Fig. 1

Photograph of part of study area.

An aerial view looking east along the north shore of Lake Opinicon. The buildings to the right of centre are the Queen's University Biology Station. Counterclockwise from the lower right corner are four large islands; Sheep Island, Cow Island, Rabbit Island, and an unnamed island.

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PATTERNS OF FEEDING AND HABITAT USE BY LITTLE BROWN BATS,
Myotis lucifugus (Chiroptera : Vespertilionidae),
OVER AND AROUND LAKE OPINICON, ONTARIO, CANADA

by

© THOMAS MICHAEL HARRISON, B.Sc. (Hons.)

A thesis submitted to the Faculty of Graduate Studies
and Research in partial fulfillment of the requirements
for the degree of
Master of Science.

Department of Biology
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ABSTRACT

Bat activity and feeding were monitored under a range of meteorological conditions. Bat dispersal was studied using chemiluminescent light tags. Insects and faeces were collected to analyze diet.

Bats were most active along shorelines and least inland. They fed mostly near the surface of the lake, showing wide variation in feeding bout times. Activity and feeding increased from mid-July to mid-August.

Bats dispersed to and then followed the nearest shoreline for at least 3.5 km from each colony. Feeding grounds of both colonies widely overlapped when the young were volant.

Bats shifted from eating largely dipterans in May to trichopterans in August. Insect activity and bat feeding declined below 12°C, during strong winds, and during increased moonlight.

Evidence is shown for reduction of intraspecific competition by expansion of feeding ranges into regions of overlap. Displacement of individual bats from home ranges could account for the geographic range of Myotis lucifugus.

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As a part-time graduate student, I frequently had to place my thesis on hold to accommodate the demands of a full-time career, much to the frustration of my supervisor, Brock Fenton. When I needed encouragement he prepared a fresh pot of tea and helped clarify the problems I was facing with the research. If my gluteus maximus (generally the starboard side) needed stimulation, he gladly obliged. The contributions I valued most from Brock were his willingness to allow me to follow my own ideas (i.e., to make mistakes) and to travel with him to Zimbabwe as a research assistant.

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Many nights my assistants and I followed bats over private property, and to those unknown people who didn't know we were there (except for one group of tourists who attacked my team claiming that we were practising witchcraft), thanks for being deep sleepers. A special thank you to Parks Canada for allowing me to trap bats in the Blockhouse and to Mr. Mike Murray who permitted me to climb around in his attic and to deploy 10-15 field observers over his property to watch for bats with "glowing green balls".

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My wife (Winkey) and I will always remember the summer of 1976 at QUBS because we had our wedding reception and party at the station. The amazing Mrs. 'B' and the 'regulars' coordinated all the preparations. We still enjoy remembering the disc jockey slumped over his turntables the next morning while Mrs. 'B' was preparing breakfast.

Finally, and most important of all, I want to mention the contributions from Winkey. Since the research began in 1975-76, our lives have undergone great changes; lovers, newly-weds, Tarah, our first child, Jamie, our second child born three months before my defense, and still we are lovers. A very special thank you, Winkey, for spending evenings on a boat listening for bats, filling globes with glowing fluid, and especially for giving me the time to do the things I wanted to complete and for raising hell when I ignored you and our family for too long a time.

TABLE OF CONTENTS

	Page
Abstract.....	i
Acknowledgements.....	ii
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	viii
Introduction.....	1
Methods and Materials.....	3
Study Area.....	3
Transect Sampling.....	3
Light-tagging.....	5
Meteorological Factors.....	5
Insects.....	6
Analysis of Data.....	6
Results.....	8
General Observations.....	8
Period-meter Analysis.....	9
Activity.....	10
Meteorological Factors.....	10
Insects.....	11
Dispersal.....	12
Mathematical Model.....	14
Discussion.....	16
Visual Observations.....	16
Activity-sampling bias.....	16

Temporal Aspects.....	18
Spatial and Dispersal Aspects.....	18
Meteorological Aspects.....	21
Insect Factors.....	24
Diet Factors.....	25
Usefulness of the Mathematical Model.....	26
Ecological and Behavioural Implications.....	28
Conclusions.....	30
Tables.....	33
Figures.....	42
References.....	58
Appendices.....	61
1. Computer programme for transforming data to dummy variables and for converting other variables.....	61
2. Summary of measured, converted and dummy variables.....	64
3. Definitions of variable names.....	68
4. Summary of Multiple Regression Analysis of passes and buzzes.....	70

LIST OF TABLES

	Page
1. Summary of period meter observations.....	33
2. ANOVA natural logarithm of buzzes.....	34
3. ANOVA natural logarithm of passes.....	35
4. Summary of mean buzzes for 3 habitats.....	36
5. Summary of comparisons feeding buzzes with temperature, windspeed, moon phases.....	37
6. Relative abundance of orders of insects determined by netting.....	38
7. Shannon indices of insect diversity.....	39
8. Relative abundance of orders of insects determined by faecal analysis 1977.....	40
9. Summary of relative abundance of insect orders determined by faecal analysis 1978.....	41

LIST OF FIGURES

	Page
1. Photograph of part of study area.....	42
2. Aerial photograph of Lake Opinicon.....	43
3. Map of Lake Opinicon area.....	44
4. Map showing transects used in the study.....	45
5. Graphs of relative hourly bat activity at three island locations.....	46
6. Graphs of relative hourly bat activity comparing three habitats.....	47
7. Graph of relative mean bat activity for July and August.....	48
8. Histogram showing relative abundance of orders of insects, July 1977.....	49
9. Histogram showing relative abundance of orders of insects, August 1977.....	50
10. Graph of relative abundance of insects through netting and faecal analysis compared with phases of moon and cloud cover.....	51
11. Histogram of relative insect abundance comparing faecal analysis and insect captures.....	52
12. Map showing bat dispersal from M. Murray's colony 21 August, 1976.....	53
13. Map showing bat dispersal from M. Murray's colony 30 August, 1976.....	53
14. Map showing bat dispersal from M. Murray's colony 21 July, 1977.....	54

15. Map showing bat dispersal from Blockhouse colony	
21 July, 1977.....	54
16. Map showing bat dispersal from Blockhouse colony	
26 August, 1977.....	55
17. Map showing bat dispersal from Blockhouse colony	
30 August, 1977.....	55
18. Scatter diagram of natural logarithm of passes versus residuals.....	56
19. Scatter diagram of natural logarithm of buzzes versus residuals.....	57

INTRODUCTION

To understand the abundance and distribution of an animal population, one must have knowledge of the relationship between the individual animal (or group of animals) and its immediate environment. One should also know how individuals interact with conspecifics and other species. Every organism lives in a matrix of space and time (Krebs 1972), and the manner in which a group of organisms uses the resources within a specified space partly defines the characteristics of its population. The number of individuals within a population is largely regulated by food supply, climate, geography, and by a wide variety of social behaviours; emigration, predation, competition, hibernation, and reproduction.

Single species aggregations, such as populations and colonies of little brown bats, are composed of individuals requiring similar resources of food and shelter (roosts), and if these resources are limited these individuals will experience high levels of intraspecific competition. Competition among members of a population may stimulate some individuals to explore and penetrate marginal and different habitats. Over time, this will encourage the dispersal of the population across a wider range as displaced individuals adapt to new and varied habitats.

The purposes of this study are 1.) to examine the use feeding bats made of the area around and over a lake, 2.) to clarify the effects of weather conditions and intraspecific competition on foraging, and 3.) to develop a model for predicting the patterns of habitat use by bats on and near the lake.

The study animals, Little Brown Bats (Myotis lucifugus), range throughout most of temperate North America, hibernating in caves or abandoned mines from early September to mid-May. The hibernacula are also sites for swarming and mating from August to October. In spring, fertilization occurs after ovulation when females leave the hibernacula and move to nursery roosts. After 50-60 d of gestation, a single young is born and usually commences flight during weaning at approximately three weeks of age. Little brown bats feed on insects, especially emergent aquatic imagoes, and are most effective at feeding in patches or swarms of insects. Although some predators occasionally feed on little brown bats (Barclay et al, 1982) mortality is largely due to flying accidents and disturbance by humans. These bats are long-lived, 10 y is common, with one banded bat at least 30 y (Keen and Hitcock 1980). Natural mortality is highest in those experiencing their first winter (Fenton and Barclay 1980). Availability of suitable roost sites (day roosts, night roosts and hibernacula) has been proposed as the major limiting factor for Myotis lucifugus populations given the availability of abundant and varied insect prey (Fenton and Barclay 1980, Barclay, 1982).

Foraging little brown bats emit ultrasonic echolocation pulses to detect and follow insect prey, and the rate at which these pulses are emitted increases as the bats close in on a target. By listening to these pulses it was possible to monitor this activity and to recognize their feeding in the study area.

MATERIALS AND METHODS

Study Area

Research was conducted on and near Lake Opinicon, South Crosby Township, Leeds County and Bedford and Storrington Townships, Frontenac County, Ontario, (latitude $44^{\circ} 34'$, longitude $76^{\circ} 19'$) during July and August of 1976 and 1977. The lake has a surface area of approximately 890 ha (approx. 1928 acres), a maximum length of 9.3 km, a maximum width of 1.6 km, and an average maximum depth of 9.8 m. Forty-five percent of the lake is less than 1.5 m deep. The total shoreline of the numerous islands and bays is nearly 52 km (Curran et al 1947, Turnbull 1975). The lake is usually ice covered from the end of November until mid-April; in 1976, the maximum water temperature of the lake was 27°C (24 June).

