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Resource Partitioning Between Little Brown Bats (Myotis  
lucifugus) and Long-legged Bats (Myotis volans) in Southern  
Alberta

by

Matthew Brett Saunders

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES  
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE  
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

JULY 1989

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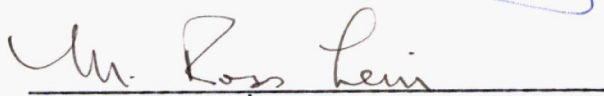
ISBN 0-315-54320-5

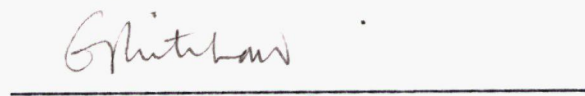
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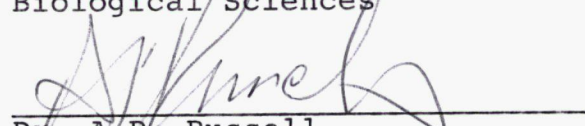
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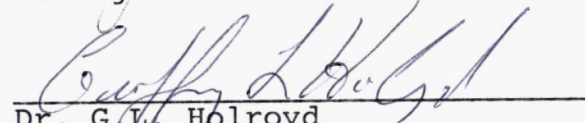
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled RESOURCE PARTITIONING BETWEEN LITTLE BROWN BATS (MYOTIS LUCIFUGUS) AND LONG-LEGGED BATS (MYOTIS VOLANS) IN SOUTHERN ALBERTA, submitted by MATTHEW BRETT SAUNDERS in partial fulfillment of the requirements for the degree of Master of Science.

  
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## ABSTRACT

Little brown bats (Myotis lucifugus) and long-legged bats (Myotis volans) are morphologically very similar, have overlapping distribution ranges, and occasionally occupy the same roosts. Despite these similarities, the two species usually feed in different habitats and on different prey taxa. Flight style is an obvious mechanism that could lead to such behavioural differences. Flight characteristics of the two species were assessed by taking direct morphological measurements and comparing properties of flight morphology between the two species. Myotis lucifugus had significantly greater wing loading and aspect ratio than did M. volans, and consequently was expected to be less manoeuvrable than M. volans. This prediction was tested by flying measured bats in a flight cage. Despite their morphological differences, both species were capable of navigating the same interstring distance in the flight cage, and hence had the same degree of manoeuvrability. This observation led to the prediction that the two species should fly in areas of similar complexity during free-flight.

Free-flight behaviour of the bats was determined using three methods. Ultrasonic equipment was used to determine the times at which bats of both species were active during the night. Bat trapping indicated the distribution of the

two species on a broad scale, and trapping in various habitat types revealed finer scale differences in habitat use by the bats. Finally, bats of both species were fitted with light-tags and released to observe and compare where they foraged.

Both species of bats foraged in all hours of the night, although most activity was concentrated in the first hour after sunset. Wing morphology and aerodynamic theory did not provide accurate predictions of where the bats flew relative to environmental clutter. Although both species foraged in the same areas, M. lucifugus fed predominantly over water, and M. volans fed near trees and along cliff edges. Diets of the two species differed significantly, and this difference was related to the habitat in which they foraged. Myotis lucifugus fed primarily on Diptera, whereas M. volans consumed mainly Lepidoptera.

This study shows that superficial morphology alone does not necessarily provide a reliable index of the behaviour of an animal. Small differences in morphology may not translate into measureable differences in behaviour. Instead, ecological aspects such as prey availability, interspecific and intraspecific relations and predation pressure must be incorporated as mechanisms that also contribute to behaviour patterns. These aspects of ecology cannot be accounted for by predictions based solely on morphology.

## ACKNOWLEDGEMENTS

I owe many people gratitude for their assistance and encouragement during all facets of this study. In particular, I wish to thank Bob Ward and his family for making my stay in the Park a pleasant one.

James Baron, Shirley Burton, Jo-Ellen Cushing, Rita (Catterson) Fowell, Colleen Kinsella, Shaune Sylvester and the rest of the staff of Writing-On-Stone were all very supportive. Ellen Gasser and Lawrence Halmrast gave me a superb introduction to the area and its history. Marge Halmrast provided the incomparable ice cream. Many thanks.

I am grateful to the Audet, Helwig, Gilchrist, MacCulloch and Penrose families who kindly permitted me to work on their property. I also wish to thank the visitors to the Park who attended my evening programs. Their inquisitive and enthusiastic responses to my 'bat talks' made it all worthwhile. I am especially indebted to Mark and Brenda Estill and their children, Nicole, Alison and Dustin, for their efforts in bat conservation.

Robert Barclay, Alvin Dyck, Paul Faure, Catherine Koehler and Heather Sims provided invaluable assistance in the field. I hope that I can reciprocate some day. Hugh Aldridge, Robert Barclay, Mark Brigham, and Jane Lancaster were very helpful during the writing stages. Thank you for your insights. Lawrence Harder guided me and showed rare

patience during data analysis. I cannot thank you enough.

Members of the bird and bat labs were all inspiring to be around. Thank you Mark Brigham, Kevin Cash, Glen Chilton, Mary-Anne Dolan, Sharon Duchesne, Paul Faure, Scott Johnson, Cathy Koehler, Robin Mackey, Dave Prescott and Diane Robinson. Thanks also to Mitch Firman for his mathematical genius. Brent Dixon gave me lodging without complaint. You are a true friend.

My supervisory committee, comprised of Drs. Robert Barclay, M. Ross Lein, Gordon Pritchard and Tony Russell, molded this project with many helpful comments. Without their guidance and experience I would still be struggling. I thank Dr. M. Ross Lein for allowing me to use his sonograph equipment. Dr. Geoff Holroyd graciously accepted the position of external examiner for this thesis. I also thank him for lending me the whirlygig traps. A tragic end.

Finally, my parents, brothers, sisters and grandparents fashioned and encouraged my desire to study biology. Their support, financial and emotional, was felt across the kilometers.

This study was funded by Natural Sciences and Engineering Research Council operating and equipment grants to R. M. R. Barclay, a grant from the Alberta Recreation, Parks, and Wildlife Foundation to R. M. R. Barclay and M. B. Saunders, and Graduate Assistantships (teaching and research) awarded to M. B. Saunders by the University of Calgary.

to Heather



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## CHAPTER I

### General Introduction

#### Introduction

Diversity in the animal kingdom has been postulated to promote the coexistence of species by giving stability to animal communities (Hutchinson 1957; MacArthur 1955). This concept has not been firmly established, in fact, more recent studies have discovered numerous exceptions to the idea (for a discussion see Begon et al. 1986). The general association between very similar species led to the theories of limiting similarity (see Abrams 1983; MacArthur and Levins 1967) and character displacement (Brown and Wilson 1956; Grant 1972; Slatkin 1980). Some researchers have considered competition a critical mechanism governing the structure of communities (e.g. Hebert 1982; Pacala and Roughgarden 1985; Schluter and Grant 1984a). Others have questioned the role of competition in community structure, and instead have advocated environmental variability as a factor determining community structure (e.g. Wiens 1977; Wiens and Rotenberry 1980). This discrepancy is difficult to resolve (see reviews in Connell 1980; den Boer 1986; Schoener 1982), and, with all probability, neither competition nor environmental variability can independently describe the nature of species interactions. Community



structure likely reflects a combination of interspecific and intraspecific relations, environmental variability and resource availability. The evolutionary nature of these components may not be revealed in short term studies of community structure.

The coexistence of species may be permitted by behavioural and morphological differences between animals of a community (e.g. Grant and Schluter 1984). Numerous examples of size-structured communities have been described including examples for mammals (Brown 1975; McNab 1971), lizards (Williams 1983), birds (Diamond 1973, 1975; Lack 1971), insects (Inouye 1977) and snails (Fenchel 1975). Most of these studies conclude that size differences between members of the community act as mechanisms that permit coexistence. Behavioural attributes such as food size preference or habitat selection, resulting from morphological differences between species, minimize niche overlap between community members and thereby permit stable coexistence (e.g. Rosenzweig 1966).

Conditions also exist whereby species of similar size can coexist. If niche overlap does not occur, species or individuals of the same size can use mutually exclusive resources located in the same area (Jarman and Sinclair 1979). Alternatively, each species may use the same resources, but if these resources are abundant, relative to the population size, a high degree of overlap in their use is possible (Bell 1980; Rosenzweig 1979). Disturbance by

predators (Slatkin 1974), or environmental variability (Connell 1980; Weins 1977) may also permit coexistence of species where this would not otherwise be possible. Species combinations that naturally benefit from their association, such as through predator avoidance, may also permit coexistence of similar species (Sinclair 1985; Ward and MacLean 1988).

Habitat is the niche dimension that has been most commonly used by researchers to separate ecologically similar species (Schoener 1974), and such differentiation is usually associated with partitioning of food resources (Hutchinson 1959; McNab 1971). The acquisition of food is a necessity for all animals, thus placing the manner of food gathering, and the morphological features that set limits on the types of food gathered, under continuous selection pressure. Use of a limited food resource by sympatric species can increase selection pressure and subsequently cause the animals to diverge behaviourally or morphologically over time. Evidence of this may appear as differences in trophic apparatus between species (e.g. Lack 1947) or between sexes of the same species (e.g. Selander 1966).

Animals are assumed to maximize their fitness while foraging (see reviews of optimal foraging theory by Pyke 1984, and Pyke et al. 1977). An animal may achieve this by minimizing the time that it spends foraging, and/or by maximizing the net return (e.g. of energy) from foraging

(Schoener 1971). The ability of an animal to maximize its fitness depends on the availability and abundance of different prey types (Pyke 1984). Features of both the predator and the prey (e.g. size, speed, manoeuvrability, etc.) determine whether that food type is accessible. Therefore, two predators that differ in morphology or behaviour may have different optimal prey. The presence or absence of predators and competitors for the available food may also limit the types of food that are available to an animal (Stephens and Krebs 1986). Correlations between behaviour, morphology, diet and species interactions may therefore be useful in assessing whether animals forage optimally.

Behaviour and morphology are frequently used to examine the degree of overlap in resource use between species (e.g. Crome and Richards 1988; Findley 1976; Grant 1986; Hill and Lein 1988). Behavioural differences in foraging strategies between species can be divided into spatial and temporal components. Spatial partitioning is determined by the degree of overlap between species in terms of the areas where food is gathered. Obviously, two or more species may consume the same prey types without competing if they feed in different areas. Aggregations of species do not necessarily indicate an absence of spatial resource partitioning. For example, many animals may congregate at a water source to drink even though they forage in different areas when they are not drinking (McKenzie and Rolfe 1986).

Temporal partitioning, as indicated by differences in the timing of food gathering by species, may reduce competition for food, and may even serve to prevent one predator from feeding on the other (Sprules 1974). Combinations of temporal and spatial partitioning are also possible (e.g. Swift and Racey 1983).

Morphological features that are potentially related to resource partitioning may include differences in jaw structure, which determines gape and 'crushing ability', differences in perceptual ability, which determines the types of and distances from which food can be detected, and locomotory adaptations, which determine the habitats in which the animals can forage. Morphology may predispose animals to feed on certain prey types (Grant 1985; Grant 1968, 1986; Zaret 1980) or to adopt particular foraging strategies (e.g. Neuweiler 1984) and can therefore serve as a valuable predictor of behaviour (McKenzie and Rolfe 1986).

Species which coexist, have similar methods of food acquisition, and have similar morphologies, are presumably faced with the greatest degree of potential competitive interaction. This situation represents an ideal opportunity to investigate whether morphology and behaviour provide a mechanism to reduce ecological overlap.

Several studies on bats have investigated the ecomorphological relationships among community members (e.g. Aldridge and Rautenbach 1987; Black 1974; Fenton 1972; Fenton and Rautenbach 1986; Findley and Black 1983;

McKenzie and Rolfe 1986; Neuweiler 1984). Wing design and echolocation call structure are invoked as having significant and predictable effects on flight capability (Aldridge 1986; Norberg 1985, 1986) and perceptive ability (Bell and Fenton 1984; Simmons et al. 1975; Simmons et al. 1979a), respectively.

The purpose of this study was to determine whether slight differences in morphology between two sympatric bat species resulted in predictable, and ecologically significant differences in their behaviour patterns. To do so, I investigated the locomotory morphologies, echolocation call structures, flight capabilities, habitat use and diets of Myotis lucifugus and Myotis volans. My objective was to compare these two species with respect to features of their flight morphologies and echolocation call structures known to affect the flight style and perceptive abilities of bats. Any differences in these features were then used to predict how the bats should fly relative to each other, and where they should forage relative to environmental clutter. Next, flight ability of individuals of both species was tested to see if morphology was a reliable predictor of flight performance. Observations on flight ability were also used to strengthen or modify the predictions on where the bats should forage. Habitat use by free-flying bats of both species was then examined by capturing foraging bats, monitoring the echolocation activity of foraging bats, and observing light-tagged individuals. The data were compared

to the initial predictions on where the bats should forage. From the observations on habitat use, predictions were made on the insect types that individuals of each species should consume. Finally, the diets of both species were determined using fecal analysis. Diets were compared between species, and with data collected on insect availability.

Several other aspects of the biology of bats, besides food and morphology, could affect their distribution and behaviour. These include the availability of water, roosts, and hibernation sites and the influence of predators. Water can effectively be ruled out as a limiting factor in the study area because abundant water was present. The Milk River flows through the study area and both species were observed to drink from it.

The role that hibernacula play in determining the abundance and distribution of these two bat species is difficult to assess. Schowalter (1980) observed both M. lucifugus and M. volans hibernating in two Alberta caves. This overlap in suitable hibernacula suggests that if one species were limited in this regard, both would be. Summer roosting requirements of these two species also overlap (pers. obs.). The overlap in the roosting ecology of the two species indicates that both species would be similarly affected if roost sites were limited. The abundance of rock crevices and large trees in the study area makes this unlikely.

The role that predators play in determining bat behaviour is also difficult to assess. Most predation occurs while bats are either at or near their roosts (Fenton 1970; and see references in Tuttle and Stevenson 1982). A variety of potential bat predators reside in the study area including several species of snakes, small mammals, and birds. Because of the overlap in their roosting biology, M. lucifugus and M. volans would presumably be equally accessible to predators and therefore would be expected to respond to them similarly.

This study provides a test of ecomorphological theory as it applies to bats, and provides insights into mechanisms that may be responsible for ecological relationships between other groups of animals. This study also provides observations on the biology of M. volans. Very little research has dealt with the ecology of this species despite its abundance in western North America.

Three general hypotheses were tested:

- 1). Differences in the flight morphology between M. lucifugus and M. volans should translate into predictable differences in their flight behaviours.
- 2). Differences in flight behaviour between M. lucifugus and M. volans should translate into observable

differences in their habitat use and foraging behaviour.

- 3). Differences in flight behaviour and habitat use by M. lucifugus and M. volans should result in differences in the diets of the two species.

### Study Area

Field work was conducted in 1987 and 1988 in and near Writing-On-Stone Provincial Park (49° 05' N, 111° 37' W) situated 40 km east of Milk River, Alberta (Fig. 1.1). The Park is located in the semi-arid, mixed grassland region of Alberta and is characterized by low precipitation, low humidity, strong winds, and hot summers (Anonymous 1980; Beaty 1975). The Milk River flows through the centre of the Park and four coulee systems converge with the river valley within the Park boundaries (Fig. 1.1). The two largest coulees, Police Coulee and Van Cleeve's (Rocky) Coulee had standing water throughout the summer in 1987 and the first half of the summer in 1988, but both dried up by late June in 1988. Davis and Humphrey coulees are smaller and contained little water from May to August in either year. The river valley and coulees are bordered by steep sandstone cliffs and hoodoo formations. A wide flood plain borders the river, although the river cuts into the cliffs in some



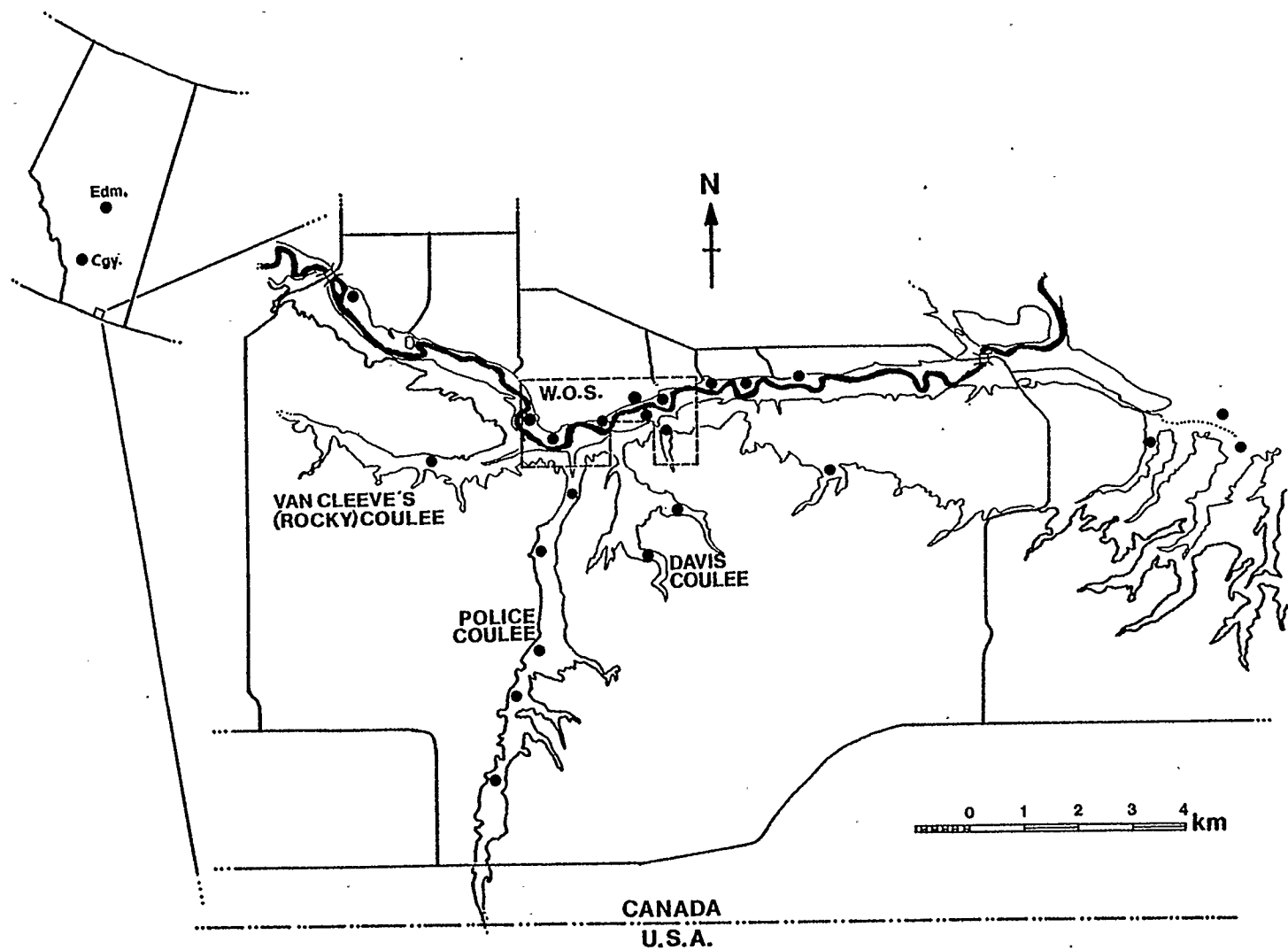


Figure 1.1 Writing-On-Stone Provincial Park (W.O.S.) and vicinity. Closed circles represent areas where bats were mist-netted in 1987 and 1988. (modified by author)

areas. Brock et al. (1980) provide a detailed description of the soils and geology of the Milk River Basin.

A variety of distinctive habitat types are located along the river, in the coulees and on neighboring private land where research was conducted. The dominant shade tree in the area is the Western Cottonwood (Populus deltoides), although other species of cottonwood (P. acuminata) and poplars (P. balsamifera, and P. tremuloides) are found in the vicinity. These trees are found in scattered groves in the river valley and in larger coulees. A variety of shrubs are distributed on the river flats and coulees subject to water availability and shelter. The most common shrubs are Water Birch (Betula occidentalis), Choke Cherry (Prunus virginiana), Yellow Willow (Salix lutea), Thorny Buffalo-berry (Shepherdia argentea), Rose (Rosa woodsii), Wild Gooseberry (Ribes oxycanthoides), Golden Currant (Ribes aureum), Saskatoon (Amelanchier alnifolia), Buckbrush (Symphoricarpos occidentalis), Skunkbush (Rhus trilobata), Ground Juniper (Juniperus communis), Creeping Juniper (Juniperus horizontalis) and Greasewood (Sarcobatus vermiculatus). Red Osier Dogwood (Cornus stolonifera) is present in the area, but is not common.

Several species of sage (Artemisia spp.) are ubiquitous in most habitats. Sagebrush (Artemisia cana) inhabits drier areas such as old flood plains, badlands, and uplands. The native vegetation of the Milk River Basin is a mosaic of mixed and short grass prairie including Spear Grass (Stipa

comata), Northern Wheatgrass (Agropyron dasystachyum), June Grass (Koelaria cristata) and Blue Grama (Bouteloua gracilis) (Anonymous 1980; J. Lancaster, pers. comm.). Two species of cactus, Prickly Pear (Opuntia polyacantha) and Pincushion (Coryphantha vivipara), are common throughout the study area.

