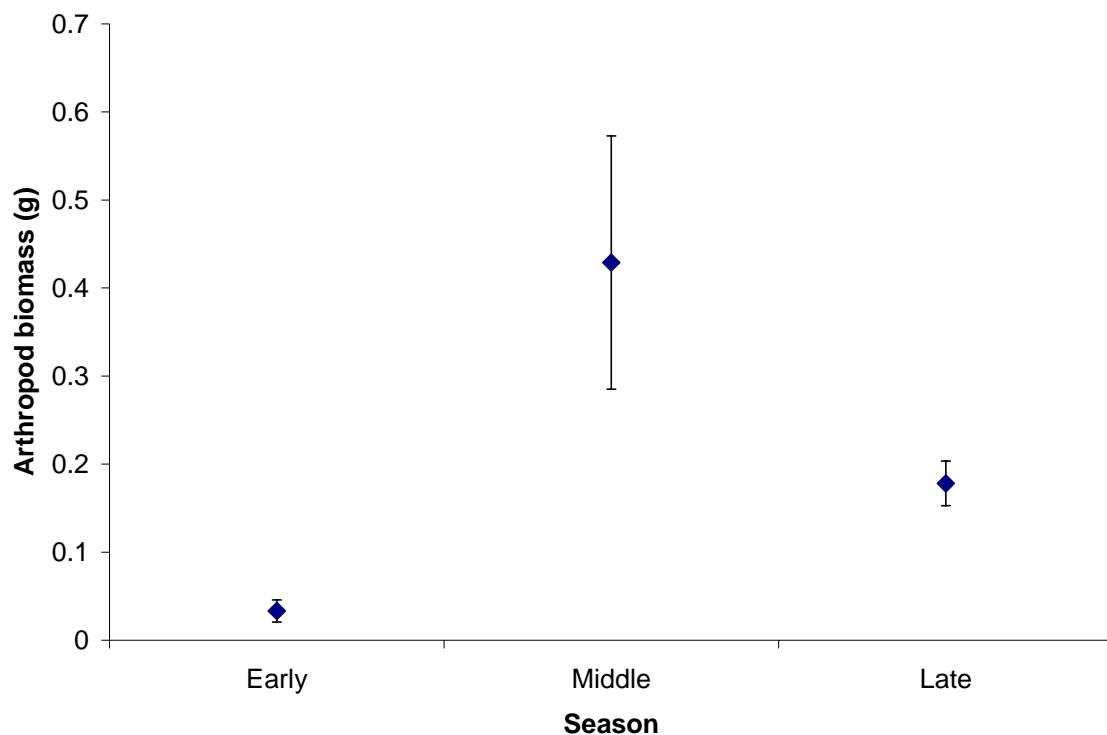


Figure 3.10: Mean (\pm SE) dry biomass of arthropods on or among the vegetation over the three seasons in 2006, Watson Lake, Yukon.

Table 3.5: The three most abundant arthropod orders captured in sweep net samples over early, middle and late summer. Note: number associated with the order is mean dry biomass (g) per night.

	Early	Middle	Late	
CORRIDOR	(n = 1)		(n = 5)	(n = 6)
Araneae	0.0071	Diptera	0.037	Coleoptera
Diptera	0.0017	Araneae	0.022	Araneae
Lepidoptera	0.00041	Coleoptera	0.017	Homoptera
EDGE	(n = 3)		(n = 6)	(n = 7)
Araneae	0.013	Diptera	0.040	Araneae
Coleoptera	0.0049	Coleoptera	0.077	Homoptera
Diptera	0.0024	Araneae	0.040	Diptera
FLOWING	(n = 1)		(n = 4)	(n = 7)
Araneae	0.012	Diptera	0.040	Hemiptera
Diptera	0.00082	Araneae	0.029	Homoptera
Homoptera	0.00050	Lepidoptera	0.010	Diptera
INTERIOR	(n = 2)		(n = 5)	(n = 8)
Araneae	0.053	Diptera	0.039	Araneae
Diptera	0.0026	Araneae	0.022	Diptera
Hymenoptera	0.00029	Coleoptera	0.011	Hymenoptera
OPEN	(n = 2)		(n = 7)	(n = 7)
Araneae	0.012	Hemiptera	0.044	Hemiptera
Diptera	0.0035	Diptera	0.035	Homoptera
Homoptera	0.00025	Orthoptera	0.024	Orthoptera
STANDING	(n = 3)		(n = 6)	(n = 7)
Diptera	0.038	Diptera	1.52	Araneae
Araneae	0.014	Araneae	0.096	Trichoptera
Coleoptera	0.003	Coleoptera	0.029	Diptera

Diet

I identified nine arthropod orders in the fecal remains from bats at the Watson Lake airport roost (Table 3.6). I divided Diptera into three groups: Chironomidae, Culicidae and all other Diptera. Over the summer, Diptera (all groups) occurred the most often (100 % of fecal pellets) and constituted the largest volume (24.59 %), followed by Lepidoptera (frequency: 45.28 %, volume: 17.57 %) and Coleoptera (frequency: 43.02 %, volume: 12.39 %). Araneae (spiders) were found in 31 % of the samples and comprised 10.76 % of the total volume over the summer. Araneae was the third most abundant food item identified in the diet during the early season. Diptera was always found in the greatest percent volume over the three light seasons. The three most abundant orders (based on percent volume) by season are listed in Table 3.7.

Percent volume of Araneae in the diet varied significantly with season ($F_{2,85} = 6.41$, $p = 0.0025$; Fig. 3.11a). There was a significantly higher volume of spiders consumed by bats early in the summer, compared to mid and late ($F_{2,85} = 6.41$, $p = 0.0025$). At the beginning of June, few spiders were consumed. This period corresponded to the Dipteran hatches recorded in the insect surveys. Diet analysis corresponded with these results; there was a high percent volume of Chironomidae in the diet during early June (Fig. 3.11b).

To determine a conservative estimate of how many spiders each bat at the airport consumed per night, I assumed that each bat consumed 4.6 g (wet-mass) of arthropods per night, half their mean body mass (Anthony and Kunz, 1977; Barclay *et al.*, 1991; Kurta *et al.*, 1989). Spiders made up 11 % of the *M. lucifugus* total diet and therefore each bat ingested 0.51 g of spiders each night. The mean dry biomass of a spider (2 mm to 15 mm) was 0.0082 g. Assuming that each spider is 70 % water, the wet mass of one spider was 0.027 g. Therefore, each bat in the colony would need to eat an average of 18.7 spiders per night. With 100 bats foraging in the area from the colony (conservative; see Chapter Two) 1870 spiders were consumed each night.

Table 3.6: Frequency of occurrence and mean percent volume of food items found in 247 *M. lucifugus* fecal pellets, collected at the Watson Lake airport roost in 2006.

Order	Frequency of occurrence (%)	Percent volume
Diptera (other)	64.91	20.25
Diptera (Chironomidae)	53.58	23.56
Lepidoptera	45.28	17.57
Coleoptera	43.02	12.39
Araneae (spider)	30.94	10.76
Trichoptera	13.58	6.91
Hemiptera	18.49	5.77
Neuroptera	12.08	1.14
Hymenoptera	7.92	0.81
Unknown	4.91	0.64
Ephemeroptera	0.75	0.14
Diptera (Culicidae)	0.75	0.06

Table 3.7: The three most abundant food items (based on percent volume) found in the fecal pellets collected at the Watson Lake airport roost, over the three light seasons in 2006.

Arthropod order	Frequency of occurrence (%)	Percent volume
EARLY (15 May to 6 June)		
Diptera (all)	100.00	37.10
Coleoptera	92.86	26.92
Araneae (spider)	85.71	21.54
MIDDLE (7 June to 3 July)		
Diptera (all)	100.00	49.63
Lepidoptera	66.67	14.97
Coleoptera	85.19	12.05
LATE (4 July to 19 August)		
Diptera (all)	100.00	42.58
Lepidoptera	82.98	21.81
Trichoptera	42.55	9.30

