THE UNIVERSITY OF CALGARY

The Influence of Developmental Constraints on the Diet and Foraging Behaviour of Big Brown Bats (*Eptesicus fuscus*) in Southeastern Alberta.

by

.

Ian Michael Hamilton

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

APRIL, 1996

Ian Michael Hamilton 1996

THE UNIVERSITY OF CALGARY FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The Influence of Developmental Constraints on the Diet and Foraging Behaviour of Big Brown Bats (Eptesicus fuscus) in Southeastern Alberta" submitted by Ian M. Hamilton in partial fulfillment of the requirements for the degree of Master of Science.

Supervisor, Dr. R. M. R. Barclay, Biological Sciences

Dr. J. R. Post, Biological Sciences

Dr. H. I. Rosenberg, Biological Sciences

Dr. G. Pritchard, Biological Sciences

External Examiner, Dr. G. C. Teskey, Psychology

May 1996 X Date

ABSTRACT

Age-related changes in foraging may relate to such factors as morphology, learning, interference from conspecifics, and differential mortality risk among age classes. I examined the development of foraging in big brown bats (*Eptesicus fuscus*) in Medicine Hat, Alberta. Juveniles ate a wider variety and softer prey than adults, and took longer to handle beetles, the predominant dietary component. Wing morphology and echolocation call structure of juveniles and adults were the same. However, juveniles were lower in mass, resulting in lower wing loading. Maintenance of low body mass by juveniles may be a strategy for reducing flight costs, lowering the risks associated with foraging and the threshold prey density above which foraging remains profitable. The presence of conspecifics may influence the emergence and location of foraging juveniles. The implications of risk-averse behaviour of juveniles on the evolution of delayed maturation in bats are discussed.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Robert Barclay, for his advice, support, and patience over my years in the 'Bat Lab'. I also thank my supervisory committee: Robert Barclay, John Post, Gordon Pritchard, Herb Rosenberg, and Campbell Teskey, for comments regarding this project. Lawrence Harder provided invaluable statistical advice. Ed McCauley and Mike Vandermeulen provided assistance with the digitizer.

This research was supported by a grant from the Bat Conservation Society of Canada, and a National Science and Engineering Research Council operating grant to Robert Barclay. I was personally funded by a National Science and Engineering Research Council post-graduate scholarship, and a University of Calgary Teaching Assistantship.

I thank the Medicine Hat Board of Education, particularly Darrell MacKinnon, and the staff and students of Elm Street School and Montreal Street School for access to the roosts. The Gladwell family kindly took the 'bat people' into their home.

I am indebted to my field assistants for their hard work and dedication. Many thanks to Cam Aldridge, Shannon Guterson, Steven McNalley, Chuck Newyar, Danielle O'Grady, and Annie Yu. I also thank those who helped us in the field: Robert Barclay, Patrick Garcia, Matina Kalcounis, Carol Stefan, and Lisa Wilkinson.

My friends and colleagues in the department gave me their support, their time, and their advice, and I offer them many thanks. Finally, I thank my other close friends, my parents, and my sisters for their support and encouragement.

iv

To my parents, Louise and Bruce Hamilton

.

.

.

,

•

.

.

TABLE OF CONTENTS

.

Approval Page	ii
Abstract	iii
Acknowledgements	iv
Dedication	v
Table of Contents	vi
List of Tables	viii
List of Figures	xi
	_
CHAPTER ONE: GENERAL INTRODUCTION	1
	1
Study Species	5
Study Site	7
General Methods	9
CHADTED TWO, DIET	15
	15
	15
Methods	18
	18
Prey Handling	18
Fecal Analysis	18
Diet Composition	20
Insect Sampling	22
Results	25
Temperature	25
Prey Handling	25
Fecal Analysis	25
Diet Composition	28
Yearlings versus Adults	28
Juveniles versus Adults	34
Insect Sampling	38
Discussion	40
Diet	40
A ge related Differences in Diet	
Prov Selection	44
Conclusiona	47
	51
CHAPTER THREE: MORPHOLOGY AND PERCEPTION	53
Introduction	53
Methods	57
Echolocation Recording	57
Wing Tracings	52
ming machines	50

Body Mass	l
$\mathbf{Results} \dots \dots \dots \dots \dots \dots \dots \dots \dots $	2
Echolocation Call Structure	2
Wing Morphology 67	7
Body Mass	7
Discussion	Ĺ
Echolocation Call Structure 71	Ĺ
Wing Morphology 75	5
Body Mass	7
CHAPTER FOUR: FORAGING BEHAVIOUR	Ł
Introduction	l
Timing, Duration, and Location of Foraging	2
Methods	5
Radio-telemetry	5
Foraging Time	7
Emergence Time	3
Time Foraging Out of Range	3
Foraging Area	Ĵ
Light-tagging)
Results)
Changes in the Foraging Behaviour of Juvenile	-
Entesicus fuscus with Age)
Comparisons of Inveniles and Adults	, 5
Foraging Time	, ĭ
Emergence Time	ý
Foraging Location 99)
Discussion 102	, ,
Development of Flight and Foraging 102	, ,
Energence and Location of Foraging	. .
Invenile and Adult Big Brown Bats 104	1
Prev Density as a Constraint on Foraging Time 104	1
An Energetic Model of Bat Foraging	5
Foraging Times of Invenile and Adult Big Brown Bats	2
Conclusions 117	, 7
	,
CHAPTER FIVE: CONCLUSIONS 118	3
LITERATURE CITED 122	2
APPENDIX ONE: Age-predictive Equations for Pups in 1994 and 1995 135	5
APPENDIX TWO: Estimated Energetic Content of a Mealworm Beetle 136	5

LIST OF TABLES

e.,

,

•

.

.

Table 2.1. Number and mass of fecal pellets produced by adult and juvenile big brown bats. Bats were held in cloth bags for at least one hour after netting; fecal pellets produced in this time were collected. All juveniles were greater than 27 days old. Results of comparisons using Mann-Whitney U tests are reported. ns = not significant. * = $P < 0.05$
Table 2.2. Number of fecal samples from <i>E. fuscus</i> that were analysed in 1994 and 1995.
Table 2.3. Percent volume of insect taxa in the diet of yearling and adult big brown batsin spring 1994 and 1995. Values are means (SE)
Table 2.4. Percent volume of insect taxa in the diet of pre-weaning juvenile and lactating female big brown bats in 1994 and 1995. Values are means (SE)
Table 2.5. Percent volume of insect taxa in the diet of fully weaned juvenile and post-lactating female big brown bats in 1994 and 1995. Values are means (SE) 32
Table 2.6. Significant effects in MANOVAs of diet composition of big brown bats,explained by percentages of major insect taxa in the diet
Table 2.7. Dietary niche breadth of yearling and adult <i>E. fuscus</i> in 1994 and 1995. Results were analysed with ANOVA. Values are least squares means. $ns = not$ significant. $* = P < 0.05$ unless otherwise stated. The effect of temperature was not significant in either season
Table 2.8. Hardness of diet of juvenile or yearling and adult <i>E. fuscus</i> in 1994 and 1995. Yearlings and adults are compared in the spring; juveniles and adults are compared in the summer. Values are calculated using the hardness index of Freeman (1981). Results were analysed with ANOVA. Values reported are least squares means. ns = not significant. * = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.
Table 2.9. Catches from suction traps by trapping date in 1995. Percent of the total catch biomass is reported for each order. Insect catches are pooled for traps at ESS and along the South Saskatchewan River

Table 2.10. Regression statistics describing line of best fit for proportions of insect taxa by mass in feces of bats and suction trap samples. The y-intercept was fixed at the origin. P_{slope} value indicates whether the slope of the regression line is significantly different from zero. H ₀ tests whether the slope of the regression line is significantly different from one. ns = not significant, * = $P < 0.05$, ** = $P < 0.01$. *** = $P < 0.001$
Table 2.11. Summary of Chi-squared values describing the distribution of data points above and below the line of equivalence for percent insect taxa in fecal samples and suction trap samples. ns = not significant, $* = 0.01 < P < 0.05 \dots 42$
Table 3.1. Comparison of echolocation search call time-frequency structures between free flying adult <i>E. fuscus</i> ($n = 21$ calls) and hand-released bats ($n = 12$ calls). Minimum, maximum, and peak frequencies refer to the fundamental. An asterisk denotes significance at the 0.05 value. All values are least-squares means (SE)
Table 3.2. Comparison of the time-frequency structure of the fundamentals of echolocation search calls emitted by hand-released pre-weaning juvenile ($n = 30$ calls), post-weaning juvenile ($n = 23$ calls) and adult ($n = 34$ calls) <i>E. fuscus</i> . Least-squares means (SE) are reported
Table 3.3. Comparison of the time-frequency structure of the fundamentals of echolocation search calls emitted by hand-released <i>E. fuscus</i> in 1994 ($n = 54$ calls) and 1995 ($n = 33$ calls). Least-squares means (SE) are reported. Asterisks denote significance. ns = not significant. * = $P < 0.05$. ** = $P < 0.01$. *** = $P < 0.001$.
 Table 3.4: Lifting surface area (LSA) and wingspan of juvenile (n = 29) and adult (n = 29) bats. All values are least squares means (SE). Values within a column followed by the same letter are not significantly different. Type I error rate was determined using Sidak's multiplicative inequality
Table 3.5. Wing loading and aspect ratio of the wings of juvenile $(n = 29)$ and adult $(n = 29)$ <i>E. fuscus</i> . Statistical significance is denoted by asterisks. ns = not significant.*** = $P < 0.001$ 69
Table 3.6. Body mass (g) of a) post-weaning juvenile and post-lactating adult female E.fuscus in 1994 and 1995 and b) yearling and adult bats in early spring 1994 and1995. Forearm length was used as a covariate in the models. Means followed bythe same letter are not significantly different at a Type I error rate adjusted usingSidak's multiplicative inequality

- Table 4.1. Comparison of the slopes of foraging time versus ambient temperature for preweaning juveniles, post-weaning juveniles and adults. Data for foraging time were arcsin-square-root transformed. P_{slope} indicates whether the slope of the regression line is significantly different from zero. Slopes followed by the same letter are not significantly different. *** = $P < 0.001 \dots 96$

Table 4.3. Mean proportion of the total time tracked that bats were out of radio-telemetry
range in 1994 and 1995. Values followed by the same letter are not significantly
different

Table 4.4. Mean foraging areas of juvenile and adult *E. fuscus* in 1995 103

LIST OF FIGURES

Fig. 1.1. Map of the study area, including the location of the two maternity colonies at Montreal Street School (MSS) and Elm Street School (ESS), the location of insect traps (*) and the extent of the South Saskatchewan River along which most bats were followed
 Fig. 1.2. Diagrams of upper canines of adult <i>E. fuscus</i> showing tooth wear patterns used to describe relative age classes (the left canine is the same in all drawings and the right canine indicates tooth wear). a) Class 1 (+1), canines very sharp and pointed; b) Class 1 (0), canines no longer pinpoint sharp and starting to round off; c) Class 1 (-1), canines rounded at tips but not yet flattened; d) Class 2 (+1), tips of canines just flattened but are not worn at an angle; e) Class 2 (0), tips of canines flattened and beginning to wear on an angle; f) Class 2 (-1), canines worn flat on an angle, but greater than two-thirds of canine left; g) Class 3, canines well worn with less than two thirds of the tooth left (modified from Christian 1956 in Holroyd 1993)
Fig 2.1. Mean (\pm SE) ambient temperature at sunset at the Medicine Hat Airport in 1994 and 1995. Triangles represent temperatures in the spring. Squares represent temperatures in the summer. Ambient temperature at sunset differed significantly between summer 1994 and 1995 ($t = 4.34$, df = 57, P < 0.001)
Fig 2.2. Time required by juvenile and adult bats to manipulate and ingest a mealworm beetle (<i>Tenebrio</i> sp.). Each bat was fed two beetles. Squares indicate the handling time for the first beetle. Filled triangles indicate handling time for the second beetle. Values are means \pm SE
Fig. 2.3. Proportion of Diptera in the diet of juvenile big brown bats and in insect trap samples. If diet is exactly equal to availability, all points would lie along the 1:1 line. Significantly more points lie above the 1:1 line than expected (see text).
Fig. 3.1. Diagram depicting the definitions of wingspan (B) and lifting surface area (LSA) in this study (adapted from Saunders 1989)
Fig. 3.2. Mean (\pm SE) interval between echolocation calls emitted by hand-released pre-weaning juvenile ($n=24$), post-weaning ($n=12$) and adult ($n=18$) <i>E. fuscus</i> . 66

Fig. 4.1. Foraging time, as a proportion of the night spent foraging, for juvenile <i>E. fuscus</i> in 1994 and 1995. Foraging time increases with age of juveniles
Fig. 4.2. Emergence time, in minutes after sunset, for juvenile <i>E. fuscus</i> in 1994 and 1995. Juvenile bats emerged earlier with age
Fig 4.3. Changes in total time foraging, as a proportion of the time between sunset and sunrise, with ambient temperature. Data for post-weaning juveniles (solid squares) and adults (open squares) are plotted
Fig. 4.4. Emergence time (minutes after sunset) of pre-weaning juvenile (n = 53), post-weaning juvenile (n = 63), and adult (n = 68) E. fuscus in 1994 and 1995. Error bars are ± SE 100
Fig. 4.5. Decline in ambient temperature during the night for 5 randomly selected warm nights (filled squares) and 5 randomly selected cool nights (open squares). The least-squares regression equation for warm nights is $(468.54 - 107.61*ln(x))^{1/2}$, and for cool nights is $(0.01013 - 0.02064*x^{-1/2})^{-1}$
Fig 4.6. Hypothesized relationship between prey availability and foraging time. As prey

÷

CHAPTER 1. General Introduction

INTRODUCTION

The foraging strategies employed by an individual animal may change with age, as a consequence of changing constraints and requirements (Werner and Gilliam 1984, Marchetti and Price 1989). For example, shifts in foraging behaviour may result from differences in body size or morphology between juveniles and adults (Werner and Gilliam 1984, Marchetti and Price 1989), or from competitive exclusion of juveniles by adults (Van Horne 1982, Schneider 1984, Jaegar et al. 1995). Risk of mortality through such factors as predation or starvation may differ among age classes (Stamps 1983, Carey and Moore 1986, Utne and Aksnes 1994), as may the currencies upon which foraging decisions are based (Davies and Green 1976, Richardson and Verbeek 1987). Foraging strategies may also change with experience, as individuals become more proficient at searching for and handling prey (Orians 1969, Buckley and Buckley 1974, Richardson and Verbeek 1987, Sullivan 1988a, b, Marchetti and Price 1989, Weathers and Sullivan 1991, Yoerg 1994). Comparisons between the foraging behaviour of adults and juveniles illustrate the influence of developmental constraints on the evolution of behavioural and life-history strategies of animals.

Juvenile flying vertebrates do not become independent from their parents until skeletal size and form are similar to those of adults (Ricklefs 1979, Barclay 1994, Hughes *et al.* 1995). However, differences in foraging strategies and diet between

juvenile and adult birds are common (Marchetti and Price 1989). As foraging differences must result from differences other than body size, flying vertebrates are ideal for testing the importance of other developmental influences on foraging.

In a review of foraging by juvenile and adult birds, Marchetti and Price (1989) reported that the majority of studies invoked morphological and experiential constraints, rather than adaptive niche differences or juvenile-adult interactions, to explain dietary differences. Age-related differences in diet have also been described for bats (Anthony and Kunz 1977, Rolseth *et al.* 1994, C. I. Stefan pers. comm.). Although juvenile bats are not fully weaned until several weeks after the onset of flight (Tuttle and Stevenson 1983), juvenile insectivorous bats begin to forage during their first flights, and insect remains are found in the fecal pellets of even the youngest flying juveniles (Jones *et al.* 1995). Constraints in terms of morphology, including wing shape and size, echolocation call structure, and jaw morphology, and experience may be important factors influencing the observed differences in foraging behaviour and diet between juvenile and adult bats.

Wing morphology is an important influence on the foraging behaviour of bats and birds (Norberg and Rayner 1987). An animal with low wing loading (the ratio of body weight to wing area), flies optimally at a lower velocity than does an animal with high wing loading (Norberg and Rayner 1987). Animals with low wing loading can also fly more maneuverably than can animals with high wing loading (Norberg and Rayner 1987). Because the power required for flight scales directly with body mass and inversely with wing area (Norberg and Rayner 1987), the cost of flight, in energy required per unit time flying, is lower for animals with low wing loading than for those with higher wing loading. While numerous studies have examined wing loading of juvenile bats before the onset of flight (Davis 1969, Pagels and Jones 1974, Hoying 1983, Powers *et al.* 1991, Jones and Kokurewicz 1994), few studies have measured wing loading of flying juvenile bats, during the period when flight actually is achieved and perfected. Hughes *et al.* (1995) reported that captive juvenile *Pipistrellus pipistrellus* had significantly lower wing loading than did adults, but no previous study has examined the wing morphology of known-aged juvenile bats in the wild.

Insectivorous bats detect prey by using echolocation, the production of sounds which reflect off surfaces. The returning echoes are compared by the bat to those being produced, giving the bat an acoustic 'picture' of its environment (Fenton 1994). The use of an acoustic, self-emitted means of prey detection may have important consequences for the ecology of bats. Echolocation may constrain prey detection and prey selection by bats (Barclay and Brigham 1991, Barclay and Brigham 1994). Although echolocating bats can distinguish small objects (Kick 1982), a flying bat has little time between detection of a potential prey item and encountering it. There may thus not be enough time to distinguish among prey (Barclay and Brigham 1994), precluding active prey selection prior to encounter.

Few studies have examined the echolocation call structure of flying juvenile bats. Calls emitted by infant bats are initially of low frequency, and are primarily used for communication (Rasmuson and Barclay 1992, de Fanis and Jones 1995). Juvenile pipistrelles (*Pipistrellus pipistrellus*) increase the frequency of calls to adult values prior to the onset of flight (Jones *et al.* 1991). Juvenile little brown bats (*Myotis lucifugus*) and big brown bats (*Eptesicus fuscus*) emit calls of lower frequency than those of adults during their first flights, with calls becoming indistinguishable from those of adults within a week of flying (Buchler 1980, Moss 1988).

In various taxa, age-related changes in prey handling time are implicated in differences in diet and energy intake of juveniles and adults (Orians 1969, Holmes 1984, Richardson and Verbeek 1987, Sullivan 1988a, Weathers and Sullivan 1991). Some prey items of insectivorous bats may require complex handling. Captive adult big brown bats remove and discard the head and elytra of mealworm beetles (*Tenebrio* sp.) and the wings of moths prior to ingestion (pers. obs.). Inefficiency of juveniles at prey handling, through lack of experience or poorly developed jaw musculature, could result in reduced dietary efficiency (Barclay *et al.* 1991) and profitability of ingesting these items (Stephens and Krebs 1986). No previous studies have investigated the prey handling abilities of juvenile and adult bats.

Inefficiency at foraging by juveniles is implicated in the evolution of delayed breeding in birds (Lack 1968, MacLean 1986, Heinsohn 1991), and may be an important factor influencing the life history strategies of bats. Juvenile bats in temperate regions have higher mortality than do adults over the period from the initiation of flight through hibernation (Racey 1982). Juvenile female bats are often not reproductive in their first autumn, possibly because they fail to achieve threshold body mass for reproduction over their first summer (Racey 1982, Speakman and Racey 1986). Age at maturity and maintenance of female reproductive activity in mammals depend on the ratio of fat to lean mass (Frisch 1984). Delayed maturity may reflect the need of individuals with low fat reserves to allocate energy to maintenance and survival during periods of low food availability (Burnett and Kunz 1982).

The purpose of my study was to identify how the diet and foraging behaviour of insectivorous bats change from the onset of flight through to adulthood, and to investigate how developmental constraints influence the foraging strategies of insectivorous bats. I examined the diet of adults and juveniles, and compared amount, composition, and diversity of prey items. I compared juvenile and adult bats in terms of flight morphology and echolocation call structure. I characterized the development of flight and foraging by juvenile big brown bats, and compared activity patterns of adults and juveniles. Finally, I considered the implications of developmental constraints on foraging on variation in the life-history strategies of bats.

STUDY SPECIES

I examined the foraging strategies of big brown bats (*E. fuscus*). *Eptesicus fuscus* is a common hibernating bat found throughout most of North and Central America (Barbour and Davis 1969, Kurta and Baker 1990). Adults typically weigh 16-24 g (Barbour and Davis 1969). *Eptesicus fuscus* has been described as a generalist forager (Whitaker 1972), although the diet is commonly dominated by beetles (Brigham 1990, Brigham and Saunders 1990, Kurta and Baker 1990, Wilkinson 1995). Tooth morphology of big brown bats is consistent with the consumption of hard prey items, such as beetles (Freeman 1981).