### Study Animals

The little brown bat (M. lucifugus) and the long-legged bat (M. volans) are both small, insectivorous bats ranging from 5.5 to 11.0 g in body mass (van Zyll de Jong 1985). Myotis lucifugus is one of the most common and widely distributed bat species in North America ranging from the Atlantic to the Pacific coast, as far north as Alaska, and south into central Mexico (Barbour and Davis 1969; Fenton and Barclay 1980; van Zyll de Jong 1985). Myotis volans is a western species ranging from the Pacific coast eastward as far as central Alberta in Canada (van Zyll de Jong 1985; Warner and Czaplewski 1984) and to North Dakota in the United States (Barbour and Davis 1969). This species extends into northern British Columbia and south to central Mexico (van Zyll de Jong 1985). The study site is near the eastern edge of the range of M. volans. It is not known what factors limit the range of this species, but suitable roosting sites may be in short supply. Myotis volans does

not exploit man-made roosts to the extent that M. lucifugus does (L. D. Harder, pers. comm).

Myotis volans can be distinguished from M. lucifugus by its distinctly keeled calcar and the presence of fur on the underside of the wing membrane extending out from the body to form a line joining the elbow and the knee (Warner and Czaplewski 1984). In my study area I could occasionally distinguish the two species by fur colour and by their behaviour. Adult M. volans generally had a darker pelage than M. lucifugus and the former species was usually less aggressive than the latter when captured. Audible vocalizations produced by the bats upon capture also differed between the species. Myotis volans often produced a bee-like buzzing sound when handled and rarely attempted to bite, while M. lucifugus bit frequently and produced continuous high pitched squawks.

Myotis lucifugus has been reported to be an opportunistic forager, often flying near water where it feeds on a variety of aquatic insects (Belwood and Fenton 1976; Buchler 1976a; Fenton and Bell 1979). Myotis volans feed primarily on moths (Black 1974), but also preys on a variety of other insect types (Warner 1985; Whitaker et al. 1977, 1981). Myotis volans may also be a faster-flying, less-maneuvrable species than M. lucifugus (Fenton and Bell 1979).

Myotis lucifugus uses a variety of roosts including trees, rocks, wood piles and caves (Fenton and Barclay

1980), and is also commonly found in man-made structures (see references in Barclay and Cash 1985). The roosting biology of M. volans is less well-known (see Warner and Czaplewski 1984), but this species has been found to roost in trees (Baker and Phillips 1965), and rock crevices (Quay 1948). Dalquest and Ramage (1946) reported a maternity colony of M. volans located in a building.

Five other species of vespertilionid bats were caught in the study area during 1987 and 1988. These were, in order of decreasing number of captures, western small-footed bat (Myotis ciliolabrum), long-eared bat (Myotis evotis), big brown bat (Eptesicus fuscus), hoary bat (Lasiurus cinereus), and silver-haired bat (Lasionycteris noctivagans). A total of six L. cinereus and two L. noctivagans were captured. Both of these species are larger than either M. lucifugus or M. volans, weighing an average of 27.6 g and 11.0 g respectively (van Zyll de Jong 1985). The larger size and low numbers of L. noctivagans, and the larger size and different foraging strategy of L. cinereus (Barclay 1985a) are assumed to minimize the degree of ecological overlap with the two study species. Eptesicus fuscus was the third most common species in the study area. These bats are also larger than the study animals (mean weight = 17.9 g, van Zyll de Jong 1985), and generally fly much higher than M. lucifugus (Kurta 1982) and M. volans (pers. obs.). These differences minimize potential interaction with the study species. Myotis ciliolabrum and

M. evotis are closest in size to the study species (mean weights are 4.9 g and 6.7 g respectively, van Zyll de Jong 1985). The smaller size of M. ciliolabrum, the gleaning foraging strategy of M. evotis (P. Faure, pers. comm.), and the highly-maneuvrable flight of both species serve as mechanisms that likely reduce niche overlap with the study species.

### General Methods

Bat trapping was carried out in the Park and on private land adjacent to the Park boundaries. Mist-nets of four different lengths (5.5, 6.1, 9.2 and 12.2 m) were used to capture bats. Nets were set singly or tiered such that the lowest string was approximately 0.2 to 1.0 m from the surface of the ground or water and the top string ranged from 2.0 to 2.5 m high for single nets and 3.5 to 4.0 m above the substrate for tiered nets. Custom nets were arranged to catch high flying bats near light poles with the bottom string 3.5 m from the ground to approximately 5.0 m at the top string. Nets were stretched across roads, across pathways through vegetation and brooks, over larger bodies of water (i.e. cattle ponds and the Milk River), along edges of tree groves, and near cliff faces where bats were active.

Upon capturing a bat, I recorded the time of capture, species, sex, and age and reproductive condition for females (i.e. pregnant versus lactating). Juvenile bats (young-of-

the-year) were distinguished from adults by the degree of fusion of the epiphyses at the metacarpal-phalangeal joints. These joints are unossified in juveniles, thereby allowing light to pass through the cartilage (see Anthony 1988 and references therein). Bats were placed into numbered, cotton bags. The total duration of the netting effort was noted to calculate trapping effort and trap success per net-hour for each month of the summer and in each hour of the night.

Each bat was banded with a coloured, numbered, plastic, split ring band on the forearm to facilitate later recognition. A strip of coloured reflective tape on each band enabled species identification on resightings in the field using a flashlight. Little brown bats were fitted with white bands with white reflective tape. Long-legged bats wore red bands with red reflective tape.

## CHAPTER II

### Morphology and Sensory Perception

#### Introduction

Morphology and sensory perception play an obvious role in food acquisition. Morphology may limit food-gathering activities between members of the same trophic group and thereby reduce competition for food resources (e.g. Grant 1986). These limitations may be directly related to size and or configuration of the body. For example, differences in tooth structure, gape, and force of jaw closure determine the size and degree of prey 'hardness' that a predator can handle (Freeman 1979). Smaller predators are generally restricted to consuming smaller items, and larger animals tend to use a greater range of prey sizes (e.g. Ashmole 1968; Hespenheide 1971; Powell and Russell 1984; Werner 1974; Wilson 1975). Morphology may also influence prey consumption by limiting where the predator can feed. In this case a predator may be capable of handling certain prey, but does not get the opportunity to do so by virtue of its morphology (e.g. Simms 1979), risks that morphology incurs (e.g. Mittlebach 1981), or perceptive ability. For example, hoary bats are physically capable of eating small dipterans, but rarely do so because of limitations set



jointly by their echolocation calls and fast, unmanoeuvrable flight (Barclay 1985a).

Evidence for the role of morphology in determining foraging strategies has been found for birds (finches, Lack 1947; Schluter and Grant 1984b; woodpeckers, Selander 1966), fish (stream fish, Gatz 1979; sunfish, Werner and Hall 1976), lizards (anoles, Schoener 1968), and mammals (weasels, Rosenzweig 1966; bats, Aldridge and Rautenbach 1987; Neuweiler 1984).

Wing shape and associated flight properties are commonly used to compare flight styles and the resultant foraging strategies in birds and bats (e.g. Norberg 1986). Aerial insectivorous birds and bats represent an extreme where flight morphology and prey gathering are inextricably linked. Besides enabling flight, wings also serve as insect scoops for foraging bats (Webster and Griffin 1962). Differences in wing morphology affect flight performance (Aldridge 1986; Neuweiler 1984; Norberg and Rayner 1987), and therefore determine, to some extent, where a bat can forage efficiently (Aldridge and Rautenbach 1987). Wing morphology may also indicate the types of insects that a bat should be capable of catching since larger flight surfaces may enable larger insects to be trapped. Highly manoeuvrable flight would also be advantageous for allowing bats to capture evasive insects. Wing morphology has therefore been used to predict where different bats should forage (Struhsaker 1961; Swift and Racey 1983), and may

also be used to predict the types of insects that a bat can catch. The reliability of such predictions in comparative studies necessarily depends on the magnitude of the differences in morphology.

Sensory ability also plays a role in determining the foraging strategies of animals since only prey that the animal can detect are available as potential food. Predators that hunt by vision are restricted to foraging during suitable light levels (Harden Jones 1956; O'Brien 1987). Environmental factors such as wind and rain are likely to reduce foraging efficiency of predators that use acoustic cues when hunting, but it is difficult to distinguish whether these factors impede perception or locomotion or both. Sound transmission for communication is inhibited by wind (Brenowitz 1986), and it is therefore not difficult to imagine how environmental noise could impede hearing. Aerial insectivorous bats are primarily acoustic predators and may adjust their foraging tactics to avoid background noise such as that produced by flowing water and the echoes reflected from environmental 'clutter' (Mackey and Barclay 1989; Neuweiler 1984).

Sympatric species that are similar in their morphology and/or sensory abilities are likely to overlap in their use of resources. However, if morphological differences translate into significant ecological differences, these differences can be used to make predictions of where the animals should forage relative to each other, and on what

they should feed. Therefore, if even small differences in morphology are present between species, predictions can be made regarding the ecological implications of these differences.

In this chapter I describe features of the morphology and echolocation calls of M. lucifugus and M. volans that are either indicative of body size or are directly related to foraging. Aspects of morphology and echolocation call structure are then used to make predictions on the relative flight style of each species, on the types of information they receive from their echolocation calls, and on where each species would be expected to feed.

Jaw morphology may also influence resource use and overlap (Freeman 1979, 1981). I have not considered this aspect of morphology since M. lucifugus and M. volans have very similar jaw structures (Freeman 1981). Also, hand-held bats of both species were fed a variety of different insects and both were capable of consuming the same types.

Therefore, locomotory and perceptual abilities of the bats are likely to be the primary determinants of the types of prey that the bats can capture, and the locations where foraging can take place.

## Methods and Materials

### Echolocation Call Recordings

The echolocation calls of both species were taped using an ultrasonic microphone coupled to a Racal 4DS tape recorder set at 76 cm/sec (system flat [ $\pm$  5 dB] from 15 to over 80 kHz; Simmons et al. 1979b). On 10 May 1987 three M. lucifugus and four M. volans were recorded as they were released in the Park. On 10 May 1988 M. volans were taped as they foraged about a yard light in the Park, and on 28 May 1988 M. lucifugus were taped as they foraged over water in Police Coulee.

To compare call duration between species, calls were randomly selected from the recordings and displayed on a Tektronix 5103N storage oscilloscope. Duration was calculated directly from the oscilloscope screen. A second set of randomly-selected calls, not necessarily excluding those used for measurement of duration, were used to produce sonograms from which minimum and maximum frequency were obtained. Sonograms were produced on a Kay Sonograph Model 6061B using the narrow band filter. Mean call duration, and minimum and maximum frequencies were compared between species.

## Morphology

Four direct morphological measurements (body mass, wingspan, forearm length and tail length) and three indices of morphology (wing loading, aspect ratio and wingtip shape index) were compared between M. lucifugus and M. volans. Measurements were taken on a total of 294 individual bats over the two years of the study. This total was comprised of 99:23 (male:female) and 83:17 M. lucifugus in 1987 and 1988 respectively, and 24:18 and 22:8 M. volans in 1987 and 1988 respectively. The low number of female bats in the sample resulted from releasing those that were pregnant or lactating. Juveniles were not considered in the analyses.

Bats were weighed ( $\pm 0.1$  g) on an O'Haus 2610 g (700 series) triple beam balance (with cage) before they were banded. The right forearm of each bat was measured using dial calipers ( $\pm 0.1$  mm). Tail length was measured with a rule ( $\pm 0.5$  mm) by placing the bat on its back and recording the distance from the tip of the tail to its point of attachment near the anus. Wingspan was not measured directly from the bat, but was instead calculated from wing tracings as described below.

Wingspan, wing area, and various components of wing area (i.e. area of the chiropatagium = handwing, and combined area of the plagiopatagium and propatagium = armwing) were determined from wing tracings of live bats (Fig. 2.1). Several conventions have been used to measure

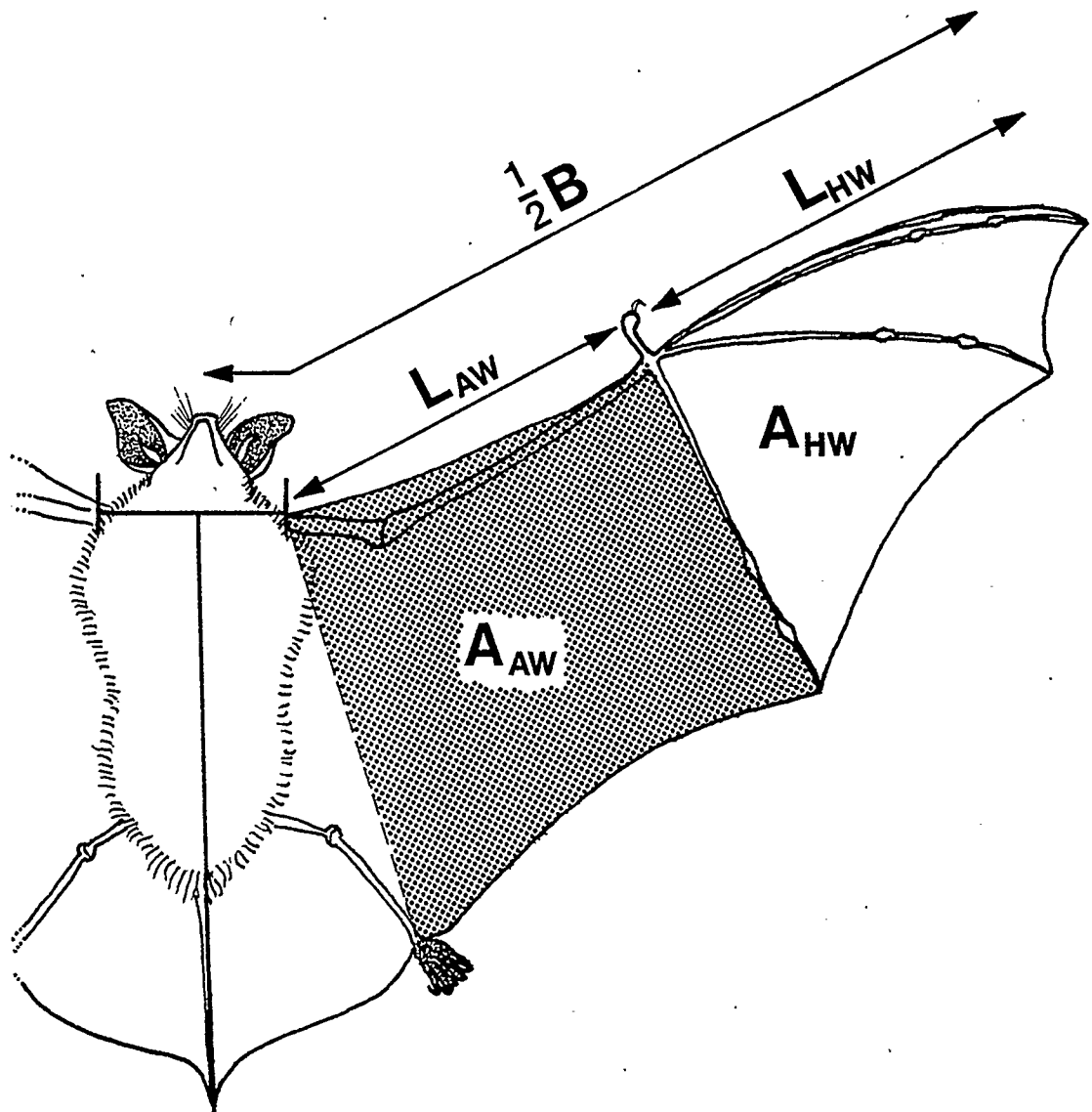


Figure 2.1 Wing tracing of bat indicating the wing dimensions measured.  $B$  = wingspan,  $L_{AW}$  = armwing length,  $L_{HW}$  = handwing length,  $A_{AW}$  = armwing area,  $A_{HW}$  = handwing area. One half of the total wing area incorporates the combined area of the arm- and handwings plus the area between the midline of the body to the proximal edge of the armwing.

wing areas in bats including the outline of the entire body, the outline of the wings plus all but the tip of the tail membrane, and only the wings (various methods described in Norberg 1981). I adopted Norberg's (1981) method where the flight surface included the combined area of both wings, the entire tail membrane and the body area in between the wings, excluding the head.

Area measurements taken from wing tracings of live bats are likely to be variable, and for this reason two tracings of the same wing were made from each bat. Wing tracings were made by placing bats on their backs with the left wing fully extended and the left foot and tail held flat. The position of both shoulders was marked and the outline of the wing and the left half of the tail membrane to the tip of the tail was traced. The respective wing areas (Fig. 2.1) were determined ( $\pm 1.0 \text{ mm}^2$ ) using electronic digitizers (1987 areas traced on a Ziess MOP digitizer; 1988 areas traced on a Houston Instruments Hipad Digitizer). Each wing area was measured three times on both wing tracings and the means were used in the analyses. One half of the wingspan (measured from the midpoint between both shoulder marks, to the point where the shoulder and wing meet, along a straight line through the base of the thumb to a perpendicular line up from the tip of the wing) was measured on each wing tracing (Fig. 2.1) using the same digitizers. This value was doubled to give total wingspan and mean wingspan was calculated from the two tracings.

Wing loading, aspect ratio and wingtip shape index are calculated as in Norberg and Rayner (1987). Wing loading is defined as the body weight (mass (M) times gravitational acceleration) divided by total wing area (S) (Eq. 2.1).

$$\text{WING LOADING} = \frac{M \times 9.8 \text{ m/sec}^2}{S} \quad \text{Eq. 2.1}$$

Aspect ratio is defined as the square of the wingspan (B) divided by wing area (Eq. 2.2).

$$\text{ASPECT RATIO} = \frac{B^2}{S} \quad \text{Eq. 2.2}$$

The wingtip shape index is comprised of a wingtip length ratio (Eq. 2.3) and a wingtip area ratio (Eq. 2.4). This index is valuable as it is independent of the overall size and shape of the armwing and handwing, but instead reflects their relative size (Norberg and Rayner 1987). The wingtip length ratio ( $T_L$ ) is the length of the handwing ( $L_{HW}$ ) divided by the length of the armwing ( $L_{AW}$ ) (Eq. 2.3). Similarly, the wingtip area ratio ( $T_S$ ) is the area of the handwing ( $A_{HW}$ ) divided by the area of the armwing ( $A_{AW}$ ) (Eq. 2.4).

$$\text{WINGTIP LENGTH RATIO } (T_L) = \frac{L_{HW}}{L_{AW}} \quad \text{Eq. 2.3}$$

$$\text{WINGTIP AREA RATIO } (T_S) = \frac{A_{HW}}{A_{AW}} \quad \text{Eq. 2.4}$$

The wingtip shape index is described in Eq. 2.5.



$$\begin{array}{c} \text{WINGTIP} \\ \text{SHAPE} \\ \text{INDEX} \end{array} = \frac{T_S}{T_L - T_S} \quad \text{Eq. 2.5}$$

Ecological consequences of differences in wing loading, aspect ratio and wingtip shape index are described in detail in the discussion. Wing loading determines flight speed with higher wing loadings contributing to faster flight (Pennycuick 1975). Aspect ratio is indicative of the efficiency of the wing where a high aspect ratio (i.e. a long, narrow wing) reduces flight costs (Vaughan 1966). Wingtip shape index represents the overall shape of the wings, with a high value representing a rounded wingtip and a low value indicating a pointed wing (Norberg and Rayner 1987).

## Results

### Echolocation Calls

Data collected on echolocation calls in 1987 and 1988 were considered separately as the recordings were made under different circumstances. In 1987 bats of both species were hand-released in the same area, while in 1988 they were taped as they foraged naturally in two different areas. Differences and similarities between the calls recorded in 1988 will be emphasized as the bats were not disturbed.

Minimum frequencies of the echolocation calls emitted by bats in both years were very consistent within species and were not significantly different between species for free-flying bats ( $t = 0.08$ , 108 df,  $p > 0.89$ ; Table 2.1). Maximum frequency and call duration were considerably more variable, and both were significantly different between species. These call characteristics were used to distinguish between species for ultrasonic monitoring of habitats (chapter IV). Mean maximum frequency was significantly higher for M. volans than for M. lucifugus ( $t = 8.03$ , 107 df,  $p < 0.001$ ). Mean duration of calls was significantly longer for M. lucifugus than for M. volans ( $t = 5.97$ , 83 df,  $p < 0.001$ ). These differences could be attributable to the differences in the areas that the bats were recorded, but when both species were hand-released and recorded in the same area and from the same distance the trend was the same (Table 2.1).

The range of call durations for M. lucifugus overlapped completely with the range of call durations for M. volans. Maximum frequencies also showed a high degree of overlap between species (Table 2.1). The most notable difference between the echolocation calls produced by free-flying and hand-held bats was that the durations were significantly shorter for the latter group in both species (M. lucifugus  $t = 20.9$ , 43 df,  $p < 0.001$ ; M. volans  $t = 26.3$ , 68 df,  $p < 0.001$ ). Minimum frequencies of calls produced by hand-held and free-flying bats did not differ significantly

Table 2.1 Echolocation call characteristics of foraging Myotis lucifugus and Myotis volans. Statistical significance is indicated by asterisks (n.s. = not significant; \*\*\* =  $p < 0.001$ ).