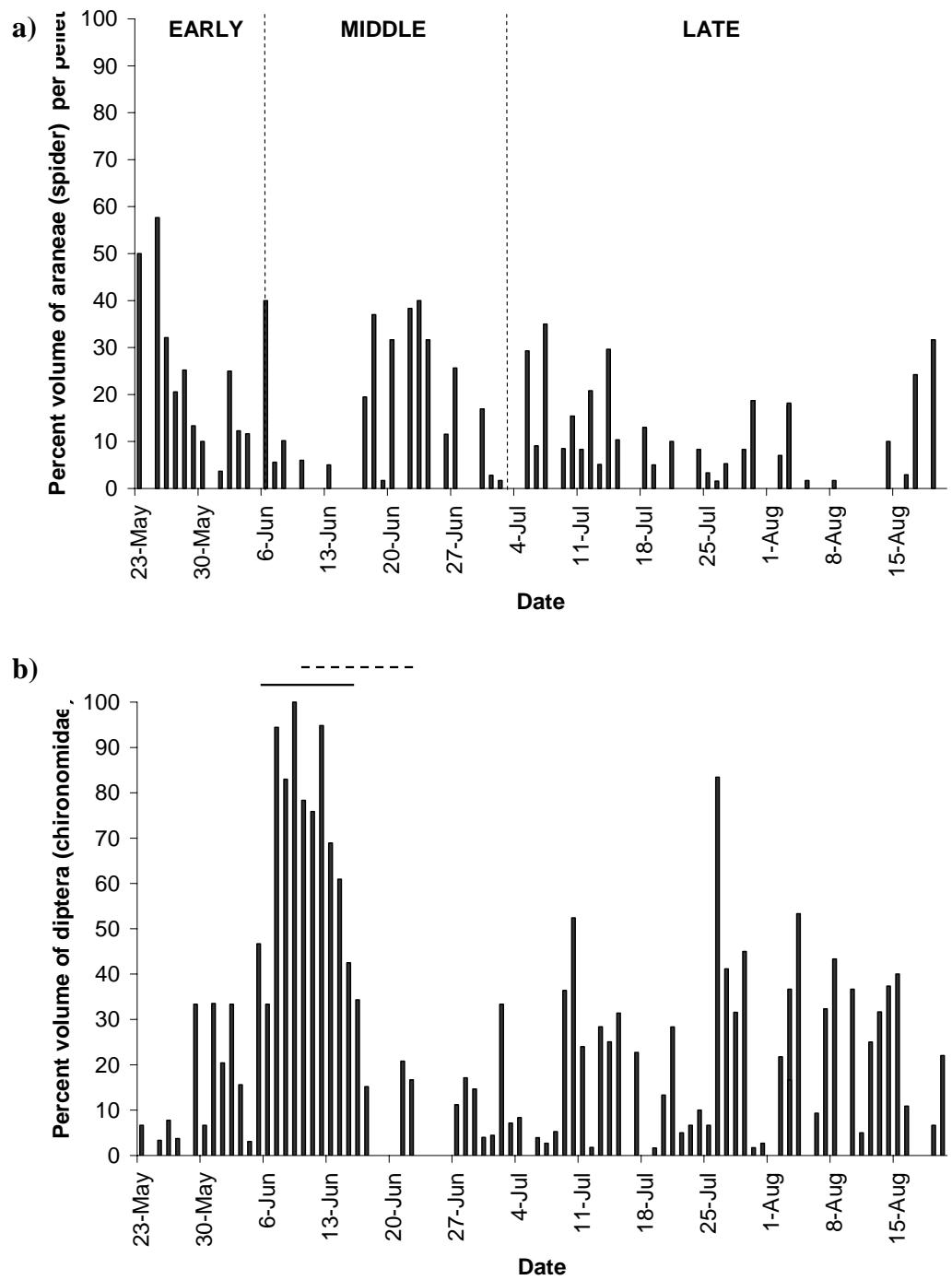
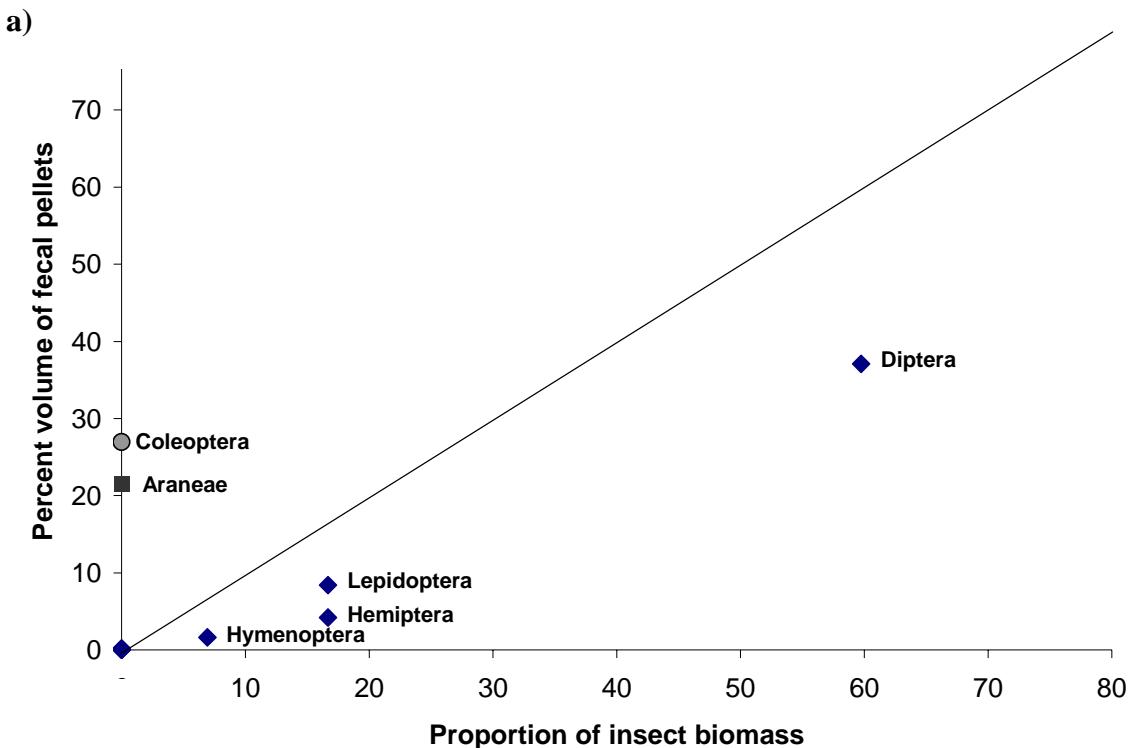


Figure 3.11: Percent volume of Araneae (spider; a) and diptera (Chironomidae; b) in the fecal pellets collected at the Watson Lake airport, in 2006, Yukon. Horizontal lines denote the chironomid hatches reported in the sweep (dashed line) and sticky trap (solid line) arthropod surveys (b).

The percent volume of insect orders in fecal pellets corresponded closely to the proportion of insect biomass available (sticky trap samples at 2 m and 4 m) during early, mid and late summer ($r^2 = 0.97$, $p < 0.0001$; $r^2 = 0.91$, $p = 0.0002$; $r^2 = 0.89$, $p = 0.0004$, respectively; Figs. 3.12 a, b, c). Coleoptera in early summer was excluded from the model because it was not present in the sticky trap samples but comprised 27 % volume of the fecal samples. Coleoptera was present in sweep net samples in the early season (Fig. 3.13). Araneae was excluded from the model in all seasons. The percent volume of insect orders in fecal pellets did not correspond to the proportion of insect biomass available in the sweep net samples in early summer ($r^2 = 0.22$, $p = 0.21$).



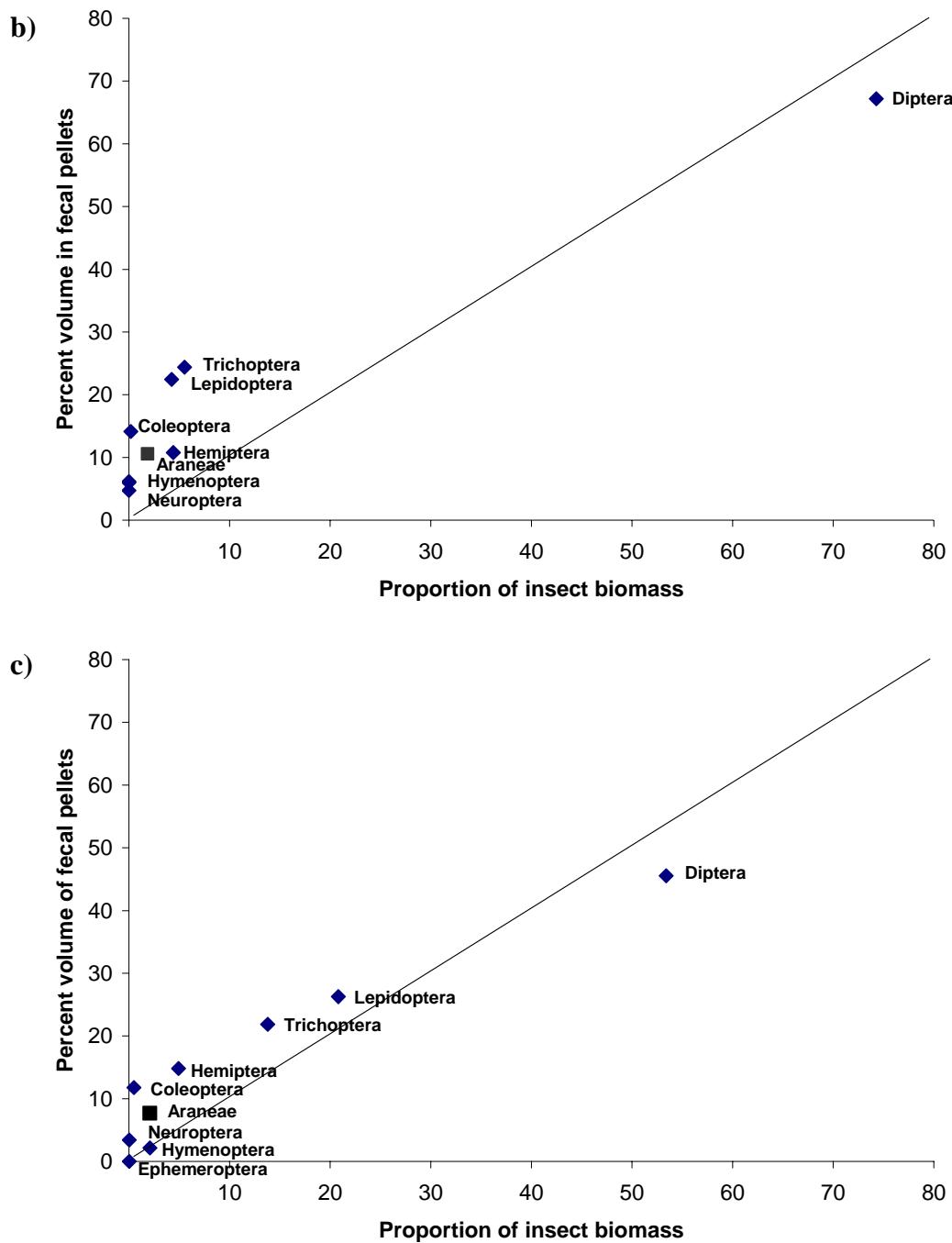


Figure 3:12: Mean percent volume of insect orders in fecal pellets and mean proportion of insect biomass in sticky trap samples (2 m and 4 m) during early (a), mid (b) and late (c) summer, Watson Lake, Yukon. Ephemeroptera and Trichoptera were not present in arthropod biomass or fecal pellets in early summer. Percent volume of Neuroptera in fecal pellets was 0.2 and it was not present in arthropod biomass in early summer. Note: solid line represents 1:1.