Little is known about the mating system of *E. fuscus*. Individuals probably mate in the fall prior to hibernation (Phillips 1966). Mating by other small hibernating insectivorous bats appears to be random, with little evidence of mate choice or defence of reproductive investment (Thomas *et al.* 1979). Some male *M. lucifugus* do, however, appear to have higher reproductive success than do others, possibly by mating with clusters of hibernating females over winter (M. Watt pers. comm.). Sperm is stored in the female's reproductive tract overwinter, with fertilization occurring in the spring (Fenton 1984a). Hibernation sites for bats are known from central Alberta (Schowalter and Gunson 1979), but it is not known where big brown bats from southern Alberta mate and hibernate.

In summer, female *E. fuscus* congregate in maternity colonies of tens to hundreds of individuals, which are often located in old buildings (Barbour and Davis 1969), or in trees (Vonhof 1995, Kalcounis 1995). The largest reported colony of *E. fuscus* was from Medicine Hat, Alberta, with 850 individuals (Schowalter and Gunson 1979). Male bats are usually solitary.

Pups are born in early summer. Bats from southern areas of North America give birth earlier than do those from northern areas (Kunz 1974). Individuals in eastern North America usually give birth to twins (Burnett and Kunz 1982), while bats in western North America usually have a single offspring (Holroyd 1993). Juveniles begin to fly at between 18 to 35 days (Kurta and Baker 1990). After juveniles are

weaned, several weeks after the initiation of flight, females and juveniles begin to leave the maternity colonies (Hamilton and Barclay 1994).

Like other bats, *E. fuscus* is long-lived relative to other small mammals (Read and Harvey 1989). The longest reported lifespan for a big brown bat is 19 years (Paradiso and Greenhall 1967). One bat at my study site was at least 19 years old. This bat, a female, was banded as an adult in 1976 and recaptured in 1994.

STUDY SITE

I conducted the study in and around the city of Medicine Hat (50°02' N, 110°40' W). Medicine Hat is located in southeastern Alberta, in the valley of the South Saskatchewan River (Fig. 1.1) and is surrounded by mixed-grass prairie and agricultural land. Riparian cottonwood (*Populus* sp.) forest and urban parkland line the banks of the South Saskatchewan River and its tributaries, Ross Creek, Bullhead Creek, and Seven Persons Creek.

Bats from two maternity colonies were included in this study. These colonies were located in the attics of two 80 to 90 year-old schoolhouses in the North Flats residential area of Medicine Hat. The two colonies were about 1 km apart, and 1 km from the South Saskatchewan River. My primary study site was at Elm Street School (ESS). ESS was occupied by at least 108 adult bats in 1994, as estimated from exit counts prior to the first flights of juveniles. Similar numbers were observed in 1995. The other colony, at Montreal Street School (MSS), was estimated to be slightly



Fig. 1.1. Map of the study area, including the location of the two maternity colonies at Montreal Street School (MSS) and Elm Street School (ESS), the location of insect traps (*) and the extent of the South Saskatchewan River along which most bats were followed.

smaller, based on the number of pups captured. A large number of potential exits at MSS precluded exit counts there.

Both colonies were composed largely of adult females and their young, although a small number of males were also resident at each colony. Males show less site fidelity than females, often roosting in houses or cliffs (Hamilton and Barclay 1994). Reproductive females roosted almost exclusively in the attics and within the walls of the two schoolhouses. In six years of netting at the Medicine Hat colonies, only two bats, one adult male and one juvenile female, have ever been captured at the colony other than where they were originally banded (Holroyd 1993, Wilkinson 1995, pers. obs.).

GENERAL METHODS

The study was conducted from 9 May through 15 August 1994 and from 10 May through 18 August 1995. Bats were also netted on 20 April and 31 September 1994. I refer to the period from the beginning of the study season until the birth of the first pup, roughly mid-June, as the 'spring' season, and the period from when the first juveniles were captured flying outside the roost in mid-July until the end of the study season as the 'summer' season.

I also obtained capture records for the summers of 1990 through 1994 (S. L. Holroyd unpublished data, L. C. Wilkinson unpublished data). Some of the capture records from 1990 and 1991 are from a third colony in Foremost, Alberta (49°28'N,

111°26′W).

To capture bats, I set monofilament mist nets approximately 7 m high near roost exits. Bats were removed from the nets, and held in cloth bags for at least one hour. Any feces produced in that time were collected. Pups were removed from the colonies, while their mothers were foraging, measured, banded (as per adults) and returned to the roost.

I weighed bats to 0.05 g using a C151 Ohaus portable electronic balance. I measured the length of the right forearm three times to 0.05 mm using vernier calipers, and averaged these values. Bats were banded on the forearm with split-ring coloured plastic bands. Each bat was given a unique combination of band number, colour, and position, depending on sex, year of capture, and age.

I assessed reproductive condition of females. Pregnancy was detected through gentle palpation of the abdomen. Later pregnancy was also detected through pronounced swelling of the abdomen. Lactation was indicated by expression of milk or noticeable swelling and bare patches around teats. Regrowth of fur around teats indicated post-lactation (Racey 1982, Holroyd 1993, Wilkinson 1995).

To obtain a general index of age for adults, I noted tooth wear, using the criteria of Christian (1956) and Holroyd (1993). Tooth wear was assessed by subjective classification of the upper canines (Fig. 1.2). If both canines were not equally worn, I used the least worn canine for the assessment. Three general categories of tooth wear were recognized, with class 1 being the least worn, and representing the youngest bats, and class 3 being the most worn, and representing the



Fig. 1.2. Diagrams of upper canines of adult E. fuscus showing tooth wear patterns used to describe relative age classes (the left canine is the same in all drawings and the right canine indicates tooth wear). a) Class 1 (+1), canines very sharp and pointed; b) Class 1 (0), canines no longer pinpoint sharp and starting to round off; c) Class 1 (-1), canines rounded at tips but not yet flattened; d) Class 2 (+1), tips of canines just flattened but are not worn at an angle; e) Class 2 (0), tips of canines flattened and beginning to wear on an angle; f) Class 2 (-1), canines worn flat on an angle, but greater than two-thirds of canine left; g) Class 3, canines well worn with less than two thirds of the tooth left (modified from Christian 1956 in Holroyd 1993).

oldest bats. Classes 1 and 2 were further subdivided into 3 subclasses: +1, 0, and -1, with +1 being the sharpest, and -1 the least sharp.

For the purposes of this study, bats were categorized into four major age classes: 1) pups, pre-volant young-of-the-year, 2) juveniles, young-of-the-year capable of sustained flight, 3) yearlings, bats that had survived their first winter, and 4) adults, those that had survived two winters or more. Unbanded bats captured in nets were aged according to ossification of the epiphyseal cartilages of the fourth metacarpalphalangeal joint of the right wing, and by relative tooth wear. The metacarpalphalangeal gap was measured using an ocular micrometer on an M-5 Wild dissecting microscope with base lighting at 6x magnification. Complete ossification of this joint indicates yearling or adult status (Kunz and Anthony 1982). Unbanded adult bats with sharp teeth (tooth class 1(+1)) were considered to be yearlings (Holroyd 1993). Unbanded adults with a tooth class of 2(+1) or greater were considered to be at least two years old (R.M.R. Barclay, unpublished data). Age of banded bats was determined based on their age when banded and the time since banding.

To examine development of pups and juveniles, I estimated their age in days since birth, by comparing forearm length and ossification of the metacarpal-phalangeal joint with those of known-aged individuals for each sex and year (Kunz and Anthony 1982, Holroyd 1993). Pups captured with an umbilicus were assumed to be less than 24 h old, and are referred to hereafter as 'known-age' individuals (Kunz and Anthony 1982, Holroyd 1993). On two occasions in 1995, pups that were known to be at least 3 days old were captured with an umbilicus at the MSS colony. On no other occasion over the two years was the same pup captured with an umbilicus on more than one night, and numerous pups that were similar in size and appearance to newborns (eyes closed, no fur) were captured with the umbilicus already having fallen off. Thus, in most cases, pups captured with an umbilicus are probably less than 24 h old.

I used known-age pups to generate age-predictive equations (Appendix 1). Age was regressed on forearm length and total gap width during periods of linear growth. Width of the epiphyseal gap decreases linearly from about 10 days after birth until several weeks after the initiation of flight (Kunz and Anthony 1982). Forearm length increases linearly from birth until shortly before the initiation of flight (Kunz and Anthony 1982, Holroyd 1993). The equations resulting from these regressions were used to estimate the ages of unknown-age pups on the first day they were captured. Because age-predictive equations based on forearm growth had less scatter than did those based on epiphyseal gap ossification, I used the forearm growth equations to age bats up to the point where forearm length began to level off, after which the epiphyseal gap equations were used.

I observed the interaction of adult females and pups at the roost in order to determine mother-pup pairs. Juvenile *E. fuscus* produce an isolation call unique to each individual (Rasmuson and Barclay 1992), and these are used by adult females to identify and locate their offspring. If an adult female allowed a pup to suckle, and flew away with the pup attached, I considered that pup to be hers. One pup in 1995 was picked up by at least two different adults, and one of those adults subsequently picked up another pup, so results from inferred mother-pup pairs should be taken with

care. Other mother-pup pairs were obtained through the capture of adults, with pups attached, in the roosts.

Age at weaning is difficult to determine. Traces of milk were not detected in fecal samples, and juveniles began to eat insects immediately upon starting to fly. Previous studies on *E. fuscus* have estimated age at weaning to be from 32 to 40 days (Kunz 1974). Based on the lactational status of mothers of known-age pups at the Medicine Hat colonies from 1990 through 1995, I estimated that juveniles were fully weaned by 35 days after birth. Thus, as an estimate of degree of independence of juveniles from their mothers, I considered those juveniles 35 days old or older to be fully weaned. Unless otherwise stated, I compared fully weaned juveniles with post-lactating females, and pre-weaning, but volant juveniles with lactating females.

CHAPTER 2. Diet

INTRODUCTION

Ultimately, successful foraging results in capture and ingestion of prey. Thus, examination of the diet of a predator provides indirect information about its foraging behaviour. Dietary analysis can also provide information about energy and nutritional intake, and allow construction of energy and nutrient budgets. Although optimal foraging models do not specifically predict the diet of a predator (Stephens and Krebs 1986), they may be useful in predicting the range of items included in the diet.

An optimally foraging predator should forage according to a decision rule, such as maximization of the net rate of intake of some currency, given that its options are constrained by numerous intrinsic and extrinsic factors (Stephens and Krebs 1986). Assuming genetically-based variability in foraging strategies, the strategy providing maximum net returns within the realm of feasible options should be favoured by natural selection. The basic optimal prey choice model predicts that a forager should maximize its average rate of net energy intake (Stephens and Krebs 1986). A forager should choose the most profitable prey item (that which maximizes net energy intake while minimizing pursuit and handling time) whenever encountered (Stephens and Krebs 1986). The decision whether to eat a less profitable item depends on its profitability and the abundance of more profitable items (Stephens and Krebs 1986).

Foraging decisions may be further influenced by a number of factors.

Morphology constrains what prey may be eaten (Freeman 1981). The currency on which foraging decisions are based may not be energy, but rather some nutrient or avoidance of a toxin (Stephens and Krebs 1986, Wilkinson 1995). Foraging decisions may be influenced by risk of predation or starvation, or by the state of the forager, such as hunger or experience (Stephens and Krebs 1986). Foraging strategies are also influenced by the ability of the predator to distinguish among potential prey items, and the cost of making that decision (Gould 1974, Stephens and Krebs 1986).

Skull morphology may constrain prey choice of bats (Freeman 1981). Bats with robust skulls eat harder prey items, such as beetles, than do bats with more gracile skulls. This correlation does not imply that bats with robust skulls are specialized as beetle strategists, but rather that they are capable of eating beetles as well as softer prey, while bats with more gracile skulls are restricted to softer prey (Freeman 1981).

Differences in the ability to handle prey are implicated in the different diets of juvenile and adult birds. Yearling Northwestern crows (*Corvus caurinus*) take more time to find and handle Japanese littleneck clams (*Venerupis japonica*) than do adults, and select a broader range of prey sizes (Richardson and Verbeek 1987). On the other hand, juvenile Eurasian dippers (*Cinclus cinclus*) reject prey items included in the diet of adults because of handling constraints (Yoerg 1994). Juvenile dippers drop a substantial proportion of medium and large prey, while adults never drop prey (Yoerg 1994). Similarly, recently independent juvenile yellow-eyed juncos (*Junco phaeonotus*) select small prey items, while older juveniles and adults show no

preference between small and large prey items (Sullivan 1988b). Several studies have reported a preference for slow-moving or stationary prey items by juvenile birds (Walton 1979, Stevens 1985, Breitwisch *et al.* 1987).

Juvenile bats may differ from adults in their ability to handle some prey items. The bones of juveniles have not fully ossified at the onset of flight and foraging, and therefore, the skulls of young bats may be less robust than are those of adults. As well, juveniles are less experienced at capturing and handling prey, and may spend more time handling novel or complicated prey items. I therefore predicted that juveniles would require more time to handle beetles, the most common item in the diet of *E. fuscus* in southern Alberta (Brigham and Saunders 1990, Wilkinson 1995). If juveniles require more time to handle beetles than do adults, beetles will be less profitable for juveniles than for adults.

If the profitabilities of prey items differ between juveniles and adults, I predicted that their diets should differ. These differences may be manifested in two ways. Adults and juveniles may differ in whether they select prey. If prey handling efficiency improves with age, adults should be more willing to pay the cost of prey discrimination than are juveniles (Gould 1974, Stephens and Krebs 1986). Thus, juveniles should eat a wide variety of prey items, while adults should select one or two prey types. Adults and juveniles may also differ in what prey is selected, if they do select prey. Juveniles may reject items that require a long time for pursuit or handling (Yoerg 1994).

METHODS

Temperature

Insect emergence and activity are correlated with ambient temperature (Sweeney and Schnack 1977, Wartinbee 1979, Zalom *et al.* 1980, Ward and Stanford 1982). As an estimate of yearly differences in insect availability, I used t-tests to compare the ambient temperature at sunset in spring and summer in 1994 and 1995. Data were obtained from hourly weather observations collected by Environment Canada at the Medicine Hat Airport, 3-4 km south of the maternity colonies. Ambient temperature at sunset was estimated by using the first reported temperature after sunset.

Prey Handling

In 1995, I hand fed juvenile male and adult male and female bats mealworm beetles (*Tenebrio molitor*). Mealworm beetles are similar in size and shape to beetles found in the diet of adults (pers. obs.). Two beetles were fed to each bat. The time from capture through ingestion was measured. Only the time actively spent manipulating the prey was recorded. Handling times for the first and second beetle were separately compared between age classes with t-tests.

Fecal Analysis

Dietary analysis can be performed through direct observation of foraging, or

analysis of stomach or fecal contents (Whitaker 1988). Direct observation of foraging by bats is difficult except under unusual circumstances, such as bats foraging under streetlights. Analysis of stomach or fecal contents is a more widely applicable technique. As bats are long-lived and have only one or two offspring a year, sacrificing individuals for stomach analysis could impact population size and structure. Thus, fecal analysis is the most widely used method of examining the diet of insectivorous bats.

Although insects may differ in digestibility and residence time in the digestive tract, fecal analysis is an effective and accurate method of estimating diet composition (Kunz and Whitaker 1983, Whitaker 1988, but see Rabinowitz and Tuttle 1982, Robinson and Stebbings 1993). Results may, however, be biased against softer-bodied prey such as mayflies (Rabinowitz and Tuttle 1982).

I collected feces from mist-netted bats returning from foraging. Feces were air dried for at least five days, and stored for later analysis. To estimate success at foraging, I measured fecal production by juvenile and adult bats in 1995. I compared the number of pellets produced by juvenile and adult bats caught as they returned to the colonies from foraging. I also compared the average mass per fecal pellet between juvenile and adult bats in August 1995, thus allowing me to calculate the mass of fecal material produced by each individual.

Immediately prior to fecal analysis, I moistened pellets with 70% ethanol, and teased them apart under an M5-Wild dissecting microscope. Up to five pellets were analyzed per bat. Large pellets were subdivided, so that all pellets or portions thereof

in a sample were roughly equal in size.

I visually estimated (to within 5 %) the proportion of each pellet or portion thereof that was composed of each insect order. Trace amounts were given a value of 1%. Proportions were estimated as the proportion of total insect remains, identifiable or not. Other ingested items, such as mist net or cloth fibres, were excluded.

Proportions were pooled across pellets for each bat. To reduce possible bias in estimations, I performed all of the fecal analysis for a year at one time. I randomly assigned numbers to each sample, and referred to each sample by its number only. Thus, when analysing a sample, I did not know whether it came from a juvenile, yearling, or adult bat.

Diet Composition

I compared the proportions of the most common taxa in the diet between age classes using MANOVA. Only taxa constituting over 10% of the diet were used in the analysis. Data were arcsine-square-root transformed (Zar 1984). I compared diet composition between age classes, and between lactation and postlactation. Data from 1994 and 1995, and from spring and summer, were analyzed separately, because different insect orders were prevalent in the diet of bats in each period.

Niche breadth indices quantitatively measure degree of resource specialization (Krebs 1989). I calculated dietary niche breadth of juvenile and adult bats using the standardized Levins' measure, B_A (Levins 1968, Hurlbert 1978; Equations 2.1 and 2.2).

$$(Equation 2.1) B = \frac{1}{\sum p_i^2}$$

where B = Levins' measure of niche breadth

 p_i = fraction of items in the diet that are of food category j

$$(Equation 2.2) \qquad \qquad B_A = \frac{B-1}{n-1}$$

where n = number of possible resource states (the number of food categories in the diet of all bats)

In calculating Levins' standardized index, I used the proportion of the identifiable component of the diet that was of each food category. Levins' index is greatest when the diet is evenly distributed among food categories. I compared the dietary niche breadth of adults and juveniles with a three-factor ANOVA. The model included terms for age class, season (lactation or postlactation) and year, and the interactions among these terms. Non-significant interactions were removed sequentially from the model. I also compared the diet of yearlings and adults in 1994 with a two-factor ANOVA, with age class and year as main effects.

I calculated average hardness of prey using the hardness index of Freeman (1981). This index assigns a value from 1 to 5 to prey items based on the strength and plasticity of an arthropod's exoskeleton. Items with a value of 1 are softest and most plastic, while items with a value of 5 are hardest and most brittle. Taxa included in category 1 are Ephemeroptera, Isoptera, Trichoptera, Plecoptera, Neuroptera,

Mecoptera, and Diptera. Category 2 includes Araneida, Odonata, Homoptera, and Lepidoptera. Category 3 includes Orthoptera and Scorpionida. Category 4 includes Hemiptera, Hymenoptera, Chilopoda, Diplopoda and Aeschnoidea. Category 5 includes only the Coleoptera. Values were assigned to each item in the diet, weighted by its prevalence in the diet. The hardness value was then summed for each bat. Results should be interpreted with caution, because several different combinations may produce the same hardness index. For example, the calculated hardness indices for a bat eating 50% Diptera and 50% Coleoptera and a bat eating 100% Scorpionida would be the same. However, the morphological requirements for the two diets may be quite different. I compared the hardness of diets of juvenile and adult bats in 1994 and 1995 with a two-factor ANOVA. I also compared the hardness of the diet of yearlings and adults in 1994 and 1995 with ANOVA.

Insect Sampling

I sampled insects with suction traps from 12 July through 15 August 1995. Traps were set every four days, weather conditions permitting. Traps were set approximately 5 m above the ground, either on a tripod or suspended from trees. Two traps were set on each trapping night, one at one of two locations in the schoolyard of Elm Street School, and the other at one of three locations on the banks of the South Saskatchewan River (see Fig. 1.1). Traps were set after sunset, but before any bats had emerged, and were taken down four hours later. To reduce bias in sampling, the traps were not lighted. Insects collected were preserved in ethanol. I identified insects to Order, and measured body length with an M5-Wild dissecting microscope.

To estimate the dry mass of captured insects, I used the length-mass conversion employed by Rogers *et al.* (1976):

(Equation 2.3) $W = 0.0305 L^{2.62}$

where W = mass in mg and L = length in mm.

To test whether bats feed selectively, I compared the composition of trap catches and fecal samples. I did not trap insects on the nights that bats were captured, so for each bat, insect samples from the nearest trapping date before and after capture were pooled and used in comparisons.

If bats fed non-selectively, then the proportions in trap and fecal samples should be equal. A regression of fecal sample proportion on trap sample proportion should therefore result in a slope significantly greater than zero, and not significantly different from one. For each order of insect, I fit a regression line, fixed at the origin, through the proportions from fecal and insect trap samples. The line was fitted through the origin to de-emphasize the effect of insects that appeared in the diet, but were rarely captured in traps (Saunders 1989). The distribution of points above and below the line of equivalence should be equal if bats fed non-selectively. Therefore, I subtracted fecal proportions from trap proportions, and compared the distribution of positive and negative values with a 50:50 ratio. I excluded insect taxa that composed a major proportion of the diet, but were never captured in traps, from this analysis.

RESULTS

Temperature

Ambient temperature at sunset was significantly higher in summer 1994 than during the same period in 1995 (Fig 2.1; t = 4.34, df = 57, P < 0.001). Temperatures did not differ significantly between the springs of 1994 and 1995 (Fig 2.2; t = -0.84, df = 70, P > 0.4).