	FREE-FLYING			HAND-RELEASED		
	<u>M. lucifugus</u>	<u>M. volans</u>	p	<u>M. lucifugus</u>	<u>M. volans</u>	p
DURATION (ms)						
mean $\pm$ S.E.	5.60 $\pm$ 0.18	4.42 $\pm$ 0.11		1.67 $\pm$ 0.06	1.23 $\pm$ 0.05	
(range)	(3.75 - 7.25)	(3.25 - 7.50)	***	(0.83 - 2.00)	(0.88 - 1.94)	***
(n)	(35)	(50)		(40)	(32)	
MIN. FREQ. (kHz)						
mean $\pm$ S.E.	39.4 $\pm$ 0.28	39.4 $\pm$ 0.25		38.7 $\pm$ 0.46	39.8 $\pm$ 0.20	
(range)	(35 - 43)	(34 - 44)	n.s.	(34 - 45)	(36 - 41)	*
(n)	(39)	(71)		(23)	(23)	
MAX. FREQ. (kHz)						
mean $\pm$ S.E.	78.7 $\pm$ 1.11	93.6 $\pm$ 1.22		70.0 $\pm$ 1.58	92.7 $\pm$ 2.59	
(range)	(56 - 96)	(72 - 120)	***	(59 - 84)	(70 - 110)	***
(n)	(38)	(71)		(23)	(23)	

within a species (M. lucifugus  $t = 1.4$ , 60 df,  $p > 0.15$ ; M. volans  $t = 1.3$ , 83 df,  $p > 0.15$ ). The maximum frequency of calls produced by free-flying M. lucifugus were significantly higher than those of hand-held bats of this species ( $t = 4.65$ , 59 df,  $p < 0.001$ ), but did not differ for M. volans ( $t = 0.4$ , 92 df,  $p > 0.70$ ). Although I made no measurements on call intensity, both species were detectable at the same range on a QMC mini bat detector (approx. 30 m) or an ultrasonic microphone (approx. 20 m).

### Morphology

Direct comparisons between the two species for several of the morphological variables measured are complicated by the fact that trapping success was unequal between years. For example, in 1987 55 M. lucifugus were caught between 1 and 15 July and 30 between 16 and 31 July. In 1988 only 17 M. lucifugus were captured in the first half of July and 82 in the second half. The same trend was true for M. volans. As a result it was difficult to compare variables that changed on a seasonal basis (e.g. body mass and wing loading). Similarly, species and sex composition of bats caught within a given period varied between years. For these reasons, data collected in 1987 and 1988 were compared separately. In order to obtain the largest sample for comparison, bats caught in May and June were considered to be from 'early' summer, and bats from July and August from

'late' summer. This classification is biologically logical as the bats increased in body mass later in the summer in preparation for hibernation.

Statistically significant differences between the species were present for several of the morphological characters examined, but these differences were not always consistent between years. Some had no obvious biological explanation and may be a result of variability in the measures. A summary of the ANOVA results of the comparison between sexes within a species is found in Table 2.2 and between species for a particular sex in Table 2.3; mean values and standard errors for measurements of each group are described in Appendix 1.

Differences in morphology were present between the early and late periods of the summer in both years for M. lucifugus, but not for M. volans in either year (Table 2.2). Body mass and wing loading were significantly greater in the late period than in the early period for M. lucifugus in both years (Table 2.2).

Wing loading and wingspan differed between sexes for M. lucifugus in 1987 (Table 2.2). Males had greater wing loadings than females early in the summer, while wing loadings were equal late in the summer (Table 2.3). Female M. lucifugus had significantly greater wingspans than males of this species (Table 2.3). Myotis volans were sexually dimorphic in more characters than M. lucifugus. Female M. volans had significantly greater wingspans and forearm

Table 2.2 Summary of ANOVA results comparing morphological measurements of Myotis lucifugus and Myotis volans between periods (pd) of the summer (early versus late), between sexes (male versus female), and the interaction term (I) between period and sex. Species are considered separately. Significance is indicated by asterisks (ns = not significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ).

variable	<u>M. lucifugus</u>						<u>M. volans</u>					
	1987			1988			1987			1988		
	pd	sex	I	pd	sex	I	pd	sex	I	pd	sex	I
body mass (g)	***	ns	ns	***	ns	ns	ns	**	ns	ns	ns	ns
wingspan (mm)	ns	***	ns	ns	ns	ns	ns	**	ns	ns	*	ns
forearm length	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	**	ns
tail length (mm)	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
wing loading ( $N/m^2$ )	***	*	*	***	ns	ns	ns	ns	ns	ns	ns	ns
aspect ratio	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
wingtip shape index	***	ns	ns	**	ns	*	ns	ns	ns	ns	ns	ns

Table 2.3 Summary of ANOVA results comparing morphological measurements of Myotis lucifugus and Myotis volans between periods (pd) of the summer (early versus late), between species (M. lucifugus versus M. volans), and the interaction term (I) between period and species. Sexes are considered separately. Significance is indicated by asterisks (ns = not significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ).

variable	MALE						FEMALE					
	1987			1988			1987			1988		
	pd	spp	I	pd	spp	I	pd	spp	I	pd	spp	I
body mass (g)	*	ns	ns	*	*	***	**	***	*	ns	ns	ns
wingspan (mm)	ns	**	ns	ns	*	ns	ns	*	ns	ns	*	ns
forearm length (mm)	ns	**	ns	ns	**	ns	ns	***	ns	ns	***	ns
tail length (mm)	ns	***	*	ns	***	ns	ns	***	ns	ns	***	ns
wing loading ( $N/m^2$ )	ns	***	ns	ns	***	***	*	ns	ns	ns	**	ns
aspect ratio	ns	***	ns	*	***	ns	ns	ns	*	ns	*	ns
wingtip shape index	ns	ns	*	ns	*	ns	ns	ns	ns	*	ns	ns

lengths than males in both years, and were significantly heavier than males in 1987 (Table 2.3). Such characteristics justified considering sexes separately.

When species were compared by sex, male and female M. volans were significantly larger than M. lucifugus with respect to wingspan, forearm length and tail length in both years (Table 2.3). Body mass was significantly greater for M. volans than for M. lucifugus in the early period in 1988, but this trend was reversed in the late period of the same year (Table 2.3). Mean mass for M. lucifugus increased more than one gram (i.e. from 6.43 g to 7.51 g) between early and late summer, while body mass for M. volans was more constant, dropping only 0.35 g over the same period (Appendix 1). This resulted in a significant interaction term between species and period for body mass (Table 2.3). Myotis volans females were consistently heavier than M. lucifugus females in 1987. Although both increased in body mass with period, M. lucifugus gained more than M. volans from the early to the late period. Body masses were not significantly different between species for males in 1987 and females in 1988.

Wing loading and aspect ratio were significantly greater for M. lucifugus than for M. volans for males in both years and for females in 1988. Females did not differ in 1987. In 1988 wing loading for M. lucifugus increased between the early and the late period. Wing loading for M. volans males decreased over the same period. Wing loading



and aspect ratio did not differ between species for females in 1987, but aspect ratio showed a significant interaction term. Mean aspect ratio for M. lucifugus was initially higher than that of M. volans, but this relationship reversed in the late period. Wingtip shape index differed between species for males in 1988, when M. volans had a significantly greater index than M. lucifugus. Wingtip shape index did not differ between males in 1987 or females in either year (Table 2.3).

## Discussion

### Echolocation Calls

The echolocation calls of a bat species vary between geographic locations, between individuals at a single location (Thomas et al. 1987) and even within individuals (Simmons et al. 1975). This variability is reflected by the range in values for each call variable described in Table 2.1, and is further evidenced by differences between my observations and previously published data on the calls of the same species. Bell (1980) and Fenton and Bell (1979) observed a conspicuous constant frequency component in the search phase calls produced by M. volans and argued that this may facilitate long-range detection of prey by this species. The CF component was not evident in the calls that I examined. Fenton and Bell (1981) describe M. volans calls

that are longer in duration than those which I report. Conversely, my recordings of M. lucifugus have maximum durations longer than those reported by Fenton and Bell (1979, 1981) and Thomas et al. (1987). The calls produced by M. lucifugus and M. volans in Milk River were similar in structure and therefore more difficult to distinguish than those previously reported.

Maximum frequency of echolocation calls differed between species, a factor that may be partially attributable to attenuation of higher frequencies if some bats were recorded further from the microphone (Thomas et al. 1987). However, when M. lucifugus and M. volans were recorded under similar circumstances, the maximum frequency of calls from the latter species were consistently higher. Including higher frequencies may enable detection of smaller targets and better range discrimination by M. volans (Simmons et al. 1979a).

Fenton and Bell (1979) indicated that the calls of M. lucifugus and M. volans were approximately 110 dB at 10 cm from the mouth, and that the frequency with the maximum energy was very similar, 45 kHz for M. lucifugus and 46 kHz for M. volans. Thus, call intensity is not likely to result in a difference in prey detection distance between these two species.

Echolocation by bats enables the detection and identification of prey and permits navigation within the environment (Griffin 1958; Simmons et al. 1979a). Call

structures vary greatly between species of bats (e.g. Fenton and Bell 1981) and different types of calls can be classified on the basis of the type information that they convey to the sender (Simmons et al. 1975). Variation in frequency sweep, intensity, duration, intercall interval and the presence or absence of harmonics, all combine to determine the information content and resolution qualities of individual calls (for discussions see Fenton et al. 1983; Fenton and Bell 1979; Neuweiler 1984; Simmons and Stein 1980).

Information on target size, shape and distance is best determined by using frequency modulated (FM) calls (Simmons et al. 1979a). Broadband FM calls permit fine resolution of stationary targets against backgrounds (Simmons et al. 1979a), and are frequently used by gleaning species (Neuweiler 1984). Long duration, constant frequency (CF) calls used by some gleaning bat species serve the same function as broadband FM calls, but depend on target movement for detection to be possible (Bell and Fenton 1984). Constant frequency calls are otherwise best suited to detecting the presence and movement of targets (Simmons et al. 1975, 1979a), and are commonly used by open air foragers (Neuweiler 1984).

Overall, M. lucifugus and M. volans use similarly structured FM calls while foraging. Mean call duration and maximum frequency were both significantly different between the two species, but the variability of calls within a

species indicates that both are capable of producing similar calls. Because of the similarities in call structure between species, prey detection capabilities are not likely to differ between species.

### Morphology

Significant differences in direct morphological measurements and the three indices of wing shape were evident between sexes within a species and between species within a sex for M. lucifugus and M. volans. I will focus on those features that showed the most consistent trends between years and on the aspects of morphology previously shown to contribute to behavioural differences between species.

Body mass, wingspan and forearm length are all useful in comparing the sizes of bats, and may also contribute to behavioural differences between groups. For example, forearm length is positively correlated with flight speed in bats (Hayward and Davis 1964). Forearm length also contributes to wingspan, and bats with longer wingspans are less capable of flying in cluttered or tight spaces because of their physical dimensions (Norberg 1981). Myotis volans was significantly larger than M. lucifugus with respect to forearm length and wingspan, but constraints based strictly on the physical size of these two species are unlikely to restrict their behaviours since differences in their linear

dimensions were very small. The longer tail length of M. volans may contribute to behavioural differences between species as it denotes a larger tail membrane, thereby reducing wing loading. The lower wing loading and large tail membrane may contribute to higher manoeuvrability by M. volans. The long tail of the barn swallow (Hirundo rustica) enables it to turn quickly and capture flying insects that are detected at close range when the bird is flying quickly (G. L. Holroyd, pers. comm.). The larger tail membrane of M. volans may serve a similar purpose. A larger tail membrane may also permit M. volans to capture larger and/or more evasive prey than M. lucifugus as the tail membrane serves as a pouch for scooping up prey (Webster and Griffin 1962).

Body mass is positively correlated with wing area and wing loading in bats (Findley et al. 1972) which in turn are related to flight speed (Struhsaker 1961; Vaughan 1966) and manoeuvrability (Aldridge 1986; Norberg 1981; Swift and Racey 1983), and thus to where the animals can fly. Body mass differed significantly between species only for females in 1987 when M. volans outweighed M. lucifugus. Body mass alone is therefore not likely to contribute to behavioural differences between the species. Since the direct measurements of morphology are all incorporated into either wing loading, aspect ratio or wingtip shape index, I will consider possible behavioural consequences of differences in these indices between species.

Wing designs of aerial feeding bats represent a compromise between minimizing flight costs and permitting the manoeuvrability (i.e. the ability to make tight turns) required to catch elusive prey (Norberg 1986). Differences in wing structure among bat species are considerable (Norberg 1986), and even small differences in morphology may significantly affect flight performance (Aldridge 1986). Flight is energetically expensive and natural selection seems to have favoured wings that minimize power requirements (Norberg 1985). Different flight styles in bats are characterized by fairly specific wing features, primarily with respect to wingspan, wing loading, aspect ratio and wingtip shape (Norberg 1981, 1985). Wing camber and the angle of attack also affect flight style (Vaughan 1966), but are difficult to measure and are not considered here.

Wing loading is positively correlated with flight speed (Vaughan 1966), but negatively correlated with agility and manoeuvrability (i.e. the ability to make tight turns) (Norberg and Rayner 1987). Bats with relatively slow and manoeuvrable flight generally have low wing loading (Norberg 1981, 1985). High wing loading is indicative of bats or birds which have relatively large body masses relative to their wing area and therefore require increased flight speed to generate sufficient lift to fly (Findley et al. 1972). Increased speed necessarily reduces manoeuvrability.

Wing loadings for bats range from  $76 \text{ N/m}^2$  for Pteropus edulis to  $3.9 \text{ N/m}^2$  for Natalus stramineus (Norberg and Rayner 1987). Wing loadings for North American bats range from  $16.5 \text{ N/m}^2$  for L. cinereus to  $6.0 \text{ N/m}^2$  for M. evotis (Norberg 1981; Norberg and Rayner 1987). Mean wing loading and aspect ratio for M. lucifugus and M. volans in the present study are lower than those presented by Norberg (1981) and Norberg and Rayner (1987), reflecting the different methods used to collect the data. The values I collected for wing loading were taken from live specimens, while those of Norberg (1981) and Norberg and Rayner (1987) were extrapolated from other studies. Precision was undoubtedly lost because the sources from which the measurements on M. lucifugus and M. volans were taken (Farney and Fleharty 1969, and Vaughan 1966 respectively) defined wing area differently than I did and were thus converted by Norberg. The values I collected correspond to theirs in that the means for M. lucifugus were greater than those for M. volans. Farney and Fleharty (1969) had the reverse relationship for wing loading than that which I report, and indicated that aspect ratios were approximately the same between species.

Various studies demonstrate that wing loading is positively correlated with flight style and habitat use by bats (e.g. Aldridge and Rautenbach 1987; Swift and Racey 1983). Bats which feed in open areas (e.g. L. cinereus, Barclay 1985a) generally have higher wing loading and fly

faster than bats which are capable of using areas with more clutter (e.g. Myotis evotis, pers. obs.). In the present study, wing loading was significantly greater for M. lucifugus than M. volans in all but the females caught in 1987.

Aspect ratio describes the relative shape of a wing. A high value indicates a long, narrow wing and a low value a relatively short, broad wing (Norberg and Rayner 1987). High aspect ratio wings are energetically more efficient than low aspect ratio wings since thin wings are subject to less drag than broad wings (Norberg 1981; Vaughan 1966). Aspect ratios of bats range from 14.3 for Tadarida fulminans (Norberg and Rayner 1987) to 4.9 for Nycteris hispida (Norberg 1981). Aspect ratios for North American bats range from 7.7 for L. cinereus (Norberg 1981) to 5.4 for Myotis sodalis (Norberg and Rayner 1987). The aspect ratios that I measured for M. lucifugus and M. volans were at the low end of this scale. However, aspect ratio was significantly greater for M. lucifugus than for M. volans in all but the females caught in 1987 when no significant difference existed between species.

The wingtip shape index describes the relative shape of the wing. High values indicate a pointed wing, while low values indicate rounded wings (Norberg and Rayner 1987). A combination of long, pointed wingtips and high aspect ratio confers swift flight on bats, while pointed wingtips in association with low wing loading may be a specialization



for hovering (Findley et al. 1972). Wingtip shape indices did not differ significantly between M. lucifugus and M. volans with the exception of males in 1988 when the mean index for M. volans was greater. Therefore, wingtip shape probably did not contribute to differences in flight performance between species.

When considered together, wing loading, aspect ratio and wingtip shape index can be used to predict the flight behaviour of bats. Bats with low wing loading and low aspect ratio (e.g. small bats with large wing area) tend to fly slowly, have high manoeuvrability and often hover well (Aldridge 1986; Norberg 1981). Bats with high wing loading and aspect ratio (e.g. large bats with narrow wings) tend to fly quickly and are less manoeuvrable (Aldridge 1986; Norberg 1981). Intermediate combinations result in flight patterns from hovering to straight flight and from slow to fast speeds (Norberg 1981).

The combination of higher wing loading and higher aspect ratio for M. lucifugus implies that this species will fly faster and be less manoeuvrable than M. volans (Aldridge 1986; Findley et al. 1972; Norberg 1981; Vaughan 1966). Myotis lucifugus should therefore be less capable of flying in cluttered habitats, and may be expected to forage in more open areas than M. volans. Field observations on these two species by Fenton and Bell (1979) contradict this prediction. Myotis lucifugus flew relatively slowly, was highly manoeuvrable as it foraged, and fed primarily over

water. Conversely, M. volans flew rapidly, and frequently fed in the open (Fenton and Bell 1979).

Differences in morphology do not imply that habitats will be used exclusively by one species since bats are not restricted to foraging within the range of highest flight efficiency that their morphology confers (McKenzie and Rolfe 1986). Morphology imposes constraints rather than rules on behaviour such that a manoeuvrable species can fly in the open. It would be less feasible for an unmanoeuvrable species to fly in clutter. It must also be established whether observed differences in morphology are biologically significant rather than just statistically significant.

#### Predictions

Prediction I: Because differences in echolocation call structure are minimal, M. lucifugus or M. volans should feed in the same manner and on similar prey (chapters IV and V).

Prediction II: Based on wing morphology M. lucifugus should be less manoeuvrable than M. volans and as a consequence should be less successful at navigating in the flight cage (chapter II) and should forage in less cluttered habitats (chapter IV).

## CHAPTER III

### Flight Cage Trials: Testing Flight Performance

#### Introduction

The flight ability of an animal can be quantitatively defined in terms of manoeuvrability and agility (Aldridge 1987). Manoeuvrability refers to the space required to alter the flight path while flying at a fixed speed and is inversely proportional to minimal turning radius and to wing loading (Norberg and Rayner 1987). Agility is defined as the ability to perform manoeuvres quickly and is not clearly linked to body size, although long wings seem to reduce agility (Aldridge 1987). Both large and small birds and bats can have wing shapes that allow them to be agile (Norberg and Rayner 1987).

Studies of aerial insectivorous bats indicate that most species forage in the open or in relatively obstacle-free space, such as near water or around the perimeter of trees (e.g. Aldridge and Rautenbach 1987; Neuweiler 1984). Therefore, in many cases, environmental clutter (i.e. the proximity to obstacles in any given direction) likely does not impose severe limitations on the flight ability of bats. Many bats seem to be more manoeuvrable than is necessary to enable them to fly in the habitats where they feed. Greater manoeuvrability is probably related to the need to capture

prey. The facts that echolocation calls are effective over only a relatively short range (Griffin 1971; Kick 1982), and that many insects fly unpredictably, requires relatively high manoeuvrability by bats. Some insect types (primarily noctuid and arctiid moths [Lepidoptera], and green lacewings [Neuroptera] in my study area) can detect and respond to the echolocation calls of bats by making evasive moves (Fullard 1987; Miller and Olesen 1979). These insects should be consumed only by bat species that can turn tightly in response to insect manoeuvres. Highly manoeuvrable bats would also be capable of feeding in relatively cluttered habitats. Less-manoevrable bats probably feed on insects that fly predictably or that can be detected from a distance (e.g. larger prey). The flight ability of such bats may limit their use of cluttered habitats. Manoeuvrability is therefore a critical aspect of the foraging ecology of bats.

Flying animals that are highly manoeuvrable, such as hovering birds and bats, require very specific morphological adaptations to achieve this type of flight (Norberg 1985). Because a direct relationship exists between morphology and behaviour, specifically that wing loading and wingspan are negatively correlated with manoeuvrability (Aldridge 1986), flight theory should provide a reliable means to predict flight performance from morphology.

Flight cages have previously been used to test and compare manoeuvrability of bats and the results are generally used to predict the habitats in which the bats can

forage (e.g. Aldridge 1986; Aldridge and Rautenbach 1987). In addition to the effect of morphology on flight performance, differences in obstacle detection resulting from differences in echolocation calls between species may also determine ability to fly in clutter (Neuweiler 1984). Therefore, to ensure that differences in flight performance are attributable to flight ability and not to differences in echolocation call structure, flight cage obstacles must be sufficiently large to allow the species being tested to detect them.