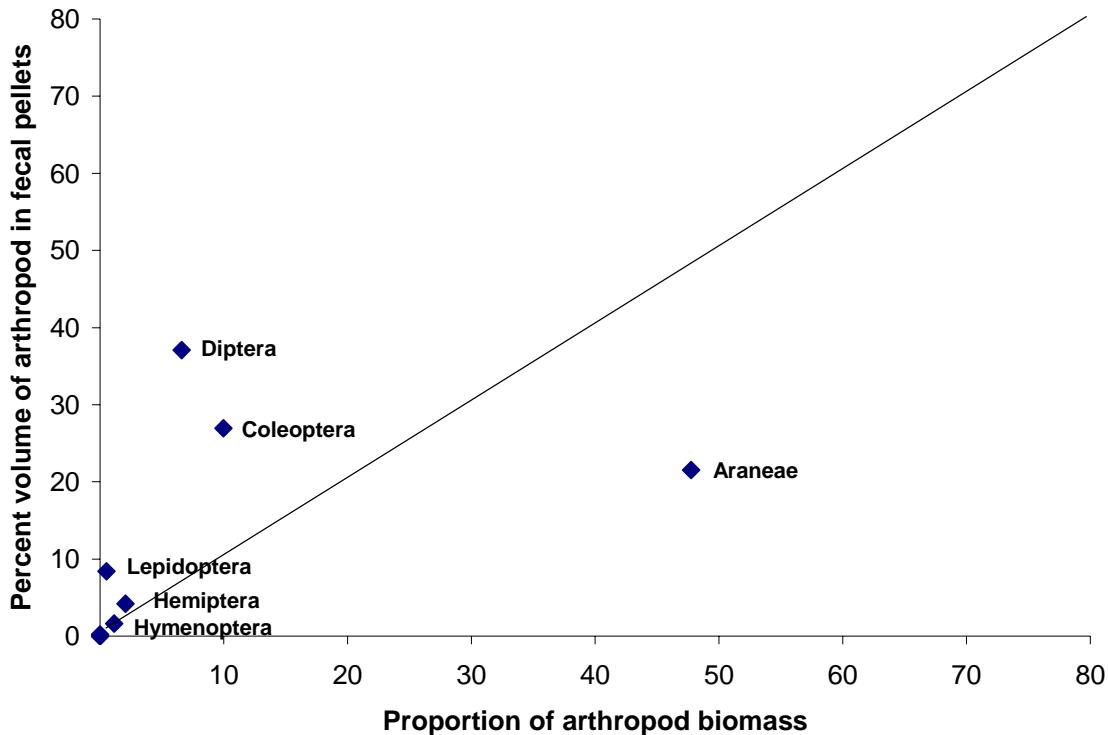


Figure 3:13: Percent volume of insect orders in fecal pellets and proportion of insect biomass in sweep net samples during early summer, Watson Lake, Yukon. Note: solid line represents 1:1.

Discussion

Timing of bat activity

The data I collected regarding activity of flying bats was consistent with the data on emergence from the Watson Lake airport maternity colony (Chapter Two) in that bats remained nocturnal over the entire summer. All bat passes, except for two, were recorded after sunset and before sunrise. However, the pattern of bat activity clearly varied over the summer. Early and late in the summer, when civil twilight ended each night and started the following morning, bat activity followed a bimodal activity pattern, whereas during mid-summer, when civil twilight persisted over the entire night, one large peak in activity was observed.

The bimodal activity pattern observed during early and late summer is typical for *M. lucifugus* in more southern locations (Anthony *et al.*, 1981; Barclay, 1982). *Myotis lucifugus* emerges at dusk and returns at dawn. During this period, it typically has two foraging bouts separated by a period of night roosting (Anthony *et al.*, 1981). The initial foraging bout lasts 40 to 185 minutes, depending on foraging success, predator activity and energetic constraints (Anthony and Kunz, 1977; Barclay, 1982). The length of the second foraging bout is dependent on the time spent night roosting and ends at dawn (Anthony *et al.*, 1981). Time spent night roosting is flexible for *M. lucifugus* (Anthony *et al.*, 1981). When nights are cool and prey densities are low, as in early summer, the night roosting period is longer than during warm nights with high prey abundance, as in late summer (Anthony *et al.*, 1981; Barclay, 1982). In the early summer, the second foraging bout may have been relatively shorter compared to late summer due to unprofitable feeding caused by cooler temperatures (Anthony *et al.*, 1981). Early and late in the summer, little brown bats typically occupy night roosts away from the maternity colony and during the lactation period, reproductive females return to the maternity roost between activity periods to nurse their young (Anthony *et al.*, 1981; Barclay, 1982). The bimodal foraging pattern that I observed early and late in the summer, as well as the emergence observations (Chapter Two), suggest that during early and late summer, bats were night roosting away from the colony. Further studies using radio telemetry would be helpful in determining where night roosts are located.

To my knowledge, the single large activity peak observed during mid-summer in Watson Lake has not been documented for *M. lucifugus* elsewhere. It is clear that the short nights present in mid-summer in Watson Lake influenced the nocturnal time budget of *M. lucifugus*. However, it is difficult to determine exactly how the time budget changed because I do not have data for individual bats. Further studies using radio telemetry and/or pit tagging would help determine this.

There are at least two possible explanations of why the activity pattern is different in mid-summer compared to early and late summer. First, bats may use the short time they have available for foraging in mid-summer by having one relatively long foraging bout each night. The majority of bat activity in mid-summer occurred over 180 minutes,

which is a reasonable length for one foraging bout for a little brown bat (Anthony and Kunz, 1977; Barclay, 1982). Variation in emergence and return time would explain the lower activity levels observed at the onset and end of each night. *Myotis lucifugus* is flexible in its foraging behaviour and has been reported to have two to four foraging bouts (Barclay, 1982), thus it may also be possible that individuals choose to have only one, long, foraging bout, when night length is restricted in mid-summer.

Having only one foraging bout may restrict the amount of energy that individuals can collect during mid-summer and bats may not be able to meet their energy demands, especially reproductive females in the late stages of pregnancy. It is possible that little brown bats in Watson Lake can meet their energy demands in mid-summer due to high arthropod abundance or through changes in their diet with season (see below). However, if energy demands are not met, bats may need to enter torpor more often. Torpor, however, can slow fetal growth and prolong gestation (Racey and Swift, 1981), thus delaying parturition (see Chapter Two). Short mid-summer nights may have contributed to the low reproductive rate and late parturition date reported at the airport colony (see Chapter Two). Further studies are needed to document torpor use by bats at northern latitudes and its influence on the timing of parturition and growth of young.

The second explanation for the foraging activity I observed is that the majority of the bats continue to have two foraging periods with a roosting period in between. This time budget may not be apparent in the overall pattern because the activity patterns of individual bats may overlap due to the short night. The timing and length of the roosting periods would vary with each individual's foraging success, energetic constraints and risk of predation (Anthony and Kunz, 1977; Barclay, 1982). For the bats that emerge early, it may be possible to have two, one-hour foraging bouts and a one-hour night-roosting period. Bats that emerge later may have shorter foraging bouts or may choose to forego the night roosting period or the second foraging period.

Habitat Use

Other than the expected increase in activity over the summer, no other significant effects of habitat or habitat with season were detected for bat activity. The lack of variation in habitat use by *M. lucifugus* in Watson Lake indicates that they use habitats that are not commonly used by southern conspecifics, in addition to the typical habitats. In more southern populations, *M. lucifugus* typically forages over water and it is occasionally captured or detected along forest corridors (Barclay, 1991; Broders *et al.*, 2004; Broders *et al.*, 2003; Buchler, 1976; Fenton *et al.*, 1980; Jung *et al.*, 1999; Parker *et al.* 1997; Saunders and Barclay, 1992; von Frenckell and Barclay, 1987). Activity within the forest interior is uncommon (e.g. Barclay, 1991). In Watson Lake, however, *M. lucifugus* was commonly detected within the forest interior and along forest corridors. Where *M. lucifugus* chose to forage in Watson Lake likely depended on various factors, including predation risk, prey availability, foraging efficiency and competition.

The emergence and return behaviour of the bats in Watson Lake (Chapter Two), suggests that perceived risk of predation was high. Bats did not use the open-field habitat unless they were emerging from or returning to the colony. As discussed in Chapter Two, when bats were in the open-field habitat while emerging and returning to the colony, they flew close to buildings, fences, or the ground. Avoidance of the open-field habitat may help explain why bat activity was significantly lower on the north side of the runway compared to the south side of the runway. Bats needed to fly over the large open runway (50 to 150 m) to access the areas on the north-side. Avoidance of large open areas by bats at high latitudes has been documented for *M. lucifugus* in Alaska and *Eptesicus nilssonii* in northern Scandinavia (Parker, 1996; Rydell, 1989a).

Bats may have used habitats such as the forest corridor and forest interior for protection from predation, specifically during brighter nights in mid-summer. The forest interior and forest corridor sites were darker due to taller vegetation. More than 80 % of the bat activity found in the ‘uncommon habitats’ (forest interior and forest corridor), was within one forest interior site and one forest corridor site situated between the maternity roost and the lake (south side of the runway). The six other corridor and interior sites, located on the north-side of the runway, had relatively low bat activity. Bat activity was

highest in the two south sites during the middle of the summer, specifically near solstice. Given the low feeding rates in these sites and low arthropod biomass, it is likely that little brown bats used these two areas primarily as protected commuting routes to and from foraging sites. Based on our observations in mid-summer (e.g. circling trees), the forest interior also may have been used for foraging.

Little brown bats in Watson Lake also likely used more sheltered sites more often than exposed sites because they provided protection from predators and the wind. In the standing water habitat, for example, bats foraged more often at the sheltered beaver pond site than at the three more open sites located on the lake, despite the insect biomass not being significantly different. Water on the beaver pond was usually calmer than the lake, especially on windy nights and little brown bats prefer to forage over clam water compared to rough water as it makes detection of prey by echolocation easier (Mackey and Barclay, 1989; von Frenckell and Barclay, 1986). The sheltered inlet of the beaver pond also may have provided cover from potential predators.