The land around the lake is tree covered for the most part with cottages concentrated at the eastern end of the lake near the village of Chaffeys Locks and Davis Lock (Fig. 1 and 2). A gravel road follows the northern shoreline along the entire length of the lake and is 2 - 1500 m from the shore.

I used two nursery colonies of Myotis lucifugus; one found in the attic and under the roof of the Rideau Canal Blockhouse at Chaffeys Locks, and the other, found in the attic of a farmhouse belonging to Mr. M. Murray. The Blockhouse colony was approximately 50 m from the lake and M. Murray's was approximately 600 m from the lake. The centre of operations for field work was the Queen's University Biology Station (Fig. 3).

Transect Sampling

In order to determine the activity of bats and the abundance of potential food insects, the lake and immediate surroundings were marked

with 16 transects (12 in water, 4 on land) by the use of adjustable Silva compasses calibrated for the 1979 variation of $12^{\circ} 15'$ West (Fig. 4). Maps of the lake were prepared indicating all transect compass bearings as a reference for my assistants. These individual transect maps showed all critical visual details (logs, rocks, conspicuous trees, weed beds, cottages, navigation beacons and buoys) that would be encountered at night along the transect. Each assistant and I travelled each transect during daylight prior to each season's field work in order to familiarize ourselves with environmental hazards and clues.

The sampling process involved several steps. First, a timetable for the entire season's sampling was prepared to ensure that each transect was covered once in each direction for each of 3 time slots (sunset to 23:00, 23:01 to 02:00, 02:01 to sunrise). Each assistant was assigned in advance to each transect for a particular time slot for the season.

To sample along a transect, one commenced at the pre-assigned end, stopped at a location, identified and recorded the position, time, temperature, moon phase, cloud cover, fog or rain. Using an ultrasonic leak detector (Simmons et al, 1979) attached to headphones, the numbers of bat passes (Fenton 1970) and feeding buzzes (Griffin et al, 1960) were counted over an elapsed time of 5 min. After recording the total numbers of passes and buzzes, insects were sampled by passing a 36 cm diameter insect sweep net 50 times through the cone of light from a large flashlight (6-V battery, plastic floating case,) aimed skyward.

Insect sampling commenced after the light had been on for 1 min. Any captured insects were immediately placed in a vial of 50% ethanol

for future counting and identification. Next, one moved to another location along the transect and repeated the process.

Light-tagging

Dispersal of bats from the two colonies was examined by the use of a chemiluminescent light tag attached to captured bats (Buchler 1976). To do this, bats were trapped (Tuttle 1974) on three occasions at each colony. Teams of observers with CB radios and binoculars were strategically positioned on and around the lake near the colony and transmitted all observations of light-tagged bats to the base radio station at the colony. All transmitted information plus the sex and condition of each bat and the release time were recorded on cassette tapes for later transcription.

The light-tags were empty gelatin pill capsules (2 x 0.7 cm), filled with the chemiluminescent fluid Cyalume_R (American Cyanamid Company; Buchler 1976), and attached to the ventral surface of the bat with surgical cement. A puff of talcum powder was applied to tagged bats to prevent residual cement from tangling the bat. Bats were tossed vertically into the air for release. Generally, the light from the capsules was visible for 2.5 h.

Meteorological Factors

The weather conditions were monitored using analytical grade thermometers and visual clues as to percent overcast and phase of moon. The wind speed was estimated using a 45-cm length of orange marker tape attached to the plastic thermometer case. The strength of the wind was determined by assessing the angle between the upright case and the fly

of the orange tape. The wind direction was taken using a compass. Conditions were not monitored during severe storms.

Insects

The insect samples were analysed in the fall of each year and classified by order (Diptera, Trichoptera, Lepidoptera, Ephemeroptera, other) and by size (≥ 4 mm, ≤ 3 mm).

Analysis of faeces obtained from two colonies (a barn and a silo) near the west end of the lake was conducted in July and August of 1977. These were not the 2 colonies used in the dispersal experiment. Insect fragments were counted and grouped to five orders, Diptera, Trichoptera, Coleoptera, Ephemeroptera, Lepidoptera using techniques similar to those used by Coutts (1972) and Belwood and Fenton (1976). A similar faecal analysis was conducted at three colonies from May to August 1978.

Analysis of Data

All data were converted to numeric values or codes and key-punched for computer analysis. The angle ($\pm 2^\circ$) and distance (± 10 m) of each sample location from the 2 colonies were measured from a topographic map and added to the data variables from each sample.

Preliminary statistical analysis for grouped data was completed using a Hewlett-Packard HP-25 programmable calculator and the HP-25 Applications Programs (1975) for linear regression and the t-statistic.

The main data analysis was done using the BMDP Biomedical Computer Programs, P-series 1977-79-81, Department of Biomathematics, University of California, Los Angeles. The first program used was P1D, Simple Data Description, to examine the data matrix for recording, transcribing and key-punching errors, and presence of outliers (extreme values). P1D

computes the number of cases read, and the following univariate statistics for each variable: mean, standard deviation, standard error of the mean, coefficient of variation, smallest and largest values, range and total frequency of all values.

A subroutine was written by Dr. L. Lefkovitch, Agriculture Canada to transform passes and buzzes to natural logarithms, and to introduce dummy variables into the multiple regression model to account for the effects of different transects, different assistants and different locations on the transects (Appendices 1, 2). All data samples in which neither passes or buzzes were recorded were deleted from the analysis. An unbalanced ANOVA was used which accommodated the unequal cell sizes, missing cells and occasional missing data in the analysis. Backward stepping multiple regression was used to discard all least significant variables from the model with $P < 0.05$ as the significance level for all F values kept in the model.

All assistants were trained to identify and count passes and buzzes from a recording I made of several situations of bats making passes and feeding buzzes. There was no further check made to validate any assistant's consistency at observing or recording passes and buzzes.

RESULTS

General Observation.

While sampling along the transects under suitable light conditions (i.e., streetlights, floodlights, bright moonlight, flashlights) I could watch the bats. No systematic sampling was done to make visual observations and the data are useful only for describing general behaviour. Of the 99 occasions when bats were seen, they were most often along shorelines (56 occasions), but also over open water (28 occasions), and inland on 15 occasions. I twice saw bats capturing insects from the surface of the water.

Insects were present either flying or on the water for 31% of the observations and I detected feeding buzzes while bats were seen during 84% of the observations. Bats were seen flying within one metre of the surface of the water on 51 occasions, within 1-3 m above the surface on 20 occasions, and above 3 m on 13 occasions. Only four times did I see bats flying high (approx. 15-30 m) above the lake but at 2 locations on the lake, I saw single bats hovering 3-4 m above the surface of the water in a strong wind. One of these bats made 3 swoops to the surface while emitting a single feeding buzz.

The sluiceway beside the mill in Chaffeys Locks was a good place to observe bats. On 11 nights I saw bats flying over the sluiceway; twice I watched groups of 5-7 bats feed by circling within the sluiceway.

Large groups of bats feeding within 2 m of the lake's surface were seen on 2 nights. At 22:15 on 24 August, 1976, approximately 45 m offshore, 15 bats circled 30-150 cm over the water and made

occasional dips to the surface. I saw many flying insects and the circling bats produced many feeding buzzes. At 21:30 on 18 August 1976, a large bloom of mayflies extended for approximately 1 km along the northwest shore of the lake and continued to 22:30. One large group of bats (approx. 40-50) fed in the insect bloom 30-150 cm above the surface. By driving a boat along the shoreline of the lake over the length of the bloom I detected 3 distinct groups of feeding bats.

On 2 other nights, I saw and listened to smaller groups of bats (N = 5-8) feeding in swarms of insects. On 9 August 1976, near a boathouse on an island, 2 bats flew in tandem along the shoreline as though one was chasing the other.

Period-meter Analysis

From 9 July to 14 August 1978, echolocation calls of bats were monitored using a broad-band microphone, period meter, and oscilloscope (Simmons et al., 1979, Fenton and Bell 1981) by one of my assistants along the transects. As bats can be identified by their calls (Fenton and Bell 1981), this allowed confirmation of the predominant bat species active in my study area. All data (N = 111 sample locations) were gathered between 21:00-02:30 with no bats detected at 70 of the sample locations. The assistant found that 63% of the calls observed swept to 40 kHz and 37% to 20 kHz (Table 1).

Myotis lucifugus was the species most active over the lake and the ones detected by the 40 kHz sensors (Fenton and Bell 1979). Other bats in the area include Myotis septentrionalis, M. leibii, Pipistrellus subflavus, Eptesicus fuscus, Lasiurus borealis and Lasiurus cinereus. Of these, Lasiurus cinereus and rarely Eptesicus fuscus were active over the lake reflected by calls sweeping to $\approx$ 20 kHz.