The flight cage was used to test whether the morphological variables measured in chapter II were reliable predictors of the flight performance of M. lucifugus and M. volans. This quantitative measure of flight ability was then used as a predictor of free-flight behaviour of the two species (chapter IV).

## Methods and Materials

Flight performance was tested in 1988 on a total of 134 little brown bats and 43 long-legged bats. Individuals of both sexes and both age groups (juvenile and adult) were included. The inclusion of juveniles in the dataset was to increase the range of wing loadings of the bats that were tested. Individual bats were flown in a flight cage 5.0 m long by 1.25 m high and 1.25 m wide (Fig. 3.1). The cage was covered with 0.6 mL plastic on all sides to prevent bats

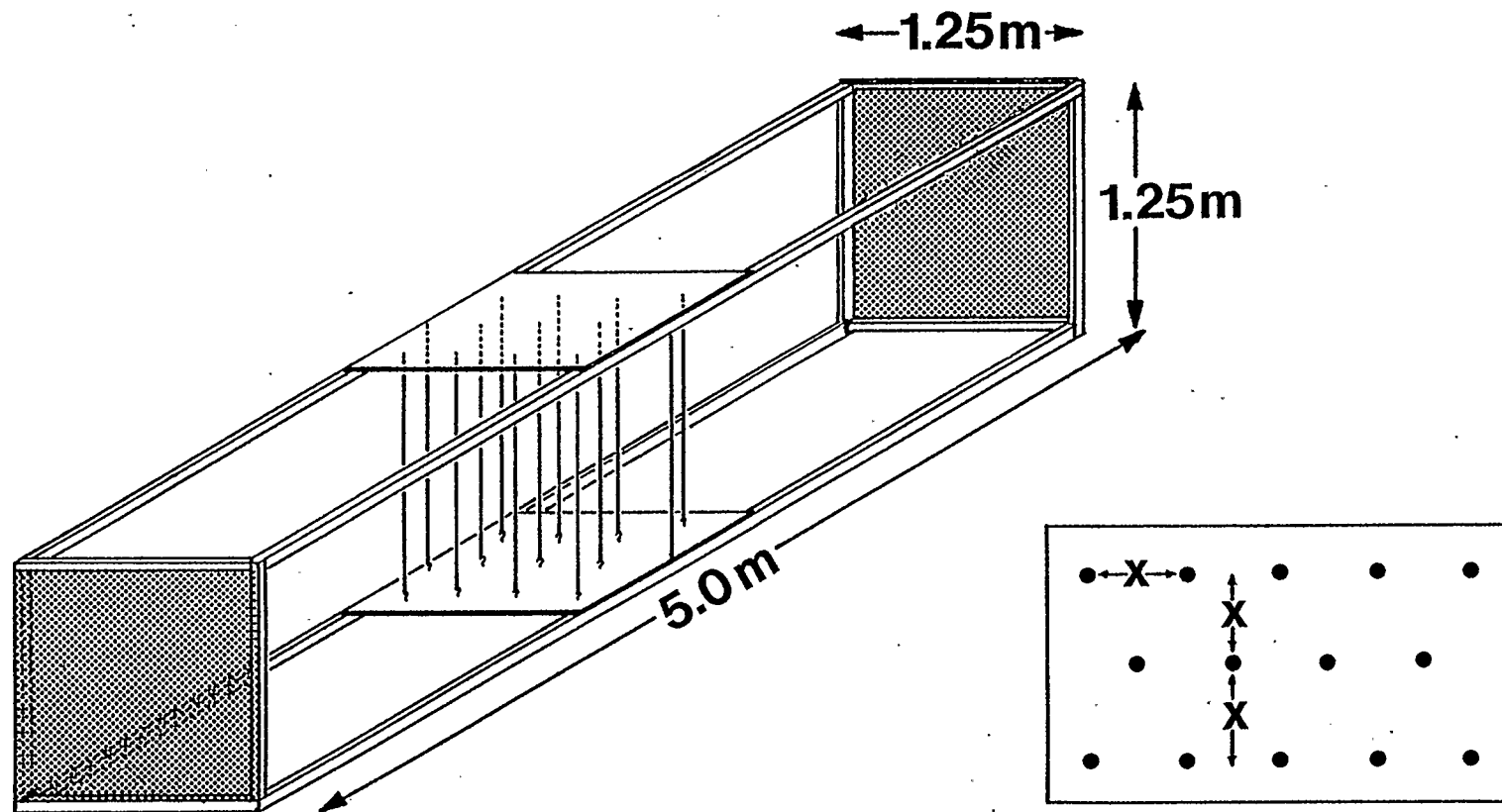


Figure 3.1 Flight cage and dimensions. The cage was covered with clear plastic, and the ends were closed with screen (stippled areas) on which the bats could land. The diagram in the lower right corner depicts the arrangement of the strings through which the bats had to fly. 'X' was either 10, 15, 20, 30, 40 or 50 cm depending on the trial (see text).

from landing during the trials. Bats could land on screens that covered the ends of the cage.

The objective for the bat was to successfully navigate through three rows of vertical nylon ropes (5.0 mm dia.) located at the centre of the cage (Fig. 3.1). These ropes were equidistant from each other within and between rows for all arrangements. The centre row was staggered such that its ropes were positioned halfway between those of the first and third rows (Fig. 3.1). Interstring distances of 10, 15, 20, 30, 40 and 50 cm were used for the tests.

To minimize the number of trials, an interstring distance of 20 cm was selected for the initial trial for each bat. Most bats were successful at this interstring distance during preliminary trials and the high degree of success probably provided positive reinforcement for the bats on subsequent runs. A bat was considered successful if it flew through a string arrangement and emerged into the opposite side of the flight cage while still in flight. Contact with the strings was permissible.

Before the flight trials began, bats were warmed by hand until they could fly voluntarily. This ensured that the bats were completely responsive when tested. Bats were released from a height of 1.0 m at the centre of one end of the cage so that they flew towards the string maze. Illumination from an overhead yard light permitted observations of the bats as they flew. Orientation of the cage and the direction in which the bats flew relative to

the light was constant in all trials. Despite the illumination, bats used echolocation to navigate while in the cage. This was known because I was able to hear portions of their calls.

After each successful trial by a bat, it was retested on the next most difficult arrangement. If unsuccessful at the first interstring distance, the bat was tested on progressively easier arrangements until it was successful. A maximum of three attempts was allowed for any arrangement. Minimum negotiable distance (MND) was recorded as the minimum interstring distance that each bat was capable of navigating.

## Results

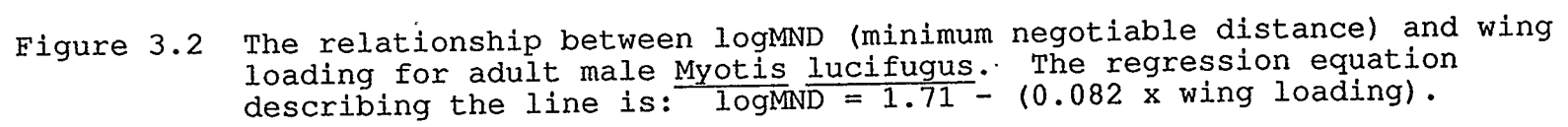
Wing loading, aspect ratio, and wingspan were regressed separately against MND for both species and sexes. The latter two measures were not correlated with MND for either sex or species (Appendix 2) and are not discussed further. Wing loading showed a curvilinear relationship to MND for the group with the largest sample size (male M. lucifugus) and was therefore plotted against logMND. Slopes of the best fit line describing the relationship between logMND and wing loading were tested for both species and sexes to see if they differed significantly from a slope of zero: Similarly, correlation coefficients of each group were



tested to see if a significant correlation existed between logMND and wing loading.

The regression of logMND against wing loading for adult females of both species, excluding obviously pregnant individuals, and adult male M. volans were not significantly different from a slope of zero (M. lucifugus females,  $n = 19$ ,  $b = 0.0021$ ,  $p > 0.95$ ; M. volans males,  $n = 22$ ,  $b = -0.028$ ,  $p > 0.70$ ; M. volans females  $n = 8$ ,  $b = 0.0005$ ,  $p = 1.0$ ). Wing loading was not significantly correlated with logMND for any of these three groups (M. lucifugus females,  $n = 19$ ,  $r = 0.0$ ,  $p > 0.95$ ; M. volans males,  $n = 22$ ,  $r = 0.12$ ,  $p > 0.70$ ; M. volans females,  $n = 8$ ,  $r = 0.0$ ,  $p = 1.0$ ; Appendix 2). Values of logMND for male M. lucifugus were significantly correlated with wing loading values ( $n = 81$ ,  $r = 0.37$ ,  $p < 0.001$ ) and the slope of the regression line was significantly different from zero ( $n = 81$ ,  $b = -0.082$ ,  $p < 0.001$ ; Fig. 3.2).

Since no apparent functional relationship existed between MND and any of the variables examined except for male M. lucifugus, regression statistics were not used to compare whether one species or sex showed higher success at navigating more difficult string arrangements. Instead, contingency tables were constructed to determine whether success in the flight cage was independent of species and sex. No significant differences in flight performance were evident between sexes of a species (M. lucifugus,  $\chi^2 = 2.07$ , 3 df,  $p > 0.55$ ; M. volans,  $\chi^2 = 7.00$ , 4 df,  $p > 0.10$ ) or



for the same sex between species (males,  $\chi^2 = 3.58$ , 3 df,  $p > 0.30$ ; females,  $\chi^2 = 3.34$ , 4 df,  $p > 0.50$ ).

To examine whether there was an overall effect of wing loading on MND, the wing loadings of all bats, including pregnant females and juveniles, were regressed against their logMND. This procedure increased the range of wing loading values present because pregnant females had high values, and juveniles had low values. No significant correlation existed between the two variables ( $n = 160$ ,  $r = 0.04$ ,  $p > 0.50$ ) and the slope of this line did not differ from zero ( $n = 160$ ,  $b = 0.029$ ,  $p = 0.60$ ).

## Discussion

There are two possible explanations for the flight cage results: either no difference in manoeuvrability exists between the species despite the statistically significant differences in wing morphology, or the difference in manoeuvrability between species was so small that it could not be detected using the flight cage and is therefore not likely to be ecologically significant. If the flight cage adequately tested manoeuvrability, then no difference in manoeuvrability existed between species or sexes.

Therefore, although wing loading was significantly different between species, this difference did not translate into a measureable difference in flight ability, and is not likely to be ecologically significant.

Aldridge and Rautenbach (1987) demonstrated that wing loading was significantly and positively correlated to MND for bats with wing loadings ranging from  $15.7 \text{ N/m}^2$  to  $6.3 \text{ N/m}^2$ . They concluded that since a smaller MND could only be achieved by having higher manoeuvrability, manoeuvrability was therefore negatively correlated with wing loading. Similarly, Aldridge (1986) found that despite the fact that Myotis yumanensis had only a slightly lower wing loading than M. lucifugus, the former species could navigate narrower string arrangements, and was therefore more manoeuvrable. Aldridge (1986) did not examine whether a correlation between MND and wing loading was present within either species. Both studies used the observed differences in flight performance to explain, or attempt to explain, observed differences in habitat use by each bat species. The effect of echolocation call structure on flight behaviour was inferred because call structure varied greatly between species (Aldridge and Rautenbach 1987), but was not considered to be a mechanism contributing to differential habitat use by M. yumanensis and M. lucifugus because their calls were structurally similar (Aldridge 1986).

In the present study, non-significant relationships existed between MND and wing loading for females of both species and for male M. volans. A significant negative relationship between MND and wing loading existed for male M. lucifugus. Therefore, individuals of this group that had higher wing loading were more successful at navigating

narrow interstring distances (Fig. 3.2). Overall, therefore, higher wing loading either had no effect or actually enhanced manoeuvrability under the experimental conditions used. This result is opposite to that predicted by aerodynamic theory (Norberg and Rayner 1987) and to that of Aldridge and Rautenbach (1987).

Although wingspan potentially sets a minimum on the size of opening through which a bat can fly (Norberg 1981), many bats in this study were successful at getting through openings less than half their wingspan (i.e. less than 10 cm between ropes). Observations on bats flying in the flight cage revealed how this was possible. At the 10 cm arrangement many bats successfully passed through the first row of strings, only to be stopped at the second or third row. Those that managed to get through all three rows flew toward the strings from near the top of the cage, tucked in their wings, glided through the strings, and began flapping flight after passing through the third row. Bats which managed to do this were invariably close to the ground by the time they got through all three rows. Although not tested in this study, if less vertical flying space was present the bats would undoubtedly have failed. This tactic also implies that rows of strings that are closer together may be easier for bats to pass through than rows spaced further apart. This observation could be tested by maintaining interstring distance while varying the distance between rows.

A slow, and apparently manoeuvrable flight style, such as that of M. evotis or M. ciliolabrum, was less effective in getting through the most difficult string arrangement than was the faster flight of M. lucifugus and M. volans (pers. obs.). Faster flight enabled the latter two species to close their wings for long enough to successfully complete arrangements narrower than those completed by the slower species. This observation suggests that the flight cage does not test relative manoeuvrability of flying bats. In fact, a bat that is obviously less manoeuvrable in free-flight may do better in such a test than a bat considered to be manoeuvrable.

Flight cage tests have been useful in defining the relative flight ability of bats that differ greatly in morphology (Aldridge and Rautenbach 1987), but the differences could also have been related to differences in wingspan. The wingspans of M. lucifugus and M. volans differed by only 2 to 8 mm (Appendix 1), a difference unlikely to be restrictive during flight tests. Therefore, these two species did not differ in manoeuvrability.

Since manoeuvrability is considered an important aspect in determining habitat use by bats (e.g. Aldridge and Rautenbach 1987, Norberg 1986), the flight cage results imply that M. lucifugus and M. volans should be capable of foraging in the same habitats. Both species were equally capable of flying through the most difficult string arrangements in the flight cage. Therefore, both should

forage under similar constraints regarding environmental clutter and prey capture.

Fenton and Bell (1979) indicated that M. volans and M. lucifugus differed in their foraging strategies. The former species was considered a 'long-range' forager as it apparently detected prey between 5 and 10 m away, whereas the latter species seemed to use short-range (i.e.  $\leq 1$  m) detection (Fenton and Bell 1979). Habitat use by the bats in the study area is investigated in chapter IV.

#### Predictions

Prediction I: similarities in flight ability and echolocation call structure between M. lucifugus and M. volans indicate that both species should forage under similar constraints; therefore, both should forage in the same habitats and consume similar prey.

## CHAPTER IV

## Habitat Use by Free-Flying Bats

## Introduction

Habitat choice by animals need not depend upon active decisions made by the animal, but instead may be predetermined by an array of intrinsic (e.g. morphology, physiology, reproductive status) and extrinsic (e.g. food availability, temperature, salinity, altitude, moisture, acidity) factors (Begon et al. 1986). The sum total of all factors that permit a species to exist describe its fundamental niche (Hutchinson 1957). These factors, in addition to interspecific and intraspecific interactions, may determine the distribution of animals and affect how resources are used (e.g. Pimm et al. 1985; Sinclair 1979). Territoriality and aggression between individuals can lead to temporal and/or spatial resource partitioning (e.g. Brown and Batzli 1985; Ebersole 1977; Orians and Willson 1964; Reith 1980). Predation pressure may also cause differential resource use (e.g. Werner et al. 1983).

Specific behaviours, such as foraging and roosting, are generally associated with particular habitat types where these behaviours are performed optimally. For example, foraging habitats differ between bat species depending on how efficiently they can obtain food within each habitat



(e.g. Findley et al. 1972), and bat species use different roosts because of morphological and physiological specializations (Kunz 1982). Use of habitats for a particular activity does not preclude other habitats from being used. For example, little brown bats consistently forage over water in certain areas (e.g. von Frenckell and Barclay 1987), but obviously pass through and forage in other habitats while in transit.

Bats have developed foraging strategies which enable them to fly in areas ranging from obstacle-free space to highly 'cluttered' space (Neuweiler 1984). Aerial insectivorous bats must avoid obstacles and capture relatively small, highly elusive quarry. These requirements impose rigorous demands on flight performance and detection ability. Consequently, certain body designs and call structures are associated with being able to forage efficiently under different conditions (Norberg 1986). In the previous two chapters I described morphological features that determine flight performance, and that should influence where bats fly. The results indicated that no significant difference in manoeuvrability existed between M. lucifugus and M. volans. Here I examine whether this similarity in flight ability results in both species using similar foraging strategies. Since both bat species were equally manoeuvrable, I predicted they would forage in the same areas. This prediction did not consider the effect of prey distribution and abundance on habitat selection by the bats.

Habitat use is best quantified using direct observations of undisturbed animals. I used three methods to determine when and where M. lucifugus and M. volans foraged. Data from mist-netting were used to make general inferences on species' distribution and periods of activity. However, this method masks fine details of habitat use because the distress calls of captured bats attract others to the area and away from where they normally forage (Tuttle 1976). Temporal aspects of bat behaviour were investigated using ultrasonic monitoring (see Fenton 1988). This method was not used to compare habitat use by bats because at a distance it was impossible to resolve whether a bat was flying near to a surface or in open space. Instead, spatial activity was examined by observing light-tagged bats (Buchler 1976b).

## Methods and Materials

### Mist-netting

Data from mist-netting were used to examine broad spatial trends in habitat use by the bats, and to compare temporal patterns of bat activity. Data from both years were combined. A total of 1418 net-hours (based on a 5.5 m net with an area of 11.3 m<sup>2</sup>) were logged, in which time 363 little brown bats and 124 long-legged bats were captured.

Spatial trends in habitat use by both species were examined by dividing areas where I caught bats into five categories and comparing the rate of bat capture (number of bats per net-hour) for both species in each area. The categories were:

- A: Treed or heavily bushed areas that provided a canopy above the net and/or a pathway across which a net was strung.
- B: Over water (excluding water in Police Coulee).
- C: Cliff edges.
- D: Police Coulee.
- E: Davis Coulee.

Categories A, B, and C were separated because of obvious differences in the degree of environmental clutter between them. Categories D and E were considered separate from the first three categories because of their different physical composition. The two coulees were separated from each other primarily because Police Coulee (category D) contained water and Davis Coulee (category E) was essentially dry. Capture success in each of these categories was compared on a monthly basis to observe seasonal shifts in bat abundance.

Temporal trends in bat activity were examined by comparing the number of bats of each species captured per net-hour in each hour after sunset. Mist-nets were not set in Police and Davis coulees in August of either year and no netting was done over water in June. Sample size was too

small to allow me to account for seasonal changes in bat abundance.

#### Ultrasonic Monitoring

To investigate temporal patterns of habitat use by the bats, the relative activity levels of M. lucifugus and M. volans were monitored remotely using the ultrasonic monitoring technique of Simmons et al. (1979b). An ultrasonic microphone with a flat frequency response ( $\pm 5$  dB) from 15 to over 80 kHz, period meter, portable oscilloscope (NLS model MS-15 miniscope) and QMC mini bat-detector (QMC Instruments) enabled me to hear and see the echolocation calls produced by bats within a radius of approximately 30 m. The oscilloscope produced a time/frequency display of the calls and enabled me to differentiate between bat species based on the pattern of frequency change with time. Since the echolocation calls were highly variable between species, except for the higher maximum frequencies used by M. volans (Table 2.1), many of the calls that were detected did not identify the caller. Calls with the higher maximum frequencies, and those with the characteristic elbow or step in the frequency sweep were considered diagnostic calls of M. volans and M. lucifugus, respectively. Only diagnostic calls were used in the analysis. From a total of 3157 calls produced by Myotis bats in 1987, I could attribute 65 percent to either M.

lucifugus or M. volans. In 1988, 31 percent of the 1078 calls I examined could not be categorized.

Relative bat activity was monitored by counting the number of bat passes and buzzes for each species in a series of five-minute intervals in a variety of different areas. A bat pass consisted of a series of search-phase calls that became louder as the bat approached, and dissipated as the bat flew by the bat detector. A rapid succession of terminal phase calls comprised a buzz (see Griffin et al. 1960 for a description). Buzzes indicated that bats were foraging, whereas passes were detected whether bats were feeding or just passing by. Therefore buzzes were examined in addition to passes because they provided more information about what bats were doing. Up to six of the available habitats (see p. 64) were monitored on a given night. Transects or circuits through all available habitat types were completed within as short a time as possible (i.e. 20 to 40 min, depending on the number of habitats monitored) to minimize the chance of missing bat activity patterns that changed during the night. All habitat types were grouped to determine if differences in temporal patterns of foraging existed between species as indicated by ultrasonic monitoring. Each night was divided into early, middle and late periods. The early period began at sunset and ended two hours later; the late period began two hours before sunrise and ended at sunrise; and the middle period

included the time between the early and late periods. The duration of the middle period changed with season.

Log-linear models were used to construct the simplest model to determine whether differences existed in relative activity levels between species and between periods of the night. Each year was considered separately because yearly differences in bat activity were evident. This difference was probably because I monitored activity throughout May, June, July and August in 1987, but equipment failure prevented me from doing so in July and August of 1988.