Prey Handling

I fed beetles to 11 juvenile male and 7 adult *E. fuscus*. Two of the adults rejected a second attempt at feeding. Four juveniles and one adult rejected any attempts at feeding. Juveniles required more time to handle beetles than did adults (Fig. 2.2). This difference was significant for both the first and second feeding attempts (t-test for unequal variances; first: t = 3.76, df = 11.3, P < 0.01; second: t = 5.40, df = 12.9, P < 0.001). I conducted a paired t-test on the sixteen bats for which I had both first and second feedings. Although handling time for the second feeding was generally shorter than for the first feeding, this difference was not significant (t = 1.69, df = 15, P > 0.1).

Fecal Analysis

The mass of fecal material produced by a bat is an index of prey capture. The number of fecal pellets produced did not follow a normal distribution, so I compared


Fig 2.1. Mean (\pm SE) ambient temperature at subset at the Medicine Hat Airport in 1994 and 1995. Triangles represent temperatures in the spring. Squares represent temperatures in the summer. Ambient temperature at sunset differed significantly between summer 1994 and 1995 (t = 4.34, df = 57, P < 0.001).



Fig 2.2. Time required by juvenile and adult bats to manipulate and ingest a mealworm beetle (*Tenebrio* sp.). Each bat was fed two beetles. Squares indicate the handling time for the first beetle. Triangles indicate handling time for the second beetle. Values are means \pm SE.

fecal production by juvenile and adult bats in 1995 with a Mann-Whitney U test. I compared the number and mass of pellets produced by juveniles 28 days old or older with those produced by adults (Table 2.1). Twenty-eight days is the age when juveniles, on average, began to forage along the river (see Chapter 4). Juveniles produced significantly fewer pellets than did adults, while the average mass per pellet for juvenile and adult bats was similar. The total mass of fecal samples (mean mass of pellets * number of pellets) was significantly lower for juveniles than for adults (Table 2.1).

I analysed a total of 181 fecal samples from 1994 and 1995 (Table 2.2), and identified nine orders of insects in the fecal pellets of juvenile and adult big brown bats in 1994 and 1995 (Tables 2.3, 2.4, 2.5). Mites (Arachnida: Acari), fur, mist net fibres and fibres from the cloth bags used for holding bats, were also found in fecal pellets.

Diet Composition

Yearlings versus Adults

In 1994, Coleoptera, Diptera, and Trichoptera comprised greater than 10% of the diet of at least one age class. The proportions of these taxa in the diet did not differ between yearlings and adults (Wilks' Lambda = 0.981, F = 0.08, df = 3, 13, P =0.97). In 1995, only Coleoptera and Diptera made up greater than 10% of the diet of at least one age class. Yearlings and adults did not differ in the proportion of Table 2.1. Number and mass of fecal pellets produced by adult and juvenile big brown bats. Bats were held in cloth bags for at least one hour after netting; fecal pellets produced in this time were collected. All juveniles were greater than 27 days old. Results of comparisons using Mann-Whitney U tests are reported. ns = not significant. * = P < 0.05.

.

•

	Juveniles		Adults		
	median (range)	n	median (range)	n	Р
Number of pellets	6 (1-20)	31	10 (1-27)	19	*
Mass/pellet (gx10 ⁻³)	6.3 (3.6-16.2)	10	5.1 (3.9-10.4)	8	ns
Total mass (gx10 ⁻²)	4.2 (0.7-13.9)	31	5.6 (0.6-15.2)	19	*

Year	Season	Age	Period	п
	<u></u>			
1994	Spring	Yearling		4
		Adult		13
	Summer	Juvenile	Pre-Weaning	30
			Post-Weaning	15
		Adult	Lactating	19
			Post-Lactating	15
1995	Spring	Yearling		9
	1 0	Adult		14
	Summer	Juvenile	Pre-Weaning	21
			Post-Weaning	21
		Adult	Lactating	13
			Post-Lactating	7

,

Table 2.2. Number of fecal samples from *E. fuscus* that were analysed in 1994 and 1995.

,

,

-

.

.

	199	94	199	95
Order	Yearlings $(n = 4)$	Adults (n=13)	Yearlings (n=9)	Adults (n=14)
Coleoptera	63.63 (9.73)	53.66 (8.48)	70.70 (10.47)	90.76 (2.70)
Hemiptera	13.41 (5.42)	3.93 (1.54)	4.64 (1.67)	5.08 (1.55)
Lepidoptera	1.13 (1.08)	7.01 (2.90)	0.83 (0.52)	0.26 (0.16)
Trichoptera	7.04 (3.86)	12.04 (4.83)	6.70 (4.44)	0.07 (0.07)
Diptera ⁻	14.19 (5.92)	20.75 (6.28)	16.78 (11.17)	3.21 (1.39)
Neuroptera	0	3.41 (3.06)	0.02 (0.02)	0
Ephemeroptera	0	0.08 (0.08)	0	0
Hymenoptera	0	1.78 (0.76)	0.22 (0.22)	0.62 (0.47)

•

.

Table 2.3. Percent volume of insect taxa in the diet of yearling and adult big brown bats in spring 1994 and 1995. Values are means (SE).

.

٠

	199	4	1995	;
Order	Juveniles (n=30)	Adults (n=19)	Juveniles (n=21)	Adults (n=13)
Coleoptera	41.54 (4.75)	73.40 (5.81)	53.89 (7.08)	65.35 (10.11)
Hemiptera	30.09 (4.03)	7.45 (1.71)	2.18 (1.34)	4.21 (1.61)
Lepidoptera	13.66 (2.70)	10.77 (4.16)	9.43 (3.58)	12.56 (8.02)
Trichoptera	7.57 (2.18)	2.70 (1.08)	9.71 (3.41)	3.04 (2.00)
Diptera	6.21 (1.54)	3.52 (1.08)	18.79 (5.65)	9.57 (5.79)
Neuroptera	0.03 (0.03)	0.11 (0.11)	4.28 (0.27)	0.08 (0.08)
Ephemeroptera	0	0.12 (0.12)	0	0
Hymenoptera	0.67 (0.27)	0.78 (0.64)	4.38 (3.14)	0.77 (0.77)

•

.

.

Table 2.4. Percent volume of insect taxa in the diet of pre-weaning juvenile and lactating female big brown bats in 1994 and 1995. Values are means (SE)

	1994	1	199:	5
Order	Juveniles (n=15)	Adults (n=15)	Juveniles (n=21)	Adults (n=7)
Coleoptera	63.39 (5.97)	74.02 (3.25)	23.84 (5.39)	38.20 (13.57)
Hemiptera	19.85 (4.07)	14.91 (2.87)	9.94 (3.87)	8.02 (2.79)
Lepidoptera	6.20 (2.22)	6.84 (2.80)	25.38 (4.93)	34.54 (13.25)
Trichoptera	1.79 (1.27)	2.86 (0.14)	3.19 (1.18)	1.74 (0.85)
Diptera	7.48 (3.15)	3.08 (0.89)	34.22 (5.38)	16.21 (8.37)
Neuroptera	0.22 (0.22)	0	0.49 (0.36)	0.32 (0.22)
Ephemeroptera	0.40 (0.40)	0	0.25 (0.24)	0
Hymenoptera	0.20 (0.20)	0.43 (0.34)	0.59 (0.33)	0.42 (0.42)
Homoptera	0	0	0	0.20 (0.20)

•

,

Table 2.5.	Percent volume	of insect taxa	in the diet	of fully	weaned juvenile	and post-
lac	tating female big	, brown bats ir	n 1994 and	1995.	Values are means	(SE)

Coleoptera and Diptera in their diet in 1995 (Wilks' Lambda = 0.804, F = 2.44, df = 2, 20, P = 0.11)

The dietary niche breadths of yearling and adult *E. fuscus* were not significantly different (Table 2.7), but bats ate a greater diversity of items in 1994 than in 1995. The effect of temperature on niche breadth was not significant. Yearlings and adults also ate prey of similar hardness, but ate softer prey in 1994 than in 1995 (Table 2.8).

Juveniles versus Adults

Coleoptera, Hemiptera, and Lepidoptera each comprised greater than 10% of the diet of at least one age class in the summer of 1994. I compared the proportions of these taxa in the diets of juveniles and adults. There were significant differences in diet between age classes (Wilks' Lambda = 0.783, F = 6.20, df = 3, 67, P < 0.001). Juvenile *E. fuscus* ate more Hemiptera and less Coleoptera than did adults (Table 2.6). There were no significant differences between the diet of bats during lactation and post-lactation (Wilks' Lambda = 0.911, F = 2.19, df = 3, 67, P = 0.10).

In 1995, Coleoptera, Lepidoptera, and Diptera were predominant (> 10% of one age class) in the diet of big browns. There was an overall significant difference in the diet between lactation and post-lactation (Wilks' Lambda = 0.771, F = 5.65, df = 3, 57, P < 0.002), but there were no significant differences between age classes (Wilks' Lambda = 0.923, F = 1.59, df = 3, 57, P = 0.20). Bats ate more Coleoptera and less Lepidoptera during lactation than during postlactation (Table 2.6).

Co	ontrast	Mean Pe	rcent Insect Taxa	
		Coleoptera	Hemiptera	Lepidoptera
Summer 1994	juvenile	51.26°*	23.65ª	6.53ª
	adult	78.72 ^b	8.08 ^b	3.52ª
		Coleoptera	Lepidoptera	Diptera
Summer 1995	lactation	60.55ª	5.93ª	9.59ª
	post-lact	26.20 ^b	24.43 ^b	22.26ª

Table	2.6.	Signifi	cant	effects	in Ma	ANOV	As of	diet	compositio	n of	big	brown	bats,
	exp	olained	by p	percenta	ges of	major	insec	t taxa	a in the die	t.			

* Means within a column and within a contrast followed by the same letter are not significantly different

•

.

Table 2.7. Dietary niche breadth of yearling and adult *E. fuscus* in 1994 and 1995. Results were analysed with ANOVA. Values are least squares means. ns = not significant. * = P < 0.05 unless otherwise stated. The effect of temperature was not significant in either season.

	Juveniles /	Yearlings	Ad	ults	
	Mean	SE	Mean	SE	Р
Spring	0.091	0.017	0.069	0.011	ns
Summer	0.110	0.009	0.056	0.009	*
			<u></u>		
<u> </u>	1994	ļ	19	95	<u></u>
	Mean	SE	Mean	SE	Р
Spring	0.125	0.015	0.035	0.012	*
Summer Lactation Post-lactation	0.094 ^{a§f} 0.069ª	0.011 0.013	0.054ª 0.100 ^b	0.01 ⁻ 1 0.015	* ^f ns

Standard Levins' Index

§ Means followed by the same letter within a year are not significantly different.

f Significance value was adjusted using Sidak's multiplicative inequality. (= P < 0.0085).

Table 2.8. Hardness of diet of juvenile or yearling and adult *E. fuscus* in 1994 and 1995. Yearlings and adults are compared in the spring; juveniles and adults are compared in the summer. Values are calculated using the hardness index of Freeman (1981). Results were analysed with ANOVA. Values reported are least squares means. ns = not significant. * = P < 0.05. ** = P < 0.01. *** = P < 0.001.

		Hardness 1	Index		
	Juveniles /	Yearlings	Ac	ults	
	Mean	SE	Mean	SE	Р
Spring	3.79	0.29	4.11	0.20	ns
Summer	3.46	0.10	4.10	0.14	***
	199	94	19	95	
	Mean	SE	Mean	SE	Р
Spring	3.45	0.26	4.45	0.21	**
Summer	4.05	0.14	3.50	0.16	*

Juvenile *E. fuscus* ate a significantly broader range of prey items than did adults (Table 2.7), and the mean hardness of prey included in the diet of juveniles was lower than for adults (Table 2.8). The dietary niche breadths of individuals were greater in 1994 than in 1995 for the pre-weaning/lactation period, and individuals also ate a broader range of items during the post-weaning/post-lactational period in 1995 than earlier in the year (Table 2.7). Bats also ate softer prey in 1994 than in 1995 (Table 2.8).

Insect Sampling

Trap catches from both river and schoolyard locations tended to be small, and included similar types of insects. I therefore pooled results for each trapping night (Table 2.9). I never found Coleoptera and Hemiptera in trap samples. Thus, to compare trap and fecal samples, I adjusted the data from fecal samples by removing Coleoptera and Hemiptera, and calculated volume of other taxa as a proportion of the adjusted value.

Three orders of insects, Diptera, Lepidoptera, and Trichoptera, were found regularly in both suction trap samples and bat fecal pellets. Regression of the proportions found in juvenile fecal pellets on the proportions from suction traps yielded slopes significantly greater than zero, but less than one, for Diptera and Lepidoptera (Table 2.10). For adults, the only significant result was for Lepidoptera, which showed a significant relationship between fecal and trap sample proportions, the slope of which was not significantly different from one (Table 2.10). A slope greater

Date	Diptera	Lepidoptera	Trichoptera	Neuroptera	Ephemeroptera	
July 12	39.09	0	0	60.91	0	
July 16	13.8	50.41	2.17	33.54	0	
July 20	0	0	0	0	100	
July 24	100	0	0	0	0	
July 28	100	0	0	0	0	
August 2	4.54	95.46	0	0	0	
August 5	11.62	52.80	11.66	23.92	0	
August 13	100	0	0	0	0	
August 16	41.43	0	58.57	0	0	

Table 2.9. Catches from suction traps by trapping date in 1995. Percent of the total catch biomass is reported for each order. Insect catches are pooled for traps at ESS and along the South Saskatchewan River.

.

Table 2.10. Regression statistics describing line of best fit for proportions of insect taxa by mass in feces of bats and suction trap samples. The y-intercept was fixed at the origin. P_{slope} value indicates whether the slope of the regression line is significantly different from zero. H_o tests whether the slope of the regression line is significantly different from one. ns = not significant, * = P < 0.05, ** = P < 0.01. *** = P < 0.001.

<u> </u>		Adults			Juveniles			
	slope	P _{slope}	Ho	-	slope	P _{slope}	Ho	
Lepidoptera	0.27	**	ns		0.33	***	**	
Diptera	0.13	ns	ns		0.20	**	**	
Trichoptera	-0.02	ns	***		0.05	ns	***	

than zero indicates that consumption of a particular type of insect is related to its availability. If selection of prey is random, the slope should be equal to one. The results from fecal and trap samples in this study imply a degree of non-random selection on the part of juveniles, but not adults.

I compared the distribution of points above and below the line of equivalence for the three insect orders (Fig 2.3, Table 2.11). The proportion of Diptera in fecal samples from juveniles was greater than in trap samples significantly more often than expected. All other comparisons were not significant.

DISCUSSION

Diet

The diets of juvenile, yearling, and adult big brown bats were dominated by beetles in 1994 and the spring of 1995. Beetles were also the most abundant item in the diet of *E. fuscus* in several previous studies (eg. Whitaker 1972, Griffith and Gates 1985, Brigham 1990, Brigham and Saunders 1990, Wilkinson 1995). Hemiptera were also a major component of the diet of big brown bats in 1994, as they have been in several other studies (Whitaker 1972, Griffith and Gates 1985), although they were rarely found in fecal samples from *E. fuscus* at my study site in previous years (Wilkinson 1995).

The diet of big brown bats in the summer of 1995 included different items than in 1994 or the spring of 1995. While beetles were a major component of the diet of



Fig. 2.4. Proportion of Diptera in the diet of juvenile big brown bats and in insect trap samples. If diet is exactly equal to availability, all points would lie along the 1:1 line. Significantly more points lie above the 1:1 line than expected (see text).

	Adults			Juveniles		
	Above	Below	Р	Above	Below	Р
Lepidoptera	13	7	ns	19	23	ns
Diptera	4	16	ns	9	33	*
Trichoptera	15	5	ns	29	13	ns

Table 2.11. Summary of Chi-squared values describing the distribution of data points above and below the line of equivalence for percent insect taxa in fecal samples and suction trap samples. ns = not significant, * = 0.01 < P < 0.05

ŝ

.

.

both juveniles and adults in the summer of 1995, they were not as dominant in the diet of big browns as in 1994. Hemiptera were a minor component of the diet of both age classes in 1995. As well, while there was no difference in dietary niche breadth between years during post-lactation, bats had a broader diet in 1994 than in 1995 during lactation. A similar difference was found in spring, with bats eating a broader range of prey in 1994 than in 1995.

The differences in dietary components and niche breadths between 1994 and 1995, as well as between this study and that of Wilkinson (1995), may have resulted from differences in prey community structure associated with ambient temperature. 1994 was significantly warmer during the summer than was 1995, and both the number and types of insects available to foraging bats would have differed between the two years. For example, it may be that Hemiptera, which were a major item in the diet only during the summer of 1994, are normally a relatively minor component of the insect community. A further influence on the diet of bats over the two years, particularly in the spring, may have been the severe flooding of the South Saskatchewan River in June 1995. Radio-tagged bats switched from foraging along the river to foraging along tributary streams for a period of about two weeks after the flood (unpublished data). Without more information on the prey base available to bats over the two years of this study, I cannot make further conclusions regarding year-toyear differences in diet.

Age-Related Differences in Diet

As predicted, juvenile and adult bats differed in dietary composition and breadth. Juveniles ate a broader range of prey items than did adults in both years. In 1994, juveniles ate fewer beetles, and more Hemiptera than did adults. Differences in insect proportions in the diet were not apparent in 1995. On return from hibernation, there were no differences between adults and yearlings for any measure of diet.

Despite feeding on a greater variety of prey, and thus encountering higher densities of potential prey, juveniles had a lower rate of prey intake than did adults. This is indicated by the fact that juveniles produced fewer fecal pellets than did adults after capture. Older juveniles and adults foraged for similar durations on warm nights (see Chapter 4). Juveniles must therefore have ingested a smaller volume of insects per minute of foraging.

Barclay (1985a) found that subadult *Scotophilus leucogaster* in Africa produced more feces than did adults. He interpreted this difference as reflecting poorer handling skills of juveniles, who were inefficient at removing indigestible parts of the prey. Juvenile *S. leucogaster* also foraged for longer than did adults (Barclay 1985a), an option which may not be available to juvenile bats in my study. Juvenile *E. fuscus* in Medicine Hat may be constrained from foraging for as long or longer than adults because declining prey availability during the night results in the rate of energetic intake falling below energy expenditures, after which it is no longer profitable to forage (see Chapter 4). Consequently, juveniles ingest a smaller volume of insects per night than do adults. Inefficiency of juveniles at discarding indigestible portions of insects may reduce the digestive efficiency of juvenile *E. fuscus*, further reducing their rate of energy intake (Barclay *et al.* 1991, Keeler and Studier 1992).

I suggest that dietary differences between juvenile and adult *E. fuscus* reflect differences in the relative profitability of different prey items, resulting from the relatively poor handling abilities of juveniles. Longer handling times for juveniles may result from inexperience or from morphological constraints on handling hard prey.

Juveniles took significantly longer than did adults to manipulate and ingest mealworm beetles. Under natural conditions, big brown bats capture, handle, and ingest insects while in flight. In this study, individuals were hand-held, and thus the handling times measured may differ somewhat from those of bats foraging naturally. However, differences between the handling times for juveniles and adults are unlikely to result from the experimental conditions. Indeed, the additional demands of flight and echolocation may further increase handling times of inexperienced juvenile bats.

Long handling times by young bats foraging on beetles result in beetles being less profitable for young bats than for adults. Profitability, defined as energy over handling time, of a 0.14 g (live mass) mealworm-sized beetle with a caloric content of 756 J (Appendix 2), would be 27.50 J/s for an adult bat, and 10.50 J/s for a juvenile bat, based on handling times from the first feeding. Based on times from the second feeding, these values would be 37.46 J/s and 13.34 J/s respectively.

Longer handling times for juveniles than for adults result in juveniles having a lower rate of energy intake than do adults. Handling time may also influence whether juveniles and adults forage selectively. The decision whether to be selective in foraging depends not only on handling time, but also on the profitability of less preferred prey types and on the availability of the preferred prey type (Stephens and Krebs 1986). However, given the higher profitability of beetles for adults than for juveniles, beetles should be the preferred prey choice of adults over a broader range of conditions than for juveniles. Therefore, beetles should make up a larger proportion of the diet of adults than of juveniles.

Although juvenile *E. fuscus* have difficulty handling hard prey, the relationship between dietary hardness and prey selection is unclear. Juveniles ate softer prey than did adults, and bats ate softer prey in 1995 than in 1994. It is difficult to elucidate whether the softer diet of juveniles is a consequence of juveniles being less selective due to lack of experience, or reflects morphological constraints on the diet of juveniles. If the skulls of juveniles are less robust than are those of adults, juveniles may be poorly equipped to capture and ingest beetles (Freeman 1981). The beaks of juvenile birds often lack the rigidity required to handle adult prey (Heppleston 1970), and juveniles often forage on softer prey items (oystercatchers, *Haematopus ostralegus*: Heppleston 1970; Darwin's finches, *Geospiza difficilis*: Price and Grant 1984). An examination of the skull morphology of juveniles relative to that of adults, and comparison of the diet predicted from skull morphology (Freeman 1981) with the observed diet may provide information on the relative importance of morphological constraints and lack of experience on prey choice by juveniles.