Foraging efficiency and prey availability were also likely factors influencing habitat choice. *Myotis lucifugus* is an aerial hawking species that forages in areas with low environmental clutter (Saunders and Barclay, 1992). Although opportunistic, it feeds heavily on aquatic invertebrates such as Trichoptera and Chironomidae (Belwood and Fenton, 1976; Fenton and Bell, 1979; Whitaker and Lawhead, 1992). Habitats such as standing water likely had the highest bat activity and highest feeding rates because it was relatively open, so prey could be taken efficiently, and it also contained large amounts of ‘preferred’ insect prey. Predation risk was likely still a factor when foraging in the exposed standing water habitat but the benefits of efficient feeding on preferred prey were high. Bats may have reduced their risk of predation while foraging by only flying high (~ 4 m) when amongst the vegetation, while over the open water they stayed close to the shoreline and kept low to the water.

Competition from diurnal insectivorous birds might occur for *M. lucifugus* in Watson Lake if the bats were active during the day. Many cliff (*Petrochelidon pyrrhonota*) and barn swallows (*Hirundo rustica*) roosted on the exterior of the Watson Lake airport. Based on our emergence observations, they were not active during the

same time period as the bats. Competition from other species of bats was unlikely around the airport. *Myotis lucifugus* is the only species documented in the study area and it is the only species I captured throughout the 2006 field season; *M. septentrionalis* has been captured 60 km north (Lausen *et al.*, 2008). The use of cluttered habitats by *M. lucifugus* in Watson Lake may thus also be the result of being the only bat species in the area. The forest interior may offer an unoccupied niche at high latitudes because specialist gleaning bat species, such as *M. septentrionalis*, are not present.

Bat activity in Watson Lake seemed to depend on the availability of roost sites in the area, specifically human settlements. For example, at the airport, there was significantly higher bat activity on the south side of the runway, where the maternity roost was located, compared to the north side of the runway. On the north side of the runway, one building was present (Bed and Breakfast) but the roof was rebuilt to exclude bats. This suggests that the majority of bats foraging in the area were from the airport colony and few bats were using natural roost sites. Likewise, the lack of human structures (e.g. buildings) at the campground and Albert Creek may explain why there was significantly lower bat activity than at the airport and in the town. Distribution of bats in other northern latitudes (e.g. Norway) has also been reported to reflect the occurrence of human settlements (Rydell *et al.*, 1994).

Diet

The diet of *M. lucifugus* in Watson Lake generally corresponded with that from studies conducted elsewhere in North America (e.g. Anthony and Kunz, 1977; Barclay, 1991; Belwood and Fenton, 1976; Fenton and Bell, 1979; Saunders and Barclay, 1992). *Myotis lucifugus* in Watson Lake was an opportunistic feeder and its diet was diverse. Dipterans, especially chironomids, were the most common prey item. Lepidoptera, Coleoptera and Trichoptera also comprised a relatively large proportion of the diet. Ephemeroptera was not a major component of the diet, unlike in New York state (Buchler, 1976). However, this is not surprising because, based on the arthropod sampling, Ephemeroptera were not common in the study area. Contrary to all other southern studies, Araneae was a common food item for *M. lucifugus* in Watson Lake.

Composition of the *M. lucifugus* diet changed throughout the summer as a consequence of the change in arthropod diversity and density in the area. The diet of little brown bats at the colony more or less corresponded to the arthropods captured in the sticky traps, with the exception of Coleoptera in early summer and Araneae throughout the entire summer. Coleoptera, in early summer, and spiders throughout the entire summer were captured primarily in the sweep net samples, suggesting that *M. lucifugus* in Watson Lake foraged not only on flying insects, but also on non-volant prey present on the vegetation. *Myotis lucifugus* foraged opportunistically on swarms of chironomids that hatched mid-summer, as has been documented elsewhere (Belwood and Fenton, 1976; Fenton and Bell, 1979).

Araneae is not a common food item for *M. lucifugus* and to my knowledge has only been documented in two studies in Alaska (Parker, 1996; Whitaker and Lawhead, 1992). Spiders have readily identifiable fragments, such as legs, and are thus unlikely to be overlooked in fecal analysis (Sheil *et al.*, 1997). In Watson Lake, Araneae were consumed throughout the summer, but made up a significantly higher proportion of the diet in early summer compared to mid and late summer, despite the biomass of Araneae remaining relatively constant over the summer. High intake of Araneae early in the summer may have been due to the lower aerial insect abundance and diversity present in early summer compared to mid and late summer. *Myotis lucifugus* is flexible in its diet and often takes one type of arthropod that is locally abundant (e.g. Araneae in this study; Anthony and Kunz, 1977).

Consumption of Araneae at high latitudes may allow bats to maintain a positive energy balance when temperatures and aerial insect densities are low (Parker 1996), especially early in the season. In Watson Lake, bats foraged in early and mid-May before flying arthropods were common and ice on the lake melted. This flexible foraging strategy may also enable reproductive female *M. lucifugus*, with high energy demands, to inhabit higher latitudes. *Myotis lucifugus* has an equal sex ratio in Alaska (Parker 1996), whereas reproductive female *M. lucifugus* are largely absent from some areas with low ambient temperatures and low insect abundance in more southern latitudes (e.g. Kananaskis, Alberta; Barclay 1991). Differences in population structure may reflect

differences in foraging abilities between the two populations. Reproductive female *M. lucifugus* in the north may be able to meet their energy demands because they exploit non-volant prey as well as volant prey, unlike individuals in more southern populations.

How little brown bats at high latitudes capture Araneae remains unclear. It is possible that bats take spiders directly out of their webs. If the webs are not detected by echolocation, a spider on a web would appear as if it was suspended in mid-air. Spider webs were abundant around the Watson Lake airport, especially in the forest interior (pers. obs). However, I did not identify spider webs in the fecal remains of *M. lucifugus* or capture any bats with spider webs on their bodies, suggesting that this method is unlikely (Schultz, 2000). It is also possible that little brown bats are capturing ballooning spiders as they are suspended in open areas (Best *et al.*, 1997). Alternatively, little brown bats may glean spiders off the vegetation. Although little brown bats are characterized as aerial hawkers, they are capable of gleaning (Ratcliffe and Dawson, 2003) and they have been documented taking other non-volant prey in more southern locations, although not in high volumes (Buchler, 1976; Fenton and Bell, 1979). Further studies are needed to observe the behaviour of *M. lucifugus* while foraging to determine how they capture spiders. In addition, identifying the spider remains to a family level would help distinguish web building spiders from non-web building spiders.

Given the differences in diet, and thus their foraging and flight style, between northern and southern populations of little brown bats, it is likely that selection has favoured different morphology as well. I explore this in Chapter Four.

CHAPTER FOUR

DOES *MYOTIS LUCIFUGUS* IN THE SOUTHERN YUKON DIFFER MORPHOLOGICALLY FROM SOUTHERN CONSPECIFICS?

Introduction

The optimal wing design and body size for a bat is influenced by many, often conflicting, selection processes, specifically involving thermoregulatory and foraging needs. The balance between these selection processes may differ with environment, foraging habitat, and prey availability, and thus morphology may also vary. Bat morphology has been reported to differ with latitude and climate (Bogdanowicz, 1990, Burnett, 1983); as latitude increases and temperature decreases, body size tends to increase. Bergmann's rule (Bergmann, 1847) states that larger body mass is advantageous at high latitudes because larger animals expend less energy per kilogram for thermoregulation due to a lower surface-to-volume ratio (Blackburn *et al.*, 1999). This allows more energy to be directed towards other activities such as reproduction and growth (Solick, 2004). Allen's rule (Allen 1977) states that body extremities (i.e. wings, feet, and ears) have been predicted to be smaller and/or shorter in warm-blooded animals of cooler climates compared to conspecifics in warmer climates because this reduces an organism's heat loss to the environment by decreasing the surface area of its extremities.

For flying animals such as bats, body mass and wing design influences more than just thermoregulation. The size and shape of the extremities (e.g. the wings), as well as mass, affect an organism's flight ability and flight style. Wing design may be shaped by foraging habitat and prey availability (Norberg and Rayner, 1987; Solick and Barclay, 2006). Bats with short, broad wings and low wing loading (mass/area), for example, are slow, manoeuvrable flyers adapted for foraging in cluttered environments and may glean insects off the vegetation (Norberg and Rayner, 1987). Bats with longer wings and high wing loading and aspect ratio (wing shape) are adapted for fast flight in more open environments (Norberg and Rayner, 1987).

In this chapter, I compare the morphology of adult, non-reproductive, female *M. lucifugus* in southern Yukon (Watson Lake; 60° 06' N, 128° 46' W) to those in southern Alberta (Calgary, Alberta, Canada; 51° 05'N, 114° 05'W). Given the differences in foraging behaviour and diet between little brown bats near the northern edge versus near the core of the range (Chapter Three), I predicted that little brown bats in the north differ morphologically from their southern conspecifics. Unlike their southern conspecifics, little brown bats in the north use the forest interior and may glean to capture spiders. However, the short, cool active season may mean that the needs for thermoregulation have a greater impact on morphology in the north. Because of the conflicting selection pressures, it is difficult to predict whether thermoregulatory or foraging needs take precedence. If thermoregulatory needs are more important (i.e. influence fitness) than foraging needs, I predicted that northern *M. lucifugus* would be larger (have a greater mass) than their southern conspecifics, based on Bergmann's rule and have smaller ears, based on Allen's rule. However, if foraging needs take precedence, greater manoeuvrability would be favoured by northern bats and they would have lower wing loading, lower aspect ratio, and shorter wings. Northern bats may also have larger ear size if they glean arthropods from the vegetation. Larger ear size is beneficial to gleaning bats because it increases their detection of non-volant insect prey by improving the directionality for low frequency sounds (Obrist *et al.*, 1993).