The amount of bat activity in each five-minute period was ranked a posteriori into one of three categories to compare whether relative levels of activity changed between each period of the night or whether they varied between species. The categories were:

- 1: no activity (0 calls or buzzes per five min)
- 2: moderate activity (1-4 calls or buzzes per five min)
- 3: high activity (5 or more calls or buzzes per five min)

Activity levels represent the number of passes or buzzes per unit time and do not distinguish whether one bat or several bats produced the calls.

#### Light-tagging

A total of 94 little brown bats (21 in 1987 and 73 in 1988) and 37 long-legged bats (18 in 1987 and 19 in 1988)

were released with light-tags. A gelatin pill capsule containing chemiluminescent cyalume<sup>R</sup> was attached either to the dorsal surface of the bat between its shoulders or to the ventrum with Skinbond<sup>R</sup> surgical cement (see Buchler 1976b for details). The bat was then released and tracked visually. Notes on where each bat flew and whether it appeared to feed or drink were recorded with a voice note recorder and later transcribed. Data were used to examine whether either species exhibited a preference in foraging habitat as measured by the amount of time they spent in any habitat.

Habitats in which bats flew were subjectively divided into six different categories based on either the relative degree of clutter or the major type of substrate present. These categories, in increasing order of complexity were:

- 1: open; > 1 m above or away from any surface.
- 2: open water; < 1 m over water surfaces that extended > 2 m in any direction.
- 3: open land; < 1 m over flat, unobstructed land surfaces.
- 4: edge; < 1 m away from an obvious physical boundary or tree line.
- 5: overstory; under canopies and between trees or hoodoo columns.
- 6: foliage; between branches of trees.

Habitats 5 and 6 were available to bats only in areas where relatively large trees were present.

Time spent in each of the six habitats was used to calculate the "habitat use index" (Equation 4.1; from Aldridge and Rautenbach 1987). This index requires that habitats are ranked in order of increasing complexity and indicates the mean complexity of the habitats used by bats.

$$\text{Habitat Use} = \sum_{H=1}^n (H \times T_H / T) \quad \text{Eq. 4.1}$$

where  $n$  is the number of habitats,  $H$  is the rank of the habitat,  $T_H$  is the total time spent in habitat  $H$ , and  $T$  is the total time that the bat was observed. A higher index value indicates that proportionately more time was spent in more cluttered habitats. This index must be interpreted carefully as time spent in more complex habitats is weighted more heavily than time spent in less cluttered habitats. For example, a bat foraging only in habitat 2 will have a habitat use index of 2.0, while a bat which forages primarily in the open (habitat 1), occasionally flying through more cluttered areas may also have a habitat use index value of 2.0 despite never actually foraging near a water surface. Therefore, this index is most useful if the bats spend most of their time in one habitat rather than dividing their activity between structurally complex habitats and obstacle-free habitats. In the latter case, the habitat use index would falsely indicate that the bats spent most of their time in habitats of moderate complexity.



Locations where the bats were released were divided into three categories based on their physical features. Sites along the Milk River Valley (including Writing-On-Stone Provincial Park and three private properties, Fig. 1.1) made up location 1. These sites had all six habitat types present. Location 2 consisted of several places in Police Coulee (Fig. 1.1). This coulee was relatively deep and wide, had several small groves of trees, and contained water for the duration of the field season in 1987 and most of 1988. Habitats 5 and 6 were not present in places where bats were released in the Coulee. Location 3 consisted of two sites in Davis Coulee (Fig. 1.1). This coulee was superficially similar to Police Coulee, but was considered to be a separate location because it possessed little water in either year. Even though this coulee was relatively dry, all six habitat types were considered to be present where bats were released in this coulee. A small puddle of water located near where bats were released was considered to be habitat type 2 despite the fact that it did not fit the specified criterion for this habitat. The relatively high degree of bat activity over this puddle justified my decision.

Of 94 little brown bats and 37 long-legged bats released with light-tags, 31 individual M. lucifugus and 19 M. volans were observed to forage. Only this subset of bats was used in the analysis of habitat use. The remaining bats were omitted from the comparison either because they behaved

abnormally or because they did not forage. Abnormally behaving bats included those with obviously clumsy flight and those that landed and attempted to remove the light-tag. Data from both years were combined to provide a sufficient sample size for comparison. A total of 403 minutes of useable observation time was logged.

## Results

### Mist-netting

Mist-netting data from 1987 and 1988 were combined since nightly patterns in the times when bats were captured were similar between years. The relative proportion of each bat species captured in June, July and August did not differ ( $\chi^2 = 1.66$ , 2 df,  $p > 0.40$ ). Proportionately more long-legged bats were captured in May (relative to little brown bats) than in any other month ( $\chi^2 = 13.09$ , 1 df,  $p < 0.001$ ; Fig. 4.1). Overall, more M. lucifugus were captured than M. volans in all months and in all habitats except in the treed area (category A) in May and in Davis Coulee (category E) in June (Fig. 4.1).

In May, June and July the relative number of bats of each species depended on the areas in which they were captured (May:  $\chi^2 = 17.14$ , 2 df,  $p < 0.001$ ; June:  $\chi^2 = 33.07$ , 3 df,  $p < 0.001$ ; July:  $\chi^2 = 11.53$ , 4 df,  $p < 0.01$ ), but relative captures were independent in August ( $\chi^2 = 2.05$ ,

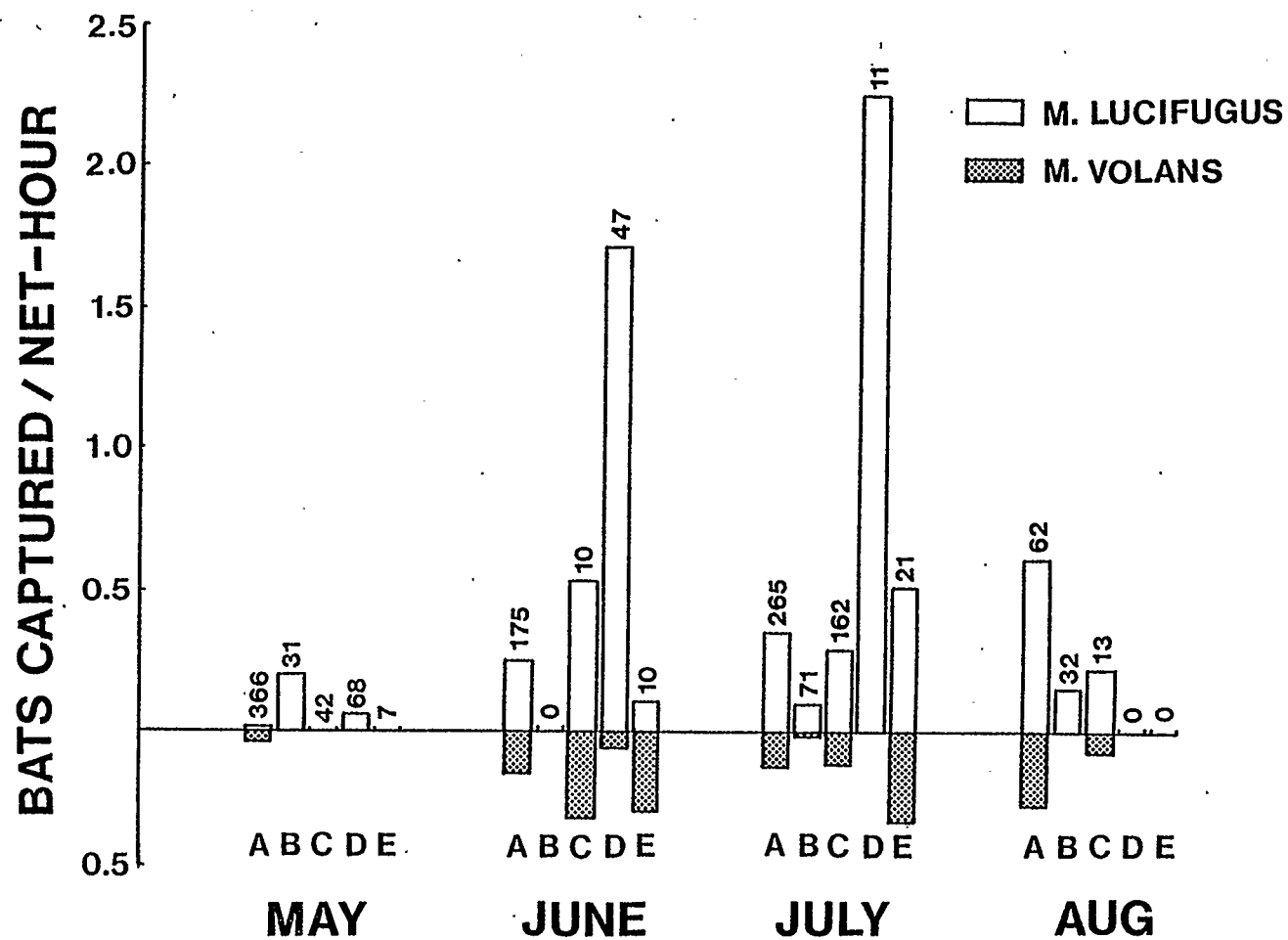


Figure 4.1 Combined mist-netting results from 1987 and 1988 represented as the number of bats captured per net-hour (based on a 5.5 m net). Areas where nets were set were: A = under canopy; B = over water; C = cliff edges; D = Police Coulee; and E = Davis Coulee. Numbers above the bars indicate the number of net-hours spent in each area.

2 df,  $p > 0.35$ ). In May, proportionately more M. lucifugus were captured over water (category B) and in Police Coulee (category D) whereas relatively more M. volans were caught in treed areas (category A; Fig. 4.1). No bats were captured along cliffs (category C) or in Davis Coulee in May (category E).

The relative number of individuals caught near trees, over water and in Davis Coulee (categories A, B and E respectively) in June, and in the same three categories plus the cliff edge category (category C) in July did not differ significantly between species (June:  $\chi^2 = 2.56$ , 2 df,  $p > 0.25$ ; July:  $\chi^2 = 2.76$ , 3 df,  $p > 0.40$ ). Combining the bat captures from these categories and comparing them to the proportion of bats of each species captured in Police Coulee revealed a significant difference in habitat use by species in June and July. Myotis lucifugus made up a much larger proportion of the total number of bats captured in Police Coulee than did M. volans in these two months (June:  $\chi^2 = 11.58$ , 1 df,  $p < 0.001$ ; July:  $\chi^2 = 8.58$ , 1 df,  $p < 0.005$ ). A total of 104 M. lucifugus and only three M. volans were captured in Police Coulee in 1987 and 1988. Similarly, more M. lucifugus ( $n = 18$ ) than M. volans ( $n = 1$ ) were captured over water (category B) in May, July and August.

The overall temporal pattern of bat captures differed significantly between species ( $\chi^2 = 23.79$ , 7 df,  $p < 0.005$ ), and this difference was a consequence of relatively more M. lucifugus and M. volans captured in the first hour after

sunset compared to the number of captures in each subsequent hour ( $\chi^2 = 14.40$ , 1 df,  $p < 0.001$ ; Fig. 4.2). The relative number of bat captures for the two species did not differ significantly between two and eight hours after sunset ( $\chi^2 = 7.74$ , 6 df,  $p > 0.75$ ; Fig 4.2). Bats of both species were captured in all hours of the night and most were captured in the first hour after sunset.

#### Ultrasonic Monitoring

Overall bat activity in 1987 changed with the period of the night (passes:  $G^2 = 39.28$ , 4 df,  $p < 0.001$ ; buzzes:  $G^2 = 121.00$ , 4 df,  $p < 0.001$ ) and levels of activity were higher for M. lucifugus than M. volans (passes:  $G^2 = 34.01$ , 4 df,  $p < 0.001$ ; buzzes:  $G^2 = 116.45$ , 4 df,  $p < 0.001$ ). Most bat activity occurred in the early and middle periods. Relative activity levels for both species did not differ significantly (passes:  $\chi^2 = 1.30$ , 2 df,  $p > 0.50$ ; buzzes:  $\chi^2 = 0.12$ , 2 df,  $p > 0.90$ ), and the relative activity levels of the two species were equal in each period of the night (passes:  $\chi^2 = 0$ , 2 df,  $p = 1$ ; buzzes:  $\chi^2 = 0$ , 2 df,  $p = 1$ ).

In 1988, the intensity of overall bat activity did not differ between periods of the night (passes:  $\chi^2 = 1.38$ , 2 df,  $p > 0.50$ ; buzzes:  $\chi^2 = 1.68$ , 2 df,  $p > 0.40$ ), relative activity levels of both species did not differ significantly (passes:  $\chi^2 = 0.002$ , 2 df,  $p > 0.95$ ; buzzes:

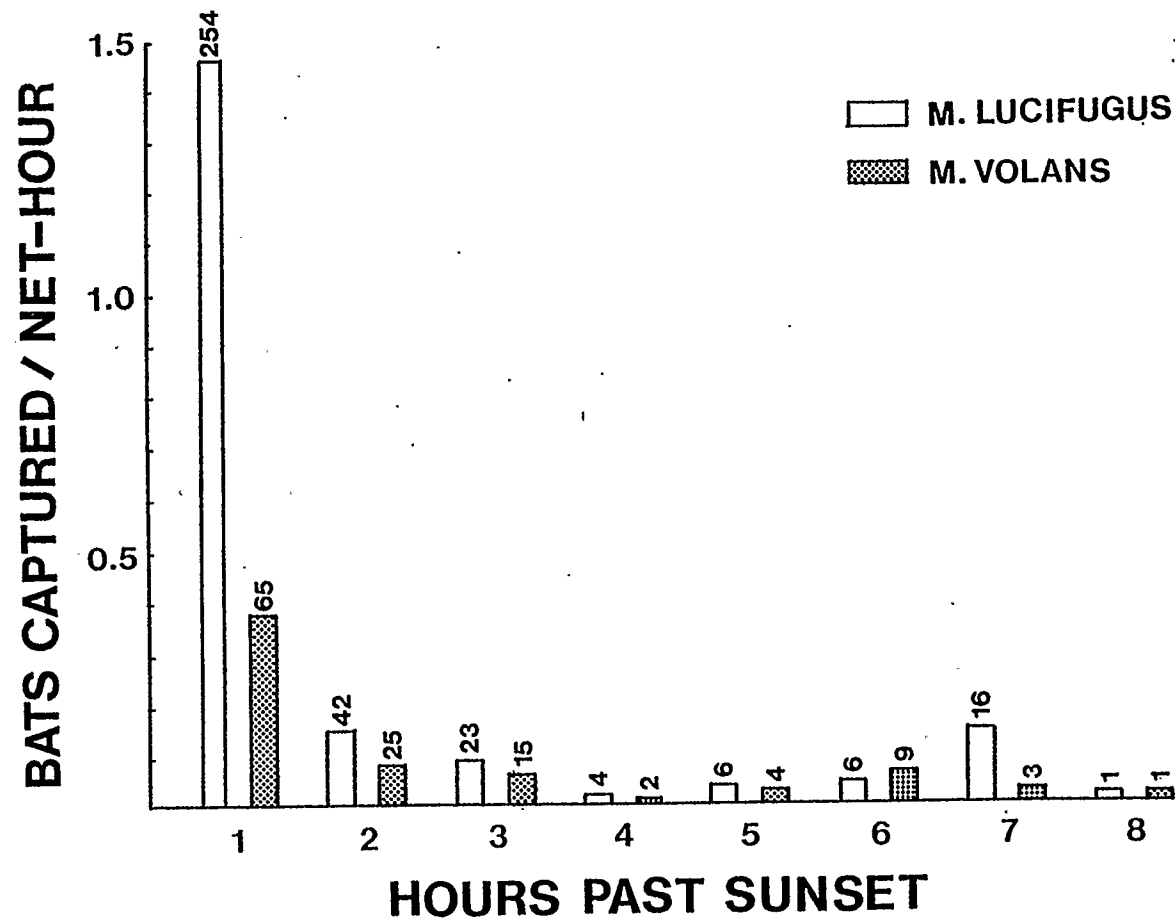


Figure 4.2 Combined mist-netting results from 1987 and 1988 represented as the number of bats captured per net-hour (based on a 5.5 m net) in each hour after sunset. Numbers above the bars indicate the number of bats caught in each hour.

$\chi^2 = 0.01$ , 2 df,  $p > 0.95$ ), and the relative levels of activity of the two species did not differ within periods (passes:  $\chi^2 = 7.86$ , 4 df,  $p > 0.05$ ; buzzes:  $\chi^2 = 0.59$ , 4 df,  $p > 0.95$ ). As in 1987, bats were active in all hours of the night and most activity occurred in the early and middle periods.

To test whether the relative activity levels of each species were associated with period of the night, further log-linear models were used. Again, these interactions were tested for the three periods of the night, three activity levels, and two species of bats.

In 1987, the number of passes by M. volans was positively related to the number of M. lucifugus passes detected in the same period ( $\chi^2 = 47.77$ , 4 df,  $p < 0.001$ ). Although the number of M. lucifugus detected did not differ between periods of the night, the number of passes by M. volans differed significantly between periods ( $G^2 = 33.09$ , 4 df,  $p < 0.001$ ) with relatively more M. volans activity in the early period. The data for buzzes were explained by the most complicated log-linear model, including interactions between period of night and the number of calls by M. lucifugus, period of night and the number of calls by M. volans and an interaction between the frequency of buzzes by each species. This observation probably results from the high number of periods in which no buzzes were detected and is unlikely to be biologically significant.

The results for passes and buzzes in 1988 were explained by the simplest log-linear model, involving no interactions between period, species and relative level of activity. Therefore, differences between periods of the night, relative levels of activity, and which species were present are all independent (passes:  $G^2 = 31.28$ , 16 df,  $p > 0.05$ ; buzzes:  $G^2 = 10.16$ , 20 df,  $p > 0.9$ ). Thus, the frequency of calls or buzzes by M. volans did not depend on the number by M. lucifugus, and the number of M. lucifugus and M. volans detected did not differ within any period.

#### Light-tagging

Data collected on habitat use by light-tagged bats in 1987 and 1988 were combined. All six of the habitat categories were present in sites along the river valley (location 1). Eighteen M. lucifugus and 14 M. volans were flown in four sites along the river for total useable observation times of 90 min for M. lucifugus and 97 min for M. volans. The habitat-use index was higher for M. volans than M. lucifugus (1.89 versus 1.46, respectively), but both spent the majority of their time in habitat 1, the least complex of the six habitats (Table 4.1). The most notable differences in habitat use were for habitats 2, 4 and 5. Myotis lucifugus spent proportionately more time foraging over water (habitat 2) than did M. volans, and M. volans spent more time along edges (habitat 4) and in



Table 4.1 Proportion of time spent by Myotis lucifugus and Myotis volans in six habitats in three different locations (see text). Habitats one through six are arranged in order of increasing complexity. Mean habitat use indices (H.U.) were calculated using equation 4.1 (see text).

species	location	n	total obs.	percent time in habitat						H.U.
			time (s)	1	2	3	4	5	6	mean + std. dev.
<u>M. luc.</u>	RIVER VALLEY	18	5406	59.9	32.8	1.7	4.7	0.7	0.4	1.46 ± 0.22
<u>M. vol.</u>		14	5807	58.6	5.5	1.9	11.5	19.1	1.8	1.89 ± 0.67
<u>M. luc.</u>	POLICE COULEE	8	10705	9.0	90.8	0.0	0.2	---	---	1.85 ± 0.19
<u>M. vol.</u>		1	402	84.6	1.2	4.2	10.0	---	---	1.40
<u>M. luc.</u>	DAVIS COULEE	5	587	90.6	0.0	3.4	6.0	0	0	1.18 ± 0.18
<u>M. vol.</u>		4	1293	78.0	1.5	4.6	15.5	0	0	1.74 ± 0.63

canopies (habitat 5) than did M. lucifugus (Table 4.1). Both species used all six habitat types, but no significant correlation existed for habitat use by the two species (Spearman rank correlation,  $r_s = 0.60$ ,  $n = 6$ ,  $p > 0.20$ ).

In Police Coulee (location 2), eight light-tagged M. lucifugus were observed for a total of 1338 min. Ninety percent of their time was spent foraging less than 20 cm above water. Signs of aggression were apparent between individuals as they foraged. Six M. lucifugus released on 29 May 1988 foraged continuously between 2247 h and 0006 h, and little spatial overlap between individuals was noticed. Each individual circled over different areas of the available water, but gradually shifted their positions over the pond as they foraged. Agonistic behaviour in the form of an upward, spiralling chase was noted on at least five occasions when two foraging individuals came in close proximity. Chases lasted no more than five seconds and ended when one bat left to forage elsewhere. It was not obvious whether the original bat or the 'intruder' stayed in the area.

Police Coulee was unique because it supported primarily little brown bats and big brown bats. Individuals of the latter species were regularly observed and heard as they foraged, but I rarely caught them because they generally fed high above the coulee bottom. Of 131 bats caught in this coulee on 13 different nights, only three were long-legged bats. Because M. volans was scarce here, three individuals

captured in WOS Park were released in the coulee to see where they foraged. Only one of these bats began to feed and most of its time was spent foraging high over the coulee bottom. This result may be a consequence of the bat being unfamiliar with the territory. The habitat-use index for M. lucifugus was greater than that for M. volans (1.85 versus 1.40 respectively). Habitats 5 and 6 were omitted from the analysis as they were not present in the area that the bats were released. No significant correlation existed in habitat use between species in this location ( $r_s = 0.20$ ,  $n = 4$ ,  $p = 1.0$ ).