While morphological and experiential constraints are commonly invoked to explain differences in foraging behaviour between juvenile and adult animals, agerelated shifts in the diets of other organisms have also been related to various other intrinsic and extrinsic factors (Werner and Gilliam 1984, Marchetti and Price 1989). Adults may exclude juveniles from habitats with high food availability or low predation risk (deer mice, Peromyscus maniculatus: Van Horne 1982; red-backed salamanders, Plethodon cinereus: Jaeger et al. 1995; tufted bats, Rhynconyteris naso: Bradbury and Vehrencamp 1977; redshank, Tringa totanus: Cresswell 1994), or interfere with foraging by juveniles (bald eagles, Haliaeetus leucocephalus: Stalmaster and Gessaman 1984). Juvenile animals are often more susceptible to predators than are adults, and consequently, choose less risky foraging strategies (yellow-bellied marmots, Marmota flaviventris: Carey and Moore 1986; anoles, Anolis aeneus: Stamps 1983). Many juvenile fishes, however, are more risk prone than are adults, choosing habitats with high predation risk and high feeding availability, in which they quickly grow to a less vulnerable size (Grant and Noakes 1987, Utne and Aksnes 1994). Juveniles and adults also may have different nutrient or energy requirements, leading to differences in foraging behaviour. Higher flight costs to adult birds may lead to greater food requirements for adults than for juveniles (Davies and Green 1976, Richardson and Verbeek 1987).

Exclusion of juvenile big brown bats by adults is unlikely. Although adult female *E. fuscus* may defend territories (Wilkinson 1995), in this study, both juveniles and adults foraged primarily in the valley of the South Saskatchewan River (see Chapter 4).

Microhabitat differences may be responsible for the observed differences in diet

between juveniles and adults. Juveniles have lower wing loading than do adults (see Chapter 3), and should therefore be able to fly more slowly and maneuverably (Norberg and Rayner 1987), facilitating foraging in spatially cluttered areas. However, light-tagged juveniles were observed foraging exclusively in open areas that were also used by adults (Wilkinson 1995, and see Chapter 4). Juvenile and adult *E. fuscus* probably encountered the same prey communities while foraging.

Predation risk is also unlikely to be an important factor influencing the diet of *E. fuscus*. Few studies have reported predation as a major factor influencing activity patterns of bats, especially in temperate regions (Erkert 1982, Kalcounis and Brigham 1994). Predation on bats occurs mostly at the roost site, rather than while foraging (Kunz 1982). There is also little reason to expect that juvenile bats would be more vulnerable to predators, as they are the same size as adults, and based on wing morphology, may be even more maneuverable.

Differences in diet could also result from different nutritional requirements of juveniles and adults. Adult female bats are in calcium debt by the end of lactation (Kwiecinski *et al.* 1987). Female bats may therefore select prey with high calcium content to replenish calcium stores prior to hibernation (Barclay 1994). However, Wilkinson (1995) did not find that female bats in Medicine Hat were selecting insects based on calcium content, and juveniles may also require calcium if ossification of bones is not completed. Although the energetic requirements of adults and juveniles differ (see Chapter 3), the high energetic cost of flight to both juveniles and adults, which may constrain foraging opportunities (see Chapter 4), and the need to

accumulate fat reserves prior to hibernation (Pistole 1989), indicate that both adults and juveniles should maximize their rate of energy intake. Thus, it is unlikely that adults and juveniles are using different currencies on which to base foraging decisions.

Prey Selection

Foraging inefficiency by juveniles could result in juveniles selecting prey that are more easily handled, or possibly in juveniles not foraging selectively (Gould 1974). Juvenile E. fuscus in Medicine Hat included more items in their diet than did adults. This suggests that juveniles may have been foraging opportunistically, while adults selectively foraged on beetles. Because beetles were never captured in insect traps, I cannot conclude that the dominance of beetles in the diet of adults reflected selective foraging, or opportunistic foraging on an abundant prey source. However, adults and juveniles used similar echolocation calls (see Chapter 3), and foraged in generally the same areas, and therefore probably encountered similar prey communities. It is therefore likely that either adults were selecting beetles above their availability, or juveniles were selecting a broad range of other insects while rejecting beetles. While juveniles ate less Coleoptera than did adults in 1994, there is little evidence that juveniles selected against beetles. In both years, a substantial proportion of the diet of juveniles was composed of Coleoptera, and at least some juveniles ate exclusively Coleoptera.

Comparison of fecal samples with samples taken from insect traps indicates that juveniles are more selective than are adults. However, results from suction traps should be interpreted with caution. Insect traps do not sample all of the prey potentially available to bats, as indicated by the lack of Coleoptera and Hemiptera in my suction trap samples. Both juvenile and adult big brown bats have been reported to fly as high as 50 m (Phillips 1966), and, at my study site, have been observed foraging much higher than the insect traps I used (Wilkinson 1995, pers. obs.).

Diptera captured in insect traps tended to be very small, and would probably have required little time for handling. Small dipterans may be more profitable than are larger prey items for juvenile bats, which are unable to efficiently handle large prey. Diptera were numerically the most common item in trap catches on all nights. As an abundant, profitable prey source, at least some juveniles may actively select dipterans (Stephens and Krebs 1986). Further examination of handling times and rate of energy intake of bats foraging on Diptera and other taxa, as well as quantification of insect availability, are necessary for a predictive model of diet choice by juvenile and adult bats.

The evidence for selective foraging by bats which use echolocation to detect prey is equivocal. The ability of bats to distinguish among prey may be constrained by the limited time between prey detection and capture for an echolocating bat (Barclay and Brigham 1994). The time between echolocation pulses gives an indication of the distance over which a bat can collect information (Fenton 1994). For a bat emitting a pulse every 100 ms, information can be collected over a distance of 17 m (see Chapter 3), and detection of prey-sized objects is only possible at an even shorter range (5 m for a 19 mm sphere; Kick 1982). A bat flying at 9 m/s, a typical flight speed for *E. fuscus* (Patterson and Hardin 1969), would have less than one second between detecting an item and encountering it. Given this time limitation, it may be most profitable for a bat to attack any potential prey item (Barclay and Brigham 1994), leaving open the possibility of post-capture prey rejection.

A bat, having captured an insect, must decide whether to ingest it, or to drop it and continue searching. A foraging bat should be more willing to pay a discrimination cost if the profitability of the most preferred prey type (energy/handling time) is much greater than is that of the second most profitable prey type (Gould 1974). Juvenile bats, which require longer to handle the preferred prey item, should therefore be less selective than are bats which are more efficient at prey handling. Prey handling should improve with experience, and the diet of older juveniles should be similar to that of adults. Indeed, by the time juveniles returned from their first hibernation, their diet was not significantly different from that of adults.

Conclusions

!

The diet of adult big brown bats conformed to that found in other studies, and to that predicted from jaw and skull morphology (Freeman 1981). Juveniles included a broader range of prey and softer prey in their diet than did adults. Juvenile *E. fuscus* also ingested a smaller volume of insects per night of foraging than did adults. These differences may be related to handling time constraints related to morphological development and learning.

Low rates of energy and nutrient intake of juvenile E. fuscus relative to adults

may constrain their foraging and life-history strategies. Daily activity patterns of juveniles will be influenced by their inefficiency at foraging (see Chapter 4). In the longer term, inability to acquire sufficient energy and nutrient (particularly polyunsaturated fat; Frank 1992) reserves prior to hibernation may lead to higher overwinter mortality and deferred reproduction by juveniles (Burnett and Kunz 1982, Rydell 1993, see Chapter 5).

.

a.

.

CHAPTER 3. Morphology and Perception

INTRODUCTION

Morphology and sensory perception play an important role in shaping the behaviour of an animal, including its foraging behaviour. Body size and configuration may influence the diet and habitat that are selected by an animal (Rosenzweig 1966, Schoener 1968, Werner and Hall 1976, Gatz 1977, Schluter and Grant 1984, Saunders and Barclay 1990, Fullard *et al.* 1991, Jones *et al.* 1993), as well as the costs of foraging (Mueller *et al.* 1981, Alatalo *et al.* 1984, Hughes *et al.* 1995). Prey selection may also be limited by perceptive ability (Barclay 1985b, Barclay and Brigham 1991, Barclay and Brigham 1994). The morphological and sensory constraints experienced by adult and juvenile animals may differ, resulting in changes in foraging strategies with age (Werner and Gilliam 1984, Marchetti and Price 1989).

The interaction among morphology, sensory systems, diet, and foraging behaviour of bats has been widely investigated. At a proximate level, morphology and sensory perception may be important determinants of the foraging behaviour and activity budget of bats. Foraging behaviour and diet of bats have been related to jaw morphology (Freeman 1981), wing morphology (Norberg and Rayner 1987), and echolocation (Fenton 1984b, Fenton 1994), and morphology and sensory perception can be used to successfully predict the foraging strategies of bats (jaw morphology: Freeman 1981; wing morphology and echolocation: Fenton and Bell 1979, Aldridge and Rautenbach 1987, Baagoe 1987, Norberg and Rayner 1987, Saunders and Barclay 1989, Fullard *et al.* 1991, Jones *et al.* 1993, Surlykke *et al.* 1993). Interspecific differences in morphology and echolocation have been particularly useful in interpreting the community structure of bats (Aldridge and Rautenbach 1987, Saunders and Barclay 1990, Fullard *et al.* 1991, Jones *et al.* 1993). At the ultimate level, the unique demands of flight and echolocation may have constrained the evolution of behavioural and life-history strategies of bats (Fenton 1994).

Flight speed, maneuverability, agility, and costs are influenced by wing morphology (Norberg and Rayner 1987), particularly wing loading and aspect ratio. Wing loading is the ratio of body weight to wing area. High wing loading is associated with high flight speed, low maneuverability, and a high energetic cost of flight (Norberg and Rayner 1987). Aspect ratio is the ratio of the square of wingspan to wing area, and is an index of wing shape; high aspect ratio indicating long, narrow wings, resulting in efficient flight through a reduction in drag (Norberg and Rayner 1987). Low aspect ratio indicates short, wide wings, which are less efficient (Norberg and Rayner 1987), but which may be advantageous for flight in clutter (Norberg and Rayner 1987).

Wing development in prevolant pups has been described for several species of bats (Davis 1969, Pagels and Jones 1974, Hoying 1983, Powers *et al.* 1991), but morphological development after the onset of sustained flights remains largely uninvestigated. Jones and Kokurewicz (1994) compared flight morphology between first year and older *Myotis daubentonii*, and found no differences. However, first-year

bats had lower body mass, and lower body condition, defined as the ratio of mass to forearm length, than did adults (Jones and Kokurewicz 1994). Hughes *et al.* (1995) measured wing loading and aspect ratio of captive flying juvenile *Pipistrellus pipistrellus*. Juveniles had lower wing loading than did adults, while the aspect ratios for juveniles and adults were similar (Hughes *et al.* 1995). Juveniles lost mass after the initiation of flight, although mealworms were provided *ad libitum* (Hughes *et al.* 1995). The authors suggested that mass loss may be adaptive for young bats by reducing the cost of flight at a time when juveniles are still inexperienced at foraging and flight.

Sensory perception also plays an important role in the foraging strategies of bats. Bandwidth, frequency, duration and intercall interval are important variables of echolocation search calls that may influence foraging. Bats that use high frequency or broadband calls can detect small insects from a greater distance than can those using low frequency calls (Barclay and Brigham 1991, but see Waters *et al.* 1995). Intercall interval influences the range in which insects may be detected (Fenton 1994). A long interval between calls will allow a bat to detect objects over a greater range.

Juvenile bats of several species produce calls of lower frequency than do adults (*M. lucifugus*: Buchler 1980; captive *E. fuscus*: Moss 1988; hipposiderid bats: Jones *et al.* 1993). Juvenile *Hipposideros speoris* and *P. pipistrellus* produce low frequency calls prior to the initiation of flight, but increase frequency of calls to within adult values prior to flight (Habersetzer and Marimuthu 1986, Jones *et al.* 1991). The developmental precursors of echolocation calls are low in frequency (Moss 1988), and

the production of low frequency calls by volant juveniles may reflect incomplete development of vocalizations prior to flight.

In this chapter, I compare the wing morphology and echolocation call structure of juvenile and adult *E. fuscus*. Based on studies of other vespertilionid bats (Jones and Kokurewicz 1994, Hughes *et al.* 1995), I predicted that juveniles would have lower wing loading than adults, while aspect ratio would not differ among age classes. I predicted that the search calls of young juvenile bats would be of lower frequency than those of adults. If the search calls of young juveniles are of low frequency because of incomplete maturation, then older juveniles should emit higher frequency calls than do younger juveniles.

Survival and reproductive success of bats is related to body mass (see Chapter 5). It therefore would be advantageous for juveniles to rapidly put on mass after starting to fly. However, an increase in mass also increases wing loading, resulting in a higher energetic cost of flight. I tested whether juveniles maintain a low body mass that reduces flight costs, as suggested by Hughes *et al.* (1995), by comparing the body mass of juveniles, using forearm as a covariate, in 1994 and 1995. The summer of 1994 was warm and dry (see Chapter 2) while 1995 was cooler and wetter, and included a period of severe flooding of the South Saskatchewan River. Reduced activity and abundance of aquatic insects is characteristic of cool temperatures and flooding (Ward 1992), and thus prey density was likely greater in 1994 than in 1995. I predicted that, if juvenile mass is limited by foraging inefficiency, then juveniles should have been heavier in 1994 than in 1995. If, however, juveniles maintain low

body mass, then they should not put on extra mass even when insects are more abundant.

METHODS

Echolocation Recording

The echolocation calls of adult and flying juvenile bats were recorded using a custom made ultrasonic microphone (Simmons *et al.* 1979) connected to a Racal 4DS instrumentation tape recorder operated at 76 cm/s (system flat \pm 5 dB from 15 to > 80 kHz). Bats were held approximately 10 m from the microphone at a standardized outdoor location and released from the hand. Calls were recorded after the bat was released, as it flew towards the microphone.

I randomly selected two to four calls per bat, which were digitized using SIGNAL Sound Analysis System (Version 2.2). For each call, a power spectrum was generated using the Discrete Fourier Transform (DFT) (sampling rate 37.8 kHz). Echolocation calls of *E. fuscus* include a fundamental and several upper harmonics. I measured the frequency of peak intensity for the fundamental, defined as the frequency at which the call amplitude is greatest. Minimum and maximum frequencies were defined as those frequencies at which the amplitude of the fundamental was no more than 30 decibels below peak amplitude. This value was chosen arbitrarily to distinguish calls from background noise. I also measured total call duration, in ms. I compared duration, minimum, maximum, and peak frequencies among pre-weaning juveniles, post-weaning juveniles, and adults, using mixed-model ANOVAs, with individual as a random factor, nested within age class. I also compared the intercall interval, defined as the silent period between calls, among age classes with a mixedmodel ANOVA, with individual as a random factor, nested within age class.

To test whether the protocol for recording echolocation calls had an influence on the structure of calls, I compared echolocation calls emitted from hand-released and free-flying adult *E. fuscus*. On 29 and 31 May 1995, I recorded echolocation calls of hand-released adult bats as described above. On 5 June 1995, echolocation calls of free flying adult bats emerging from ESS were recorded. I generated power spectra using DFT and compared the duration, minimum and maximum frequencies, and frequency of peak intensity of calls produced by hand-released and free-flying bats. I compared call structure using a mixed-model ANOVA, with individual as a random factor, nested in the term for treatment as a fixed effect.

Wing Tracings

I traced the wings of 29 adult females and 29 juvenile females mist-netted in the summer of 1995. Bats were placed on their backs on a sheet of paper with the left wing and tail membrane fully extended and held flat. The wing and tail membrane of each bat was traced using a non-toxic felt pen. The positions of both shoulders were marked. Wing tracings were digitized using Sigma-ScanTM (Jandel Scientific, San Rafael, CA 94901). I also measured the mass of each bat with a C151 Ohaus portable electronic balance. A number of conventions have been used for reporting wing area of bats. I used the same definition as Norberg (1981). Lifting surface area (LSA) was calculated as the area of the wings and tail membrane and the body excluding the head. I measured the area of the left wing, and the left half of the tail membrane and body (Fig 3.1). The midpoint of the bat was determined by drawing a line from halfway between the shoulders to the tip of the tail. The area was doubled to obtain total LSA.

I used the same definition of wingspan (B) as Saunders (1989). Wingspan was defined as twice the distance from the midpoint between the shoulders to the left shoulder, plus the distance of the straight line from the shoulder, through the base of the thumb, to a perpendicular line through the tip of the wing (Fig 3.1).

I calculated wing loading and aspect ratio for each bat. Wing loading (S) is the ratio of body weight to LSA:

(Equation 3.1)
$$S = \frac{M * 9.8 m/s^2}{LSA}$$
 (3.1)

where M = body mass.

Aspect ratio (A) is the ratio of the square of wingspan to lifting surface area:

$$(Equation 3.2) A = \frac{B^2}{LSA} (3.2)$$

I compared LSA, wingspan, wing loading and aspect ratio between age classes and seasons (pre-weaning/lactation versus post-weaning/post-lactation) using two-factor



Fig. 3.1. Diagram depicting the definitions of wingspan (B) and lifting surface area (LSA) in this study (adapted from Saunders 1989).
ANOVAs, with age class and season as main effects. As in all analyses, interactions between effects were removed sequentially if not significant.

Body Mass

I compared the body masses of juvenile and adult females in late summer 1994 and 1995 with ANCOVA. All adults were post-lactating, and all juveniles were weaned. The model included terms for age class and year as fixed effects. Forearm length and capture date were included as covariates in the model. Data from one capture per bat were used. Most bats were only captured once during the summer. If a bat was captured more than once in one year, I randomly selected one capture.

I used records from 1990, 1991 and 1993 to compare the masses of juvenile and adult bats during the month of September, immediately prior to mating and hibernation. Because of the small sample size, I pooled data over the three years. Forearm length and capture date were used as covariates.

As an index of the condition of bats returning from hibernation, I compared the mass of yearling and adult females in April and May in 1994 and 1995 using ANCOVA. All bats were nonreproductive or not yet detectably pregnant. The model included terms for age class and year as fixed effects. Forearm length and capture date were used as covariates. If a bat was captured several times during this period, I used the mass from the first capture only.

Echolocation Call Structure

The protocol for recording echolocation calls did not affect the frequency structure of search calls. Hand-released and free flying adult *E. fuscus* did not differ in minimum or maximum frequency or frequency of peak intensity of echolocation calls (Table 3.1). However, hand-released bats did produce shorter echolocation calls than did free-flying bats. Individuals varied significantly for all variables (minimum: F = 8.80, df = 9, 22, P < 0.001; maximum: F = 4.88, df = 9, 22, P < 0.01; peak: F = 4.31, df = 9, 22, P < 0.01; duration: F = 6.10, df = 9, 22, P < 0.001).

Juvenile and adult bats did not differ in minimum or maximum frequency, frequency of peak intensity, or duration of echolocation search calls (Table 3.2). There were significant differences in echolocation call structure between years (Table 3.3). Bats emitted longer calls of lower minimum and peak frequencies in 1994 than in 1995. The terms for individual were significant in all models (minimum: F = 7.65, df = 30, 51, P < 0.001; maximum: F = 3.83, df = 30, 51, P < 0.001; peak: F = 6.06, df = 30, 51, P < 0.001), indicating that individual bats differed in their echolocation call structure.

Intercall interval of pre-weaning juvenile, post-weaning juvenile, and adult bats were not significantly different (Fig 3.2; F = 1.21, df = 2, 15, P > 0.3). Adults, however, tended to have a longer interval between echolocation calls than did juveniles. Table 3.1. Comparison of echolocation search call time-frequency structures between free flying adult *E. fuscus* (n = 21 calls) and hand-released bats (n = 12 calls). Minimum, maximum, and peak frequencies refer to the fundamental. An asterisk denotes significance at the 0.05 value. All values are least-squares means (SE).

,

	Hand-released	Free-flying	F	df _{denom}	Р
Minimum (kHz)	26.74 (0.26)	26.59 (0.20)	0.021	9	ns
Peak (kHz)	30.39 (0.47)	29.34 (0.35)	0.756	9	ns
Maximum (kHz)	38.73 (1.16)	39.50 (0.88)	0.057	9	ns
Duration (ms)	5.82 (0.48)	9.94 (0.36)	7.61	9	*

•

· ·

	Juven	iles	Adults	F	df _{denom}	Р
	Pre-weaning	Post-weaning				
• • • • • •						
Minimum (kHz)	27.60 (0.23)	26.74 (0.23)	28.02 (0.29)	0.98	30.91	ns
Peak (kHz)	34.18 (0.39)	35.03 (0.39)	33.80 (0.49)	0.40	31.15	ns
Maximum (kHz)	46.35 (0.60)	48.01 (0.60)	47.27 (0.76)	0.53	31.82	ns
Duration (ms)	4.91 (0.24)	4.93 (0.22)	4.60 (0.28)	0.15	30.27	ns

.