Methods

Field Work

From May to August 2006, I captured bats using mist nets of various lengths (2.6 to 18 m). I placed mist nets in a variety of locations including: around two maternity colonies (Watson Lake Airport and Hougens Department store), near water bodies (Watson Lake, beaver ponds) and across narrow forest trails and access roads. Upon capture, I immediately placed bats in individual cloth bags for one hour so they could empty their digestive system and an accurate body mass could be obtained. I recorded the species, sex, age, and reproductive condition of all bats captured. Juvenile bats were distinguished from adults by the degree of epiphyseal fusion of the fourth metacarpal joint (Anthony, 1988). Female reproductive condition was classified as: non-

reproductive (furred, unswollen nipples), pregnant (recognized by palpitation of the abdomen), lactating (swollen nipples), or post-lactating (bare unswollen nipples) (Racey, 1988). I only used data from adult females (non-reproductive and not obviously pregnant) in morphological analyses.

I determined body size by measuring mass and forearm length. I measured the mass of each bat, to the nearest 0.1 g, using a calibrated digital scale. I used calipers to measure the length of the right forearm of each bat to the nearest 0.01 mm. The average of three forearm measurements was used to reduce error. I also measured ear length (from the base to the tip of the ear) using a ruler, to the nearest 0.5 mm. The average of three ear-length measurements was used to reduce error.

To determine the wing dimensions (wing area and span), I photographed the extended right wing and tail membrane of adult female bats, using a digital camera (Canon PowerShot A410; Harley and Miller-Butterworth, 2000; Saunders and Barclay, 1992; Solick, 2004). I placed bats on a white background, beside a ruler, and took photographs directly vertical to the bat (Harley and Miller-Butterworth, 2000).

Image Processing

I downloaded digital photographs to a computer and ensured that the right wing tip and midline of the bat's body were visible on all photographs (Harley and Miller-Butterworth, 2000); I discarded ones that did not meet those criteria. To calculate wing area and linear measurements, I loaded images of 51 bats into Paint Shop Pro 7.0 and traced the right wing membrane, the right half of the tail membrane and the right half of the body between the wings (excluding the head) according to the methods in Harley and Miller-Butterworth (2000). I then analyzed the traced photographs (in portable pixel format (.ppm) in "BatWing.exe" (version 1.0, copyright 2000, E.H. Harley).

"BatWing.exe" calculated the wing area (cm^2) and wing span (cm; Fig. 4.1). Using those outputs, I calculated the aspect ratio ($\text{wing span}^2 / \text{wing area}$) and wing loading (mass/wing area) for each bat (Fig. 4.1).

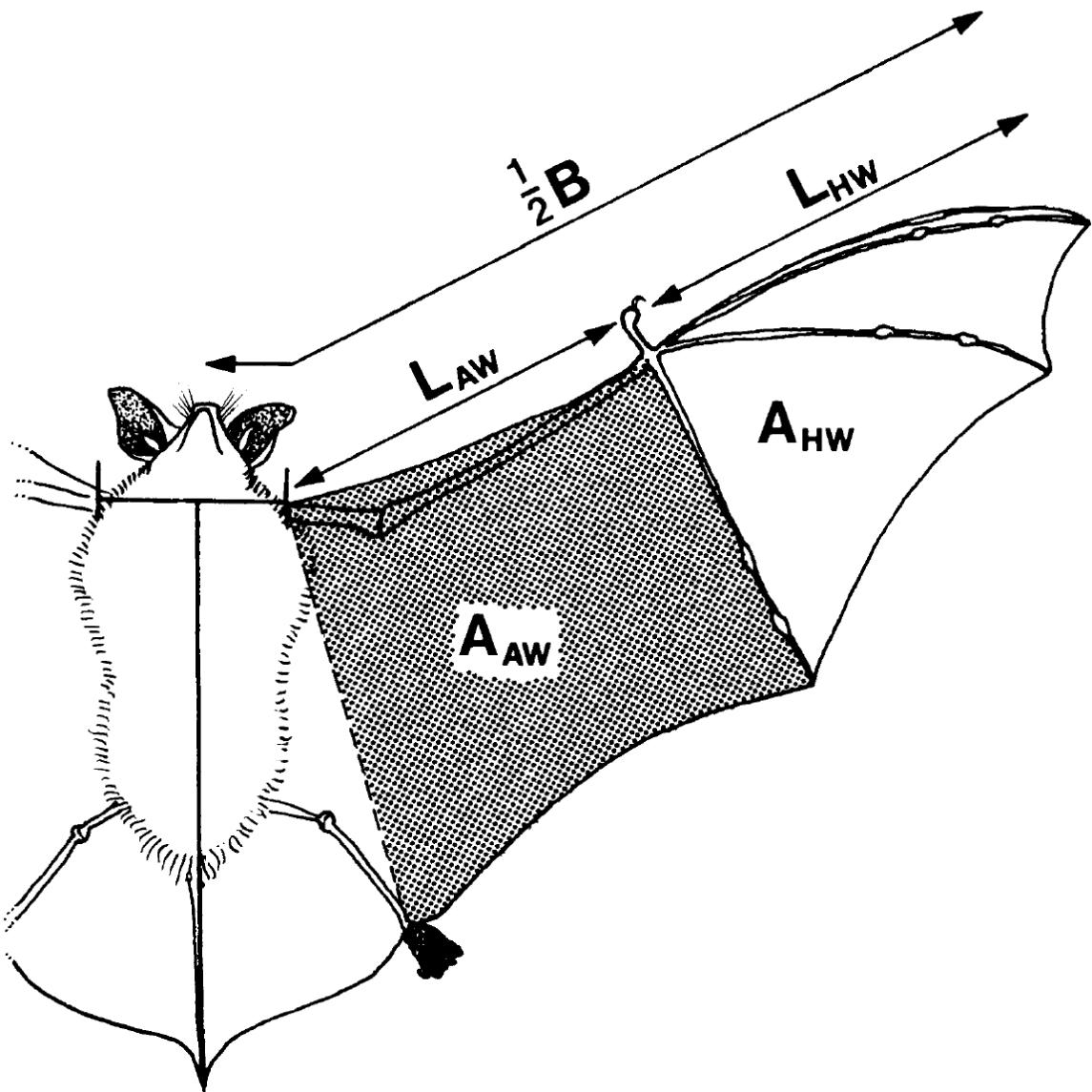


Figure 4.1:

Outline of a bat indicating the wing dimensions measured (Saunders and Barclay, 1992). B = wingspan. Wing area was measured as the combined area of the area between the midline of the body, and the proximal edge of the arm-wing (A_{AW}), the area of the arm-wing (A_{AW}), and the area of the handwing (A_{HW}).

Statistical Analysis

I compared the morphological measurements of adult, non-reproductive, female bats in Watson Lake ($60^{\circ} 06' N$, $128^{\circ} 46' W$) to adult, non-reproductive, female bats from Calgary, Alberta ($51^{\circ} 05' N$ $114^{\circ} 05' W$). Bats in both areas are *M. l. lucifugus* (Fenton and Barclay, 1980). Photographs and measurements of Calgary bats were taken by Joanna Coleman (Ph.D. Candidate, University of Calgary) in 2006. Methods for capturing and measuring bats in Calgary were the same as Watson Lake (see above). I conducted all image processing of the Calgary bat wing photos. I analyzed Calgary and Watson Lake data using JMP IN statistical software (version 7.0.1). Model residuals were tested for normality using the goodness of fit, Shapiro-Wilk W test. A $W > 0.85$ indicated that the assumption of normality was satisfied. I used $\alpha = 0.05$ and report means \pm SE.

Data were analyzed in two ways. First, to determine if there were overall differences in morphology (ear length, wing area, wing span, aspect ratio), I used ANOVA to test the effects of location (Watson Lake and Calgary). Second, I included forearm length as a covariate into the same models, to determine if bats of similar linear size differed in morphology. To test differences in wing loading, I used the same two types of models but also incorporated Julian day as a continuous, numerical, covariate and the Julian day with location interaction. Julian day was included in the model to account for changes in mass over the summer. I also tested if there were differences in, forearm length with location, or mass with location, Julian date and the interaction between Julian date and location.

Results

Size

I compared 51 non-reproductive adult female *M. l. lucifugus* from Watson Lake to 31 from Calgary. The ANOVA describing body mass explained a significant proportion of the variation ($F_{3, 75} = 5.77$, $p = 0.0013$). Location (north and core, i.e. Watson Lake and Calgary, respectively) had a significant effect on body mass ($F_{1, 75} = 12.39$, $p = 0.0007$). Little brown bats near the northern edge of the range had a significantly smaller body mass than little brown bats near the core of the range, on average 7.3 % smaller

(Table 4.1). Julian date and the interaction between Julian date and location had no significant effect ($F_{1,75} = 1.42, p = 0.24$; $F_{1,75} = 0.06, p = 0.81$, respectively) on body mass.

Forearm length varied significantly with location ($F_{1,78} = 5.65, p = 0.02$). Little brown bats in Watson Lake had significantly shorter forearms than little brown bats in Calgary, by an average of 1.1 % (Table 4.1). Likewise, the wingspans of little brown bats in Watson Lake were significantly shorter than little brown bats in Calgary (with forearm as a covariate: $F_{2,79} = 13.16, p < 0.0001$, without forearm: $F_{1,79} = 15.15, p = 0.0002$). Ear length was not significantly different between locations (with forearm: $F_{2,78} = 2.13, p = 0.12$; without forearm: $F_{1,79} = 2.45, p = 0.12$).

Wing morphology

The model describing variation in wing area explained a significant portion of the variation (with forearm: $F_{2,79} = 10.43, p < 0.0001$; without forearm: $F_{1,79} = 13.64, p = 0.0004$). Little brown bats in Watson Lake had a significantly smaller wing area than Calgary little brown bats, even after accounting for differences in body size (Table 4.1). The wing loading of little brown bats did not differ significantly by location (with forearm: $F_{4,74} = 2.49, p = 0.05$; without forearm: $F_{3,75} = 1.72, p = 0.17$), although the difference was almost significant when forearm was included in the model. Watson Lake little brown bats had slightly lower wing loading than Calgary little brown bats (Table 4.1). Aspect ratio also did not differ by location (with forearm: $F_{2,79} = 1.84, p = 0.16$; without forearm: $F_{1,79} = 1.52, p = 0.22$), although Watson Lake bats had slightly lower aspect ratios than Calgary bats (Table 4.1).