Activity

The number of passes recorded in a 5-min period ranged from 0 to 335, ($\bar{x} = 14.06$, $SE = 0.76$, $N = 1351$), and the number of buzzes ranged from 0 to 96 ($\bar{x} = 1.68$, $SE = 0.14$, $N = 1351$), with the most frequently occurring number of passes being, in increasing order, 5 per min, 1 per min and none. The most frequently occurring number of buzzes were, in increasing order, less than one per min, one per min and none. When the number of passes and buzzes recorded in 3 classes of habitat are compared: inland, shore (approx. 15 m on either side of the shoreline), and open water, bats show a significant preference for shorelines. The arithmetic mean number of buzzes differs among all these habitats (Tables 2, 3, 4). Bats were significantly more active and fed more over water than land (Tables 2, 3).

While monitoring activity throughout the night at specified locations I detected large variability in the number and distribution of peak activity periods. These variations in activity peaks occurred throughout both summers and across all 3 classes of habitat (Figs. 5, 6). Night periods did not significantly contribute to the model predicting either activity or feeding. A plot of the relative mean number of bat passes shows that although there was variation in activity over the summer, the peaks of activity were higher in mid-August than in July (Fig. 7).

Meteorological Factors

Temperature ranged from 7°C to 27°C with most temperature readings occurring between 16°C and 21°C (approx. 66% of all recordings). Temperature had little impact on bat activity or feeding except that activity virtually ceased below 12°C (Table 5). The most frequently observed wind speed category was medium (42% of the total), and zero

wind or light winds accounted for 43% of the observations. Wind speed has a significant negative affect on activity and feeding (Tables 2, 3) with most feeding occurring in zero or light winds. Wind direction was largely from the west (35%) and south (32%) reflecting the SW to NE direction of Lake Opinicon and the westerly flow of air in this area of Canada. Winds at night were variable 22% of the time.

Bat feeding should be strongly correlated to the phases of the moon as insect activity keys on the moon (H. F. Howden, pers. comm.). Although the moon was not visible for 63% of the sampling, I found moonlight to be a significant factor in depressing both bat activity and feeding (Tables 2, 3, 5), (Fig. 10).

Cloud cover showed no relationship to feeding activity and similarly light rain and fog had no pronounced effects on feeding. The sky was clear 45% of the time of observation with overcast skies occurring 30% of the nights. Rain was observed and felt 3% of the observation time.

Insects

Insects were captured at 19% of the total transect sample points ($N = 1351$), and insects were observed or encountered flying near our motor boats at 12% of the sample points when no insects were captured ($N = 144/1207$). The most common orders captured, Diptera, Trichoptera and Ephemeroptera, accounted for 90% of the total captured (Table 6). The most frequent insect abundances were between 2 and 10 insects per sample with the largest single abundances in samples being 98 (all Diptera) and 200+ (all Ephemeroptera). The presence of insects was positively correlated with bat feeding but was not significantly related to bat activity (Tables 2, 3). Insect length (>4 mm or <3 mm) played no direct role in predicting activity or feeding. A sharp

decline in insect abundance was noted in strong winds.

Insects were captured on 63% of the sampling nights of 1977.

Shannon indices suggest that insect abundances and variety were diverse over both summers and differed between July and August (Table 7), (Figs. 8, 9).

The variability in orders of insects and the relative abundances of insects within the samples indicate that food resources were patchy. Only 8 samples consisted of a single order (Diptera). When the abundance of insects is examined with respect to moon phase and cloud cover for the entire summer 1977, the percent abundance increases during periods of no moon (new phase) and/or cloud cover (Fig. 10). The 2 nights in early August showing large insect samples indicate 2 samples of 100+ insects that were taken in large blooms of emerging dipterans and ephemeropterans. There were major shifts in insect captures from Trichoptera to Diptera between July and August in 1976 and from Diptera to Ephemeroptera in 1977 (Table 6). A partial shift from Trichoptera to Diptera appears in faecal pellets during July and August 1977 from Hughson's Silo colony (Table 8).

When relative insect abundance as shown by faecal analysis and net sampling are compared there is an inverse relation between Diptera and Trichoptera (Fig. 11). The Hughson's Silo colony where faeces were analyzed in 1977 was reexamined in more detail in 1978 and showed that the bats made a change in diet of approximately 50% Diptera in May 1978 to 93% Trichoptera in August 1978. The bats of the M. Murray colony and the Opinicon Lodge colony (approx. 100 m from Blockhouse colony) showed a similar diet change over the summer (Table 9).

Dispersal

A total of 208 bats (165 adult females, 4 adult males, 33 juvenile females, 6 juvenile males) was light-tagged, released and followed by a

team of observers; 155 of those tagged were from the Blockhouse colony and the other 53 from M. Murray's house. The general direction, route taken and distance travelled until lost by 'lighted bats' were transcribed from cassettes to maps. During 1976 I concentrated my observers near the colonies (approx. 1 km). Once the most common routes taken by bats had been detected, observers were placed further afield. M. Murray's bats mostly followed an open field directly south-west to the lake (Figs. 12, 13, 14). Bats from both colonies used the shorelines of the lake more than open water during dispersal. In bright moonlight, bats from the Blockhouse colony (Figs. 15, 16, 17) dispersed inland or remained along shorelines in the lee near the colony when the wind was strong. During conditions of light winds from the south-east bats moved out more over the lake and were observed along shorelines further from the colony (approx. 3-4 km). There was a slight tendency for tagged bats to remain in lee areas when winds were light but not enough to keep bats from crossing the lake.

Bats from the Blockhouse explored and fed in the immediate vicinity (approx. 100 m) of the colony when released, whereas the M. Murray's colony bats moved very quickly to the lake about 600-700 m away, averaging 15-20 min for the flight.

Bats from both colonies were observed flying and dipping in common areas of the lake (Figs. 13, 14, 16, 17).

Light-tagged bats were released at an average rate of 1 per 3 min. Bats flew most often at 1/2 to 3/4 canopy height and next often within 1 m of the lake surface. Bats were followed most often along shorelines of the lake and islands, next most often inland, and least often over open water. On 2 occasions, while walking with CB radios, observers watched bats making dives at the globes at the tip of the extended antennae of the

radios. This also occurred once in a boat.

Loops or dips were observed with 2 'lighted' bats; one individual made 7 loops in 1 min all with simultaneous feeding buzzes. Twenty-seven bats were seen making dips without feeding buzzes being heard. On 22 occasions light-tagged bats roosted in trees. Nineteen light-tagged bats were observed returning to and entering the colonies between 21:20 and 00:41, and on 2 occasions, groups of 2 or 3 bats returned together. The mean elapsed time between the release of the first bat and the return of bats to enter the colony was 106.3 min (SE = 6.9, N = 19) with a maximum elapsed time of 2 h 31 min and a minimum elapsed time of 45 min.

I tabulated the greatest distances tagged bats achieved at known times after the first bat had been released; these were bats that had been continuously followed by a team of observers in boats. The maximum distance a tagged bat was followed was 3.5 km from its colony, and the fastest bat covered 2 km over the lake (i.e., not along a shoreline) in 5 min.

Of the 208 light-tagged bats 69 were 'lost' immediately within 100-200 metres of the colony. Of the remaining 139 bats that were followed for considerable distances 13 individuals dispersed into home ranges of different colonies from their own. All instances of bats feeding beyond their colony home range occurred after the 21 July and when the young were volant.

Mathematical Model

Three transformations were attempted to fit the data (e.g., linear, square root, natural logarithm). Since both the linear and square root transformations distinctly showed means and variances that were positively

correlated (greater means accompanied by greater variances), they were rejected. The natural logarithm ($\log_e(x+1)$) transformation of passes and buzzes reduced, but not completely eliminated the amount of scatter of the residuals (Figs. 18, 19). Simultaneously included in the regression analysis were the variables: year, surfaces (water or land), surfaces within transects, location (open water, shoreline, inland), assistants, insects (presence or absence), windspeed and moonlight.

Both passes and buzzes could not be predicted with the same combination of variables. In the case of passes as the dependent variable, presence of insects was not significant (Table 3). For buzzes as the dependent variable, the year was not a significant predictor (Table 2).

When individual assistants are considered, two had a negative effect on observed levels of passes and four had a negative effect on observed levels of buzzes. It appears that the variability in passes and buzzes can be accounted for by a combination of physical factors (surfaces and shorelines), meteorological factors (windspeed and moonlight), sampling factors (assistants and year) and presence of insects. Using this model, 18% of the total variation in buzzes and 20% of the total variation in passes can be explained (Tables 2, 3).

DISCUSSION

Visual Observations

Although Buchler (1976) and Whitaker et al (1977) report Myotis lucifugus foraging within 3 m over the ground, most evidence suggest that they feed over water and near shorelines (Barbour and Davis 1969; Belwood and Fenton 1976; Anthony and Kunz 1977; Fenton and Bell 1979; Fenton and Barclay 1980; this study). My visual contacts with bats support the findings of Fenton and Bell (1979) for Myotis lucifugus who reported them feeding from the surface or within a metre of the surface of the lake and in groups of individuals. By capturing Eptesicus fuscus and Myotis lucifugus in nets over a stream, Kurta (1982) found that the median capture heights for the 2 species differed (M. lucifugus - 1.5 m, E. fuscus - 4.9 m) as well as the median capture distances from shore (M. lucifugus - 0.9 m, E. fuscus - 2.7 m). Most of the occasions on which I saw groups of bats and individuals feeding, they were within 1.5 m of the water's surface; this height is consistent with Kurta's reports for Myotis lucifugus.