Table 3.2. Comparison of the time-frequency structure of the fundamentals of echolocation search calls emitted by hand-released pre-weaning juvenile (n = 30 calls), post-weaning juvenile (n = 23 calls) and adult (n = 34 calls) *E. fuscus*. Least-squares means (SE) are reported.

.

Table 3.3. Comparison of the time-frequency structure of the fundamentals of echolocation search calls emitted by hand-released *E. fuscus* in 1994 (n = 54 calls) and 1995 (n = 33 calls). Least-squares means (SE) are reported. Asterisks denote significance. ns = not significant. * = P < 0.05. ** = P < 0.01. *** = P < 0.001.

•

.

.

	1994	1995	F	df _{denom}	P
Minimum (kHz)	26.48 (0.19)	28.43 (0.22)	6.08	30.79	*
Peak (kHz)	31.84 (0.32)	36.83 (0.38)	18.74	30.99	***
Maximum (kHz)	47.17 (0.49)	47.25 (0.58)	0.01	31.58	ns
Duration (ms)	5.65 (0.18)	3.97 (0.22)	9.94	30.11	**



Fig. 3.2. Mean (\pm SE) interval between echolocation calls emitted by hand-released pre-weaning juvenile (n=24), post-weaning (n=12) and adult (n=18) E. fuscus.

The age by season interactions for both lifting surface area and wingspan were significant (age by season - LSA: F = 4.67, df = 1, 54, P < 0.05; wingspan: F = 5.90, df = 1, 54, P < 0.05). Pre-weaning juvenile bats had smaller lifting surface areas than did post-weaning juveniles, lactating females, and post-lactating females (Table 3.4). Pre-weaning juveniles also had shorter wingspans than did older bats (Table 3.4).

Juvenile bats had lower wing loading than did adults (Table 3.5). Bats did not differ in wing loading between lactation and post-lactation (F = 0.02, df = 1, 55, P > 0.8). The age by season interaction was not significant and was removed from the model. Aspect ratio did not differ significantly between age classes or seasons (Table 3.5; model F = 2.57, df = 2, 55, P > 0.05).

Body Mass

Post-weaning juvenile bats were lighter than were post-lactating females, although this difference was significant in 1994 only (Table 3.6). The effect of capture year differed between adult and juvenile bats (age by year interaction: F =5.26, df = 1, 34, P < 0.05). Adult bats were heavier in 1994 than in 1995, while juvenile bats did not differ significantly between years (Table 3.6). Forearm length was a significant covariate in the model (F = 27.37, df = 1, 34, P < 0.001). Forearm length is an index of skeletal size, and bats with larger forearms, and hence, larger skeletons, were heavier. I also included a term for capture date as a covariate in the model; however, body mass was not significantly related to capture date (F = 0.84, df Table 3.4. Lifting surface area (LSA) and wingspan of juvenile (n = 29) and adult (n = 29) bats. All values are least squares means (SE). Values within a column followed by the same letter are not significantly different. Type I error rate was determined using Sidak's multiplicative inequality.

Age	LSA (cm ²)	Wingspan (B) (cm)	
Pre-weaning Juvenile	134 31 (2 97)a	28 71 (0 37)a	
Post-weaning Juvenile	157.82 (4.81) ^b	30.81 (0.60) ^b	
Lactating Adult	159.19 (3.12) ^b	31.78 (0.39) ^b	
Post-lactating Juvenile	165.93 (4.30) ^b	31.51 (0.54) ^b	

Table 3.5. Wing loading and aspect ratio of the wings of juvenile (n = 29) and adult (n = 29) *E. fuscus*. Statistical significance is denoted by asterisks. ns = not significant. *** = P < 0.001.

.

.

.

•

	Juvenile	Adult	F	df _{denom}	P
Wing Loading (N/m^2)	10.37 (0.24)	12.54 (0.29)	37.19	55	***
Aspect Ratio	6.06 (0.09)	6.20 (0.09)	1.36	55	ns

.

.

.

.

Table 3.6. Body mass (g) of a) post-weaning juvenile and post-lactating adult female *E. fuscus* in 1994 and 1995 and b) yearling and adult bats in early spring 1994 and 1995. Forearm length was used as a covariate in the models. Means followed by the same letter are not significantly different at a Type I error rate adjusted using Sidak's multiplicative inequality.

. .

•

	1994	n	1995	n
a) Juvenile	18.12 (0.59) ^a	13	17.20 (0.68)ª	10
Adult	23.49 (0.65) ^b	10	19.50 (0.78) ^a	7
b) Yearling	14.52 (0.67)ª	6	16.44 (0.57) ^{ab}	9
Adult	18.78 (0.41) ^c	18	17.94 (0.30) ^{bc}	28

.

= 1, 34, P > 0.3). Thus, neither juvenile nor adult bats in 1994 and 1995 gained mass over the sampling period, although sample sizes were low, particularly for adult females in 1995.

In September 1990, 1991, and 1993, juvenile bats were significantly lighter than were adults (Table 3.7). Forearm length and capture date were both significant covariates (FA: F = 4.59, df = 1, 23, P < 0.05; capture date: F = 4.80, df = 1, 23, P < 0.05). Bats were heavier later in September, but the rate of increase cannot be estimated, because data were pooled over the three years.

Yearling bats in spring 1994 were significantly lighter than were adults (Table 3.6). In 1995, however, the masses of yearlings and adults were not significantly different (Table 3.6; age by year interaction: F = 7.22, df = 1, 55, P < 0.05). Yearling bats in 1994 were lighter than yearlings in 1995. Forearm length was marginally significant as a covariate in the model (F = 4.02, df = 1, 55, P = 0.05). Capture date was not significant (F = 0.19, df = 1, 55, P > 0.6).

DISCUSSION

Echolocation Call Structure

The frequency-time structure of search-phase calls did not differ among preweaning juveniles, post-weaning juveniles, and adults. This contrasts with the findings of Moss (1988), who found that juvenile *E. fuscus* at 21 days produced echolocation calls of lower frequency and longer duration than did adults. Pre-weaning juveniles in Table 3.7. Least-squares mean body mass of juvenile (n = 15) and adult (n = 15) *E. fuscus* captured in September 1990, 1991 and 1993. Data were pooled over the three years. Forearm length and capture date were significant covariates in the model. *** = P < 0.001.

•

	Juveniles	Adults	F	df _{denom}	Р
Mass (g)	18.62 (0.44)	23.31 (0.51)	40.31	23	***

this study ranged in age from 21 to 35 days, which may have masked any differences in the echolocation call structure of the youngest bats. As well, the 21-day-old juveniles in Moss' study were not yet foraging on their own, while in Medicine Hat, juveniles begin to fly and forage at 21 days. Juveniles of foraging age did not differ from adults in echolocation call structure in either population (Moss 1988). Masters *et al.* (1995) also reported that the approach-phase calls of juvenile *E. fuscus* were lower in frequency than were those of adults. However, juveniles in their study were much older than in this study (Masters *et al.* 1995).

The echolocation calls of both adults and juveniles in this study were of higher frequency and, generally, longer duration than those reported by Moss (1988). These differences probably reflect different experimental protocols. Bats in the present study were recorded in the field, while those in Moss' (1988) study were recorded in a foam-padded recording chamber. *E. fuscus* has been previously reported to emit shorter calls when flying near surfaces (Griffin 1958). This effect may also explain the shorter call duration of hand-released bats compared with free-flying bats. Hand-released bats flew near to the ground (< 3 m), while free flying bats flew at an altitude of approximately 5-10 m.

Both juvenile and adult bats emitted lower frequency echolocation calls in 1994 than in 1995. Recordings from 1995 were of poorer quality than were those from 1994. It was difficult to obtain clear recordings from a number of bats, indicating that call amplitude may have also been lower in 1995 than in 1994. The cause of this relationship is unclear, but may be related to different environmental conditions over the two years. Bats in 1995 were often recorded on cool nights with intermittent rain.

Echolocation calls recorded in spring 1995 were generally of lower frequency and narrower bandwidth than were calls recorded in the summers of 1994 and 1995. Individuals also differed significantly in both spring and summer. Bats are flexible in terms of echolocation call structure, particularly in relation to habitat variation (Kalko and Schnitzler 1993). However, I found substantial differences between individuals from the same population recorded at the same location. Masters *et al.* (1995) found a high degree of variability in echolocation calls between individual *E. fuscus*, which may provide information on identity and group membership. The individual distinctiveness of echolocation calls was greater for adults than juveniles (Masters *et al.* 1995). Given the flexibility and variability of echolocation call structure, comparisons of echolocation calls between age groups should be interpreted with caution.

Based on intercall interval, adults and juveniles are able to detect objects at a similar distance. Because *E. fuscus* is intolerant of overlap between pulse and echo, the intercall interval provides an indication of the range over which individuals can collect information (Fenton 1994). The intercall intervals of pre-weaning juvenile *E. fuscus*, post-weaning juveniles, and adults correspond to distances of 17 m, 16 m, and 20 m respectively (speed of sound in air = 341 m/s). For a bat flying at 9 m/s, an average flight speed for *E. fuscus* (Patterson and Hardin 1969), these distances correspond to a maximum time to target of 1.9 s for pre-weaning juveniles, 1.8 s for post-weaning juveniles, and 2.2 s for adults. The distance at which bats can detect

prey-sized objects would be even smaller (5 m or less, Kick 1982). The flight speeds of juveniles and adults may differ (see below), and it is unlikely that adults have significantly more time between prey detection and prey capture than do juveniles.

Foraging by juveniles relative to adults is not influenced by differences in the structure of echolocation calls. Within a season, structures of calls emitted by juveniles and adults were the same. As a result, the information available from returning echoes should be the same for juvenile and adult *E. fuscus*. For example, similar-sized insects would be available as prey to juvenile and adult bats. However, the abilities of juvenile and adult bats to interpret echolocation calls is unknown. As suggested by Buchler (1980), lack of experience at the use of echolocation may influence the foraging behaviour of juveniles.

Wing Morphology

At the onset of flight, juvenile bats have smaller wings than do adults. Juveniles have a shorter wingspan, and smaller lifting surface area. By the time juveniles are fully weaned, wingspan and wing area are equivalent to those of adults, but juveniles have lower mass and thus a lower wing loading.

In various species of bats, wing loading of pups is high, but decreases to within adult values prior to the onset of flight (Davis 1969, Pagels and Jones 1974, Hoying 1983, Powers *et al.* 1991). Wing growth then continues after the onset of flight, while mass remains constant, or even decreases, resulting in a continued decrease in wing loading after the onset of flight. Hughes *et al.* (1995) found that juvenile bats had lower wing loading than did adults but that aspect ratio was similar between age classes. First-year and > 1 yr old *Myotis daubentonii* are not different in terms of flight morphology, although first-year individuals are lighter than older individuals (Jones and Kokurewicz 1994).

Aspect ratio was similar between juvenile and adult *E. fuscus*, indicating that the wings of juveniles and adults were of similar shape. In other species, aspect ratio of pups is generally low compared with that of adults, but increases to within adult values prior to the onset of flight (O'Farrell and Studier 1973, Powers *et al.* 1991, Hughes *et al.* 1995).

The lower wing loading of juveniles has several implications for their foraging and activity strategies. Juvenile bats should be able to fly more slowly and more maneuverably than adults. Juveniles would therefore be expected to be able to capture slow flying insects more efficiently, and possibly to forage in cluttered habitats where their maneuverability may be advantageous. The pectoralis muscle, one of the major flight muscles, is fully developed in juvenile *M. lucifugus* two weeks prior to flight (Schutt *et al.* 1995). However, juveniles are inexperienced at flight and foraging and their flight is slow and uncoordinated (Buchler 1980, Brown *et al.* 1983, pers. obs.). Radio-tagged juvenile *E. fuscus* returning to the maternity colonies in Medicine Hat had more difficulty entering the colony than did adults (pers. obs.). Low wing loading may not confer the advantage of high maneuverability to juveniles, probably because of lack of flight experience. Juveniles may be more maneuverable than if they were heavier, but are not necessarily more maneuverable than adults.

Body Mass

Low wing loading may be advantageous to young bats in another way. The cost of forward flight at minimum power speed, P_{mp} , is a function of wingspan (B), wing area (LSA), and body mass (M) (Norberg and Rayner 1987).

(Equation 3.3)
$$P_{mp} \propto M^{1.56} B^{-1.79} LSA^{0.34}$$

At the time of weaning, juvenile and adult *E. fuscus* had similar wingspans and lifting surface areas. However, the cost of flight can be minimized by maintaining a low body mass. A decline in mass after the initiation of flight is common in bats (Kleiman 1969, Rakhmatulina 1971, Maeda 1972, Kunz 1973, Funakoshi and Uchida 1981, Hughes *et al.* 1995) and birds (Ricklefs 1968). Decline in mass may be a result of nutritional stress and increased energetic demands during flight (Kunz 1973), or may be an adaptive strategy that reduces flight costs (Hughes *et al.* 1995).

Unlike individuals in previous studies, juvenile big brown bats in Medicine Hat did not decline in mass after the initiation of flight. Nevertheless, juvenile bats were lighter than adults in 1994, and had lower wing loading than did adults in 1995. The cost of flight for juvenile bats, therefore, should be lower than for adults (Norberg and Rayner 1987). In 1994, assuming that wingspan and wing area of juveniles and adults were the same as in 1995, the power required for continuous forward flight at minimum power speed was 22.9% higher for adults than for juveniles (see Chapter 4).

Juvenile bats are less efficient foragers than are adults (see Chapter 2). Prey

handling times for juveniles are longer than for adults, juveniles have a lower rate of energy intake than do adults, and juveniles forage for a shorter duration on cool nights (see Chapter 4). Total energy intake per night of foraging is therefore lower for juveniles. Juveniles also do not use torpor to the same extent as do adults (S. McNalley, unpublished data). The low mass, and therefore wing loading, of juveniles may therefore be a consequence of energetic stress. If accumulation of mass by juveniles is limited by their rate of energy intake, then an increase in prey availability and decrease in thermoregulatory costs resulting from warmer temperatures should result in increased body mass.

Results from 1994 and 1995 indicate that body mass of juveniles is not limited by rate of prey capture. The warmer temperatures in 1994 should have resulted in higher rates of prey encounter for all bats. Indeed, adult bats attained a greater body mass in late summer 1994 than in 1995, supporting the hypothesis that insects were more abundant in 1994. Juveniles, however, attained the same mass in both years. This suggests that there may be an optimal mass for juvenile bats, and that further accumulation of mass is costly. The cost of high body mass may be increased risk of mortality from exhaustion or starvation during periods of low food availability. By reducing flight costs, juveniles can reduce flight time and its risks, and are better able to maintain themselves in a positive energy budget despite lower foraging efficiency (see Chapter 4). By maintaining a low body mass, juveniles keep the energetic cost of flight low at a time when the risks associated with the development of flight and foraging remain high. There may be a cost to bats which maintain a low body mass, in terms of reproduction the following spring. Reproduction by female bats is correlated with the accumulation of fat deposits the previous season (Speakman and Racey 1986, McWilliam 1987). Juvenile bats must make a trade-off between maintaining a low body mass in the late summer that increases the probability of surviving the post-fledging period, and the future reproductive benefits of accumulating fat reserves. By maintaining a low body mass, juveniles may sacrifice reproduction the following year (see Chapter 5). However, because bats are long-lived, the fitness costs associated with delaying reproduction should be low (Stearns 1992).

Yearling and adult bats were of similar mass in May 1995, indicating that, either the juveniles that survived over winter attained a similar mass to adults prior to hibernation in 1994, lost mass at a slower rate during hibernation, or were able to make up for lost mass better than were adults in spring. In spring, yearlings and adults foraged for similar lengths of time per night (Chapter 4) and had similar diets (Chapter 2), so it is unlikely that yearlings were able to increase mass more rapidly than were adults. If my hypothesis is correct and it is advantageous for juvenile bats to keep their body mass low while becoming proficient at flight and foraging, juveniles may delay fat deposition as long as possible. Bats can deposit large amounts of fat in a short time immediately prior to hibernation (Ewing *et al.* 1970). Both juvenile and adult bats increased mass in September, although the data were pooled over 3 years, and may not be an accurate measure of changes in mass. By measuring mass only during late summer in 1994 and 1995, I may have missed the most critical period for fat deposition. Further examination of fat deposition during the period from weaning to hibernation would be informative.

•

.

.

•

CHAPTER 4. Foraging Behaviour

INTRODUCTION

As an animal develops, its activity budget may change in response to various intrinsic and extrinsic factors. For a variety of reasons, ranging from morphological constraint to competitive exclusion, juveniles and adults often forage in different habitats (e.g. oystercatchers, *Haematopus ostralegus*: Goss-Custard *et al.* 1982; anoles, *Anolis aeneus*: Stamps 1983; redshank, *Tringa totanus*: Cresswell 1994; garter snakes, *Thamnophis atratus*: Lind and Welsh 1994; gobies, *Gobiusculus flavescens*: Utne and Aksnes 1994, see Chapter 2), and allocate time differently (yellow-bellied marmots, *Marmota flaviventris*: Carey and Moore 1986). Because juvenile animals are also often less efficient foragers than are adults, they may require more time than adults to meet their daily energy and nutrient requirements (bats, *Scotophilus leucogaster*: Barclay 1985a; juncos, *Junco phaeonotus*: Sullivan 1988b).

The development of foraging behaviour has not been described for most species of bats. However, because juvenile bats rapidly achieve adult form and function (see Chapter 3), bats may illustrate the influence of factors such as changes in experience, risk-sensitivity, and social interactions on the ontogeny of foraging behaviour. Furthermore, the acquisition of nutrient and energy reserves may be advantageous to juvenile bats by increasing the probability that they will reproduce the next year (see Chapter 5), at the cost of increasing immediate foraging risks (see Chapter 3). As a result, the optimal short-term and long-term strategies for juvenile bats may be in conflict.

The foraging behaviours of various species of bats do change with age. Juvenile *M. lucifugus* progress from short practise flights, through a flycatching stage, to aerial hawking, over about a week (Buchler 1980), and juveniles of several species of insectivorous bats differ from adults in dietary composition or diversity (Rolseth *et al.* 1994, C. I. Stefan pers. comm., see Chapter 2). As well, many young bats lose mass after beginning to fly (Hughes *et al.* 1995). While this may reflect the demands of learning to fly and forage (Kunz 1973), mass loss also reduces the wing loading of inexperienced young bats (see Chapter 3, Hughes *et al.* 1995), allowing them to forage in spatially complex habitats (Norberg and Rayner 1987), and reduce the cost of flight compared with adults (Hughes *et al.* 1995). The early stages of foraging by *E. fuscus* have not been described.

Timing, Location, and Duration of Foraging

Lack of experience at foraging may influence the timing, location and duration of foraging by juveniles relative to adults. Buchler (1980) suggested that juvenile microchiropterans, inexperienced in the use of echolocation, may be confused by the auditory clutter resulting from the echolocation calls of bats emerging *en masse* from the maternity colony. Newly volant juveniles, therefore, should emerge later than adults, and emerge solitarily to avoid auditory interference from conspecifics. Buchler (1980) reported that juvenile *M. lucifugus* emerge later than adults. Auditory clutter would also hinder foraging by newly volant juvenile bats. Juveniles should therefore forage away from adults and other juveniles. Hereafter, I will refer to this hypothesis as the 'acoustic clutter' hypothesis.

In contrast to the above, juveniles may need to associate with adults to learn where to forage. The cues juvenile bats use to find profitable patches of insects are not known, although there is some evidence for association between foraging female bats and their offspring (Brown et al. 1983, Brigham and Brigham 1989, R. Ransome pers. comm.). Juveniles may also use the presence of foraging adults as an indicator of high-quality foraging sites (Buchler 1980). Echolocating bats emit 'feeding buzzes', a rapid series of signals, prior to prey capture. Other bats may use feeding buzzes as a cue to locate patches of insects and both adult and juvenile M. lucifugus are attracted to the echolocation calls of conspecifics (Barclay 1982). The response of juveniles to the echolocation calls of conspecifics is stronger than is that of adults (Barclay 1982). If juveniles either follow their mothers to foraging sites, or use the echolocation calls of adults to find areas of high insect abundance, then juveniles and adults should emerge at the same time and forage in the same locations. Because I was unable to place radios on mother-pup pairs, distinguishing between these two hypotheses, which I will hereafter refer to together as the 'social facilitation' hypothesis, was not possible in my study.

Morphological and/or learning constraints result in juvenile big brown bats capturing fewer insects while foraging than do adults (see Chapter 2). Consequently rates of energy and nutrient intake are lower for juveniles than for adults. Juvenile bats also do not use daily torpor to the same extent as adults (S. McNalley unpublished data). Given their higher energy requirements for thermoregulation and lower intake from foraging, recently independent juvenile bats would need to forage for longer than adults to achieve the same prey intake.