Table 4.1: Mean (\pm SE) morphological measurements of adult, non-reproductive, female, *M. lucifugus* in 2006 in Watson Lake, Yukon and Calgary, Alberta.

Variable	Watson Lake	Calgary
Body mass (g)	8.15 ± 0.10 (n = 49)	8.79 ± 0.17 (n = 31)
Forearm length (mm)	38.61 ± 0.10 (n = 51)	39.02 ± 0.15 (n = 31)
Ear length (mm)	11.06 ± 0.13 (n = 51)	10.77 ± 0.13 (n = 30)
Wingspan (cm)	24.60 ± 0.18 (n = 51)	25.77 ± 0.22 (n = 31)
Wing area (cm ²)	52.11 ± 0.65 (n = 51)	55.98 ± 0.73 (n = 31)
Wing loading (N/m ²)	7.67 ± 0.13 (n = 48)	7.73 ± 0.17 (n = 31)
Aspect ratio	5.83 ± 0.06 (n = 51)	5.94 ± 0.07 (n = 31)

Discussion

Differences in body and wing morphology were observed between *M. l. lucifugus* near the northern edge of the range (Watson Lake) and near the core of the range (Calgary). These results suggest that both thermoregulatory and foraging factors may have influenced the morphological variation. Bats in Watson Lake had a thermoregulatory advantage because they had significantly smaller wings (surface area and wingspan) than Calgary bats, even when accounting for body size. Therefore, northern bats may have lost less heat to the environment through their extremities than southern bats (Allen's rule –Allen 1877, Lindsay, 1987). However, contrary to Bergmann's rule (Bergmann, 1847) and previous studies (Bogdanowicz, 1990; Burnett, 1983), body size was smaller in the northern population. Bats in Watson Lake had a smaller mass than Calgary bats and thus northern bats may have lost more heat via their bodies.

Differences in body mass have many important physiological and ecological consequences (McNab, 1971) and thus they influence more than just thermoregulation. Northern bats may be smaller because they may not be able to maintain a larger body size due to low insect abundance in early summer (Chapter Three). Higher food intake is required by an increase in body size, due to an increase in metabolism (McNab, 1971). A greater body mass also affects a bat's flight ability and flight style. If Watson Lake bats had a greater body mass, their wing loading would have been greater and they would be

less manoeuvrable. If gleaning or foraging in cluttered habitats is favoured because of predation risk or prey abundance and distribution, greater manoeuvrability would be selected.

Differences in body size and wing morphology of *M. lucifugus* between Watson Lake and Calgary may be influenced by foraging habitat, foraging behaviour and prey availability (Solick and Barclay, 2006). The significantly smaller wings, and perhaps lower aspect ratio (not significant), lower wing loading (not significant), observed in Watson Lake indicate that northern *M. lucifugus* are more manoeuvrable than *M. lucifugus* in Calgary and may thus be better adapted to foraging in cluttered environments and possibly gleaning (Norberg and Rayner, 1987). These results correlate with my behavioural observations and bat activity and diet data (Chapter Three). In Watson Lake, *M. lucifugus* foraged more in cluttered environments, such as the forest interior, than more southern conspecifics do (Barclay, 1991). They also relied heavily on non-volant prey such as spiders early in the summer when aerial insect abundance was low. Greater manoeuvrability and foraging needs in the north therefore may be favoured in comparison to thermoregulatory needs because greater manoeuvrability may allow northern bats to maintain a positive energy balance when temperatures and aerial insect densities are low (Parker 1996). It may also enable them to use cluttered environments, such as the forest interior, for foraging or to avoid predation (Chapter Three).

Further research is needed to examine thermoregulatory and roosting behaviour of northern bats. How do northern bats survive in the north given their small size? Do they depend on roost sites that are thermally stable and warm (e.g. heated buildings) or can they survive in natural roost sites? How often do northern bats (reproductive/non-reproductive and male/female) enter torpor?

CHAPTER 5

GENERAL CONCLUSIONS

In my study, I examined the behaviour, diet and morphology of *M. lucifugus* near the northern limit of its range in Yukon Canada. I hypothesized that the short reproductive season, low temperatures and short nights limit the foraging opportunities of northern Canadian bats. I predicted that to cope with potential energy deficits, bats at high latitudes modify their foraging behaviour over the summer (i.e. where they foraged, when they foraged and what they foraged on).

Based on the behaviour of bats at the airport colony, the perceived risk of predation was high in Watson Lake and it was likely one of the major factors influencing foraging behaviour. Contrary to my prediction, little brown bats remained nocturnal throughout the summer. They consistently emerged from and returned to the airport colony after sunset and before sunrise, respectively. Almost no bat activity was detected before sunset and after sunrise. When emerging from and returning to the roost, bats consistently flew in the most protected areas (i.e. close to buildings, fences and the ground), which were often not the most direct routes to their destination. Although I did not detect any significant changes in habitat use with season, predator avoidance likely influenced habitat choice. Little brown bats only used the open-field habitat when emerging from and returning to the roost. They also used habitats not commonly used in more southern latitudes such as the forest interior (Barclay, 1991). Bats may have used habitats such as the forest interior for protection from predation, specifically during brighter nights in mid-summer.

It appeared that the length of the night in mid-summer provided ‘sufficient’ foraging time for the bats in Watson Lake and it was not ‘necessary’ to forage before sunset or after sunrise. However, short mid-summer nights seemed to impose time constraints on little brown bats in the north and they appeared to have a different nocturnal time budget than southern conspecifics. During mid-summer, when civil twilight persisted over the entire night, one large peak in activity was observed instead of the typical bimodal activity pattern for *M. lucifugus* in southern populations (Anthony *et al.*, 1981; Barclay, 1982) and that I observed in early and late summer.

Low temperatures present in Watson Lake also seemed to have a considerable influence on the foraging behaviour and diet of *M. lucifugus*. Northern bats were active over a range of temperatures (2.7 °C to 17.9 °C), from mid-May to mid August. They foraged during nights with light rain (< 3 mm) and nights with blowing snow. Northern little brown bats seemed to be more flexible in their foraging behaviour than in more southern populations. When ambient temperatures and aerial insect abundance were low in early summer, little brown bats foraged extensively on non-volant prey, specifically spiders. Spiders are not a common food item for *M. lucifugus* and to my knowledge have only been documented in two studies in Alaska (Parker, 1996; Whitaker and Lawhead, 1992). Consumption of spiders at high latitudes may allow bats to maintain a positive energy balance when temperatures and aerial insect densities are low (Parker 1996) especially early in the season. This flexible foraging strategy may also enable reproductive female *M. lucifugus*, with high energy demands, to inhabit higher latitudes. How little brown bats at high latitudes capture spiders remains unclear and further research is required to determine this.

Greater manoeuvrability and foraging needs in the north may be favoured in comparison to thermoregulatory needs because greater manoeuvrability allows northern bats to forage in more cluttered environments, such as the forest interior, and possibly glean. Differences in habitat use and diet may allow bats to maintain a positive energy balance when temperatures and aerial insect densities are low (Parker 1996). Northern *M. lucifugus* was more adapted to foraging in cluttered environments and possibly gleaning than those in Calgary because they had significantly smaller wings. Northern bats were also significantly smaller (body mass and wing forearm) than Calgary bats.

My study identified that northern *M. lucifugus* has both similarities and differences in its foraging behaviour to more southern conspecifics. This indicates that it may not be accurate to extrapolate the ecology of northern subarctic bats from studies on more southern populations. Further research is needed to understand the ecology of bats at the northern extent of their range. Specifically, studies are needed to examine the reproductive biology and the thermoregulatory and roosting behaviour of northern bats. What is the average length of gestation of female bats in northern populations? What is

the average mass of a bat pup at birth? At what age do female bats first reproduce? How do the over-winter-mortality rates and longevities of northern bats compare to more southern populations? In addition, given that bats remain nocturnal over the summer in the north, how do they obtain enough energy to survive? How much torpor do they use? Does torpor use differ from more southern populations? Do they depend on roost sites that are thermally stable and warm (e.g. heated buildings) or can they survive in natural roost sites?

Due to the harsher conditions and the short season, I predict that unlike in southern populations, female *M. lucifugus* do not reach sexual maturity until their second fall (see also Schowalter *et al.*, 1979). I hypothesize that because of lower reproductive rates, northern bats have a longer life expectancy than individuals in more southern populations. Because bat activity was significantly higher in areas with heated buildings (e.g. airport and town) than areas with few or no buildings (e.g. campground and Albert Creek), I hypothesize that reproductive, female northern bats depend on thermally stable, warm, roosts to successfully reproduce.

LITERATURE CITED

- Allen, J.A. 1877. The influence of physical conditions in the genesis of species. Radical Review 1: 108-140.
- Altringham, J.D. 1996. Bats biology and behaviour. Oxford University Press. New York.
- Anthony, E.L.P. 1988. Age determination in bats. In: Kunz, T.H. (ed.). Ecological and behavioral methods for the study of bats. Washington DC: Smithsonian Institution Press, pp 31-43.
- 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, *Myoits lucifugus*: effects of reproductive status, prey density and environmental conditions. Oecologia 51: 151-156.
- Ashton, K.G., M.C. Tracy and A. Queiroz. Is Bergmann's rule valid for mammals? The American Naturalist 156: 390-415.
- Baker, J.K. 1962. The manner and efficiency of raptor depredations on bats. Condor 64: 500-504.
- Barclay, R.M.R. 1982. Night roosting behavior of the little brown bat, *Myotis lucifugus*. Journal of Mammalogy 63: 464-474.
- Barclay, R.M.R. 1984. Observations on the migration, ecology and behavior of bats at Delta Marsh, Manitoba. Canadian Field-Naturalist 98: 331-336.
- Barclay, R.M.R. 1989. The effect of reproductive condition on the foraging behaviour of female hoary bats, *Lasiurus cinereus*. Behavioural Ecology and Sociobiology 24: 31-37.
- Barclay, R.M.R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. The Journal of Animal Ecology 60:165-178.
- Barclay, R.M.R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. The American Naturalist. 144: 1021-1031.
- Barclay, R.M.R., M.A. Dolan and A. Dyck. 1991. The digestive efficiency of insectivorous bats. Canadian Journal of Zoology 69: 1853-1856.
- Barclay, R.M.R. and M.B. Fenton. 1980. *Myotis lucifugus*. Mammalian Species 142: 1-8.