Activity-sampling Bias

The use of ultrasonic detectors to monitor activity allows observation of bats without disturbance in a wide variety of habitats over prolonged periods of time. Some biases in my technique are reflected in the kinds and levels of activity recorded.

First, the sensitivity and angle of detection on the leak detector infer that bats can be observed in only 8.3% ($\pm 2.8\%$) of the approximately 395 m^2 ($\pm 50 \text{ m}^2$) potential area of detection at each sample point along a

transect (Downes 1982). At a point on open water, it is possible, by aiming the detector over one side of the boat, that an observer could miss a large amount of activity on the opposite side or directly overhead.

Second, along the roadways used as inland transects, the frequent trees and rock cuts on both sides of the roadway could act as flight corridors for bats moving to feeding areas, or flying to roosts, rather than hunting insects. The low levels of feeding inland could be accounted for by this bias and may reflect a different pattern of habitat use.

The very high levels of activity recorded along shorelines represent a common behaviour of Myotis lucifugus (Barbour and Davis 1969; Belwood and Fenton 1976; Anthony and Kunz 1977; Fenton and Bell 1979; Fenton and Barclay 1980; Kurta 1982). However, there was a strong bias for my assistants aiming sensors in the direction of the shoreline. It is possible that these biases predetermined the high levels of activity recorded along shorelines and decreased the levels recorded over open water.

The ANOVA shows the varying impact that assistant observers had on the levels of passes and buzzes recorded. Although each person was trained using audio cassette recordings of actual bat sounds the individual person's judgement in the field was not consistent with all others.

There was greater accuracy in observing low levels of passes and buzzes because of the long periods of time between individual passes or buzzes. The presence of outliers in the scatterplots (Figs. 18, 19) demonstrate the lack of accuracy at very high levels of activity.

Temporal Aspects

My data support the work of Kunz (1973) and Fenton et al (1977) who found that major foraging bouts of bats parallel the early evening and pre-dawn periods of insect activity but that other peaks of bat activity occur during the night (Figs. 5 and 6). The activity and feeding periods were highly variable in all 3 classes of habitat studied, likely because of the use of night roosts near the feeding areas for digestion prior to the next bout (Barclay 1982) and the spatial and temporal patchiness of insect swarms during the middle of the night. My data also agree with those of Kunz (1973) and Barclay (1982) who noted that the predawn activity period was centred at the diurnal roosts (nurseries). I found no specific pattern in the temporal variation in the feeding peaks during the middle of the night confirming the work of Bradbury and Vehrencamp (1976).

The general but erratic increase in activity between July and mid-August (Fig. 7) suggests evidence for the increased energy demands of lactating females in early July, and the doubling of the potential population of bats using the lake when the young are volant from mid-July to mid-August.

I noted that the times of emergence and return to the colonies varied over the summer and keyed on the level of ambient light as did those found by Kunz (1973).

Spatial and Dispersal Aspects

Refuging predators are carnivorous animals that disperse in a circadian pattern from some fixed point or area (e.g., a nursery colony) into their home range and return to the same fixed point or area

(Hamilton and Watt 1970). The size of the home range of a member of a refuging species is a function of available food resources, the amount of energy required to commute to the feeding areas in the home range, the energy required to search for individual prey items, and the local weather and climate (McNab 1963; Schoener 1968). Adult female Myotis lucifugus and their volant young emerge from nursery colonies in the evenings to feed and return to the colonies shortly before dawn. Lactating females may return several times during the night to nurse non-volant young.

My observations of light-tagged Myotis lucifugus support their role as refuging predators on Lake Opinicon. If food resources remain constant, refuging species are forced to increase their home range size as their population increases in order to expand the area in which food resources can be obtained. This may place an increased energy demand on individuals commuting to food resources and raise the level of intraspecific competition within the population for these resources (Hamilton and Watt 1970). The feeding areas from both colonies in this study overlapped considerably. This overlap occurred at a time when both colony populations had increased with young and the overlap was concentrated in regions of the collective home ranges that were most distant from the colonies and most distant from the initial feeding areas of the colonies. This suggests that little brown bats do not defend feeding territories within the colony home range. My data and those of Fenton and Morris (1976) support Morrison (1978) who interprets the many patches of potential food being unlocated and unused in the range of a foraging predator (Pielou 1959)

as the reason why foraging ranges can be broadly overlapping in refuging predators. Little brown bats from the colonies I studied overlap their home range foraging areas at a time when the total population in each colony has nearly doubled. This supports a model of foraging time developed by Morrison (1978) which predicts that the increased commuting time required to locate distant patches of food is equivalent to the additional searching time needed to find food patches nearby. The observed overlap may also be an indicator for the beginning of the dissolution of the home ranges which occurs at the end of each summer. A reduction of intraspecific competition could occur through the bats exploitation of the insect fauna which are near the centre of dispersal and by expanding their foraging ranges (Figs. 12-17). I found that the bats foraged on a variety of insects throughout the summer but changed their food preferences as insects belonging to certain orders became very abundant (Tables 8, 9). This allows bats to commute shorter distances to available resources in order to gain the required food and facilitates the existence of a large population of individuals in a collective colonial home range. Natural selection will favour the most efficient forager - - one that minimizes its commuting distance and quickly harvests the food resource. Myotis lucifugus uses the strategy of an opportunistic feeder considering its size and energy requirements (McNab 1970, Fenton and Morris 1976), and at the same time the strategy of a feeding generalist by consuming a variety of nutritionally different resources (Buchler 1976; Covich 1976; Anthony and Kunz 1977). My data suggest the use of ~~these~~ twin strategies by Myotis lucifugus on Lake Opinicon because these bats regularly used nearby known feeding areas directly after emergence, and then after feeding in these sites, followed shorelines to find insects in lee areas (Figs. 12-17). The apparently

undefended overlapping feeding areas (Figs. 14, 16, 17), the prey patches over the lake (Figs. 8, 9), and the flexibility in diet (Tables 8, 9) allow these bats to use the strategy of opportunistic generalists.

The selection of diurnal and nocturnal roosts near abundant although patchy food resources is consistent with the model of foraging dispersal presented by Bradbury and Vehrencamp (1976). This roosting behaviour suggests that the colonies of M. lucifugus using L. Opinicon are large as a result of the unique shape, direction, and nature of shoreline habitats and the shallow and muddy bottom of the lake that encourages abundant levels of aquatic insects. The small number of human dwellings nearby and the large number of trees present many potential roosting sites.

Meteorological Aspects

Bat activity is influenced by weather factors through the bats' responses to low temperatures, strong winds, and moonlight, and through the responses of insects to the same factors. Barclay (1982) found that female Myotis lucifugus used night roosts more on colder nights and during the spring, as these roosts provided small, warm spaces where the bats can maintain a high body temperature at a minimal cost near the feeding areas. The decreasing activity of bats below 12°C that I observed reflects the use of night roosts to maintain efficiently a high body temperature and also the lack of suitable insect prey for the bats. Anthony and Kunz (1977) noted that insect availability was relative to temperature and that few insects were available below 10°C. The variability in mean numbers of passes I observed over the range of 12 - 24°C could reflect the influence of temperature on both emergence times and locations of aquatic insects. Temperatures at the surface of the

water can be altered by the wind and the number of consecutive days of warm, sunny weather. These conditions, in turn affect the size of the alate population of aquatic insects.

Myotis lucifugus cannot maintain themselves energetically when they spend long periods of time searching for the very few aerial insects that are active at temperatures below 10°C and my data show that very little activity occurred below this temperature.

The topography of Lake Opinicon (especially the shorelines), and many of the larger islands in the lake are orientated in a northeast to southwest direction. When winds are from the north, the major portion of the lake's shoreline is positioned such that the wind would cause lee areas to form along the north side of the lake and along the south side as well, because the wind would rise to go over the trees along the shoreline prior to reaching the shore. The attraction of shorelines for feeding in Myotis lucifugus are the high likelihood of insects staying in the lee areas associated with the shorelines and the movement of emergent blooms occurring in open water to the shores when the wind is strong.

In very strong gusty winds bats may expend considerable amounts of energy dispersing into exposed areas. Inland and shoreline regions would offer protection and easier flying prospects when used for movement to and from roosts. At some locations on the lake, winds may bring insects from the open water to specific locations downwind and bats familiar with the topography could glide and hover into the wind over these locations to capture larger insects being blown downwind. The energy costs of gliding into the wind or hovering over an optimum location might be balanced with the success of capturing larger insect prey in the wind stream.

Bryant (1975) found that wind intensity was an important correlate of aerial insect abundance throughout an entire summer season and my data suggest that the increased activity of bats in zero or light winds reflects the larger numbers of aerial insects present under these low wind conditions.

Bradbury and Vehrencamp (1976) and Bell (1980) found no decrease in bat activity during bright moonlight. Furthermore, Bradbury and Vehrencamp (1976) found that, regardless of moon-phase or time of moonrise, there was a major peak in aerial insect abundance during the first hour after sunset with continued additional peaks during the night, with no clear relationship between the peaks and levels of moonlight.

A flying bat could present an easy target to predators (especially owls) in bright moonlight and because insects are most abundant in the first hour after sunset, bats could afford to roost or restrict their flying to wooded areas during moonlight if they fed in the initial emergence period of insects. The benefits of feeding in the twilight insect abundance period may be high enough to allow bats to disregard the risks of predation in moonlight during the initial feeding bout of the evening, thereby helping to explain the weak decline in bat feeding activity during moonlight.