Bats must accumulate sufficient energy and nutrient reserves prior to hibernation to survive over winter and reproduce the following spring (Racey 1982, Speakman and Racey 1986, Frank 1992). I therefore predict that, if the long-term benefits of further foraging exceed the immediate costs of foraging, then juveniles should attempt to maximize energy or nutrient intake per night and forage for longer than adults. However, foraging may be costly, particularly for juveniles. The costs of foraging include the energetic cost of flight (Avery 1985), and the risk of incidental mortality while foraging, while the returns from foraging decline over time as insect availability decreases over the night (Jones and Rydell 1994). The short-term costs of lengthy foraging bouts may exceed the longer term fitness benefits of accumulating energy and nutrient reserves. The behaviour of juveniles relative to adults should therefore depend on the relative short-term costs and benefits to foraging.

In this chapter, I describe the foraging behaviour of juvenile *E. fuscus*, in relation to three questions: 1) how does the foraging behaviour of juvenile bats change with age, 2) do the timing of emergence and location of foraging by juvenile and adult bats fit the predictions of either the acoustic clutter or social facilitation hypotheses, and 3) how does the foraging behaviour of juveniles compare with that of adults, particularly on cool nights when prey densities are low? I determined activity patterns

through the use of radio-telemetry and light-tags. This allowed me to measure emergence time, foraging duration, and foraging location of juvenile and adult bats.

METHODS

Radio-telemetry

I determined activity patterns of bats by attaching radiotransmitters (Holohil Systems Ltd, Woodlawn, ON, models BD-2, BD-2/B, BD-2T, mass 0.67-0.9 g) to adult and juvenile big brown bats. Transmitters did not exceed 5% of the mass of the bat (Aldridge and Brigham 1991). To eliminate any possible interaction between ageand sex-related differences in foraging behaviour, I placed radios on female bats only. A small area between the shoulder blades of each bat was trimmed with dissecting scissors, and the transmitter was attached using Skinbond^R surgical adhesive. In 1994, bats were netted and radio-tagged opportunistically, to keep constant the number of bats with radios over the entire monitoring period (two to three each of juveniles and adults). In 1995, bats were netted regularly, and I tagged two juveniles and two adults, if possible, every eight days, regardless of how many bats already carried radios. If several individuals of appropriate mass and age were captured on one night, transmitters were attached to randomly chosen individuals. The battery life of each transmitter was approximately three weeks; however, most transmitters were removed by the bats in one to two weeks.

I tracked yearling and adult bats from 10 May through 17 June 1994, and from

14 May through 19 June 1995. I tracked juvenile and adult bats from 10 July through 11 August 1994, and from 15 July through 18 August 1995. Bats were not tracked on the night they were captured. On subsequent nights, bats were followed while foraging by one or two trackers, each with a Merlin 12 receiver (Custom Electronics, Urbana, IL) and 5-element Yagi antenna. Another observer, also with a receiver and antenna was stationed at the day-roost to record emergence and return times.

On nights when two trackers were available (May, July, and August 1995), the location of foraging bats was determined through triangulation. Observers recorded the compass bearing and signal strength for each bat at synchronized times, usually every 3-5 minutes, and at least once every 15 minutes. Compass bearings taken from standardized locations were used to triangulate the position of bats on a map of the Medicine Hat area overlain by a 250 m x 250 m grid. When only one tracker was available, he or she attempted to maintain contact with the bat at all times, noting signal strength and direction every 3-5 minutes. Bats were generally followed for the entire night, if possible. However, most bats spent at least part of the night out of radio-telemetry range.

The observer at the maternity colony recorded presence or absence of each bat, along with signal strength and fluctuation, at least once every 10 minutes from shortly after sunset until sunrise. Bats were monitored more frequently during peak emergence from the colony or when the signal fluctuated, indicating movement. It was usually possible to determine emergence time of each bat to within five minutes or less, and return times to within 10 minutes.

Foraging Time

I defined foraging time as the time that bats were away from the day-roost, usually the maternity colony, totalled over all foraging bouts over the night. Adult female bats from the Medicine Hat colonies have not been recorded night-roosting away from the maternity colony, except during storms (Wilkinson 1995). No juveniles or adults in 1994 or 1995 were observed night-roosting away from the colonies, so I assumed that a bat was active for the entire period during which she was away from the day-roost. For statistical purposes, foraging time was converted to the proportion of the night, defined as the time from sunset to sunrise, that the bat spent foraging. This value was arcsine-square-root transformed (Zar 1984).

To examine changes in foraging time with age of juvenile bats, I used a mixedmodel ANCOVA, with year as a fixed effect, and age in days and ambient temperature at emergence as covariates. As repeated observations were made for each individual, a random term for individual was nested in the term for year. Ambient temperature at emergence was estimated from hourly weather data issued by Environment Canada for the Medicine Hat Airport, and was defined as the temperature recorded closest in time to emergence of each bat.

To compare the foraging times of juvenile and adult *E. fuscus*, I used a mixedmodel ANCOVA, with age class and year as fixed effects, and ambient temperature at emergence as a covariate. Because few lactating adults were radioed in 1994, and few postlactating adults were radioed in 1995, I pooled telemetry data for lactating and post-lactating adults within each year, and compared foraging time among adults, preweaning juveniles and post-weaning juveniles. A random term for individual was nested in the age class-by-year interaction. As in all analyses, other interactions were removed from the model if not significant. A similar model was used to compare the foraging times of yearling and adult bats in 1994 and 1995.

Emergence Time

I defined emergence time as the time, in minutes after sunset, when a bat emerged for its first foraging bout. Data were inverse transformed. I used a mixedmodel ANCOVA to examine changes in emergence time of juvenile bats with age. The model included terms for year as a fixed effect, age and ambient temperature at emergence as covariates, and a random term for individual nested within year.

I also compared the emergence times of adults, pre-weaning juveniles and postweaning juveniles with ANCOVA. Terms for age class and year as fixed effects, and ambient temperature at emergence as a covariate, were included in the model. A random term for individual was nested in the interaction between age and year. I similarly compared log emergence time for yearling and adult bats in 1994 and 1995 using ANCOVA.

Time Foraging Out of Range

The study area, to the limits of radio-telemetry coverage, covered approximately 120 km² along the valley of the South Saskatchewan River (Wilkinson 1995). In 1995, the study area was expanded to include the valleys of Ross and Bullhead Creeks. Many bats, however, could not be detected in this area for at least part of each night. The time spent foraging out of range is important, because it meant that bats were foraging along the river valley more than 13 km from the maternity colonies, or possibly over prairie (Wilkinson 1995). For statistical comparisons, I calculated time foraging out of range as a proportion of the total time that the bat was either being tracked or searched for. This value was arcsin-squareroot transformed. I compared time out of range between age classes and years using ANCOVA, with ambient temperature at emergence as a covariate. A random term for individual was nested in the interaction between age class and year. Ambient temperature at emergence was included as a covariate.

Foraging Area

Minimum convex polygons were drawn around foraging locations as determined by triangulation on one night per bat in 1995. For most bats, only one night provided enough radio-telemetry data to delineate foraging area. I randomly chose one night if I was able to plot the foraging area for an individual on several nights. Only bats that were tracked for more than 45 minutes, or for the entire time spent foraging were used in this analysis. The area over which bats foraged during the observation period was compared between juveniles and adults with ANCOVA, with ambient temperature at emergence as a covariate.

Light Tagging

Chemoluminescent fishing lures (American Cyanamid Company, Charlotte, NC.; 0.15 g) were attached to the ventral surface of newly volant juvenile bats (< 28 days old), using Skinbond^R adhesive. Light tags emit light for approximately 2 h, and are visible up to 30 m away. Only bats netted on emergence were light-tagged. Bats were released, and activity noted by an observer speaking into tape recorders. The observer noted whether the bat was flying or had landed, and subjectively assessed whether the bat was flying in clutter (defined as within tree branches, or within 1 m of trees or buildings) or in open areas.

RESULTS

I radio-tagged a total of twenty-five bats in the summers of 1994 and 1995. A total of six adults and five juveniles were tagged in 1994, and seven adults and seven juveniles were tagged in 1995. A total of 177 bat-nights of telemetry data were obtained over the two summers.

In the spring seasons of 1994 and 1995, I radio-tagged a total of twenty bats. I tagged five yearlings and six adults in 1994, and five yearlings and four adults in 1995. A total of 84 bat-nights of telemetry data were obtained in the two springs.

Changes in the Foraging Behaviour of Juvenile Eptesicus fuscus with Age

Juvenile E. fuscus in Medicine Hat began to fly about three weeks after they

were born. Juveniles were first captured flying outside of the roost on 7 July 1994 and on 14 July 1995, corresponding to 19 and 21 days after the first pups were captured in the roost. The youngest known-aged juveniles captured outside the roost were 18 days old in 1994 and 21 days old in 1995.

I light-tagged a total of five juvenile bats on 18 July and 22 July 1995. One bat, aged 21 days, immediately landed and did not fly again for at least 1 hr. The other four bats, ranging in age from 21 to 25 days, either landed or flew out of range within 5 - 10 minutes of release, so I was not able to statistically analyse the time spent in open versus cluttered areas. However, juvenile bats flew almost exclusively in open areas over the observation period, and landed frequently. Because these bats often attempted to groom off the light tag after landing, it is unclear whether bats without light tags would have landed as frequently. Despite frequent landings, it did not appear that juvenile bats were using a 'flycatching' foraging strategy, as described by Buchler (1980) for *M. lucifugus*. Juvenile *E. fuscus* flew continuously for a period of at least several minutes while foraging.

Newly volant juveniles that carried radios also landed frequently, making as many as seven flights per night in 1994. Adults (n = 25 bat-nights) and juvenile bats older than 29 days (n = 28 bat-nights) did not make more than three flights per night. In 1995, none of the radio-tagged bats made more than three flights in a single night (n = 130 bat-nights). As bats aged they switched from making many short foraging bouts to fewer, longer foraging bouts, and the maximum time spent foraging per night increased (Fig. 4.1). There was a significant effect of the interaction between age and



Fig. 4.1. Foraging time, as a proportion of the night spent foraging, for juvenile *E. fuscus* in 1994 and 1995. Foraging time increases with age of juveniles.

temperature at emergence on time spent foraging by juvenile bats (F = 14.02, df = 1, 97, P < 0.001). Older juveniles were more sensitive to differences in temperature than were younger juveniles. Foraging times of juveniles did not differ between years (F =0.008, df = 1, 11.64, P > 0.9) but there were significant differences between the foraging times of individuals (F = 7.41, df = 10, 97, P < 0.001).

Emergence time of juvenile bats was also significantly related to age (Fig 4.2; F = 16.69, df = 1, 103, P < 0.001). Juveniles emerged sooner after sunset with increasing age. The term for individual was significant in the model (F = 3.24, df = 10, 103, P < 0.002), but there were no differences in emergence time between years (F = 2.01, df = 1, 11.69, P > 0.1).

Within a week after starting to fly, juvenile bats began to fly in the same areas as adults. Newly volant juvenile bats could be tracked from ESS for the duration of the night. These bats usually foraged within 20 m of the roost exit. Older juveniles switched from foraging close to the maternity colony to foraging along the South Saskatchewan River (see below). In 1994, two juveniles carrying radios first flew out of range of ESS at an age of 28 days. In 1995, juveniles (n = 3) were first tracked away from the maternity colony at ages ranging from 23 to 25 days. All juveniles were tracked to the South Saskatchewan River on their first flight away from ESS. A light-tagged individual aged 25 days also flew out of visual range towards the South Saskatchewan River in 1995.



Fig. 4.2. Emergence time, in minutes after sunset, for juvenile *E. fuscus* in 1994 and 1995. Juvenile bats emerged earlier with age.

Comparisons of Juveniles and Adults

Foraging Time

As compared to newly volant juvenile bats, adults and fully weaned juveniles made fewer, but longer foraging forays. Adults foraged for a substantial proportion of the night, even on cool nights. There was a significant effect of the interaction between age class and ambient temperature at emergence on the foraging time of bats in the summer (F = 3.85, df = 2, 145, P < 0.05). I used the ESTIMATE procedure in SAS (SAS Institute Inc. 1985) to compare the slopes of the relationship between ambient temperature and foraging time among the three age classes (Table 4.1). For all age classes, foraging time increased significantly with ambient temperature. The slope for post-weaning juveniles was significantly greater than was that for adults (Fig. 4.3). The slope for pre-weaning juveniles was intermediate and did not differ significantly from that for adults or post-weaning juveniles.

The proportion of the night spent foraging did not differ significantly between yearlings and adults (Table 4.2; F = 0.34, df = 1, 20.42, P > 0.5), or between years (F = 0.09, df = 1, 20.22, P > 0.7). The effect of temperature was significant (F = 39.73, df = 1, 63, P < 0.001). Bats foraged for longer on warm nights than on cold nights.

In both the spring and summer, the terms for individual, nested in the age-byyear interaction, were significant in the model (spring: F = 2.8, df = 16, 63, P < 0.01; summer: F = 3.95, df = 23, 145, P < 0.001). Individual bats differed from one another in the amount of time they spent foraging per night. Table 4.1. Comparison of the slopes of foraging time versus ambient temperature for preweaning juveniles, post-weaning juveniles and adults. Data for foraging time were arcsin-square-root transformed. P_{slope} indicates whether the slope of the regression line is significantly different from zero. Slopes followed by the same letter are not significantly different. *** = P < 0.001.

Age Class	Slope	SE	п	P _{slope}
Pre-weaning Juveniles	0.039 ^{ab}	0.010	52	***
Post-weaning Juveniles	0.063ª	0.009	60	***
Adults	0.032 ^b	0.008	65	***


Fig 4.3. Changes in total time foraging, as a proportion of the time between sunset and sunrise, with ambient temperature. Data for post-weaning juveniles (solid squares) and adults (open squares) are plotted.

Table 4.2. Foraging times and emergence times of yearling and adult bats in the springs of 1994 and 1995. Emergence time is in minutes after sunset. Foraging time is time away from the day-roost as a proportion of total night length.

.

.

•

.

.

...

Age Class	Emergence	SE	n	Foraging	SE	n	=
Yearling	66.6	4.8	45	0.23	0.02	40	
Adults	60.1	3.6	49	0.25	0.02	44	

Emergence Time

I compared the emergence time of pre-weaning juveniles, post-weaning juveniles, and adults, but did not find a significant difference in emergence time among age classes (Fig. 4.4; F = 0.39, df = 2, 32.93, P > 0.6). There were no significant differences in emergence time between years (F = 2.52, df = 1, 39.91, P > 0.1) and ambient temperature was not a significant influence (F = 2.43, df = 1, 153, P > 0.1). The term for individual, nested within the age-by-year interaction, was significant (F = 2.39, df = 24, 153, P < 0.001).

The emergence times of yearling and adult bats were not significantly different (Table 4.2; F = 0.32, df = 1, 18.92, P > 0.5). Emergence times also did not differ between years (F = 1.49, df = 1, 18.72, P > 0.2), or with ambient temperature (F = 0.18, df = 1, 73, P > 0.8). The term for individual was significant (F = 4.99, df = 16, 73, P < 0.001).

Foraging Location

The data for time spent foraging out of range were not normally distributed, despite various attempts at transformation. Results from ANCOVA should therefore be interpreted with caution. There was a significant effect of age class on the proportion of the total time spent out of range (F = 7.61, df = 2, 23.91, P < 0.01). Young juvenile bats were out of telemetry range for a significantly smaller proportion of total time foraging (Table 4.3). The effects of ambient temperature at emergence and of year were not significant (temperature: F = 1.23, df = 1, 108, P > 0.2; year: F



Fig. 4.4. Emergence time (minutes after sunset) of pre-weaning juvenile (n = 53), postweaning juvenile (n = 63), and adult (n = 68) *E. fuscus* in 1994 and 1995. Error bars are \pm SE.

Table 4.3. Mean proportion of the total time tracked that bats were out of radio-telemetry range in 1994 and 1995. Values followed by the same letter are not significantly different.

 Age Class	Foraging Time	SE	n	
 Pre-weaning Juvenile	0.37ª	0.09	38	
Post-weaning Juvenile	0.91 ^b	0.03	44	
Adults	0.90 ^b	0.03	55	

.

= 2.19, df = 1, 25.24, P > 0.1).

The areas covered by juvenile and adult bats while foraging were not significantly different (F = 0.96, df = 1, 4, P > 0.3). Due to the small sample size, it is difficult to make conclusions regarding home ranges. There was a trend for juveniles to have larger home ranges than did adults (Table 4.4). The effect of ambient temperature was not significant in the model (F = 0.07, df = 1, 4, P = 0.80).

DISCUSSION

Development of Flight and Foraging

The early stages of flight and foraging of newly volant *E. fuscus* were similar to those described for newly volant juvenile *M. lucifugus* in upstate New York (Buchler 1980). Juveniles of both species begin to fly at approximately 3 weeks, and initially make many short flights in the vicinity of the maternity colony. Buchler (1980) found no evidence of successful foraging by newly volant *M. lucifugus*. In this study, I found chitinous material in the fecal pellets of the youngest volant juvenile *E. fuscus* (see Chapter 2).

For the first several nights of foraging, juvenile *M. lucifugus* initially use a 'flycatching' strategy. Young juveniles perch on a tree trunk and make forays into forest clearings after detecting potential prey (Buchler 1980). I did not observe a similar behaviour in juvenile *E. fuscus*. Light-tagged juvenile *E. fuscus* foraged continuously for several tens of seconds to several minutes, and were never observed

Age Class	Foraging Area (km ²)	SE	n	
Juveniles	4.44	0.48	4	
Adults	2.90	1.34	3	

5

Table 4.4. Mean foraging areas of juvenile and adult E. fuscus in 1995.

•

.

.

.

to make brief forays from a perch.

Within a week after starting to fly, radio-tagged juvenile bats foraged along the South Saskatchewan River. Foraging duration increased gradually, and juveniles gradually began to emerge earlier with age. By the time bats returned from hibernation, there were no discernible differences between the foraging behaviour of yearling and adult bats. The foraging behaviour of juvenile *M. lucifugus* also gradually merges with that of adults (Buchler 1980).

Emergence and Location of Foraging Juvenile and Adult Big Brown Bats

Although juvenile bats emerged earlier with increasing age, emergence time did not differ among pre-weaning juveniles, post-weaning juveniles, and adults. Because each age class of juveniles includes bats that may differ in age by as much as two weeks, much of the variation in emergence time with age was lost due to the breadth of each age class. Support for either the acoustic clutter hypothesis or the social facilitation hypothesis on the basis of emergence time is therefore equivocal.

Newly volant juveniles fly and forage in the vicinity of the maternity colonies, while older juveniles and adults forage along the South Saskatchewan River. This supports the hypothesis that newly volant juveniles avoid the activity of older juveniles and adults (Buchler 1980). However, it is also consistent with the hypothesis that inexperienced juveniles may be unable to fly long distances, and thus cannot forage further from the colony.

After their first few days of flight, foraging juveniles were tracked to the same

general area as adults. The first foraging bouts away from the maternity colonies were to the South Saskatchewan River, indicating that juveniles did not fly randomly from the colony, but were using some cue to find profitable foraging areas. This may have been by following their mothers or other bats (Buchler 1980), or by using other cues, such as the calls of frogs or the sound of running water (Buchler and Childs 1981). Bats were often seen emerging from or returning to the colony in pairs (pers. obs.), although this may result from bottlenecks at the colony, rather than social behaviour (Kalcounis and Brigham 1994). Even with random entrance and exit patterns, some 'pairs' of bats would be observed. The composition of putative pairs of bats could not be determined, but if some members of the colony follow others to foraging sites, this behaviour should also be exhibited by juveniles. The general pattern of emergence and foraging location provides little support for the acoustic clutter hypothesis, but does not allow for it to be rejected either. Social interactions may be important in determining when and where older juvenile bats forage, by providing cues by which juvenile bats may find profitable patches of prey. These hypotheses are not mutually exclusive (Buchler 1980), and newly volant juvenile bats may switch from avoiding to maintaining contact with conspecifics as flight ability and experience at echolocation improve.

Prey Density as a Constraint on Foraging Time

There was no indication that juvenile bats attempted to maximize nightly energetic or nutrient intake by foraging for longer than adults. Rather, juveniles foraged for less time than adults on cool nights, and for the same length of time on warmer nights. Ambient temperature was also a significant influence on the amount of time spent foraging by individuals in all age classes. These results suggest that the time available for foraging may be limited by declining prey density through the night.

A significant positive relationship between ambient temperature and foraging duration has been found previously for *E. fuscus* at this site (Wilkinson 1995). Correlation between insect availability and foraging time has also been reported for hoary bats, *Lasiurus cinereus*, in Manitoba (Barclay 1985b). Many other studies have found that insectivorous bats do not emerge below a threshold temperature (Leonard and Fenton 1983, Avery 1985, Wai-Ping and Fenton 1989, Rydell 1989, Audet 1990, Grinevitch *et al.* 1995). As insect abundance and activity are related to ambient temperature (Ward and Stanford 1982), an examination of how foraging time changes with temperature would be informative.