Five M. lucifugus and four M. volans were flown in Davis Coulee (location 3) for a total of 9.8 and 21.6 min, respectively. A small puddle (approximately 2 m<sup>2</sup>) was located near the site where the bats were released. Because this was the only water available in the coulee, and despite its small size, it was considered to be habitat type 2. Both species flew primarily in the open (habitat 1), but M. volans tended to fly close to the cliff walls at the sides of the coulee (habitat 4) and as a result had a higher habitat use index than M. lucifugus (1.74 versus 1.18 respectively). The amount of time spent in different habitats was significantly correlated between species ( $r_s = 0.96$ ,  $n = 6$ ,  $p < 0.02$ ).

Repeated measures analysis of variance and Bonferroni contrasts were also used to compare habitat use by the bats. This analysis considers each habitat type as a variable that

changes with the amount of time spent in it by individual bats. Years were combined for this analysis, but the three locations were again considered separately.

No significant difference was noted in habitat use between species in any of the six habitat types in location one ( $B = 3.36$ , 5 df,  $p > 0.05$ ). Myotis volans spent more time in canopies (habitat 5) than did M. lucifugus, and M. lucifugus fed low to the water (habitat 2) proportionately more than did M. volans, but these differences were not significant ( $p > 0.05$ ). Differences in habitat use by species in these two areas approached significance ( $0.05 < p < 0.10$ ).

At location 2, M. lucifugus fed low over water (habitat 2) significantly more than did M. volans, and M. volans flew low over land and along cliff edges (habitats 3 and 4, respectively) significantly more than did M. lucifugus ( $B = 3.591$ , 3 df,  $p < 0.05$ ). Only one M. volans was released in this location.

Both species were relatively common in Davis Coulee (location 3) as indicated by mist-net captures (Fig 4.1, habitat 5). In this coulee M. volans spent significantly more time flying along cliff edges than did M. lucifugus (habitat 4;  $B = 3.59$ , 5 df,  $p < 0.05$ ). M. volans also spent more time over the small puddle near where the bats were released, but not significantly more.

Overall, M. lucifugus and M. volans were active at the same time, with most of their activity occurring in the

first two hours after sunset. Although both bat species showed complete overlap in their foraging habitats, M. lucifugus fed predominantly over water when it was available, and M. volans tended to forage relatively high above the ground, and often flew along cliff edges while feeding. Myotis lucifugus was more abundant than M. volans in all areas, but the relative proportions of each species were similar in Davis Coulee where water was virtually absent.

#### Discussion

Temporal differences in the activity patterns of M. lucifugus and M. volans were not evident on a hourly basis during the night at any of the three locations in either year of the study. However, mist-netting indicated that M. volans were relatively more abundant in May compared to the other months. Myotis volans seems more cold tolerant than M. lucifugus (Schowalter 1980) and this may explain why proportionately more were captured early in the season. Individuals of both species were present in the Park by 9 May 1987 and 17 May 1988, but on nights in May when ambient temperature was  $\leq 10^{\circ}\text{C}$  only long-legged bats were captured. This occurred on 31 May 1987 and 31 May 1988 when four and two long-legged bats were caught respectively. In May, most bat activity was concentrated around two light poles in the Park, presumably to capture insects that aggregated there.

Insectivorous bats are frequently attracted to insect swarms at light sources (Bell 1980; Belwood and Fullard 1984; Fenton and Barclay 1980; Fenton and Morris 1976; Furlonger et al. 1987).

Activity levels of M. lucifugus and M. volans were positively associated, indicating that both species became active at approximately the same time of the night, and that one did not forage longer than the other. Activity levels were generally higher for M. lucifugus than for M. volans, undoubtedly reflecting the greater abundance of the former species.

The prevalent peak in bat activity for both species in the early period of the night is comparable to findings in other studies (e.g. Fenton 1970; Kunz 1973; O'Farrell and Bradley 1970), but the bimodal pattern of activity characteristic of insectivorous bats (Erkert 1982) was not evident in the study area. Myotis lucifugus in Iowa also exhibited a unimodal pattern of activity, most bats being caught in the first three hours after sunset (Kunz 1973). Unimodal activity patterns can result when mist-netting is carried out far from diurnal roosts because bats may fly further just after sunset relative to later in the night (Fenton 1970). This situation was unlikely in the present study because suitable roost sites seemed abundant in the Park and because mist-netting was carried out in a variety of locations. In the Park, most places were within 100 to 200 m of a known colony including individuals of both M.

lucifugus and M. volans. Therefore, I was likely to catch bats soon after they began to fly. Hourly intervals may not be sufficiently small to accurately assess changes in activity patterns by bats (Erkert 1982), but were necessary because of the relatively small number of bats caught after the first hour past sunset. A small increase in the number of both species was noticed between six and seven hours after sunset, but this increase was not significant.

Insectivorous bats are capable of filling themselves within 45 to 95 minutes (Gould 1955) and may therefore be expected to exhibit temporal differences in activity patterns more so than animals which must forage for extended periods of time. Evidence for temporal partitioning of prey resources has been demonstrated for several species of insectivorous bats. The observed differences in foraging times have been attributed to interspecific competition for similar prey types (Reith 1980), and to differences in the times that preferred prey were available (Swift and Racey 1983). In one study, Plecotus auritus and Myotis daubentonii occupied the same roost, but departed at different times because the latter species fed on insects that were active later in the evening (Swift and Racey 1983). Insect trapping and analysis of the diets of M. lucifugus and M. volans (chapter V) may provide insights into why the foraging times of these two species overlap.

Flight cage trials implied that both species should be capable of foraging in similar circumstances. This

prediction was substantiated by observations of light-tagged bats as both species used the same habitats. However, M. lucifugus spent proportionately more time feeding low over water when it was available, and M. volans spent relatively more time feeding high up and along cliff edges. Myotis lucifugus frequently forage over water (Fenton and Bell 1979; von Frenckell and Barclay 1987), but they also feed in a variety of other habitats (Aldridge 1986; Herd and Fenton 1983). The foraging behaviour of M. volans is poorly documented, but this species is reported to be a high level, open air forager (Bell 1980; Fenton and Bell 1979). Myotis volans was also flexible in its foraging because this species was netted at treetop level around the park lights, and under canopies of cottonwood groves. The difference in habitat use, despite obvious morphological correlates to explain it, suggests that these two species divide their food resources on a spatial basis at least part of the time.

On a broad scale, the two species were unequally distributed through the study area. Myotis lucifugus was usually present in areas where M. volans was found, but other areas supported large numbers of M. lucifugus and lacked M. volans. This pattern was most obvious in Police Coulee (location 2) where M. lucifugus was common, but few individuals of M. volans were present. Interspecific aggression could cause this distribution pattern. Intraspecific aggression between little brown bats foraging in Police Coulee resulted in small, but exclusive zones



around individual bats, and these zones were defended during brief skirmishes. Although no interspecific interactions were witnessed, if little brown bats were also aggressive toward long-legged bats, this could explain why very few of the latter species were found in Police Coulee. Hoary bats in Manitoba (Barclay 1984) and Hawaii (Belwood and Fullard 1984) were aggressive toward conspecifics and maintained individual foraging zones.

The agonistic behaviour that I observed between individual of M. lucifugus in Police Coulee is apparently unusual for this species. Myotis lucifugus is reported to be non-territorial (Fenton and Barclay 1980), although individuals may return to the same foraging site regularly (Hough 1957). Barclay (1982) witnessed a group of approximately 25 little brown bats feeding together in a small area with no apparent signs of aggression. In areas other than Police Coulee I saw no signs of interspecific or intraspecific aggression. In Davis Coulee, where individuals of M. lucifugus and M. volans were approximately equal in abundance, both species fed in the same habitat types. This indicates that the high number of bats in Police Coulee and/or the relative abundance of insects may have promoted the aggression between little brown bats. In Hawaii, the relative number of agonistic calls by L. cinereus was positively correlated with the number of bats feeding in an area, and negatively correlated with the density of available insects. More individuals fed at a

site when insect densities were higher (Belwood and Fullard 1984). I have no insect-trapping data to indicate what prey densities were when I observed the agonistic interactions between individuals of M. lucifugus.

When prolonged hot, dry weather dried up all of the available water in Police coulee by the end of June in 1988, the number of M. lucifugus caught at this site dropped by over 50 percent. Between June and July 1988, captures of M. lucifugus in Police Coulee dropped from 0.07 to 0.03 bats per net-hour.

Wing morphology indicated that M. lucifugus should be less manoeuvrable than M. volans. The two most difficult habitats in which to fly (habitats 5 and 6) were used infrequently by bats, and were occupied only during an approach or exit from a temporary roost on a tree. The relatively open areas where each species foraged likely did not require very different flight styles or impose rigorous constraints on the morphology of the bats that could fly there. Therefore, I suggest that prey capture may be a more important source of selection pressure on flight ability in insectivorous bats than habitat complexity.

Flight morphology and echolocation call structure do not explain the observed difference in habitat use. My observations on habitat use by both species concur with those of previous studies, but disagree with predictions based on morphology. Aggressive behaviour is a potential mechanism to explain the observed habitat use. Little brown

bats were intolerant of conspecifics foraging in close proximity and may be equally aggressive towards other species. This species was also more belligerent than M. volans when handled. Myotis lucifugus apparently prefers feeding near water, perhaps because of the relatively high numbers of prey that are associated with water (Barclay 1985a; Barclay, unpubl. data), and may prevent other species from using this habitat. If insect distributions differ between habitats, the differential habitat use by little brown bats and long-legged bats should result in dietary differences between the species regardless of the mechanism promoting habitat partitioning.

#### Predictions

Prediction I: the diets of M. lucifugus and M. volans should differ in accordance with the types of insects found in given habitat types. Myotis lucifugus should consume insects that are associated with water, and M. volans should feed on high-flying insects found over land.

## CHAPTER V

### Diet

#### Introduction

Diet varies considerably between different species, and may also vary between age groups (e.g. Werner 1977) and sex classes (e.g. Snyder and Wiley 1976) within a species. Individuals may be selective in their choice of diet for energetic (Barclay 1989; Fleming 1988) and/or nutritional (Belovsky 1978) reasons, or they may feed opportunistically based on the abundance and availability of prey. Morphology sets limits on absolute size and hardness of food that can be ingested (e.g. Freeman 1979, 1981; Grant 1986; Heithaus et al. 1975; Hespenheide 1971). In other cases morphology can restrict access to certain food types (e.g. Harder 1985).

In addition to these intrinsic factors affecting resource use, a variety of extrinsic factors also determine food use. Environmental conditions that influence insect distribution (e.g. moonlight, wind, rain, ambient temperature; Kunz 1988) alter the foraging strategies of insectivorous bats (Anthony et al. 1981; Barclay 1982, 1985a). Interspecific and intraspecific relations may also affect habitat use by bats (see chapter IV), and consequently may cause different species to consume

different insect types. Predation pressure can also lead to dietary differences between individuals by causing shifts in habitat use (e.g. Mittelbach 1981). However, predation is usually not considered an important aspect of the ecology of temperate bats when they are foraging. Predators usually focus their attention on roosting bats, or those entering or leaving their day roosts (e.g. Fenton 1970; Twente 1954; and see references in Tuttle and Stevenson 1982).

Currently there is a debate on whether insectivorous bats are opportunistic (e.g. Belwood and Fenton 1976; Fenton 1985; Fenton and Morris 1976; Rydell 1986; Vaughan 1980) or selective (e.g. Black 1974; Buchler 1976a; Freeman 1979; Swift et al. 1985) foragers. Others view foraging strategies used by bats as being subject to insect availability which may depend on season (e.g. Barclay 1985b), nightly changes in insect activity (e.g. Eckrich and Neuweiler 1988), and/or limitations imposed by morphology and perceptive ability (Barclay 1985a). Part of the difficulty in determining whether bats are specialist or generalist foragers is that it is impossible to determine exactly what a bat perceives as available food. Larger prey are probably perceived more readily by bats, and such items may therefore appear as more available food items than small prey. The sizes and types of prey that bats can consume are therefore constrained by echolocation abilities (Barclay 1985a), by feeding morphology (e.g. jaw morphology, Freeman 1979), and by possible optimal foraging considerations such

as handling time, digestion efficiency and energy content of prey. A bat which "preferentially" consumes large prey could do so either for energetic reasons, or simply because such items are perceived as being more available. It is difficult to distinguish between these two conclusions.

Components of an animals' diet may be investigated in a variety of ways (see Lehner 1979). Direct observations of foraging animals, or of adults provisioning food to offspring, are practical if prey are relatively large or foraging animals can be closely approached. Animals which consume relatively small prey, and those for which direct observations are difficult (e.g. crepuscular or nocturnal foragers and aquatic animals) require alternative techniques. Stomach analysis, fecal analysis and examination of culled parts are three techniques commonly used to determine the diets of bats (Whitaker 1988). Using culled insect parts as an index of the types of prey consumed is inaccurate for aerial feeders because few or no parts are culled when prey are small (Coutts et al. 1973; LaVal and LaVal 1980). Stomach analysis requires that specimens are sacrificed, and is therefore undesirable in ecological studies where it is important to avoid disturbing the population. Fecal analysis is a non-destructive method of analyzing diet and has been found to be more accurate than (Kunz and Whitaker 1983), or in good agreement with, results from stomach analysis (Whitaker et al. 1981). Problems associated with differential rates of digestion of

different insect types are minimized because food passes through the digestive system of bats quickly (Whitaker 1988).

If soft-bodied prey (e.g. Ephemeroptera) comprise a large portion of the diet, fecal analysis may provide an unreliable measure of diet (Dickman and Huang 1988; Rabinowitz and Tuttle 1982). In the study area, only Diptera, Neuroptera and Ephemeroptera could be considered soft-bodied. The first two orders were easily recognized by the presence of wing pieces in the feces, and Ephemeroptera were rare in the Park. Only one mayfly was captured in over 20 h of whirlygig trapping. Fecal analysis was therefore judged to be a reliable method of assessing diets of the two species. However, fecal analysis usually cannot provide information on the sizes of insects consumed by bats. Different sizes and types of prey may have different digestion efficiencies (e.g. based on their relative chitin content) which may bias the interpretation of the relative proportions of different prey types that the bats actually consume. In this study both species are subject to the same analysis technique and the results therefore provide a comparative assessment of the prey consumed by individuals of both species.

Methods of estimating the availability of insects to bats are limited in their effectiveness for a variety of reasons. For example, small insects may be trapped in large numbers, but are not readily detectable by bats.

Conversely, large insects may be more available to bats than their numbers indicate because of their large size (Kunz 1988). Certain insects may also be prone or impervious to capture by bats by virtue of size, flight speed, activity patterns (Black 1974; Yack 1988), and/or their ability to detect and elude the bats (Fullard 1987; Miller and Olesen 1979). It is also naive to assume that bats captured near where insect sampling is taking place have not foraged in other areas prior to being captured. Bats may take insect prey from an array of insects different from that sampled by the insect trap. Comparing measures of insect availability to the prey types consumed by bats is therefore tenuous.

A variety of traps have been designed to collect insects, but all of these devices are biased in some respect (see Graham 1969; Southwood 1966). Most traps are either prone to catching certain insect types, or have limited success in catching large, or very small, or fast-flying insects. Whirlygig traps are generally considered to take a random sample of flying insects, but may attract mosquitoes (Graham 1969).

Despite limitations in assessing the proportions of insect types consumed by bats and in measuring prey availability, synchronous comparisons between the feeding ecologies of two or more species using the same methods provides a measure of the degree of difference between species. Because all species are exposed to the same conditions, differences in diet are therefore related to



behaviour and not merely to methodological deficiencies. Therefore, similarities or differences in habitat use, timing of foraging bouts, sensory capabilities and differences in trophic morphology should be reflected in diet. Dietary differences between two or more similar species therefore indicate that food resources are being partitioned.

I used fecal analysis to compare the diets of M. lucifugus and M. volans. I also compared the diets of individuals with an index of insect availability taken at the same time that the bats were foraging. This allowed me to assess whether dietary differences exist between sexes and species, and whether the bats selected certain types of insects from those available.

## Methods and Materials

### Fecal Analysis

Feces were collected from all bats captured in mist-nets in 1987 and 1988 in order to compile dietary information. Bats were kept in cotton bags for at least one hour after capture and any fecal pellets produced were collected. In order to avoid biasing fecal analysis, individual fecal samples were identified by bat number rather than by species. The bat that produced the sample was identified only after fecal analysis was completed.

Fecal samples ranged from one to 44 pellets. Only feces collected in 1988 were analyzed as no effort was made to trap insects concurrent with bat trapping in 1987. Feces from a total of 136 M. lucifugus and 52 M. volans were examined. Juveniles were omitted from the comparisons leaving 120 M. lucifugus and 48 M. volans samples.

Feces were dried in an oven at 60°C for 24 h before being weighed on a digital Mettler balance ( $\pm$  0.0001 g). Samples containing more than one pellet were subdivided into portions of approximately equal size. Individual pellets were placed in petri dishes, softened in 70 percent ethanol, and teased apart using two probes. Insect parts were identified to order (suborder for Hemiptera) using a Wild (6X to 31X) zoom dissecting scope. Diagnostic features such as mouthparts, head capsules, eyes, scales and wings were used to classify the insects present (Whitaker 1988). Estimates of the percentage of each pellet (by volume) comprised by each insect taxon present were recorded. These proportions were then arcsine transformed and the transformed data were used in the comparisons between species and with insect availability data.

### Insect Trapping

Three types of insect traps were used in 1988. Depending on the night and location, up to eight sticky traps, two Malaise traps, and a whirlygig trap (see Holroyd

1983 for the design) were operational at the same time and in the same area that mist nets were set to capture bats. The first two trap types were ineffective at catching insects, and therefore only the results obtained from the whirlygig trap were analyzed. The whirlygig trap consisted of two rectangular insect nets (25 X 57 cm) on opposite sides of a central pivot pole. The nets had screen enclosures that guided insects into a collecting bottle. Seventy percent ethanol in the collecting bottle served to kill the insects. One net was low (i.e. 55 cm from the ground); the other was high (i.e. 355 cm). The distance from the center of one net to the centre of the other was 4.7 m (= diameter of sweep circle). An electric motor turned the arms with the nets at 10 to 12 rpm.

The whirlygig trap was used in Writing-On-Stone Provincial Park on 11 nights in 1988. The trap was set in a total of six different locations within the Park over this period. Bats of both species were caught in only three of these areas on eight different nights. On the three remaining nights either no bats were captured or those that were captured were several hundred metres from the whirlygig trap and in different habitat types. A total of 39 M. lucifugus and 26 M. volans was captured near (i.e.  $\leq 10$  m) where the whirlygig trap was operating. Forty-five of these 65 bats (72 percent) were caught in the first two hours after sunset.

The whirlygig trap was operated for one-hour sampling periods, two or three times per night, totalling 1325 minutes of trapping for the summer. After each sampling period the insects from both collecting bottles were combined, separated by order (suborder for Hemiptera), counted, dried at 60°C in an oven for 24 h, and weighed on a digital Mettler balance ( $\pm 0.0001$  g) to determine the total dry weight of insects of each taxon. The dry weight of each taxon was then compared to the corresponding proportion of each taxon in the feces from bats caught either at or near the same time that the insects were captured.

Similar studies have compared either the number (e.g. Anthony and Kunz 1977; Swift et al. 1985) or the biomass (e.g. Barclay 1985a; Whitaker et al. 1977) of insects of different orders in the feces to those in the insect traps. I adopted the latter method because it was impossible to discern the number of insects of each taxon represented in the feces. Such a technique requires that the number of eyes, head capsules, or legs found in the feces can be extrapolated to estimate the minimum number of insects in the feces. This would be feasible for insects that were ingested whole, but not possible for larger insects that were only partially consumed. Insect number also does not account for differences in prey size which is likely used as a cue by foraging bats.

Feces from bats that were captured while the whirlygig was not operating were compared to insect samples caught

during the closest sampling period prior to catching the bats. The maximum time between the end of an insect sampling period and capture of a bat was 75 minutes. Buchler (1975) indicated that most insects consumed by M. lucifugus had a transit time of 35 to 170 minutes through the digestive system. Certain insect types may take as long as 20 h to void (Kunz and Whitaker 1983).

## Results

### Fecal Analysis

Multiple analysis of variance (MANOVA) was used to compare diets (by the relative proportion of each insect taxon in the feces) between sexes of a species, and between species. The diets of male and female bats of the same species were compared on nights when both sexes were captured to see if individuals of both sexes consumed the same insect types in the same proportions. Of 32 nights when bats of either species were caught, 11 nights had both male and female M. lucifugus (56 males and 21 females), and 6 nights had both sexes of M. volans (15 males and 9 females). The day on which the feces were collected from the bats was used as a variable in the analysis to take into account differences in diet caused by shifts in prey populations over the season.