Another reason for reduced bat activity during moonlight may be the availability of larger insect prey (moths and beetles) which are strongly attracted to light. These insects would fly at higher altitudes because of their attraction to moonlight, causing bats hunting these to be undetected by our sensors (Downes 1982). The larger size of many moths and beetles compared to midges, mayflies and caddisflies would be such that bats need to eat fewer food items to maintain the same energy intake, and that lower feeding activity would be observed under these conditions. The question of the relationship between the activity patterns of Myotis

5

lucifugus and the phases and level of moonlight still requires more intensive study.

Insect Factors

Local emergences of imagoes of aquatic insects are an important source of food for Myotis lucifugus (Barclay and Fenton 1980) but occur rarely at a sampling site (Figs. 8, 9, 10). The irregular occurrences of large insect captures in sampling over the summer of 1977 on Lake Opinicon suggests that aerial insects are patchily distributed in space and time. The variation in depth and type of lake bottom could be factors affecting the distribution of emerging aerial aquatic insects. The Shannon (1948) indices indicate a low diversity and a fairly strong evenness in abundance of insect orders when sampling over the lake throughout both summers. It reflects a food resource which is generally abundant but varying in composition, even though this resource is patchy in space and time.

The very low capture rate (19% of all sample points) even though insects were seen but not captured indicates a biased sampling procedure. The use of a cone of light to draw insects in the immediate area to a central location did improve our chances of captures but many potential "captures" escaped the movement of the net through the light. As well, at specific cold and/or windy locations on the lake insects would not be present for sampling. Many moths and beetles would not be attracted to the light in the short (2-3 min) time that it was on for sampling.

The insects that are suitable as prey are approximately equal to or greater in length than the wavelength of the echolocation sounds emitted by the bats attempting to capture them (Gould 1955) which for Myotis

lucifugus is 4-12 mm (Anthony and Kunz 1977). My data show that the presence of insects was positively correlated to feeding buzzes regardless of size (Table 2) and support Woodsworth (1981) who found that the increase in the pass-to-buzz ratio detected in the spatially uniform presence of insects was less than the increase in ratio that occurred in the concentrated groups (patches) caused by a light source.

Diet Factors

Schoener (1969) defined an optimal diet as one that yields the maximum net energy unit per unit of feeding per unit of energy requirement. Natural selection would favour a feeding strategy that maximizes net caloric intake per unit time (Emlen 1966). If so, active bats should be expected to maximize their foraging efforts at a time when insects of a certain size are most active or most abundant.

Although bat faeces were examined for detection of four orders of insects and therefore indicated the relative abundance of only those four orders in the diet, analysis of faeces suggested selective feeding by Myotis lucifugus. Schoener (1969) predicted that when a single species population predominates in an area, prey items are selected largely on abundance and relative energy value. Theoretically, predators respond to rising prey abundances by being increasingly selective in prey consumed (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Charnov 1976). Myotis lucifugus exhibits flexibility in diet, moving from being a generalist to being a specialist when the abundance of larger, more energetically profitable insects increases. My analysis of faeces shows a dramatic shift from Diptera to Trichoptera from May to August in faeces taken from 3 colonies of M. lucifugus in 1978 (Table 9).

Aquatic Dipterans were found by investigators (Belwood and Fenton 1976; Anthony and Kunz 1977) to be common items in the diet of M. lucifugus although some colonies showed preferences for Ephemeroptera and Trichoptera (Buchler 1976). Anthony and Kunz (1977) showed that the diet of M. lucifugus remained diverse throughout the summer but females were more selective in July when insect abundance was high, taking more beetles and mayflies. Kunz (1973) noted that lactating females had the highest consumption of insects, with pregnant females eating considerably less. The shift in food preference shown by faecal analysis (Table 9) demonstrates the influence of lactation in females to increase energy intake by concentrating on insect species of greater yield in energy per unit captured when insects in general are in greater abundance. M. lucifugus has a life cycle that is synchronous to these variations in abundance of insects; lactation occurs during times of increasing numbers of insects and weaning of young during times of highest insect abundance.

Usefulness of the Mathematical Model

The multiple regression analysis (MRA) models employed in this project cannot be used to describe a causal situation in nature. Their usefulness centres on predicting the values of the dependent variables (passes and buzzes) from a combination of independent (predictor) variables that collectively maximize the reduction in unexplained variance in the passes or buzzes. There is a danger in trying to increase the coefficient of multiple correlation (R^2) by adding more independent variables to the equation. I found that by inserting the variable 'passes' into the regression equation for buzzes that the $R^2 = 0.629$ whereas, without 'passes' being included, the $R^2 = 0.163$. Although this shows a strong correlation

between passes and buzzes it does not mean that the variable 'passes' can be used to directly predict buzzes (i.e., feeding activity).

Another difficulty with MRA concerns the intercorrelation among the independent (predictor) variables used in the equation. Since the regression coefficients of any one independent variable relies on the other independent variables in the model, a certain combination of these variables can provide misleading R^2 values. By using dummy variables to account for the interactions between certain variables I was able to reduce the intercorrelation. Much of the confounding between variables could have been eliminated by collecting data from a constant set of individual sites rather than from transects.

In studies where variables are difficult to control (e.g. ecology, social sciences) the use of MRA has yielded small R^2 and regression coefficients which are inconsistent when studies are repeated. A way to test my model would have been to use one half the data to develop the model and then use the remainder of the data to test the model.

The adjusted ANOVA resulting from backward step-wise regression revealed 8 of 89 variables to be significant ($P < 0.05$) at predicting levels of passes or buzzes. Field observations of little brown bats confirms the importance of water surfaces to these animals and, that location is a critical determinant of activity and feeding. This is supported by my observations that transects which largely followed shorelines rather than open water were more likely to have high levels of activity and feeding. The presence of insects as a predictor for both activity and feeding suggests that bats are not eating just insects caught through netting and/or that bats do not feed continuously whenever insects are present.

The most interesting variable in the model is moonlight. Much discussion has surrounded the role moonlight plays in bat activity (Bradbury and Vehrencamp, 1976; Bell, 1980) but very few studies rely on the large sample from which my data is drawn. In my analysis the presence of insects is a positive predictor of both passes and buzzes, and moonlight is a depressor of both passes and buzzes. This suggests that insect activity may also be depressed by moonlight. Insects may fly to the shade from moonlight offered by trees along the shorelines of L. Opinicon and as such be a positive influence on bat feeding.

I propose that given the variation caused by different observers (assistants) and the likely variation in bat activity from year to year, that little brown bats are most active and feed along shorelines in the presence of volant aquatic insects under the conditions of zero or light winds and low or zero moonlight.

Ecological and Behavioural Implications

M. lucifugus appears to reduce levels of intraspecific competition for food by demonstrating a generalized diet but with flexibility in shifting to the abundant resources of insect blooms and to insects of higher energy content when abundance is high or when physiological demands are excessive (e.g., lactation). The change in diet of females may reflect a partitioning of food to allow newly volant young access to the continually abundant dipterans of the lake. Group feeding by these bats in large emergent blooms of insects may reduce competition for the more limited insects along shorelines.

M. lucifugus on Lake Opinicon has a stable population abundance until the young are born and flying, when an increased demand and

competition for food forces both the lactating females and young further into the collective home range and into less optimal habitats. The strong tendency for little brown bats to hunt along shorelines and in areas nearby colonies where there are many insects available during the initial evening emergence period of the insects, and the bats' dispersal along shorelines to regions of (1) wide overlap between the 2 colonies' home ranges and of (2) optimal feeding, show clear habitat partitioning.

M. lucifugus secures its role as a nocturnal predator of aerial insects by emerging from its colonies when diurnal insectivorous and raptorial birds have gone to roost for the night. This emergence parallels the evening flight of insects allowing bats to rapidly fill their stomachs. Subsequent feeding bouts by individuals occur as they move along shorelines away from the colonies to locate patches or blooms of insects near the surface of the lake shore. Variation in choice of size and species of insects allows M. lucifugus to optimize the use of food resources.

CONCLUSIONS

1. Bats were most active along shorelines (within 15 m of the water's edge), and near the surface of L. Opinicon (with 1-3 m of the surface).
2. Most flying bats are either feeding or searching for food. The rate of buzzes increases in the presence of insects.
3. Bats emerged from colonies shortly after dusk and returned as the green colour of vegetation was becoming visible in the morning. Bats have several feeding-bouts during the night and show wide variation in feeding bout timing within 3 different habitats (shorelines, open water, inland) and at different locations on the lake. Both activity and feeding increased during August.
4. Bats dispersed from the colonies to at least 3.5 km away and returned frequently within 0.75 - 2.5 h. During dispersal, bats followed shorelines or travelled inland. They remained in lee areas during strong winds. Bats from 2 colonies fed in common areas of the lake and quickly flew to the lake shoreline when dispersing.
5. Insects were active between temperatures of 10° and 25°C , and the number of insects sharply declined in strong winds and increasing moonlight. Lake Opinicon provides bats with abundant, diverse and patchily distributed insect resources. Faecal analysis indicates that bats shift their diet from May to August. Groups of bats fed in blooms of emerging aquatic insects.

6. Temperature, wind speed, and moonlight affected both the presence of insects and the feeding of bats. Bats fed most during zero or light winds, but feeding declined as moonlight levels increased and when ambient temperatures fell below 10°C .