An Energetic Model of Bat Foraging

The relationship between foraging decisions and insect density, and consequently ambient temperature, may be expressed as an energetic model. For example, the decision whether to emerge depends on whether the expected net returns of foraging exceed those from remaining in the roost and entering torpor (Avery 1985, Rydell 1989). As the gains of foraging are a function of feeding rate, which is a function of insect density, there is a threshold insect density below which bats should not emerge (Avery 1985, Rydell 1989). A similar approach may be useful in illustrating when bats should return to the roost, rather than continue foraging. Ambient temperature declines through the night (Fig. 4.5), and consequently, prey availability may decline to a point where it is no longer profitable to forage. An energetic model incorporating foraging efficiency and flight costs may be used to predict how threshold prey densities for foraging change in response to changes in these variables. Because juvenile and adult *E. fuscus* differ in both energy intake and the cost of flight (see Chapters 2 and 3), such a model may therefore be useful in elucidating observed differences in behaviour between juvenile and adult bats.

It is profitable for bats to continue to forage so long as the net benefits of foraging (gains of foraging, G_f , minus the costs of foraging, C_f) exceed the net benefits of returning to the roost ($G_r - C_r$) (Avery 1985). There is no gain to be had from returning to the roost, such that, by rearranging this inequality, bats should forage so long as the gains of foraging are greater than the difference between the cost of foraging and the cost of roosting (from Avery 1985):

$$(Inequality \ 4.1) \qquad \qquad G_f > C_f - C_r$$

The costs associated with roosting are very small. C_r for a 9.2 g *Eptesicus* nilssoni at 10 °C is 14 J/h (calculated from Hock 1951 in Rydell 1989). For 17 - 23 g *E. fuscus*, this value would be larger, but still negligible compared to flight costs of 10 kJ/h (see below). Therefore, to simplify the model, I have assumed that the cost of



Fig. 4.5. Decline in ambient temperature during the night for 5 randomly selected warm nights (filled squares) and 5 randomly selected cool nights (open squares). The least-squares regression equation for warm nights is $(468.54 - 107.61*ln(x))^{1/2}$, and for cool nights is $(0.01013 - 0.02064*x^{-1/2})^{-1}$.

.

roosting is zero. This yields the following inequality, for which foraging remains profitable when true:

$$(Inequality 4.2) G_f > C_f$$

The rate of prey capture declines through the night as temperature declines. I have assumed that insect density (N_p) is linearly proportional to ambient temperature T_a :

$$(Equation \ 4.1) \qquad \qquad N_p = a + bT_a$$

where a and b are constants relating ambient temperature to prey availability.

Number of prey captured (N_{et}) per unit time (t) is a function of number of prey available (N_p) and handling time (t_h) following equation 4.2 (type II functional response: Holling 1959).

$$(Equation \ 4.2) \qquad \qquad N_{et} = \underbrace{cN_{p}t}_{1 \ + \ cN_{p}t_{h}}$$

where c is a constant for search efficiency.

Energy intake (E_{ii}) is directly proportional to the rate of prey capture. Energy intake per unit time:

$$(Equation \ 4.3) \qquad \qquad E_{it} = mE_pN_{et}$$

where *m* is a coefficient for the assimilation of energy from prey, and E_p is the energetic value of each prey item. The assimilation efficiency for *Myotis* spp. may range from 0.91 for mealworm (*Tenebrio molitor*) larvae (O'Farrell *et al.* 1972), to less than 0.70 for moths (Barclay *et al.* 1991). For insects that occur naturally in the diet of *E. fuscus*, particularly beetles, a low assimilation efficiency, comparable to that of moths, is likely.

The cost of foraging per unit time (E_{ft}) is assumed to be constant. This cost results from the direct energetic cost of flight. Assuming that the cost of foraging equals the power required for steady, forward flight (P_{mp}) , then E_{ft} increases with increasing mass (M) as per Thomas (1975):

$$(Equation \ 4.4) \qquad P_{mp} = 58.4 M^{0.79}$$

(Equation 4.5)
$$E_{ft} = P_{mp}t$$

Rate of energy intake is highest just after emergence, and is higher on warm nights than on cold nights. As prey density declines, energy intake (E_{it}) eventually falls below the expenditures resulting from flight and foraging (E_{ft}) (Fig. 4.6). After this time, bats are using more energy for flight than they can acquire and should not continue to forage. The predicted threshold temperature at which bats should return to the roost is therefore a function of search and handling efficiencies and flight costs.

In this model I have assumed that prey density is linearly proportional to ambient temperature, that bats follow a type II functional response, and that cost of flight is constant over the night. Although the first of these assumptions is undoubtedly unrealistic, the model should be robust to changes in the relationship between ambient temperature and prey density so long as prey density declines with ambient temperature. Although many species of insects may exhibit an all-or-none response to temperature (Ward and Stanford 1982), dropping out of the assemblage below a threshold temperature, the thresholds likely differ among species, and total insect density should therefore be a relatively continuous function of ambient temperature. Rydell (1989) found that insect density in southern Sweden decreased continuously with ambient temperature.

The feeding rate of pregnant northern bats (*E. nilssoni*) follows a type Π functional response (Rydell 1989). The model should be robust to changes in the functional responses of juvenile and adult bats, so long as the rate of energy intake is a function of handling time.

Finally, cost of flight is unlikely to remain constant over the night. Foraging bats increase in mass over the night, and flight costs should increase correspondingly. The qualitative predictions of the model should be robust to violations of this assumption, however, because increased flight costs will further shorten the period of the night when it is profitable for bats to forage.

I was unable to estimate the value of constants a, b, and c in equations 4.1 and



Fig 4.6. Hypothesized relationship between prey availability and foraging time. As prey encounter rate declines through the night, it eventually reaches a threshold where the energetic returns from foraging equal the cost of flight. After this threshold, it is no longer profitable for bats to forage.

.

4.2, because of the biases inherent in insect sampling. However, qualitative predictions of this model may be tested. Increased handling time should result in bats truncating foraging bouts earlier in the night. Therefore, bats that are less efficient foragers should forage for less time when prey availability is limiting. A further prediction of the model is that as cost of foraging increases, if handling time remains constant, foraging time should decrease. This may be tested by experimentally manipulating the weight of radio-telemetered bats.

A number of natural experiments may test the influences of encounter rate and flight costs on foraging time. During pregnancy, female bats increase mass, and therefore flight costs. Following this model, I predict that pregnant bats should forage for less time than non-reproductive females. Foraging time for female *E. nilssoni* decreases in late pregnancy, resulting in a negative daily energy budget (Rydell 1993). The predicted foraging times of juvenile and adult bats, which differ in both flight costs and encounter rate, should also differ according to the model (see below).

Foraging Times of Juvenile and Adult Big Brown Bats

I propose that the relatively poor foraging efficiency of juveniles compared with adults results in juveniles gaining lower returns from foraging than do adults. As a result, the costs of foraging exceed the gains at a higher prey density for juveniles than for adults, and juveniles should therefore return to the roost earlier than do adults when prey availability is limiting. On warm nights, however, foraging by both juveniles and adults may not be limited by prey availability, but rather set by daily energy and nutrient requirements. Furthermore, by reducing flight costs, juveniles can increase the length of the period over which foraging remains profitable. Otherwise, juvenile bats may not be able to meet minimum daily energy and nutrient requirements on some nights.

For adults in 1994, the cost of forward flight (Equations 4.4 and 4.5) was 181.01 J/min, based on mass. For juveniles the cost of forward flight was 147.28 J/min. In 1995, the cost of forward flight for adults was 156.20 J/min, and for juveniles was 141.46 J/min. To balance foraging costs, an adult bat foraging on mealworm-sized beetles (see Appendix 2) would need to capture 0.34 beetles per minute in 1994 and 0.30 beetles per minute in 1995 (Equation 4.3), with an assimilation efficiency of 0.70 (Barclay *et al.* 1991). Juveniles would need to capture 0.28 beetles per minute in 1994 and 0.27 beetles per minute in 1995.

By rearranging equation 4.2, the threshold product of search efficiency and prey density is obtained.

$$(Equation \ 4.6) \qquad \qquad cN_p = \frac{N_{et}}{1 - t_h N_{et}}$$

Using handling times from the first feeding in Chapter 2, the threshold value of cN_p below which bats should cease foraging is 0.40 beetles/min for both adults and juveniles in 1994, 0.34 beetles/min for adults in 1995, and 0.38 beetles/min for juveniles in 1995. If search efficiency (c) is the same for juveniles and adults and over the two years, then adults should have returned to the roost at the same time as

juveniles in 1994, while in 1995, juveniles should have returned to the roost earlier than adults. The activity patterns of bats fit the qualitative predictions of the model in 1995 but not in 1994. On cool nights, juveniles returned to the roost earlier than did adults in both years.

A critical assumption I have made is that search efficiency is the same for juvenile and adult bats. If juveniles are less efficient at locating prey than are more experienced adults, this would result in the threshold prey density at which to cease foraging being higher for juveniles. Consequently, juveniles should return earlier in the night than would be predicted if search efficiencies were the same.

Furthermore, I assumed that bats were foraging entirely on beetles, which is a reasonable assumption for most adults. However, a large proportion of the diet of many bats, especially juveniles in both years and adults in 1995, consists of other insects (see Chapter 2). Predicted foraging times for bats capturing other insects depend on the handling time and energetic content of these insects, and the relationship between ambient temperature and insect densities. However, these values are not available for insects other than beetles. In general, decreased handling time should reduce the differences in foraging time between adults and juveniles.

By the time bats return from hibernation, search and handling efficiencies of young bats should be similar to those of adults. The diet of yearlings and adults in spring do not differ (see Chapter 2). Therefore, yearlings should be able to forage for as long or longer than adults, depending on flight costs. I did not find any significant differences in foraging times between juveniles and adults. Rydell (1993) also predicted that younger female *E. nilssoni* would forage for longer than would adults to compensate for poor foraging efficiency, but did not find differences in foraging time with age. He suggested that the time available for foraging was limited (Rydell 1993), which is consistent with predictions from the above model. However, Barclay (1985a) found that juvenile *Scotophilus leucogaster* in Africa foraged for longer than did adults. Prey availability may not be as important a constraint for tropical bats as it is for bats in temperate regions. Ambient temperature in tropical or warm temperate regions may not drop far enough during the night for insect availability to fall below the threshold level. In Barclay's (1985a) study, ambient temperature remained above 17 °C (R.M.R. Barclay, pers. comm.).

An alternative explanation for the short foraging times of juveniles is that juveniles require less energy than do adults. Flight costs are lower for juveniles than for adults (see Chapter 3). If it is not advantageous for juveniles to accumulate further mass, because it would increase flight costs, juveniles may be able to meet their daily energy requirements by consuming fewer insects than do adults. The poorer foraging efficiency of juveniles would therefore be compensated for by their lower flight costs (Hughes *et al.* 1995). This may be the case on warm nights, if prey availability is not limiting. However, differences in daily energy requirements alone do not explain why juveniles should forage for less time than do adults on cool nights, but not on warm nights. Furthermore, while flight costs of juveniles are lower than for adults, daily energy requirements of juveniles are not known. Juvenile *E. fuscus* rarely use long bouts of torpor (S. McNalley, unpublished data), and may therefore expend significantly more energy than do adults during the day.

Conclusions

Numerous intrinsic and extrinsic factors influence the foraging behaviour of juvenile and adult big brown bats. The development of foraging is rapid. Within a week after starting to fly, juveniles forage at the same time and in the same location as adults. Juveniles may be less efficient than adults at locating and handling prey, and may follow adults to profitable locations. The evidence for this, however, is not conclusive. Inefficiency at foraging by juveniles may result in short foraging times being the optimal strategy for juveniles. As a consequence, juveniles may be less able than are adults to accumulate sufficient energy and nutrient reserves to satisfy both short- and long-term requirements. High juvenile mortality both during the pre-hibernation period and over winter may therefore be a consequence of developmental constraints on foraging time.

The foraging strategies of juvenile *E. fuscus* are influenced by morphological development and learning. Juvenile *E. fuscus* took longer than did adults to manipulate and ingest beetles. Longer handling times for juveniles may reduce their rate of prey capture relative to adults, and influence the degree to which juvenile *E. fuscus* are selective in terms of prey and habitat. Juvenile and adult big brown bats differed in the composition, diversity, and volume of prey captured. Although not conclusive, these results suggest that juvenile *E. fuscus* forage opportunistically, while adults may be selective, either by rejecting less profitable prey, or by foraging in higher quality habitats than juveniles.

Juvenile *E. fuscus* did not differ from adults in wing shape or size, or in echolocation call structure. As in birds, skeletal growth and flight in bats appear to be incompatible (Charlesworth 1980). Despite similarities in wing size between juvenile and adult *E. fuscus*, however, the lower body mass of juveniles allows them to reduce flight costs significantly. Juveniles did not accumulate more mass in 1994, when prey availability was high, than in 1995, which indicates that there may be a cost to further increasing mass.

The costs of increasing mass include a reduction in the time over which foraging is profitable, given declining prey availability through the night. This may be particularly important for juveniles, for which the rate of energy intake is low because of poor handling abilities, and perhaps lower prey detection and capture abilities. Higher flight costs may increase the risk of the rate of energy intake decreasing below flight costs prior to acquiring enough energy and nutrients to satisfy minimum daily requirements.

Activity patterns of juveniles may be influenced by foraging inefficiency in a number of other ways. Location and time spent foraging change with age, as bats gain experience in flight and foraging. The echolocation calls emitted by conspecifics may hinder foraging by newly-volant juveniles, but provide information on profitable foraging sites to older juveniles.

In this study, I have examined the influence of developmental constraints on the foraging strategies of juvenile bats themselves. Developmental constraints, however, may also influence the long-term foraging and life-history strategies of bats. For example, early experience at foraging may influence the foraging behaviour of adults (Yoerg 1994), and juvenile survivorship and reproduction (Burnett and Kunz 1982, MacLean 1986, Heinsohn 1991, Rydell 1993). The physiological and developmental trade-offs faced by juvenile animals as a result of foraging inefficiency will ultimately influence the evolution of life-histories (Stearns 1992).

Compared with other eutherian mammals, bats exhibit delayed maturation (Read and Harvey 1989). While most mammals reach sexual maturity before completion of morphological development (Sadlier 1969), most bats delay sexual maturity until after they are morphologically indistinguishable from adults (Tuttle and Stevenson 1982). Age at sexual maturity of female bats ranges from two months in *Pipistrellus mimus* (Isaac and Marimuthu 1996) to seven years in *Rhinolophus* *ferrumequinum* (Ransome 1990). In Medicine Hat, the proportion of yearling female *E. fuscus* that are reproductive is variable from year to year, ranging from 0-90% of individuals (Holroyd 1993, unpublished data). Over 90% of adults are reproductive in all years (unpublished data).

Delayed maturation in bats probably reflects a number of factors. Most morphological development occurs before juvenile bats begin to fly, and flight may be a constraint on the life-history evolution of flying vertebrates. Juvenile birds also delay sexual maturity until after finishing morphological development (Charlesworth 1980). Demographic factors may also be important. Mortality of adults is low, reflecting low rates of predation, especially in temperate regions (Erkert 1982, Kalcounis and Brigham 1994). However, mortality of juveniles is relatively high (Tuttle and Stevenson 1982, Burnett and Kunz 1982, Ransome 1990). The evolution of delayed maturity may have been favoured if early maturation carries a cost of increasing risk of juvenile mortality (Stearns 1992).

Age of maturity and maintenance of female reproductive activity is dependant on the acquisition of fat reserves in mammals (Frisch 1984). Delayed maturity of bats may reflect failure to achieve a threshold body condition for reproduction over the first foraging season (Racey 1982, Speakman and Racey 1986, McWilliam 1987). This may be a direct consequence of foraging inefficiency, as juveniles may not be able to accumulate energy and nutrient reserves as rapidly as can adults. Accumulating fat reserves, however, also increases flight costs, possibly increasing the risk of mortality for juvenile bats. Juvenile bats may therefore face a trade-off between current survival and future reproduction.

The costs associated with delayed maturation should be low for female bats. Yearling female bats have smaller offspring and give birth later than do adults (Schowalter et al. 1979, Ransome 1990). The offspring of young female *R*. *ferrumequinum* start to fly and forage later than do those of older females (Ransome 1990). Given that a yearling female bat has a long remaining lifespan, she should take few risks for any given offspring (Schaffer 1974).

Natural selection has favoured the rapid acquisition of adult form and function by juvenile *E. fuscus*. However, juvenile *E. fuscus* begin to fly and forage before foraging abilities are equal to those of adults. As a consequence of constraints related to development, juveniles capture fewer and different prey than do adults, and forage for less time than do adults when prey availability is low. Juveniles do not accumulate as much mass as do adults in the post-weaning stage, which, rather than being a direct consequence of foraging inefficiency, allows juveniles to reduce flight costs, thereby compensating somewhat for their reduced rate of energy intake. In the longer term, however, failure to accumulate further mass may be costly to an individual in that it may limit the opportunity for reproduction the following year.

- Alatalo, R. V., L. Gustaffson and A. Lundberg. 1984. Why do young passerine birds have shorter wings than older birds? Ibis 126: 410-415.
- Aldridge, H. D. J. N. and R. M. Brigham. 1988. Load carrying and manoeuvrability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. J. Mamm. 69: 379-382.
- Aldridge, H. D. J. N. and I. L. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. J. Anim. Ecol. 56: 763-778.
- Anthony, E. L. P. and T. H. Kunz. 1977. Feeding strategies of the little brown bat, Myotis lucifugus, in southern New Hampshire. Ecology 58: 775-786.
- Audet, D. 1990. Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). J. Mamm. 71: 420-427.
- Avery, M. I. 1985. Winter activity of pipistrelle bats. J. Anim. Ecol. 54: 721-738.
- Baagoe, H. J. 1988. The Scandanavian bat fauna: adaptive wing morphology and free flight in the field. Pp. 57-74 in Recent advances in the study of bats (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.). Cambridge University Press: Cambridge. 470 pp.
- Barbour, R. W. and W. H. Davis. 1969. Bats of America. University Press of Kentucky: Lexington. 286 pp.
- Barclay, R. M. R. 1982. Interindividual use of echolocation calls: eavesdropping by bats. Behav. Ecol. Sociobiol. 10: 271-275.
- Barclay, R. M. R. 1985a. Foraging behavior of the African insectivorous bat, *Scotophilus leucogaster*. Biotropica 17: 65-70.
- Barclay, R. M. R. 1985b. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. Can. J. Zool. 63: 2507-2515.
- Barclay, R. M. R. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. Am. Nat. 144: 1021-1031.

- Barclay, R. M. R. and R. M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivores so small? Am. Nat. 137: 693-703.
- Barclay, R. M. R. and R. M. Brigham. 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. Anim. Behav. 48: 1013-1021.
- Barclay, R. M. R., M. A. Dolan, and A. Dyck. 1991. The digestive efficiency of insectivorous bats. Can. J. Zool. 69: 1853-1856.
- Bradbury, J. W. and S. L. Vehrencamp. 1977. Social organization and foraging in emballonurid bats. IV. Parental investment patters. Behav. Ecol. Sociobiol. 2: 19-29.
- Breitwisch, R., M. Diaz, and R. Lee. 1987. Foraging efficiencies and techiques of juvenile and adult northern mockingbirds (*Mimus polyglottos*). Behaviour 101: 225-234.
- Brigham, R. M. 1990. Prey selection by big brown bats (*Eptesicus fuscus*) and common nighthawks (*Chordeiles minor*). Am. Midl. Nat. 124: 73-80.
- Brigham, R. M. and A. C. Brigham. 1989. Evidence for association between a mother bat and its young during and after foraging. Am. Midl. Nat. 121: 205-207.
- Brigham, R. M. and M. B. Saunders. 1990. The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. Northwest Sci. 64: 7-10.
- Brown, P. E., T. W. Brown and A. D. Grinnell. 1983. Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. Behav. Ecol. Sociobiol. 13: 287-298.
- Buchler, E. R. 1980. The development of flight, foraging, and echolocation in the little brown bat (*Myotis lucifugus*). Behav. Ecol. Sociobiol. 6: 211-218.
- Buchler, E. R. and S. B. Childs. 1981. Orientation to distant sounds by foraging big brown bats (*Eptesicus fuscus*). Anim. Behav. 29: 428-432.
- Buckley, F. G. and P. A. Buckley. 1974. Comparative feeding ecology of wintering adult and juvenile royal terms (Aves: Laridae, Sterninae). Ecology 55: 1053-1063.