Five taxa of insects (Coleoptera, Diptera, Heteroptera, Lepidoptera, and Neuroptera) and a category of 'other' insect types, including Homoptera, Hymenoptera and Trichoptera, were considered in the dietary analysis. The first five taxa comprised over 80 percent of the diets of both species of bats. On average, Lepidoptera made up the largest portion of the diet of M. volans whereas Coleoptera, Diptera and Lepidoptera were common in the diet of M. lucifugus (Table 5.1).

No significant differences existed in the diets between male and female M. lucifugus ( $F = 0.13$ , 6 df,  $p > 0.99$ ). Diet varied amongst days ( $F = 2.43$ , 60 df,  $p < 0.001$ ) with Diptera and Lepidoptera contributing most to this difference. A significant difference was noted between male and female M. volans for Neuroptera ( $F = 42.66$ , 1 df,  $p < 0.001$ ), and again diet differed amongst days ( $F = 7.40$ , 30 df,  $p < 0.001$ ). When all components of the diet were combined and dietary differences were examined using MANOVA (describing sexes based on all components of the diet) the difference in the percentage of Neuroptera in the diet between sexes contributed to a significant difference in diet between sexes ( $F = 25.31$ , 6 df,  $p < 0.001$ ), and amongst days ( $F = 7.40$ , 30 df,  $p < 0.001$ ). However, Neuroptera were rarely found in the diet of M. volans, and did not comprise more than 13 percent of the diet of an individual of either sex.

Table 5.1 Least squares mean weight (corrected for size of the fecal sample) of insect taxa appearing in the diets of Myotis lucifugus and Myotis volans in 1988. The 'other' category consisted of Homoptera, Hymenoptera and Trichoptera.

	<u>M. lucifugus</u> (n = 120)	<u>M. volans</u> (n = 47)
	LS mean weight $\pm$ S.E. (mg)	LS mean weight $\pm$ S.E. (mg)
Coleoptera	5.89 $\pm$ 1.21	2.72 $\pm$ 1.60
Diptera	6.42 $\pm$ 1.09	2.43 $\pm$ 1.44
Lepidoptera	7.25 $\pm$ 1.56	18.06 $\pm$ 2.06
Heteroptera	1.90 $\pm$ 0.51	0.41 $\pm$ 0.67
Neuroptera	0.95 $\pm$ 0.26	0.13 $\pm$ 0.34
Other	2.53 $\pm$ 0.52	1.61 $\pm$ 0.69

Since the diets of males and females of the same species did not differ (except for Neuroptera with M. volans), sexes were combined for further analyses. Daily differences in diet warranted interspecific comparisons of diet only on days when individuals of both species were captured (19 of 32 nights). Diet differed significantly between days ( $F = 2.24$ , 108 df,  $p < 0.001$ ) and between species ( $F = 7.20$ , 6 df,  $p < 0.001$ ). Diptera and Lepidoptera contributed most to the difference between species. Myotis lucifugus ate significantly more Diptera ( $F = 6.57$ , 1 df,  $p < 0.02$ ) and fewer Lepidoptera ( $F = 40.17$ , 1 df,  $p < 0.001$ ) than did M. volans.

#### Insect Trapping versus Diet

To investigate whether either species foraged selectively or opportunistically, the diets of both bat species were compared with the index of insect availability from whirlygig trap samples. To see if diets of this subset of bats (i.e. only those bats caught when the whirlygig trap was operational) differed between species, the relative proportions of insect types consumed were compared using MANOVA. The diets of this group of bats differed between days ( $F = 4.13$ , 42 df,  $p < 0.001$ ), and between species ( $F = 2.91$ , 6 df,  $p < 0.02$ ). As with the larger data set, M. lucifugus consumed significantly fewer Lepidoptera ( $F = 14.72$ , 1 df,  $p < 0.001$ ) than did M. volans.



Diptera comprised 70 to 90 percent of the total number of insects caught in the whirlygig trap on all sampling dates (Fig. 5.1). Lepidoptera and Neuroptera were the next most frequently captured insect types. Lepidoptera comprised 50 to 80 percent of the total dry weight of the insects sampled between 7 June and 7 July (Fig. 5.2). Diptera and Neuroptera made up most of the remaining dry weight on those nights. Between 21 and 29 July, the relative dry weights of each of these orders fluctuated considerably, and no taxon comprised more than 50 percent of the total sample weight on these nights. Heteroptera, Homoptera, Hymenoptera and Trichoptera comprised less than ten percent of the insect biomass in the trap on all nights (Fig. 5.2).

Shifts in the composition of the diets of both species from night to night were parallel (see Fig. 5.3 for the trend for Diptera). However, on several nights M. lucifugus and M. volans consumed Trichoptera and Heteroptera in high proportions relative to their index of availability. Trichoptera frequently occur in large swarms (Chapman 1969), and the bats may have exploited a swarm not sampled by the whirlygig trap. Myotis lucifugus generally consumed Diptera in proportion to their availability, whereas Diptera were under-represented in the diets of M. volans. The reverse was true for Lepidoptera.

The percentages of each insect taxon by weight in the feces of bats were plotted against the relative biomass of

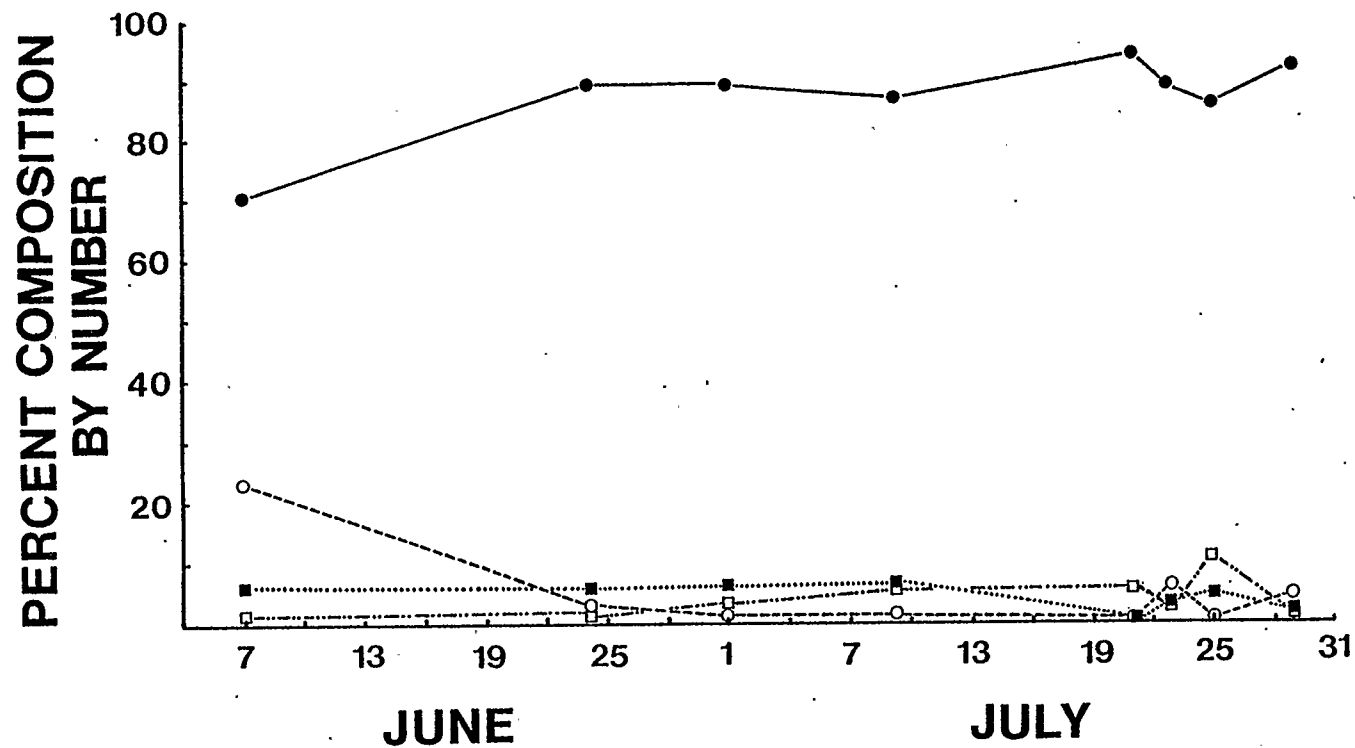


Figure 5.1 Percent composition of insect taxa (by number) in the whirlygig trap.  
 ●—● = Diptera, ○---○ = Neuroptera, ■.....■ = Lepidoptera, and □-.-.-□ =  
 the combined total of Coleoptera, Heteroptera, Homoptera, Hymenoptera and  
 Trichoptera.

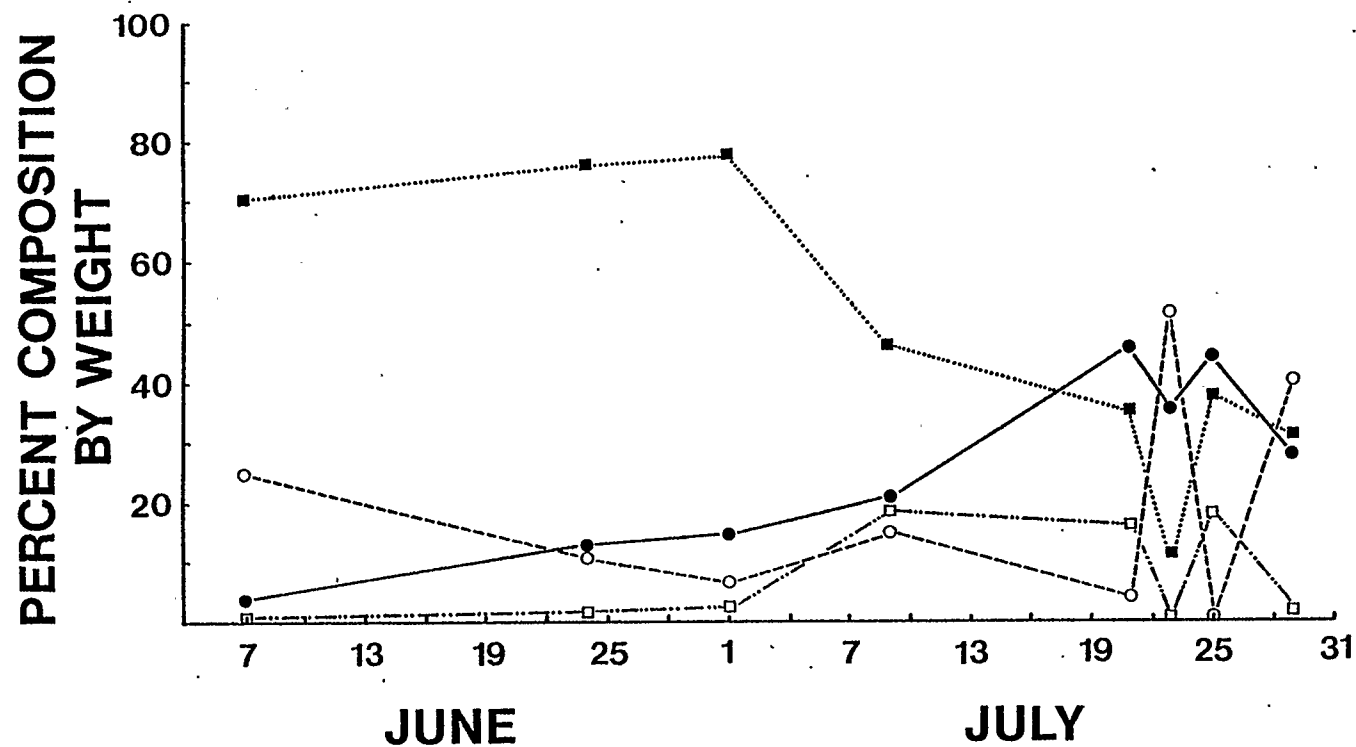


Figure 5.2 Percent composition of insect taxa (by weight) in the whirlygig trap.  
 ●—● = Diptera, ○—○ = Neuroptera, ■—■ = Lepidoptera, and □—□ = the combined total of Coleoptera, Heteroptera, Homoptera, Hymenoptera and Trichoptera.

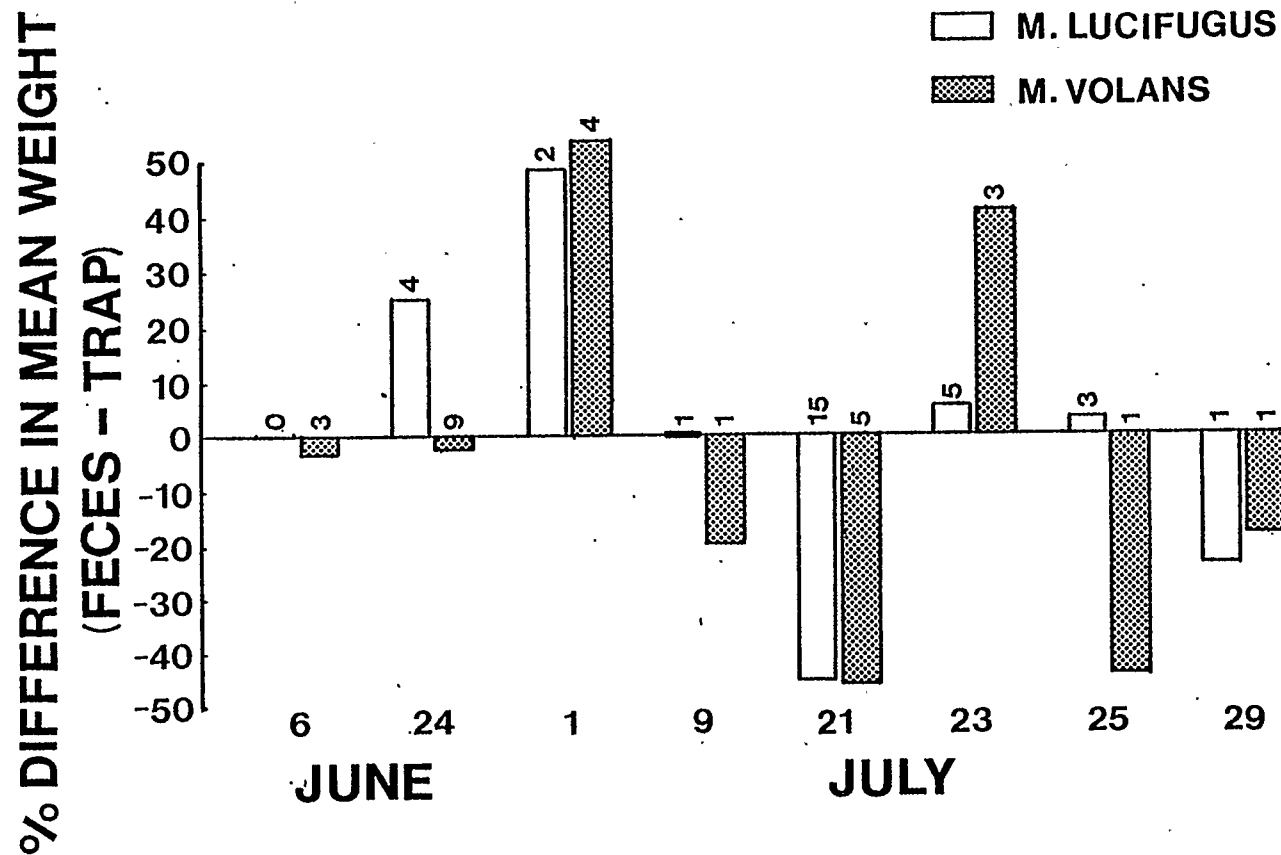


Figure 5.3 Percent difference in the mean dry weight of Diptera in the feces of Myotis lucifugus and Myotis volans and the dry weight of Diptera in the whirligig trap on given nights. Numbers above the bars indicate the number of bats captured.

each insect taxon caught in the whirlygig trap. Since insect size was not discernible from remains in the feces of bats, insects of all sizes within a taxon were grouped in the trap samples. One thirteen-lined June beetle (Polyphylla decilineatus) was omitted from the insect trap data as it was too large for either bat species to consume. Eight insect taxa were considered in this analysis: Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, Neuroptera and Trichoptera.

If a species preferentially selects certain prey types (i.e. for optimal foraging reasons), then those types of prey should be common in the diet except when their availability is low (i.e. a type I functional response curve; see Holling 1959). The high degree of variability in the diet of M. lucifugus (Table 5.1) suggests that individuals of this species are not selective foragers. However, long-legged bats have high proportions of moths in their diet in this and other studies (Table 5.1; Black 1974; Warner 1985). To examine whether M. volans preferentially selects moths from an array of available insects, the percentage of Lepidoptera (by weight) in the feces was plotted against moth density (as indicated by the rate that moths were captured in the whirlygig trap at the same time; Fig. 5.4). Although there was an increase in the proportion of moths in the feces as moth availability increased, at the highest rates of moth capture moths were

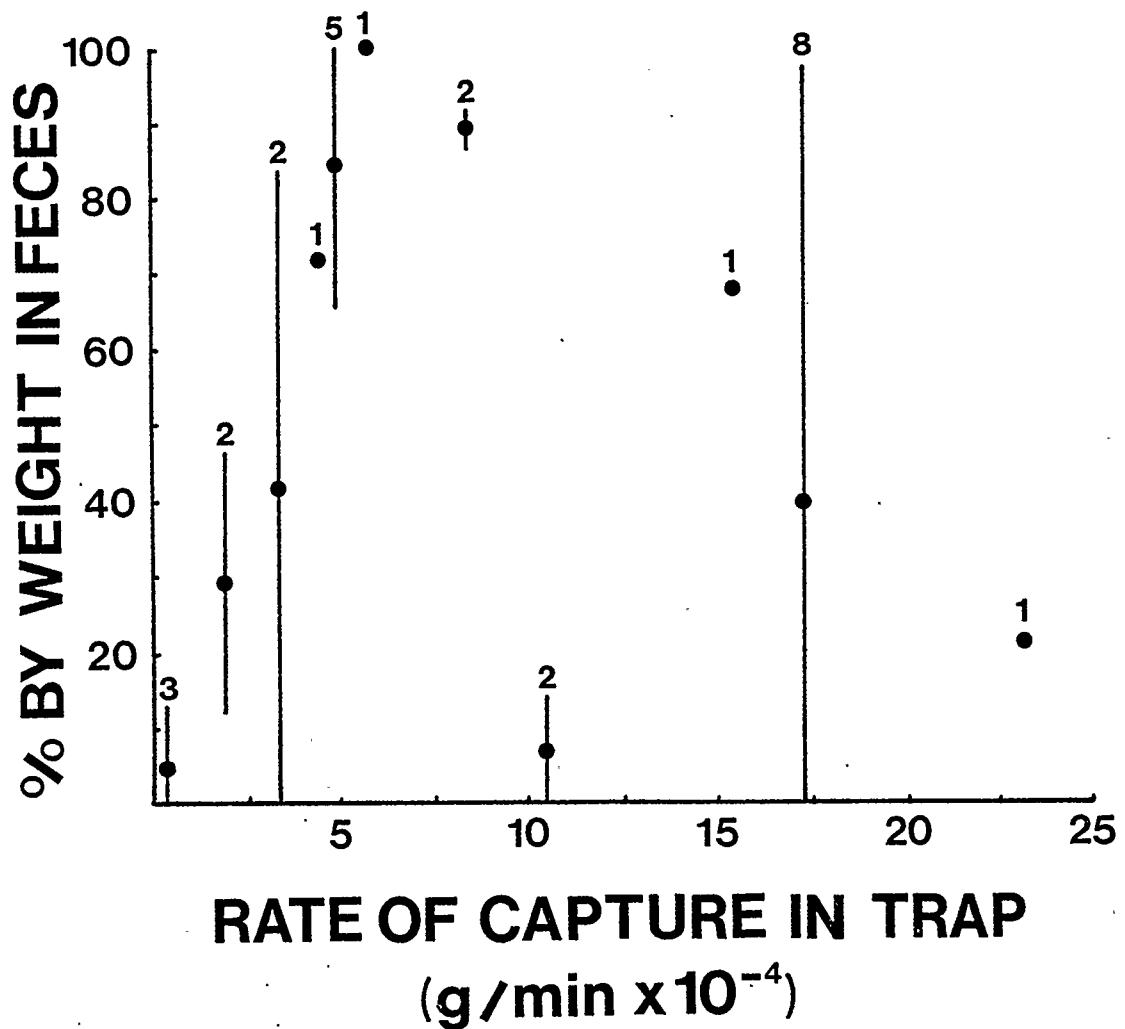


Figure 5.4 Percent composition of Lepidoptera in the feces of *Myotis volans* versus the density of moths available to the bats (measured as the dry weight of moths captured per minute in the whirlygig trap). Bars indicate the range in values above and below the mean. Numbers above the bars indicate the number of bats captured.

less common in the diet. Diets were highly variable between individual M. volans regardless of moth availability.

Barring the obvious methodological problems of measuring insect availability, if bats consumed insects at random from those available, the percentage of each insect taxon in the feces should reflect the proportion of each taxon in the trap in a 1:1 relationship. This hypothesis was tested by fitting a regression line, fixed at an intercept of zero, through the data points for each insect taxon and bat species. If a significant correlation existed, the slope of the line was tested to see if it differed from a slope of one (i.e. random selection of prey).