- Barclay, R.M.R., C.L. Lausen and L. Hollis. 2001. What's hot and what's not: define torpor in free-ranging birds and mammals. Canadian Journal of Zoology 79: 1885-1890.
- Barclay, R.M.R., C.E. Thompson, F.J.S. Phelan. 1982. Screech owl, *Otus asio*, attempting to capture little brown bats, *Myotis lucifugus*, at a colony, Canadian Field Naturalist 96: 205-206.
- Barclay, R.M.R., J. Ulmer, J.A. C. MacKenzie, M.S. Thompson, L. Olsen, J. McCool, E. Cropley and G. Poll. 2004. Variation in the reproductive rate of bats. Canadian Journal Zoology 82: 688-693.
- Belwood J.J. and M.B. Fenton. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 54: 1674-1976.
- Bender D.J., E.M. Bayne and R.M. Brigham. 1996. Lunar condition influences coyote (*Canis latrans*) howling. American Midland Naturalist 136 : 413-417.
- Bergmann, C. 1847. Ueber die verhältnisse der wärmeökonomie der thiere zu ihrer Grösse. Gottinger Studien 3: 595-708.
- Best, T.L., B.A. Milam, T.D. Haas, W.S. Cvlikas and L.R. Saidak. 1997. Variation in diet of the grey bat (*Myotis grisescens*). Journal of Mammalogy 78: 569-583.
- Birch, L.C. 1957. The meaning of competition. The American Naturalist 856: 5-18.
- Blackburn, T.M. K.J. Gaston and N. Loder. 1999. Geographic gradients in body size : a clarification of Bergmann's rule. Diversity and Distributions 5: 165-174.
- Bogdanowicz, W. 1990. Geographic variation and taxonomy of Daubenton's Bat, *Myotis daubentonii*, in Europe. Journal of Mammology 71: 205-218.
- Bowers, M.A. 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. Journal of Mammalogy 69:210-204.
- Brigham, R.M. and R.M.R. Barclay. 1992. Lunar influence on foraging and nesting activity of common poorwills (*Phalaenoptilus nuttallii*). Auk 109: 315-320.
- Broders, H.C., G.J. Forbes, S. Woodley and I.D. Thompson. 2004. Range extent and stand selection for roosting and foraging in forest dwelling northern long-eared bats and little brown bats in the greater Fundy ecosystem, New Brunswick. Journal of Wildlife Management 70: 1174-1184.

- Broders, H.G., G.M. Quinn, and G.J. Forbes. 2003. Species status, and the spatial and temporal patterns of activity pf bats in southwest Nova Scotia, Canada. *Northeastern Naturalist* 10:383-398.
- Buchler, E.R. 1976. Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). *American Naturalist* 110: 619-628.
- Buchler, E.R. 1980. The development of flight, foraging, and echolocation in the little brown bat (*Myotis lucifugus*). *Behavioral Ecology and Sociobiology* 6: 211-218.
- Burnett, C.D. 1983. Geographic and climatic correlates of morphological variation in *Eptesicus fuscus*. *Journal of Mammalogy* 64: 437-444.
- Cagle, F.R. and L. Cockrum. 1943. Notes on a summer colony of *Myotis lucifugus*. *Journal of Mammalogy* 24: 474-492.
- Case, T.J. and M.E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences (PNAS)* 71: 3073-3077.
- Case, T.J., R.D. Holt, M.A. McPeek and T.H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 109: 28-46.
- Catto, C.M.C., A.M. Hutson, P.A. Racey, P.J. Stephenson. 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology (London)* 238: 623-634.
- Chappell, M.A. 1980. Thermal energetics and thermoregulatory costs of small arctic mammals. *Journal of Mammalogy* 61: 278-291.
- Clarke, J.A. 1983. Moonlight's influence on predation/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13: 205-209.
- Danks, H.V. 2004. Seasonal adaptations in arctic insects. *Integrative and Comparative Biology* 44: 85-94.
- Davis, W.H. 1966. Population dynamics of the bat *Pipistrellus subflavus*. *Journal of Mammalogy* 47: 383-396.
- Downes, J.A. 1965. Adaptations of insects in the arctic. *Annual Review of Entomology* 10: 257-274.
- Duverge, P.L., Jones, G., Rydell, J., and R.D. Ransome. 2000. Functional significance of emergence timing in bats. *Ecography* 23: 32-40.

- Encarnacao, J.A., U. Kierdorf, D. Holweg, U. Jasnoch and V. Wolters. 2005. Sex related differences in roost selection by Daubenton's bats *Myotis daubentonii* during nursery period. Mammal Review 35:285-294.
- Environment Canada. 2008. Watson Lake climate normals and averages. Last accessed 5 May 2008 from: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/
- Erkert, H.G. 1978. Sunset-related timing of flight activity in Neotropical bats. Oecologia 37: 59-67.
- Erkert, H.G. 1982. Ecological aspects of bat activity rhythms. In: Kunz, T.H. (ed.). The ecology of bats. New York: Plenum Press, pp 201-242.
- Fenton, M.B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. Canadian Journal of Zoology, 47:597-602.
- Fenton, M.B. and R.M.R. Barclay. 1980. *Myotis lucifugus*. Mammalian Species 142: 1-8.
- Fenton, M.B. and G.P. Bell. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Canadian Journal of Zoology 57: 1273-1277.
- Fenton, M.B., I.L. Rautenbach, S.E. Smith, C.M. Swanepoels, J. Grosell and J. Van Jaarsveld. 1994. Raptors and bats: threats and opportunities. Animal Behavior 48: 9-18.
- Fenton, M.B., C.G. van Zyll de Jong, G.P. Bell, D.B. Campbell, and M. Laplante. 1980. Distribution, parturition dates and feeding of bats in south-central British Columbia. Canadian Field Naturalist 94: 416-420.
- Firman M.C., C. Godwin, and R.M.R. Barclay. 1995. Bat fauna of the west Shuswap and south Thompson river region, BC. Report prepared for Wildlife Branch, Ministry of Environment, Lands and Parks, Victoria, BC.
- Fujita, M. 1986. A latitudinal comparison of growth and development in the little brown bat *Myotis lucifugus* with implications for geographic variation in adult morphology. Thesis Boston University.
- Gilbert, S.B. and S. Boutin. 1991. Effect of moonlight on winter activity of sheshoe hares. Arctic and Alpine Research 23: 61-65.
- Gilbert, B.S., D.B. Cichowski, D. Talarico and C.J. Crebs. 1985. Summer activity patterns of three rodents in the southwestern Yukon. Arctic 39 : 204-207.

- Grindal, S.D., T.S. Collard, R.M. Brigham, R.M.R. Barclay. 1992. The influence of precipitation on reproduction by myotis bats in British Columbia. *American Midland Naturalist* 128: 339-344.
- Grinevitch, L., S.L. Holroyd and R.M.R. Barclay. 1995. Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. *Journal of Zoology (London)* 235: 301-309.
- Harley, E.H. and C.M. Miller-Butterworth. 2000. A software assistant for measuring bat wings. *Bat Research News* 41: 99-102.
- 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*). *Canadian Journal of Zoology* 72: 744-749.
- Hamilton, W.D. 1971. Geometry of the selfish herd. *Journal of Theoretical Biology* 31: 295-311.
- Henry, M., D.W. Thomas, R. Vaundry and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* 83: 767-774.
- Herd, R.M. and M.B. Fenton. 1983. An electrophoresic, morphological and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology* 61: 2029-2050.
- Hollis, L. and R.M.R. Barclay. 2008. Developmental changes in body temperature and use of torpor by the Big Brown Bat (*Eptesicus fuscus*). In Lovegrove, B.G. and A.E. McKechnie (eds.) *Hypometabolism in mammals: hibernation, torpor and cryobiology*. University of KwaZulu-Natal, Pietermaritzburg. pp 359-366.
- Holroyd, S.L., R.M.R. Barclay, L.M. Merk and R.M. Brigham. 1993. A survey of the bat fauna of the dry interior of British Columbia: A summary by species with recommendations for future work. Report prepared for Ministry of the Environment, Wildlife Branch, Victoria British Columbia.
- Holt, R.D., and T.H. Keitt. 2005. Species' borders: a unifying theme in ecology. *Oikos* 108: 3-6.
- Holt, R.D., T.H. Keitt, M.A. Lewis, B.A. Maurer and M.L. Taper. 2005. Theoretical models of species' borders: single species approaches. *Oikos* 108: 18-27.