TABLES AND FIGURES

Table 1. Summary of period-meter observations taken at 111 sample locations along transects during July and August 1978.

	Inland		Shoreline		Water	
Lowest frequency of call (kHz)	20	40	20	40	20	40
Number of occurrences of lowest frequency	1	10	14	14	0	2

Table 2

ANOVA of abbreviated model of variables affecting natural
logarithm of number of buzzes.

Refer to Appendix 3 for definitions of terms used to name
variables.

Table 2

Analysis 1
Dependent Variable Buzz

Natural Logarithm Buzz

Adjusted Analysis Of Variance - Each Term Adjusted For All Other Terms

Variation	D.F.	Mean Square	F value
Surf	1	9.16613	14.497
Tr/s	14	1.23936	1.960
Year	1	1.95553	3.093 NS
Locn	2	3.74667	5.926
Assn	6	4.12393	6.523
Insc	1	4.14231	6.552
Wnsp	1	4.17493	6.603
Moon	1	9.32029	14.741
Residual	890	0.63226	
Total	917	0.75258	

18.46 Per Cent Reduction In Total SS

Parameter Estimates With Their Standard Errors

Parameter		Deviation From Grand Mean	S.E.
Surf 1	+	0.2382825	0.06258
Surf 2	-	0.2382825	0.06258
Year 1	+	0.0685705	0.03899
Year 2	-	0.0685705	0.03899
Locn 1	-	0.0615393	0.08722
Locn 2	+	0.1354116	0.05051
Locn 3	-	0.0738723	0.05781
Assn 1	+	0.2374041	0.10108
Assn 2	-	0.2560209	0.09101
Assn 3	+	0.0297532	0.09801
Assn 4	-	0.0629690	0.10700
Assn 5	+	0.1320644	0.11824
Assn 6	-	0.0659164	0.11859
Assn 7	-	0.0143153	0.46236
Insc 1	+	0.0813211	0.03177
Insc 2	-	0.0813211	0.03177
Wnsp	-	0.0829495	0.03228
Moon	-	0.0702538	0.01830
Grand Mean =		0.6028	

Note: Refer to Appendix 3 for definition of terms

Table 3

ANOVA of abbreviated model of variables affecting the natural logarithm of the number of passes.

Refer to Appendix 3 for definitions of terms used to name variables.

Table 3

Analysis 2

Dependent Variable Pass

Natural Logarithm Pass

Adjusted Analysis Of Variance - Each Term Adjusted For All Other Terms

Variation	D.F.	Mean Square	F value
Surf	1	8.2267	8.272
Tr/s	14	2.7400	2.755
Year	1	9.9750	10.030
Locn	2	11.8439	11.910
Assn	6	7.4810	7.522
Insc	1	2.5185	2.532 NS
Wnsp	1	13.7169	13.793
Moon	1	4.7811	4.808
Residual	890	0.9945	
Total	917	1.2172	

20.70 Per Cent Reduction In Total SS

Parameter Estimates With Their Standard Errors

Parameter		Deviation From Grand Mean	S.E.
Surf 1	+	0.22574	0.07849
Surf 2	-	0.22574	0.07849
Year 1	+	0.15487	0.04890
Year 2	-	0.15487	0.04890
Locn 1	-	0.17778	0.10939
Locn 2	+	0.26436	0.06335
Locn 3	-	0.08658	0.07251
Assn 1	+	0.27656	0.12677
Assn 2	-	0.32030	0.11415
Assn 3	+	0.10747	0.12293
Assn 4	+	0.09726	0.13420
Assn 5	+	0.39457	0.14829
Assn 6	+	0.22208	0.14873
Assn 7	-	0.77764	0.57988
Insc 1	+	0.06341	0.03985
Insc 2	-	0.06341	0.03985
Wnsp	-	0.15035	0.04049
Moon	-	0.05032	0.02295
Grand Mean =		2.275	

Note: Refer to Appendix 3 for definition of terms

Table 4. Summary of the simple arithmetic mean numbers of feeding buzzes per 5 minutes for three classes of habitat for 1976, 1977 combined.

	Class of Habitat		
	Inland	Shore	Water
$\bar{x}$ feeding buzzes	0.36	1.94	1.45
(SE)	(0.08)	(0.18)	(0.19)
N	250	707	398

Table 5. Summary of comparisons between simple arithmetic mean feeding ($\bar{X}$ buzzes) and moon phases, temperature, wind speed and wind direction.

	Temperature					
	12°C	15°C	18°C	21°C	24°C	27°C
$\bar{X}$ buzzes	0.89	2.32	1.52	1.79	0.93	2.09
(SE)	(0.33)	(0.45)	(0.18)	(0.30)	(0.21)	(1.09)
N	111	235	399	404	159	22

	Windspeed (determined by angle of fly of ribbon from upright thermometer case)			
	Zero	Light	Medium	High
$\bar{X}$ buzzes	1.83	2.41	1.45	0.93
(SE)	(0.34)	(0.41)	(0.16)	(0.29)
N	272	307	569	204

	Wind direction (determined by Silva compass)							
	N	NE	E	SE	S	SW	W	NW
$\bar{X}$ buzzes	2.7	2.5	0.9	1.04	1.8	1.2	1.7	1.7
(SE)	(0.69)	(0.77)	(0.23)	(0.25)	(0.32)	(0.16)	(0.32)	(0.53)
N	114	141	123	80	128	234	137	100

	Moon phases				
	None	Quarter	Half	Gibbous	Full
$\bar{X}$ buzzes	1.88	2.55	1.18	1.49	0.71
(SE)	(0.20)	(1.00)	(0.26)	(0.45)	(0.18)
N	902	61	102	126	155

Table 6. Summary of relative abundance of insect orders by netting through a cone of light, July and August, 1976, 1977.

Figures represent percentage of total abundance for each order in each of July and August.

(N) = number of insects

		1976		1977	
July	Diptera	32.5	(215)	80.2	(478)
	Trichoptera	46.3	(306)	1.2	(7)
	Coleoptera	5.1	(34)	0.3	(2)
	Lepidoptera	2.1	(14)	2.0	(12)
	Ephemeroptera	2.6	(17)	12.6	(75)
	Thysanoptera	11.0	(73)	3.5	(21)
	Other	0.3	(2)	0.2	(1)
August	Diptera	67.9	(142)	59.6	(630)
	Trichoptera	14.4	(30)	0.4	(4)
	Coleoptera	1.0	(2)	0.4	(4)
	Lepidoptera	8.1	(17)	2.1	(22)
	Ephemeroptera	7.2	(15)	33.0	(349)
	Thysanoptera	1.0	(2)	4.5	(48)
	Other	0.5	(1)	0.1	(1)

Table 7. Shannon (1948) indices of diversity for insect samples, July and August 1976, 1977.

The Shannon expression $H = - \sum_{i=1}^k p_i \log p_i$ was converted to the

$$n \log n - \sum_{i=1}^k f_i \log f_i$$

computing formula of $H = \frac{n \log n - \sum_{i=1}^k f_i \log f_i}{n}$ for convenience in doing calculations. The maximum diversity is $H_{\max} = \log k$ and the relative diversity $J = \frac{H}{H_{\max}}$ (Pielou, 1948).

n = sample size

f_i = proportion of observations in category i

k = number of categories

p_i = proportion of observations in category i

$$p_i = \frac{f_i}{n}$$

	H	J
July 1976	0.57	0.67
Aug 1976	0.46	0.54
July 1977	0.31	0.36
Aug 1977	0.41	0.48

Table 8. Relative abundance of orders of insects determined by analysis of 2274 insects parts from bat faecal pellets, July and August, 1977.

Figures represent percentage of total abundance for each order in each of two months.

Colony	Insect Order	July		August	
Hughson's Barn	Diptera	29.6	(63)	14.3	(1)
	Trichoptera	67.6	(144)	42.9	(3)
	Coleoptera	2.4	(5)	28.6	(2)
	Lepidoptera	0.5	(1)	14.1	(1)
Hughson's Silo	Diptera	4.5	(68)	25.5	(137)
	Trichoptera	93.8	(1423)	68.5	(368)
	Coleoptera	1.5	(19)	3.7	(20)
	Lepidoptera	0.5	(7)	2.2	(12)

(N) = number of insect parts

Table 9. Summary of relative abundance of insect orders found by analysis of bat faecal pellets removed from 3 nursery colonies, May to August, 1978.

Figures represent percentage of total abundance for each order in each of four months.

(N) = number of insect parts

1978	Order	Hughson's Silo	Opinicon Lodge	Mike Murray's
May	Diptera	52.6 (141)	21.8 (88)	44.6 (45)
	Trichoptera	42.5 (114)	75.2 (303)	54.5 (55)
	Coleoptera	4.9 (13)	2.7 (11)	0.0 (0)
	Lepidoptera	0.0 (0)	0.3 (1)	0.9 (1)
June	Diptera	31.2 (53)	15.7 (21)	5.1 (11)
	Trichoptera	64.1 (109)	79.1 (106)	82.8 (178)
	Coleoptera	3.5 (6)	3.7 (5)	11.2 (24)
	Lepidoptera	1.2 (2)	1.5 (2)	0.9 (2)
July	Diptera	3.5 (57)	2.0 (17)	1.9 (3)
	Trichoptera	95.2 (1574)	96.1 (826)	93.6 (146)
	Coleoptera	0.9 (15)	1.4 (12)	4.5 (7)
	Lepidoptera	0.4 (7)	0.6 (5)	0.0 (0)
August	Diptera	3.1 (15)	4.2 (14)	9.1 (11)
	Trichoptera	92.5 (454)	93.8 (316)	83.5 (101)
	Coleoptera	3.7 (18)	0.89 (3)	7.5 (9)
	Lepidoptera	0.81 (4)	1.19 (4)	0.0 (0)

Fig. 1

Photograph of part of study area.