A high degree of variability existed between the percentage of insects of each type in the feces of both species of bats and in the trap. This variability resulted in correlation coefficients ranging from zero for Heteroptera to 0.75 for Lepidoptera. Only Diptera and Lepidoptera exhibited a significant correlation between points for both species (Table 5.2). The slopes of the lines describing the relationship between proportions of Diptera and Lepidoptera in the feces and trap was closer to a slope of one for M. volans than for M. lucifugus.

Forcing the regression line through zero de-emphasized the effect of bats which consumed insect types not frequently captured in the whirlygig trap as these points were weighted less heavily. Chi-square tests with Yates

Table 5.2 Regression statistics describing the best fit line for the proportion of insect taxa by weight in the feces of bats versus in the whirlygig trap. P SLOPE values indicate whether a significant correlation exists between points of the regression. The y-intercept is fixed at the origin.  $H_0$  tests whether the slope of the regression line is significantly different from a slope of one. Statistical significance is indicated by asterisks (ns = not significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ).

	<u>M. lucifugus</u>			<u>M. volans</u>		
	slope	P SLOPE	$H_0$	slope	P SLOPE	$H_0$
Coleoptera	0.90	ns	ns	1.54	ns	ns
Diptera	0.34	*	***	0.59	*	ns
Hemiptera	0.00	ns	ns	0.00	*	ns
Homoptera	0.07	ns	***	0.05	ns	***
Hymenoptera	0.09	ns	**	0.04	ns	***
Lepidoptera	0.52	***	***	0.72	***	*
Neuroptera	0.03	ns	***	0.02	ns	***
Trichoptera	0.37	ns	ns	0.74	ns	ns



continuity correction (Zar 1984) were used to see whether the distribution of points on either side of the line of equivalence was biased toward one side or the other (Table 5.3). Points above this line indicated that insects of that taxon were selected preferentially; points below the line indicated that bats avoided or could not capture those insects. Alternatively, a high representation of an insect type in the diet could indicate that those insects were not readily captured by the trap, and points below could indicate that the the insects were attracted to the trap. The latter two alternatives are unlikely (Graham 1969).

Overall, bats of both species consumed Diptera, Lepidoptera and Trichoptera in proportion to their availability (Table 5.3). Both species consumed fewer Hymenoptera and Neuroptera than expected by the number of these insects caught in the whirlygig trap. Myotis volans consumed proportionately more Coleoptera than expected, while M. lucifugus consumed beetles in proportion to their availability. The reverse was true for Heteroptera. Curiously, Heteroptera comprised less than 0.25 percent of the insect biomass in the trap samples, but were frequently found in the feces of M. lucifugus. Myotis volans consumed Homoptera in proportion to their availability, but M. lucifugus took fewer of these insects than expected (Table 5.3).

Table 5.3 Summary of Chi-squared analysis describing the distribution of data points above or below the line of equivalence for the proportion of insect taxa in the feces versus in the whirlygig trap samples. '=' indicates that as many points are above the equivalence line as below; '+' indicates that more points are above than below (i.e. a greater representation of the insect type in the feces than in the trap); '-' indicates that more points are below the line (i.e. more of the insect type in the trap than in the feces. Statistical significance is indicated by asterisks (ns = not significant; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ).

INSECT ORDER	<u>M. lucifugus</u>	p	<u>M. volans</u>	p
Coleoptera	=	ns	+	**
Diptera	=	ns	=	ns
Heteroptera	+	***	=	ns
Homoptera	-	**	=	ns
Hymenoptera	-	*	-	*
Lepidoptera	=	ns	=	ns
Neuroptera	-	***	-	***
Trichoptera	=	ns	=	ns

## Discussion

All insect taxa captured in the whirlygig trap were represented in the diets of both bat species, but the relative proportions of the taxa differed between species. Overall, M. lucifugus consumed proportionately more Diptera and fewer Lepidoptera than did M. volans. This dietary difference could result from the fact that both species foraged in different habitats where the types of available insects differed. Alternatively, the two species may have different types of insects available to them because of limitations set by their morphology and/or their echolocation calls. Finally, different species of bats may actively select different types of prey from those available for consumption.

Myotis lucifugus usually foraged over water, and M. volans usually foraged over land. This differential use of habitat may have been sufficient to cause the difference in diet. However, when both species foraged in the same area, diet still differed; specifically, M. volans consumed proportionately more moths than did M. lucifugus. It is possible that smaller scale habitat separation was responsible for such differences in the diet. On the other hand, long-legged bats may preferentially select moths, or moths may be less available for consumption by little brown bats because of morphological differences.

Overall, several insect taxa made up relatively large proportions of the diet of M. lucifugus, whereas moths were usually the major component in the diet of M. volans. Myotis lucifugus may have exploited local insect abundances of insects, whereas M. volans seemed to consume high proportions of moths independent of their availability. However, diet was variable amongst individual long-legged bats, and when moths were abundant in the whirlygig trap not all individuals consumed high proportions of moths. These observations indicate that although moths were usually the major dietary component, long-legged bats were not feeding selectively.

My observation that components in the diet of M. lucifugus were variable and those of M. volans were relatively constant concurs with findings in other studies. In different areas, the diet of M. lucifugus was comprised primarily of Ephemeroptera (Buchler 1976a), chironomids and other Diptera (Whitaker et al. 1977), Diptera, Lepidoptera and Coleoptera (Whitaker et al. 1981), and Diptera and Trichoptera (Belwood and Fenton 1976). Despite this dietary variability, the diet usually consists of insects found near water (Fenton and Barclay 1980). Myotis volans feeds primarily on moths wherever it is found (Black 1974; Warner 1985; Whitaker et al. 1977, 1981), although other insect types are also found in its diet (Bell 1979; Warner and Czaplewski 1984).

Consistencies in the diet of a species, such as in M. volans, should not be assumed to represent selective foraging. Low variability in the diet may be present because only one type of insect is available to consume (e.g. a hatch of one type of insect may be exploited), or because other types of prey may not be available to the foraging bat. For example, although in terms of overall insect density, areas near water often appear to be the optimal habitats in which to forage (Barclay 1985a; von Frenckell and Barclay 1987), this situation ignores differences in actual prey availability imposed by morphology. If long-legged bats are more efficient than little brown bats at capturing evasive prey (such as moths), and areas away from water have higher moth densities, this might explain why long-legged bats rarely forage over water. The larger tail membrane of M. volans may enable it to capture larger prey than M. lucifugus, or it may allow the former species to catch evasive insects (e.g. moths) by giving it a greater margin of error (i.e. less chance of missing) when scooping prey in its tail.

Black (1974) classified North American insectivorous bats as either moth or beetle strategists based on the relative frequency of these insects in their diets. Freeman (1979, 1981) related this dichotomy to skull characteristics that predispose bats to consuming hard-bodied (e.g. beetles) or soft-bodied (e.g. moths) insects. She also indicated that the former category of bats was likely more capable of

taking a wide variety of insects than the latter (Freeman 1981). Neither M. lucifugus nor M. volans would be expected to differ with respect to the insect types that they consume because they have similar jaw morphologies (Freeman 1981).

Considerable research on the foraging strategies of bats has taken place since Black's (1974) study. Many studies on aerial insectivorous bats agree that they forage opportunistically by taking prey in proportion to their availability (e.g. Fenton 1985; Swift et al. 1985; Warner 1985). However, these bats frequently respond to local insect aggregations (Anthony and Kunz 1977; Bell 1980; Belwood and Fenton 1976) where they may preferentially select certain sizes (Anthony and Kunz 1977; Fenton and Morris 1976) and/or types (Vaughan 1980) of insects. Foraging bats may also become more selective in the insects they consume as the abundance of insects increases (Anthony and Kunz 1977). 'Selective opportunism' may best describe the foraging strategies of most bats because of their flexibility in altering their foraging behaviour in accordance with local prey populations (Fenton and Morris 1976). This trend is not universal as some bat species appear to be highly selective in the types of insects they consume (e.g. Whitaker and Black 1976).

Moths made up greater than 50 percent of the insect biomass available to bats on all but two nights when many Neuroptera were caught, and two nights when Diptera comprised the majority of the total insect dry weight. The

peaks in biomass of Neuroptera do not necessarily indicate that the insects were available to the bats because Neuroptera can detect the echolocation calls of bats and evade capture (Miller and Olesen 1979). An indication of the ability of Neuroptera to avoid predation by bats is that green lacewings (Chrysopidae) were relatively common in the whirlygig trap, but rarely appeared in the feces of either species of bat. Some moths can also evade bats (Fullard 1987), but the high numbers of moths in the Park, many of which likely could not detect bats, permitted bats to have high proportions of these insects in their diet.

Despite the fact that M. volans consumed more moths than did M. lucifugus, both species seemed to respond to insect availability in a similar manner when they fed in the same area because the presence or absence of an insect type in the diet of one species was usually reflected in the diet of the other species. This observation fits the description of aerial insectivores as temporal dietary opportunists (Fenton and Morris 1976; Warner 1985).

Comparisons of morphology and echolocation calls between the two bat species indicated that both should be capable of locating and consuming the same insect types. This prediction was verified through dietary analysis, but significant differences in the proportions of different insect taxa in diets were apparent. Several different scenarios may explain the observed pattern, and the way in which these results are interpreted may have implications

for further studies on foraging strategies. Diet is often assumed to be a consequence of morphology in the sense that morphology determines habitat use, which in turn determines the types of insects that are available to bats (e.g. Aldridge 1986; Aldridge and Rautenbach 1987). However, morphology may set direct limitations on the types of prey that can be consumed, and consequently bats of a particular morphology may forage most efficiently in habitats where suitable insects are available.



## CHAPTER VI

## Conclusions

Myotis lucifugus and M. volans differed significantly in wing morphology, but these differences did not translate into significant differences in their flight ability as measured by one test. Aerodynamic theory predicted that the greater wing loading and aspect ratio of M. lucifugus should have translated into faster and less manoeuvrable flight by this species relative to that of M. volans. If differences in flight capability are present between the two species, they were not detectable in flight cage tests.

Reports on these two species foraging under natural conditions indicate that M. lucifugus flies more slowly and is capable of making tighter turns than is M. volans (Fenton and Bell 1979). These observations are the reverse of what would be predicted by my measurements of flight morphology. My field observations on the flight of these bats did not reveal noticeable differences in their flight ability, although differences in the habitats in which they flew were apparent. Thus, the aspects of morphology that I measured did not allow me to accurately predict the observed pattern of habitat use. Although I measured wing characters that have been successfully used to predict flight behaviour in the past, in this case those measures were insufficient to do so.

Studies that have accurately predicted flight behaviour from morphology dealt with species that were distinctly different from one another (e.g. Aldridge and Rautenbach 1987; Crome and Richards 1988; Fenton and Rautenbach 1986). The reliability of such predictions necessarily depends upon the magnitude of the morphological differences between species. Therefore, behaviour of bats with less extreme characters (e.g. similar trophic apparatus, intermediate wing loading and aspect ratio) may not be predictable. Differences in the aspects of morphology that I measured on M. lucifugus and M. volans were small and predictions from these differences were not ecologically informative. Characters other than those with intuitively-obvious relationships to behaviour may need to be examined.

Flight performance of M. lucifugus and M. volans indicated that both species were capable of flying in the same areas. Observations of free-flying bats confirmed this prediction. However, each species spent significantly more time in particular habitat types than did the other. Myotis lucifugus fed primarily over water, and M. volans foraged relatively high above the ground and often along cliff or tree edges. None of these habitats requires the degree of manoeuvrability that both of these species demonstrate. Therefore, their manoeuvrability is probably more related to the need to catch insects than it is the ability to fly in areas with high degrees of clutter. The convention for many researchers to use morphology to predict behaviour and then

relate behaviour to diet (e.g. Aldridge 1986; Aldridge and Rautenbach) may be incorrect in some cases. Instead, diet may be a direct consequence of morphology, and therefore the forager may feed in particular habitats based on the distribution of suitable prey.

Considerable dietary overlap was noted between the two bat species, but each seemed to 'specialize' on particular types of insects. This specialization was not attributable to differences in echolocation calls between species because the same types of insects were present in the diets of both species. The diet of M. lucifugus seems to be determined by the habitats in which it spent most of its time when foraging. Because M. lucifugus fed predominantly over water, its diet consisted primarily of insects that are commonly associated with water (especially Diptera). When M. lucifugus foraged away from water and in the same areas where M. volans foraged, its diet showed greater overlap with that of the latter species. The relative proportion of Diptera in the diet between species did not differ significantly in this circumstance. However, M. volans consumed significantly more Lepidoptera than did M. lucifugus in all circumstances. This observation indicates that M. volans may be better suited to capturing moths than is M. lucifugus, and that its use of habitat may be a consequence of where moths are commonly found.

Some species of bats consistently feed over water (e.g. Myotis daubentoni, Jones and Rayner 1988; Myotis adversus,

Thompson and Fenton 1982; and M. lucifugus, Fenton and Barclay 1980) and it is possible that certain morphological characteristics permit this type of flight. However, Findley's (1972) study of phenetic relationships amongst Myotis bats categorized M. lucifugus and M. volans into a group of bats considered to have the same mode of foraging. Therefore, it is not clear why M. volans does not feed low over water, given that insect abundance is generally high there (Barclay 1985a; von Frenckell and Barclay 1987). Myotis lucifugus is able to increase its wingbeat frequency and decrease the negative elevation of its wings when flying close to water surfaces (Aldridge 1988). This ability prevents wing contact with the water and permits this species to fly close to the water for extended periods of time. Photographs of M. volans drinking while in flight indicated that these bats are less capable of foraging low over water (J. S. Altenbach, pers. comm.). Comparative investigations of skeletal and muscle configuration of the pectoral girdle of species that feed over water, and those that do not, might provide valuable insights into why this difference exists.

The differences in habitat use and the types of prey consumed by the bats in this study indicate that resource partitioning is occurring. However, wing morphology, echolocation call structure and flight behaviour do not provide an obvious explanation of why this ecological difference was present between species. Social interactions

may be partly responsible for the observed pattern. Myotis lucifugus was aggressive towards conspecifics as they fed over water in Police Coulee, and the absence of potentially competing species implicates interspecific aggression as a potential mechanism promoting differential habitat use. In other areas, however, this segregation was less obvious and both species foraged together with no obvious signs of aggression. Differences in the distribution of suitable prey may contribute to this difference. The only place where M. volans tended not to be found was over water, whether at the river, or in Police Coulee. Myotis lucifugus was found in all areas. If long-legged bats cannot forage efficiently over water, as seems the case, insects low over the water are effectively unavailable to them, and consequently these bats feed where they can do so more economically.

The ability to predict behaviour from morphology is an inviting concept to those seeking to explain patterns of community organization, implications of limiting similarity, and mechanisms of resource partitioning between species. Studies on bats have had varying success with this idea, although most demonstrate that ecomorphological theory can provide correct predictions concerning behaviour when morphological differences are large (e.g. Aldridge and Rautenbach 1987; Crome and Richards 1988; Fenton and Rautenbach 1986; Findley 1976). Other investigations have accurately predicted various aspects of bat behaviour, but

could not provide clear explanations of how these predictions related to the ecology of the bats (e.g. Aldridge 1986; and see Findley and Wilson 1982). I have shown that morphological differences between M. lucifugus and M. volans cannot be used to accurately predict their respective flight performance or aspects of their feeding ecology. This finding serves as a precaution to those who believe morphology closely reflects ecology and wish to use morphology as a means to investigate the ecological structure of bat communities (e.g. Findley and Wilson 1982).

My findings also have broader implications with respect to animal communities. For example, the geographic distribution of foragers that are limited in the size of prey that they can consume (e.g. fish, Werner 1974; lizards, Powell and Russell 1984; birds, Ashmole 1968, Grant 1986; and mammals, Freeman 1981, Simms 1979) may be related to the distribution of suitable prey rather than a reflection of the types of habitats that are available. Morphology can lead to habitat selection and subsequently to diet, but morphology can also restrict diet, which in turn determines habitat use. These relationships should be investigated in any study of community structure. Wiens and Rotenberry (1980) have demonstrated that morphology is an unreliable index of ecology in various bird populations and they advocated the need for further field studies. My study emphasizes that need.

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Appendix 1. Mean morphological measurements of Myotis lucifugus and Myotis volans in 1987 and 1988. Each summer was divided into early (1 May to 30 June) and late (1 July to 31 August) periods. Only measurements from adult bats were included. Pregnant and lactating females were excluded.

variable (mean $\pm$ S.E.)	<u>M. lucifugus</u>							
	EARLY				LATE			
	MALE		FEMALE		MALE		FEMALE	
	1987	1988	1987	1988	1987	1988	1987	1988
sample size	44	31	15	12	55	52	8	7
body mass (g)	6.48 (0.09)	6.43 (0.09)	6.22 (0.13)	6.76 (0.15)	6.94 (0.08)	7.51 (0.11)	7.22 (0.17)	7.67 (0.19)
wingspan (mm)	242.9 (0.001)	248.4 (0.002)	248.4 (0.002)	250.4 (0.001)	244.2 (0.001)	250.1 (0.001)	248.3 (0.003)	255.0 (0.002)
forearm length (mm)	37.6 (0.18)	37.4 (0.20)	38.2 (0.25)	37.6 (0.25)	37.2 (0.16)	37.3 (0.13)	37.6 (0.37)	37.6 (0.22)
tail length (mm)	37.8 (0.28)	37.0 (0.43)	38.3 (0.47)	38.3 (0.84)	36.5 (0.28)	37.7 (0.26)	36.8 (0.80)	38.6 (0.84)
wing loading (N/m <sup>2</sup> )	5.94 (0.07)	5.58 (0.07)	5.47 (0.11)	5.80 (0.13)	6.18 (0.06)	6.33 (0.09)	6.18 (0.22)	6.26 (0.10)
aspect ratio	5.53 (0.03)	5.46 (0.03)	5.55 (0.07)	5.50 (0.04)	5.44 (0.03)	5.38 (0.03)	5.37 (0.07)	5.43 (0.07)
wingtip shape index	2.03 (0.07)	1.53 (0.03)	1.91 (0.12)	1.74 (0.09)	1.72 (0.03)	1.49 (0.03)	1.72 (0.13)	1.44 (0.11)

(continued...)

Appendix 1 (continued)

variable (mean $\pm$ S.E.)	<u>M. volans</u>							
	EARLY				LATE			
	MALE		FEMALE		MALE		FEMALE	
	1987	1988	1987	1988	1987	1988	1987	1988
sample size	7	12	10	6	17	10	8	2
body mass (g)	6.64 (0.23)	6.81 (0.14)	7.32 (0.17)	6.95 (0.38)	6.93 (0.14)	6.46 (0.14)	7.44 (0.19)	7.20 (0.00)
wingspan (mm)	248.1 (0.002)	254.6 (0.002)	252.1 (0.002)	258.7 (0.003)	248.6 (0.001)	252.4 (0.002)	255.5 (0.002)	261.5 (0.004)
forearm length (mm)	38.6 (0.23)	38.1 (0.31)	39.6 (0.28)	39.4 (0.34)	38.1 (0.23)	37.9 (0.12)	39.2 (0.31)	38.8 (0.40)
tail length (mm)	41.8 (0.83)	42.8 (0.47)	43.2 (0.51)	44.0 (1.73)	42.6 (0.33)	43.3 (0.65)	42.4 (1.32)	44.0 (0.00)
wing loading (N/m <sup>2</sup> )	5.57 (0.19)	5.42 (0.13)	5.91 (0.19)	5.41 (0.23)	5.77 (0.10)	5.14 (0.12)	6.04 (0.13)	5.36 (0.11)
aspect ratio	5.28 (0.09)	5.26 (0.05)	5.23 (0.07)	5.34 (0.08)	5.27 (0.04)	5.17 (0.03)	5.43 (0.12)	5.19 (0.05)
wingtip shape index	1.69 (0.09)	1.63 (0.06)	1.91 (0.13)	2.01 (0.25)	1.82 (0.09)	1.68 (0.18)	1.97 (0.08)	1.44 (0.02)

Appendix 2. Descriptive statistics for wing loading, aspect ratio, and wingspan regressed against logMND (minimum negotiable distance). Probability values for CORR describe whether points in the regression are significantly correlated. Probability values for SLOPE describe whether the slope of the regression line is significantly different from a slope of one. Sexes are considered separately. Pregnant females were omitted from the analyses. Statistical significance is indicated by asterisks (ns = not significant; \*\*\* =  $p < 0.001$ ).

## WING LOADING

	<u>M. lucifugus</u>		<u>M. volans</u>	
	male	female	male	female
n	81	19	22	8
r <sup>2</sup>	0.14	0.004	0.015	0.010
corr	***	ns	ns	ns
slope	***	ns	ns	ns

## ASPECT RATIO

	<u>M. lucifugus</u>		<u>M. volans</u>	
	male	female	male	female
n	82	19	23	8
r <sup>2</sup>	0.003	0.002	0.021	0.105
corr	ns	ns	ns	ns
slope	ns	ns	ns	ns

(continued...)



## Appendix 2 (continued)

## WINGSPAN

	<u>M. lucifugus</u>		<u>M. volans</u>	
	male	female	male	female
n	82	19	23	8
r <sup>2</sup>	0.001	0.042	0.016	0.009
corr	ns	ns	ns	ns
slope	ns	ns	ns	ns