- Humphrey S.R. and J.B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. American Society of Mammalogy Special Publication No 4. Allen Press: Lawrence, Kansas, pp 83.
- Issac, S.S. and G. Marimuthu. 1993. Early outflying and late homeflying in the Indian pygmy bat under natural conditions. *Oecologia* 96: 426-430.
- Jung, T.S., I.D. Thompson, R.D. Titman, and A.P. Applejohn. 1999. Habitat Selection by forest bats in relation to mixed-wood stand types and structure in central Ontario. *Journal of Wildlife Management* 63: 1306-1319.
- Jung, T.S., B.G. Slough, D.W. Nagorsen, T.A. Dewey, T. Powell. 2006. First records of the Northern Long-eared Bat, *Myotis septentrionalis*, in the Yukon Territory. *Canadian Field-Naturalist* 120: 39-42.
- Kotler, B.P., J.S. Brown, and O. Hasson. 1991. Factors affecting gerbil behavior and rates of owl predation. *Ecology* 72: 2249-2260.
- Kramer, K.M. and E.C. Birney. 2001. Effect of light intensity on activity patterns of patagonian leaf-eared mice, *Phyllotis xanthopygus*. *Journal of Mammalogy* 82: 535-544.
- Kunz, 1988. Methods of Assessing the Availability of Prey to Insectivorous Bats. In: Kunz, T.H. (ed.). *Ecological and Behavioural Methods for the Study of Bats*. Washington DC: Smithsonian Institution Press, pp 191-205.
- Kunz, T.H., and E.L.P. Anthony. 1982. Age estimation and post natal growth in the bat *Myotis lucifugus*. *Journal of Mammalogy* 63: 23-32.
- Kunz, T.H. and E.L.P. Anthony. 1996. Variation in the timing of nightly emergence behavior in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Contributions in Mammalogy: A Memorial Volume Honoring Dr. J. Knox Jones, Jr. 225-235.
- Kunz, T.H. and W.R. Hood. 2000. Parental care and postnatal growth in the chiroptera. In: Crichton, E.G. and P.H. Krutzsch (eds.). *Reproductive Biology of Bats*. New York: Academic Press, pp 415-454.
- Kurta, A., G.P. Bell, K.A. Nagy and T.H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62: 804-818.
- Lausen, C. 2006. Bat survey of Nahanni National Park reserve and surrounding areas, Northwest Territories. Report prepared for Parks Canada and Canadian Parks and Wilderness Society.

- Lausen, C.L., T.S. Jung, and J.M. Talerico. 2008. Range extension of the northern long-eared bat (*M. septentrionalis*) in the Yukon. *Northwestern Naturalist* 89:115-117.
- Lindsay, S.L. 1987. Geographic size and non-size variation in Rocky Mountain Canada and USA *Tamiasciurus hudsonicus*: significance in relation to Allen's rule and vicariant biogeography. *Journal of Mammalogy* 68: 39-48.
- Lee, Y. and G.F. McCracken. 2001. Timing and variation in the emergence and return of mexican free-tailed Bats, *Tadarida brasiliensis Mexicana*. *Zoological Studies* 40: 309-316.
- Lewis, S.E. 1993. Effect of climate variation on reproduction by pallid bats (*Antrozous pallidus*). *Canadian Journal Zoology* 71: 1429-1433.
- Mackey, R.L. and R.M.R. Barclay. 1989. The influence of physical clutter and noise on the activity of bats over water. *Canadian Journal of Zoology* 67: 1167-1170.
- Marimuthu, G. 1984. Seasonal changes in the precision of the circadian clock of a tropical bat under natural photoperiod. *Oecologia* 61: 352-357.
- Meiri, S., T. Dayan. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* 30: 331-351.
- Meiri, S.T., Y. Yom-Tov, and E. Geffen. 2007. What determines conformity to Bergmann's rule? *Global Ecology and Biogeography* 16:788-794.
- McNab, B.K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52: 845-854.
- Nagorsen, D.W. and R.M. Brigham. 1993. Bats of British Columbia. Vancouver: UBC Press, pp 81-85.
- National Research Council Canada. 2006. Sunrise/Sunset Calculator. Accessed 31 August 2006 from: http://www.hia-ihc.nrc-cnrc.gc.ca/sunrise_e.html
- Neuweiler, G. 2000. The biology of bats. Oxford University 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. *Philosophical Transactions of the Royal Society of London* 316: 335-427.

- Obrist, M.K., M.B. Fenton and J.L. Eger. 1993. What ears do for bats: a comparative study of pinna sound pressure transformation in chiroptera. *Journal Experimental Biology* 180: 119-152.
- Parker, D.I. 1996. Forest ecology and distribution of bats in Alaska. Thesis University of Alaska Fairbanks.
- Parker, D.I., B.E. Lawhead, and J.A. Cook. 1997. Distributional Limits of Bats in Alaska. *Arctic* 50: 256-265.
- Price M.V., N.M. Waser and T.A. Bass. 1984. Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammalogy* 65: 353-356.
- Prestrud, P. 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. *Arctic* 44: 132-138.
- Racey, P.A. 1988. Reproductive assessment in bats. In: Kunz, T.H. (ed.). *Ecological and behavioral methods for the study of bats*. Washington DC: Smithsonian Institution Press, pp 31-43.
- Racey, P.A. and S.M. Swift. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *Journal of Reproduction and Fertility* 61: 123-129.
- Racey, P.A. and S.M. Swift. 1985. Feeding ecology of *Pipistrellus pipistrellus* (chiroptera: Vespertilionidae) during pregnancy and lactation. *Journal of Animal Ecology* 54: 205-215.
- Ratcliffe, J.M. and J.W. Dawson. 2003. Behavioural flexibility: the little brown bat (*Myotis lucifugus*) and the northern long eared bat, *M. septentrionalis*, both glean and hawk prey. *Animal Behaviour* 66: 847-856.
- Rawn D.F.K., W.L. Lockhart, P. Wilkinson, D.A. Savoie, G.B. Rosenberg, and D.C.G. Muir. 2001. Historical contamination of Yukon Lake sediments by PCBs and organochlorine pesticides: influence of local sources and watershed characteristics. *The Science of the Total Environment* 280: 17-37.
- Reynolds, D.S. and T.H. Kunz. 2000. Changes in body composition during reproduction and postnatal growth in the little brown bat, *Myotis lucifugus* (Chiroptera: Vespertilionidae). Ecoscience 7: 10-17.
- Rydell, J. 1989a. Occurance of bats in northernmost Sweden (65°N) and their feeding ecology in summer. *Journal Zoology London* 227: 517-529.

- Rydell, J. 1989b. Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. *Oecologia* 80: 562-565.
- Rydell, J. 1991. Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. *Holarctic Ecology* 14: 203-207.
- Rydell, J., A. Entwistle and P.A. Racey. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 76: 243-252.
- Rydell, J. and J.R. Speakman. 1995. Evolution of nocturnality in bats: Potential competitors and predators during their early history. *Biological Journal of the Linnean Society* 54: 183-191.
- Rydell, J., K.B. Strann and J.R. Speakman. 1994. First record of breeding bats above the Arctic Circle: northern bats at 68-70° N in Norway. *Journal of Zoology London* 233: 335-339.
- 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.
- Schonewille, B. and T. Murphy-Kelly. 2005. Albert Creek bird banding and migration monitoring station annual report 2004. Report prepared for Yukon Government, Environment Canada, Bird Studies Canada and Yukon Bird Club.
- Schowalter, D.B., J.R. Gunson and L.D. Harder. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. *Canadian Field-Naturalist* 93: 243-251.
- Schultz, M. 2000. Diet and foraging behaviour of the golden-tipped bat, *Kerivoula papuensis*: a spider specialist? *Journal of Mammalogy* 81: 948-957.
- Scudder, G.G.E. 1997. Environment of the Yukon. In: Danks, H.V. and J.A. Downes (eds.). *Insects of the Yukon*. Ontario Canada: Biological survey of Canada (Terrestrial Arthropods), pp 13-57.
- Sendor, T. and M. Simon. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology* 72: 308-320.
- Shiel, C.B. and J.S. Fairley. 1999. Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland. *Journal of Zoology* 247: 439-447.
- Shiel, C., C. McAney, C. Sullivan and J. Fairley. 1997. Identification of arthropod fragments in bat droppings. An occasional publication of the Mammal Society: No. 17.

- Solick, D.I. 2004. Morphology and behaviour of *Myotis evotis*. Thesis University of Calgary.
- Solick, D.I. and R.M.R. Barclay. 2006. Morphological differences among western long-eared myotis (*Myotis evotis*) populations in different environments. *Journal of Mammalogy* 87: 1020-1026.
- Slough, B.G. and T.S. Jung. *In press*. The terrestrial mammals of the Yukon Territory: a review. *Canadian Field-Naturalist*
- Speakman, J.R. 1990. The function of daylight flying in British bats. *Journal Zoology* London 220: 101-113.
- Speakman, J.R. 1991. Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology* 5: 518-524
- Speakman, J.R., Rydell, J., Webb, J.P., Hayes, J.P., Hays, G.C., Hulbert, A.R., and R.M. McDevitt. 2000. Activity patterns of insectivorous bats and birds in northern Scandinavia (69°N), during continuous midsummer daylight. *Oikos* 88: 75-86.
- Speakman, J.R., R.E. Stone, and J.E. Kerslake. 1995. Temporal patterns in the emergence behaviour of pipistrelle bats, *Pipistrellus pipistrellus*, from maternity colonies are consistent with an antipredator response. *Animal Behavior* 50: 1147-1156.
- Stevens, G.C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics? *American Naturalist* 133:240-256.
- Taylor, L.R. 1963. Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* 32: 99-117.
- Thomas, D.W. and R.K. LaVal. 1988. Survey and census methods. In: Kunz, T.H. (ed.). *Ecological and Behavioural Methods for the Study of Bats*. Washington DC: Smithsonian Institution Press, pp 105-124.
- Topping M.G., J.S. Millar and J.A. Goddard. 1999. The effects of moonlight on nocturnal activity in bushy-tailed wood rats (*Neotoma cinerea*). *Canadian Journal of Zoology* 77: 480-485.
- Underwood, L.S. 1975. Continuous light and physiology of arctic birds and mammals. *International Journal of Biometeorology* 19: 304-310.
- Verboom, B. and H. Huitema. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology* 12: 117-125.

- von Frenckell, B. and R.M.R. Barclay. 1986. Bat activity over calm and turbulent water. Canadian Journal of Zoology 65: 219-222.
- Whitaker, J.O. 1988. Food habits analysis of insectivorous bats. In: Kunz, T.H. (ed.). Ecological and Behavioural Methods for the Study of Bats. Washington DC: Smithsonian Institution Press, pp 171-178.
- Whitaker, J.O. and B. Lawhead. 1992. Foods of *Myotis lucifugus* in a maternity colony in Central Alaska. Journal of Mammalogy 73: 646-648.