An aerial view looking east along the north shore of Lake Opinicon. The buildings to the right of centre are the Queen's University Biology Station. Counterclockwise from the lower right corner are four large islands; Sheep Island, Cow Island, Rabbit Island, and an unnamed island.

Fig. 2

Aerial photograph of Lake Opinicon area.

This high altitude photograph shows the topography of the area around the lake in April 1976. Some ice remains on the lake. The circles show bat nursery colonies.

Fig. 3

Fig. 4

Map showing the location of all transects

water

land

Fig. 5

Graphs showing relative hourly patterns of bat activity at 3 island locations on two different nights in 1976.

Solid line (————) represents the percentage of the total activity (passes) at 15-min intervals. The total number of passes recorded for that night (N) is indicated for all 3 locations.

These graphs represent data taken before the thesis study began and are to illustrate the wide variation in activity periods overnight at 3 similar habitat locations.

Fig. 6

Graphs showing the relative hourly patterns of bat activity (passes) for three classes of habitat (inland, shoreline, openwater) July and August, 1976-77.

N represents the total passes for July and August for both years.

Solid line (—) represents the percentage of total activity (passes) for inland locations (N = 1247) at hourly intervals.

Dashed line (---) represents the percentage of total activity (passes) for shoreline locations (N = 5802) at hourly intervals.

Dash-dot line (-.-.-) represents the percentage of total activity (passes) for open water locations (N = 2123) at hourly intervals.

Fig. 7

Graph showing the relative mean activity (passes) per 5 minutes (●—●, N = 1351 5 minute samples) for July and August, 1976, 1977.

Open circles show the number of 5 minute samples taken for each date.

Fig. 8

Histograms showing the relative abundance of orders
of insects captured during July, 1977.

PERCENT OF TOTAL INSECTS

Fig. 9

Histogram showing the relative abundance of orders
of insects captured during August, 1977.

30
10
5
0

Fig. 10

Graphs showing the percentage abundance of insects over all transects for July and August 1977 and in the faecal analysis for Hughson's Silo colony in 1977 compared with the phases of the moon and cloud cover.

The solid (●) and open (○) circles show the dates of the new and full moons respectively.

The solid line (—) indicating a sine wave shows the cyclic relative amount of moonlight.

The thick solid lines (■ ■) show nights of partial or complete overcast skies.

The bar graphs show the percentage abundance of insects. In the case of insect captures the percent is based on the total number of insects captured in 1977 (N = 1664). In the case of faecal analysis the percent is based on the number of insect parts found in the faeces (N = 2274).

Fig. 11

Histograms comparing the percentage insect abundance as shown by captures and analysis of bat faecal pellets.

Fig. 12 - 17

Map showing dispersal of light-tagged Myotis lucifugus from the two colonies on stated dates.

The large arrows ( ) show the mean direction flown by light-tagged bats after release. The number in the large arrow is the total number of bats that flew in that direction.

A solid line with small arrowhead ( ) indicates the approximate route of a single light-tagged bat after release.

The solid circle ( ) near the compass arrow indicates the moon phase on that night.

The small circles ( ) show the locations of the 2 nursery colonies.

Fig. 12

N = 14 bats

M. Murray Colony

21 August 1976

Fig. 13

N = 18 bats

M. Murray Colony

30 August 1976

Fig. 14
 N = 20 bats
 M. Murray Colony
 21 July 1977

Fig. 15
 N = 27 bats
 Blockhouse Colony
 25 July 1977

Fig. 16

N = 35 bats

Blockhouse Colony

26 August 1977

Fig. 17

N = 25 bats

Blockhouse Colony

30 August 1977

Fig. 18

Scatter Diagram of natural logarithm of passes (horizontal axis) versus residuals, July and August, 1976-77.

Fig. 19

Scatter Diagram of natural logarithm of buzzes (horizontal axis)
versus residuals, July and August, 1976-77.

BAT ACTIVITY AND FEEDING - NATURAL LOGARITHM BUZZ

SCATTER DIAGRAM - VARIABLE RES (VERTICAL AXIS) VERSUS VARIABLE YEXP (HORIZONTAL AXIS)

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APPENDICES

APPENDIX 1: Computer programme for transforming data to dummy variables
and converting other variables.

```
SUBROUTINE TRANS(Y,NG)
  DIMENSION Y(1)
C
C SKIP COMPLETELY IF NEITHER BUZZES NOR PASSES - OTHERWISE TRANSFORM
C
      J=Y(7)+0.01
      K=Y(8)+0.1
      IF(J.EQ.999.OR.K.EQ.999.OR.(J.EQ.0.AND.K.EQ.0)) NG=-1
      IF(NG.LT.0) RETURN
      Y(7)=ALOG(Y(7)+1.0)
      Y(8)=ALOG(Y(8)+1.0)
C
C DUMMY VARIABLES FOR TRANSECTS AND LAND : 36 REFERS TO SURFACE.
C   TRANSECTS : 37-39 OVER LAND   40-50 OVER WATER
C
      DO 100 I=36,89
100    Y(I)=0.0
      J=Y(1)+0.1
      IF(J.NE.99) GO TO 1
      NG=-1
      RETURN
1    Y(36)=1.0
      IF(J.GE.13) Y(36)=-1.0
      IF(J.LE.12) GO TO 5
      IF(J.EQ.16) GO TO 2
      K=24+J
      Y(K)=1.0
      GO TO 10
2    DO 3 I=37,39
3    Y(I)=-1.0
      GO TO 10
5    IF(J.EQ.12) GO TO 7
      K=39+J
      Y(K)=1.0
      GO TO 10
7    DO 8 I=40,50
8    Y(I)=-1.0
10   CONTINUE
C
C YEAR Y(2) CAN BE LEFT IN THIS POSITION
C
      J=Y(2)+0.1
      IF(J.EQ.76) Y(2)=1.0
      IF(J.EQ.77) Y(2)=-1.0
C
C INTERACTION : YEARS AND SURFACES Y(51)
      Y(51)=Y(2)*Y(36)
```

```
C
C CONVERT MONTH AND DAY INTO WEEK
C
      J=Y(4)+0.1
      J=K+(J-7)*5
C
C GENERATE DUMMIES FOR WEEKS WITHIN EACH YEAR Y(52-69)
C
      IF(Y(2).GT.0.0) GO TO 15
      IF(J.EQ.10) GO TO 13
      K=J+51
      Y(K)=1.0
      GO TO 20
13     DO 14 I=51,59 -
14       Y(I)=-1.0
      GO TO 20
15     IF(J.EQ.10) GO TO 17
      K=60+J
      Y(K)=1.0
      GO TO 20
17     DO 18 I=61,69
18       Y(I)=-1.0
20     K=0
C
C TIME SLOTS Y(70-71) DUSK, MIDDLE, DAWN
C
      J=Y(5)+0.1
      IF(J.GE.1800.AND.J.LT.2200) K=1
      IF(J.GE.2200.OR.J.LT.200) K=2
      IF(J.GT.200.AND.J.LT.600) K=3
      IF(K.GT.0) GO TO 21
      NG=-1
      RETURN
21     IF(K.EQ.3) GO TO 22
      J=69+K
      Y(J)=1.0
      GO TO 25
22     Y(70)=-1.0
      Y(71)=-1.0
25     CONTINUE
C
C LOCATIONS - Y(72-73) INLAND V SHORE V WATER
C
      J=Y(6)+0.1
      IF(J.EQ.3) GO TO 26
      K=71+J
      Y(K)=1.0
      GO TO 30
26     Y(72)=-1.0
      Y(73)=-1.0
30     CONTINUE
C
C CONVERT WIND DIRECTION INTO SINE AND COSINE Y(74-75)
C VARIABLE DIRECTION (11, 74 AND 75)
C INCLUDE Y(89) ALWAYS WITH 74 AND 75
```

```

      J=Y(11)+0.1
      X=J*0.785398
      Y(74)=SIN(X)
      Y(75)=COS(X)
      Y(89)=1.0
      IF(J.EQ.9) Y(89)=-1.0
C
C CONVERT FOG TO DUMMY LEAVE IN Y(15)
C
      J=Y(15)+0.1
      IF(J.EQ.0) Y(15)=-1.0
C
C INSECT ABUNDANCE Y(76) PRESENT U ABSENT
C
      J=Y(16)+0.1
      IF(J.LT.9) GO TO 35
34      NG=-1
      RETURN
35      IF(Y(19).GT.8.OR.Y(22).GT.8.OR.Y(25).GT.8.OR.Y(28).GT.8)
1      GO TO 34
      Y(76)=-1.0
      IF(J+Y(19)+Y(22)+Y(25)+Y(28).GT.0.5) Y(76)=1.0
C
C INSECT SIZE Y(77) 4MM OR GREATER
C Y(78) 3MM OR LESS
C
      Y(77)=(Y(17)+Y(20)+Y(23)+Y(26)+Y(29))/5.
      Y(78)=(Y(18)+Y(21)+Y(24)+Y(27)+Y(30))/5.
C
C DUMMY FOR ASSISTANTS - Y(79-84)
C
      J=Y(31)+0.1
      IF(J.EQ.7) GO TO 40
      K=J+78
      Y(K)=1.0
      GO TO 45
40      DO 41 I=79,84
41      Y(I)=-1.0
45      CONTINUE
C
C ANGLES FROM COLONY MM (85-86) AND BH(87-88)
C
      J=Y(32)+0.1
      X=J*0.785398
      Y(85)=SIN(X)
      Y(86)=COS(X)
      J=Y(34)+0.1
      X=J*0.785398
      Y(87)=SIN(X)
      Y(88)=COS(X)
C
      RETURN
      END

```

APPENDIX 2: Summary of measured, converted and dummy variables.