- Burnett, C. D. and T. H. Kunz. 1982. Growth rate and age estimation in *Eptesicus* fuscus and comparison with *Myotis lucifugus*. J. Mamm. 63: 33-41.
- Carey, H. V. and P. Moore. 1986. Foraging and predation risk in yellow-bellied marmots. Amer. Midl. Nat. 116: 267-275.
- Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press: Cambridge.
- Christian, J. J. 1956. The natural history of a summer aggregation of big brown bats, *Eptesicus fuscus fuscus*. Am. Midl. Nat. 55: 66-95.
- Cresswell, W. 1994. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? J. Anim. Ecol. 63: 589-600.
- Davies, N. B. and R. E. Green. 1976. The development and ecological significance of feeding techniques in the reed warbler (*Acrocephalus scirpaceus*). Anim. Behav. 24: 213-229.
- Davis, R. 1969. Growth and development of young pallid bats, *Antrozous pallidus*. J. Mamm. 50: 729-736.
- de Fanis, E. and G. Jones. 1995. Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat *Plecotus auritus*. J. Zool., Lond. 235: 85-97.
- Erkert, H. G. 1982. Ecological aspects of bat activity rhythms. Pp. 201-242 in Ecology of bats (T. H. Kunz, ed.). Plenum Press: New York. 425 pp.
- Ewing, W. G., E. H. Studier, and M. J. O'Farrell. 1970. Autumn fat deposition and gross body composition in three species of *Myotis*. Comp. Biochem. Physiol. 36: 119-129.
- Fenton, M. B. 1984a. Sperm competition? The case of vespertilionid and rhinolophid bats. Pp. 573-587 in Sperm competition and the evolution of animal mating systems (R. L. Smith, ed.). Academic Press: Orlando.
- Fenton, M. B. 1984b. Echolocation: implications for ecology and evolution of bats. Quart. Rev. Biol. 59: 33-53.
- Fenton, M. B. 1994. Echolocation: its impact on the behaviour and ecology of bats. Ecoscience 1: 21-30.

- Fenton, M. B. and G. P. Bell. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). Can. J. Zool. 57: 1271-1277.
- Freeman, P. W. 1981. Correspondence of food habits and morphology in insectivorous bats. J. Mamm. 62: 166-173.
- Frank, C. L. 1992. The influence of dietary fatty acids on hibernation by goldenmantled ground squirrels (*Spermophilus lateralis*). Physiol. Zool. 65: 906-920.
- Frisch, R. E. 1984. Body fat, puberty and fertility. Biol. Rev. 59: 161-188.
- Fullard, J. H., C. Koehler, A. Surlykke and N. L. McKenzie. 1991. Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in southwestern Australia. Aust. J. Zool. 39: 427-438.
- Funakoshi, K. and T. A. Uchida. 1981. Feeding activity during the breeding season and postnatal growth in the Namie's frosted bat, Vespertilio superans superans. Jap. J. Ecol. 31: 67-77.
- Gatz, A. J., Jr. 1979. Community organization in fishes as indicated by morphological features. Ecology 60: 711-718.
- Gould, J. P. 1974. Risk, stochastic preference, and the value of information. J. Econ. Theory 8: 64-84.
- Goss-Custard, J. D., S. E. A. le V. dit Durell, S. McGrorty and C. J. Reading. 1982. Use of mussel, *Mytilus edulis*, beds by oystercatchers, *Haematopus ostralegus*, according to age and population size. J. Anim. Ecol. 51: 543-554.
- Grant, J. W. A. and D. L. G. Noakes. 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salevlinus fontinalis*. Can. J. Fish. Aquat. Sci. 44: 1390-1396.
- Griffin, D. R. 1958. Listening in the dark. Yale University Press: New Haven. 413 pp.
- Griffith, L. A. and J. E. Gates. 1985. Food habits of cave-dwelling bats in the central Appalachians. J. Mamm. 66: 451-460.
- Grinevitch, L., S. L. Holroyd, and R. M. R. Barclay. 1995. Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. J. Zool., Lond. 235: 301-309.

Habersetzer, J., and G. Marimuthu. 1986. Ontogeny of sounds in the echolocating bat *Hipposideros speoris*. J. Comp. Physiol. 158A: 247-257.

•

- Hamilton, I. M. and R. M. R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). Can. J. Zool. 72: 744-749.
- Heinsohn, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. Am. Nat. 137: 864-881.
- Heppleston, P. B. 1970. Anatomical observations on the bill of the oystercatcher (*Haematopus ostralegus*) in relation to feeding behaviour. J. Zool., Lond. 161: 519-524.
- Hock, R. J. 1951. The metabolic rates and body temperatures of bats. Biol. Bull. 101: 289-299.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entom. 91: 385-398.
- Holmes, W. G. 1984. Predation risk and foraging behavior of the hoary marmot in Alaska. Behav. Ecol. Sociobiol. 15: 293-302.
- Holroyd, S. L. 1993. Influences of some extrinsic and intrinsic factors on reproduction by big brown bats (*Eptesicus fuscus*) in southeastern Alberta. M.Sc. Thesis, University of Calgary.
- Hoying, K. M. 1983. Growth and development of the eastern pipistrelle bat, *Pipistrellus subflavus*. M.A. Thesis, Boston University.
- Hughes, P. M., J. M. V. Rayner, and G. Jones. 1995. Ontogeny of 'true' flight and other aspects of growth in the bat *Pipistrellus pipistrellus*. J. Zool., Lond. 235: 291-318.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.
- Isaac, S. S. and G. Marimuthu. 1996. Postnatal growth and age estimation in the Indian pygmy bat *Pipistrellus mimus*. J. Mamm. 77: 199-204.
- Jaeger, R. G., J. A. Wicknick, M. R. Griffis, and C. D. Anthony. 1995. Socioecology of a terrestrial salamander: juveniles enter adult territories during stressful foraging periods. Ecology 76: 533-543

- Jones, G. and T. Kokurewicz. 1994. Sex and age variation in echolocation calls and flight morphology of Daubenton's bat *Myotis daubentonii*. Mammalia 58: 41-50.
- Jones, G. and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Phil. Trans. R. Soc. Lond. B 346: 445-455.
- Jones, G. P. M. Hughes, and J. M. V. Rayner. 1991. The development of vocalizations in *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during post-natal growth and the maintenance of individual vocal signatures. J. Zool., Lond. 225: 71-84.
- Jones, G., P. L. Duverge, and R. D. Ransome. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. Symp. Zool. Soc. Lond. 67: 309-324.
- Jones, G., M. Morton, P. M. Hughes, and R. M. Budden. 1993. Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. J. Zool., Lond. 230: 385-400.
- Kalcounis, M. C. 1995. Roost-site selection by big brown bats. M.Sc. Thesis, University of Regina.
- Kalcounis, M. C. and R. M. Brigham. 1994. Impact of predation risk on emergence by little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae), from a maternity colony. Ethology 98: 201-209.
- Kalko, E. K. V. and H.-U. Schnitzler. 1993. Plasticity in echolocation signals of European pipistrelle bats in search flight: implications for habitat use and prey detection. Behav. Ecol. Sociobiol. 33: 415-428.
- Keeler, J. O. and E. H. Studier. 1992. Nutrition in pregnant big brown bats (*Eptesicus fuscus*) feeding on June beetles. J. Mamm. 73: 426-430.
- Kick, S. A. 1982. Target-detection by the echolocating bat, *Eptesicus fuscus*. J. Comp. Physiol. 145: 431-435.
- Kleiman, D. G. 1969. Maternal care, growth rate and development of the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*), and serotine (*Eptesicus serotinus*) bats. J. Zool., Lond. 157: 182-211.
- Krebs, C. J. 1989. Ecological methodology. Harper and Row: New York. 654 pp.

- Kunz, T. H. 1973. Population studies of the cave bat (*Myotis velifer*): reproduction, growth, and development. Occ. Pap. Mus. Nat. Hist. Univ. Kans. 15: 1-43.
- Kunz, T. H. 1974. Reproduction, growth and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. J. Mamm. 55: 1-13.
- Kunz, T. H. 1982. Roosting ecology. Pp. 1-56 in Ecology of bats (T. H. Kunz, ed.). Plenum Press: New York. 425 pp.
- Kunz, T. H. and E. L. P. Anthony. 1982. Age estimation and post-natal growth in the bat *Myotis lucifugus*. J. Mamm. 63: 23-32.
- Kunz, T. H. and J. O. Whitaker. 1983. An evaluation of fecal analysis for determining food habits of insectivorous bats. Can. J. Zool. 61: 1317-1321.
- Kurta, A. and R. H. Baker. 1990. Eptesicus fuscus. Mamm. Spec. 356: 1-10.
- Kwiecinski, G. G., L. Krook and W. A. Wimsatt. 1987. Annual skeletal changes in the little brown bat, *Myotis lucifugus lucifugus*, with particular reference to pregnancy and lactation. Am. J. Anat. 178: 410-420.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen: London.
- Leonard, M. L. and M. B. Fenton. 1983. Habitat use by spotted bats (*Euderma* maculatum, Chiroptera: Vespertilionidae): roosting and foraging behaviour. Can. J. Zool. 61: 1487-1491.
- Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press: Princeton, New Jersey.
- Lind, A. J. and H. H. Welsh. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Anim. Behav. 48: 1261-1273.
- MacLean, A. A. E. 1986. Age-specific foraging ability and the evolution of deferred breeding in three species of gulls. Wilson Bull. 98: 267-279.
- Maeda, K. 1972. Growth and development of the large noctule, *Nyctalus lasiopterus* Schreber. Mammalia 269: 143-152.
- Masters, W. M., K. A. S. Raver, and K. A. Kazial. 1995. Sonar signals of big brown bats, Eptesicus fuscus, contain information about individual identity, age and family affiliation. Anim. Behav. 50: 1243-1260.

- Marchetti, K. and T. Price. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. Biol. Rev. 64: 51-70.
- McWilliam, A. N. 1987. The reproductive and social biology of *Coleura afra* in a seasonal environment. Pp. 324-350 in Recent advances in the study of bats (M. B. Fenton, P. A. Racey, and J. M. V. Rayner, ed.). Cambridge University Press: Cambridge. 470 pp.
- Moss, C. F. 1988. Ontogeny of vocal signals in the big brown bat, *Eptesicus fuscus*.
 Pp. 115-120, in Animal sonar: processes and performance (P. E. Nachtigall and P. W. B. Moore, eds.). Plenum Press: New York. 869 pp.
- Mueller, H. C., D. D. Berger, and G. Allez. 1981. Age and sex differences in wing loading and other aerodynamic characteristics of sharp-shinned hawks. Wilson Bull. 93: 491-499.
- Norberg, U. M. 1981. Allometry of bat wings and legs and comparison with bird wings. Phil. Trans. R. Soc. Lond. B 292: 359-398.
- Norberg, U. M. and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Phil. Trans. R. Soc. Lond. B. 316: 335-427.
- O'Farrell, M. J. and E. H. Studier. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). Ecology 54: 18-30.
- O'Farrell, M. J, E. H. Studier, and W. G. Ewing. 1972. Energy utilization and water requirements of captive *Myotis thysanodes* and *Myotis lucifugus* (Chiroptera). Comp. Biochem. Physiol. A 39: 549-552.
- Orians, G. H. 1969. Age and hunting success in the brown pelican (*Pelicanus occidentalis*). Anim. Behav. 17: 316-319.
- Pagels, J. F. and C. Jones. 1974. Growth and development of the free-tailed bat, *Tadarida brasiliensis cynocephala* (Le Conte). Southwest. Nat. 19: 267-276.
- Paradiso, J. L. and A. M. Greenhall. 1967. Longevity records for American bats. Am. Midl. Nat. 78: 251-252.
- Patterson, A. and J. Hardin. 1969. Flight speeds of five species of vespertilionid bats. J. Mamm. 50: 152-153.

>

- Phillips, G. L. 1966. Ecology of the big brown bat (Chiroptera: Vespertilionidae) in northeastern Kansas. Am. Nat. 75: 168-198.
- Pistole, D. H. 1989. Sexual differences in the annual lipid cycle of the big brown bat *Eptesicus fuscus*. Can. J. Zool. 67: 1891-1894.
- Powers, L. V., S. C. Kandarian, and T. H. Kunz. 1991. Ontogeny of flight in the little brown bat, *Myotis lucifugus*: behavior, morphology, and muscle histochemistry. J. Comp. Physiol. A. 168: 675-685.
- Price, T. D. and P. R. Grant. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. Evolution 38: 483-494.
- Rabinowitz, A. R. and M. D. Tuttle. 1982. A test of the validity of two currently used methods of determining bat prey preferences. Acta Theriol. 27: 283-293.
- Racey, P. A. 1982. Ecology of bat reproduction. Pp. 57-104, in Ecology of bats, (T. H. Kunz, ed.). Plenum Press: New York. 425 pp.
- Rakhmatulina, I. K. 1971. The breeding, growth and development of pipistrelles in Azerbaidzhan. Soviet J. Ecol. 2: 131-136.
- Ransome, R. D. 1990. The natural history of hibernating bats. Christopher Helm: London. 235 pp.
- Rasmuson, T. M. and R. M. R. Barclay. 1992. Individual variation in the isolation calls of newborn big brown bats (*Eptesicus fuscus*): is variation genetic? Can. J. Zool. 70: 698-702.
- Read, A. F. and P. H. Harvey. 1989. Life history differences among the eutherian radiations. J. Zool., Lond. 219: 329-353.
- Richardson, H. and N. A. M. Verbeek. 1987. Diet selection by yearling northwestern crows (*Corvus caurinus*) feeding on littleneck clams (*Venerupis japonica*). Auk 104: 263-269.
- Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110: 419-451.
- Ricklefs, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. Biol. Rev. 54: 269-290.
- Robinson, M. F. and R. E. Stebbings. 1993. Food of the serotine bat, *Eptesicus serotinus* is faecal analysis a valid qualitative and quantitative technique? J. Zool., Lond. 231: 239-248.

- Rogers, L. E., W. T. Hinds, and R. L. Buschborn. 1976. A general weight vs. length relationship for insects. Ann. Ent. Soc. Amer. 69: 387-389.
- Rolseth, S. L., C. E. Koehler, and R. M. R. Barclay. 1994. Differences in the diets of juvenile and adult hoary bats, *Lasiurus cinereus*. J. Mamm. 75: 394-398.
- Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. J. Mamm. 47: 602-612.
- Rydell, J. 1989. Feeding activity of the northern bat, *Eptesicus nilssoni* during pregnancy and lactation. Oecologia 80: 562-565.
- Rydell, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. J. Mamm. 74: 503-509.
- Sadlier, R. M. F. S. 1969. The ecology of reproduction in wild and domestic animals. Methuen: London. 321 pp.
- SAS Institute, Inc. 1985. SAS user's guide. SAS Institute, Inc.: Cary, N.C.
- Saunders, M. B. 1989. Resource partitioning between little brown bats (*Myotis lucifugus*) and long-legged bats (*Myotis volans*) in southern Alberta. M.Sc. Thesis, University of Calgary.
- Saunders, M. B. and R. M. R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73: 1335-1345.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. Ecology 55: 291-303.
- Schluter, D. and P. R. Grant. 1984. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. Evolution 38: 856-869.
- Schneider, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. Ecology 65: 1820-1827.
- Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704-726.
- Schowalter, D. B. and J. R. Gunson. 1979. Reproductive biology of the big brown bat (*Eptesicus fuscus*) in Alberta. Can. Field. Nat. 93: 48-54.

- Schowalter, D. B., J. R. Gunson, and L. D. Harder. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. Can. Field-Nat. 93: 243-251.
- Schutt, W. A., M. A. Cobb, J. L. Petrie, and J. W. Hermanson. 1994. Ontogeny of the pectoralis muscle in the little brown bat, *Myotis lucifugus*. J. Morph. 220: 295-305.
- Simmons, J. A., M. B. Fenton, W. R. Ferguson, M. Jutting, and J. Palin. 1979. Apparatus for research on animal ultrasonic signals. Life Sci. Misc. Publ., R. Ont. Mus. 31 pp.
- Speakman, J. R., and P. A. Racey. 1986. The influence of body condition on sexual development of male brown long-eared bats (*Plecotus auritus*) in the wild. J. Zool., Lond. 210: 515-525.
- Stalmaster, M. V. and J. A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. Ecol. Monogr. 54: 407-428.
- Stamps, J. A. 1983. The relationship between ontogenetic habitat shifts, competition, and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behav. Ecol. Sociobiol. 12: 19-33.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press. 249 pp.
- Stephens, D. W. and J. R. Krebs. 1986. Foraging theory. Princeton University Press: Princeton, New Jersey. 247 pp.
- Stevens, J. 1985. Foraging success of adult and juvenile starlings, Sturnus vulgaris: a tentative explanation for the preference of juveniles for cherries. Ibis 127: 341-347.
- Sullivan, K. A. 1988a. Age-specific profitability and prey choice. Anim. Behav. 36: 613-615.
- Sullivan, K. A. 1988b. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. Ecology 69: 118-124.
- Surlykke, A., L. A. Miller, B. Mohl, B. B. Andersen, J. Christensen-Dalsgaard, and M. B. Jorgensen. 1993. Echolocation in two very small bats from Thailand: *Craseonycteris thonglongyai* and *Myotis siligorensis*. Behav. Ecol. Sociobiol. 33: 1-12.
- Sweeney, B. W. and J. A. Schnack. 1977. Egg development, growth, and metabolism of *Sigara alternata* (Say) (Hemiptera: Corixidae) in fluctuating thermal environments. Ecology 58: 265-277.
- Thomas, D. W., M. B. Fenton, and R. M. R. Barclay. 1979. Social behaviour of the little brown bat, *Myotis lucifugus*. I. Mating behaviour. Behav. Ecol. Sociobiol. 6: 129-136.
- Thomas, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus* hastatus and *Pteropus gouldii*. J. exp. Biol. 63: 273-293.
- Tuttle, M. D. and D. Stevenson. 1982. Growth and survival of bats. Pp. 105-150, in Ecology of bats, (T. H. Kunz, ed.). Plenum Press: New York. 425 pp.
- Utne, A. C. W., and D. L. Aksnes. 1994. An experimental study on the influence of feeding versus predation risk in the habitat choice of juvenile and adult twospotted goby *Gobiusculus flavescens* (Fabricius). J. Exp. Mar. Biol. Ecol. 179: 69-79.
- Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63: 992-1003.
- Vonhof, M. J. 1995. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. M.Sc. Thesis, University of Calgary. 103 pp.
- Wai-Ping, V. and M. B. Fenton. 1989. Ecology of spotted bat (*Euderma maculatum*) roosting and foraging behavior. J. Mamm. 70: 617-622.
- Walton, K. C. 1979. Diet of meadow pipits Anthus pratensis on mountain grassland in Snowdonia. Ibis 1121: 325-329.
- Ward, J. V. 1992. Aquatic insect ecology. Wiley: New York. 438 pp.
- Ward, J. V. and J. A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Ann. Rev. Entomol. 27: 97-117.
- Wartinbee, D. C. 1979. Diel emergence patterns of lotic Chironomidae. Freshwater Biol. 9: 147-156.
- Waters, D. A., J. Rydell, and G. Jones. 1995. Echolocation call design and limits on prey size: a case study using the aerial hawking bat *Nyctalus leisleri*. Behav. Ecol. Sociobiol. 37: 321-328.

- Weathers, W. W. and K. A. Sullivan. 1991. Foraging efficiency of parent juncos and their young. Condor 93: 346-353.
- Werner, E. E. and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.
- Werner, E. E. and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191: 404-406.
- Whitaker, J. O., Jr. 1972. Food habits of bats from Indiana. Can. J. Zool. 50: 877-883.
- Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp 171-190 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.).
 Smithsonian Institute Press: Washington, D.C. 533 pp.
- Wilkinson, L. C. 1995. The influence of reproduction on foraging behaviour and diet of big brown bats (*Eptesicus fuscus*) in southeastern Alberta. M.Sc. Thesis, University of Calgary. 105 pp.
- Yoerg, S. I. 1994. Development of foraging behaviour in the Eurasian dipper, *Cinclus cinclus*, from fledging until dispersal. Anim. Behav. 47: 577-588.
- Zalom, F. G., A. A. Grigarick, and M. O. Way. 1980. Diel flight periodicities of some Dytiscidae (Coleoptera) associated with California rice paddies. Ecol. Entomol. 5: 183-187.
- Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall: Englewood Cliffs, NJ. 718 pp.

.

<u>1994</u>

.

Females:	
Forearm Length (mm):	age = 0.57 (0.03) x - 8.52 (1.13) $r^2 = 0.95$
Metacarpal-Phalangeal Gap (mm):	age = 47.61 (2.99) - 7.58 (0.71) x $r^2 = 0.91$
Males:	
Forearm Length:	age = 0.58 (0.04) x - 10.1 (1.09) $r^2 = 0.94$
Metacarpal-Phalangeal Gap:	age = 42.80 (1.61) - 6.36 (0.65) x $r^2 = 0.93$

<u>1995</u>

Females:

Forearm Length	age = 0.55 (0.03) x - 9.00 (1.17)
	$r^2 = 0.92$

Metacarpal-Phalangeal Gap age = 49.09 (5.62) - 6.95 (0.99) x $r^2 = 0.81$

Males:

Forearm Length age = 0.64 (0.04) x - 10.96 (1.32) $r^2 = 0.90$

Metacarpal-Phalangeal Gap age = 49.55 (5.31) - 7.88 (1.18) x $r^2 = 0.79$ APPENDIX 2: Estimated energetic content of a mealworm beetle (Tenebrio molitor)

From Keeler and Studier (1992):

Energetic content of culled June beetle (Phyllophaga spp.): 4510 cal/g dry mass

Dry mass of culled June beetle: 0.0856 g

Energy / June beetle: 386 cal

Wet mass of whole June beetle: 0.3034 g

Energetic content of live June beetle: 1272 cal/g

Live mass of mealworm beetle (g): 0.1422 ± 0.066

Energetic content of mealworm beetle: 181 cal/beetle (756 J/beetle)