VARIABLE	MIN	MEAN	MAX	VARIANCE
1 SECT	1.00000	8.19608	16.00000	0.18803387D+02
2 YEAR	-1.00000	-0.20697	1.00000	0.95820652D+00
3 MONT	7.00000	7.55864	8.00000	0.24706049D+00
4 DAY	1.00000	17.89325	31.00000	0.78433520D+02
5 TIME	55.00000	1477.08932	2459.00000	0.96252275D+06
6 LOCA	1.00000	2.13943	3.00000	0.42546620D+00
7 PASS	0.69315	2.27532	5.56452	0.12171560D+01
8 BUZZ	0.00000	0.60281	4.57471	0.75257701D+00
9 TEMP	8.00000	19.07081	99.00000	0.10954678D+03
10 WNSP	0.00000	1.52070	3.00000	0.88670311D+00
11 WNDR	0.00000	3.68627	8.00000	0.74630829D+01
12 MOON	0.00000	1.01307	9.00000	0.26126970D+01
13 CLUD	0.00000	1.65142	9.00000	0.35751943D+01
14 RAIN	0.00000	0.09041	9.00000	0.55343036D+00
15 FOG	-1.00000	-0.84967	9.00000	0.80180469D+00
16 DIPT	0.00000	1.19608	8.00000	0.67292322D+01
17 >4MD	0.00000	0.28867	15.00000	0.15316272D+01
18 <3MD	0.00000	1.06645	95.00000	0.24127532D+02
19 TRIC	0.00000	0.04793	2.00000	0.93665286D-01
20 >MT	0.00000	0.05011	8.00000	0.19377861D+00
21 <3MT	0.00000	0.00871	4.00000	0.28277299D-01
22 THYS	0.00000	0.12745	3.00000	0.36650844D+00
23 >4MY	0.00000	0.01852	3.00000	0.29100529D-01
24 <3MY	0.00000	0.05882	10.00000	0.21900058D+00

25	EPHE	0.00000	0.22222	4.00000	0.840421660+00
26	P4MP	0.00000	0.21351	52.00000	0.572971920+01
27	P3MP	0.00000	0.06100	12.00000	0.384497140+00
28	OTHE	0.00000	0.20697	5.00000	0.993102920+00
29	P4MD	0.00000	0.05338	6.00000	0.133461870+00
30	P3MD	0.00000	0.03050	8.00000	0.156102470+00
31	ASST	1.00000	2.84096	8.00000	0.267478730+01
32	ANMM	0.00000	255.22658	350.00000	0.196607730+04
33	DIMM	0.00000	2722.16776	6860.00000	0.334200870+07
34	ANBH	0.00000	184.38126	272.00000	0.281495590+04
35	DIBH	0.00000	2329.01634	6040.00000	0.244361000+07
36	SURF	-1.00000	0.59259	1.00000	0.649541580+00
37	TR/S	-1.00000	0.01525	1.00000	0.134990720+00
38	Y38	-1.00000	-0.00545	1.00000	0.114474120+00
39	Y39	-1.00000	-0.04575	1.00000	0.720593580-01
40	Y40	-1.00000	-0.02832	1.00000	0.121334370+00
41	Y41	-1.00000	-0.00545	1.00000	0.145008470+00
42	Y42	-1.00000	-0.02070	1.00000	0.129342150+00
43	Y43	-1.00000	-0.00654	1.00000	0.143904890+00
44	Y44	-1.00000	0.01307	1.00000	0.163405820+00
45	Y45	-1.00000	-0.00654	1.00000	0.143904890+00
46	Y46	-1.00000	-0.01525	1.00000	0.134990720+00
47	Y47	-1.00000	0.00545	1.00000	0.155913600+00
48	Y48	-1.00000	-0.01743	1.00000	0.132738420+00
49	Y49	-1.00000	-0.00763	1.00000	0.142798930+00
50	Y50	-1.00000	-0.01634	1.00000	0.133865760+00

51	T*SR	1.00000	-0.08061	1.00000	0.99458545D+00
52	Y52	-1.00000	-0.00871	0.00000	0.86480733D-02
53	Y53	-1.00000	-0.00871	0.00000	0.86480733D-02
54	W/YR	-1.00000	-0.00436	1.00000	0.13067144D-01
55	Y55	-1.00000	0.00327	1.00000	0.20709047D-01
56	Y56	-1.00000	0.00327	1.00000	0.20709047D-01
57	Y57	-1.00000	0.02179	1.00000	0.38783283D-01
58	Y58	-1.00000	0.00000	1.00000	0.17448201D-01
59	Y59	-1.00000	0.00763	1.00000	0.25023580D-01
60	Y60	0.00000	0.00545	1.00000	0.54228647D-02
61	Y61	-1.00000	-0.00545	0.00000	0.54228647D-02
62	Y62	-1.00000	0.00763	1.00000	0.18480505D-01
63	Y63	-1.00000	-0.00109	1.00000	0.98134249D-02
64	Y64	-1.00000	0.04793	1.00000	0.56587860D-01
65	Y65	-1.00000	0.02505	1.00000	0.35358503D-01
66	Y66	-1.00000	0.03050	1.00000	0.40508146D-01
67	Y67	-1.00000	0.00871	1.00000	0.19553199D-01
68	Y68	-1.00000	0.01743	1.00000	0.28049218D-01
69	Y69	-1.00000	0.03377	1.00000	0.43569421D-01
70	NIPE	-1.00000	-0.12200	1.00000	0.43002782D+00
71	Y71	-1.00000	0.28867	1.00000	0.77263051D+00
72	LOCN	-1.00000	-0.12092	1.00000	0.44883144D+00
73	Y73	-1.00000	0.26580	1.00000	0.77987565D+00
74	DIWN	-1.00000	-0.09147	1.00000	0.46054436D+00
75	Y75	-1.00000	0.22459	1.00000	0.48167550D+00

76	INSC	-1.00000	0.27451	1.00000	0.92565270D+00
77	INSZ	0.00000	0.12484	10.40000	0.35460602D+00
78	Y78	0.00000	0.24510	19.00000	0.10543216D+01
79	ASSN	0.00000	0.22113	1.00000	0.17242096D+00
80	Y80	0.00000	0.33660	1.00000	0.22354438D+00
81	Y81	0.00000	0.26797	1.00000	0.19637779D+00
82	Y82	0.00000	0.11438	1.00000	0.10140698D+00
83	Y83	0.00000	0.08061	1.00000	0.74192866D-01
84	Y84	0.00000	0.12309	1.00000	0.10805934D+00
85	Y85	-1.00000	-0.00334	1.00000	0.49180998D+00
86	Y86	-1.00000	-0.10568	1.00000	0.49808934D+00
87	Y87	-1.00000	0.07574	1.00000	0.47953703D+00
88	Y88	-1.00000	-0.01352	1.00000	0.51562788D+00
89	Y89	1.00000	1.00000	1.00000	0.00000000D+00

DEFINITIONS OF VARIABLE NAMES

1	SECT	Transect
2	YEAR	Year
3	MONT	Month
4	DAY	Day of Month
5	TIME	Time of Day (24h clock)
6	LOCA	Location (Inland, Shore, Water)
7	PASS	Passes
8	BUZZ	Buzzes
9	TEMP	Temperature ($^{\circ}\text{C}$)
10	WNSP	Windspeed
11	WNDR	Wind direction
12	MOON	Phase of Moon
13	CLUD	Cloud Cover
14	RAIN	Rainfall
15	FOG	Fog
16	DIPT	Dipteran Insects
17	>4MD	Dipterans longer than 4 mm
18	<3MD	Dipterans less than 3 mm
19	TRIC	Trichoptera Insects
20	>4MT	Trichoptera >4 mm
21	<3MT	Trichoptera <3 mm
22	THYS	Thysanoptera Insects
23	>4MY	Thysanoptera >4 mm
24	<3MY	Thysanoptera <3 mm
25	EPHE	Ephemeroptera
26	>4MP	Ephemeroptera >4 mm

27	<3MP	Ephemeroptera <3 mm
28	OTHE	Other Insects
29	>4MO	Other >4 mm
30	<3MO	Other <3 mm
31	ASST	Assistants
32	ANMM	Angle from M. M. Colony
33	DIMM	Distance from M. M. Colony
34	ANBH	Angle from B. H. Colony
35	DIBH	Distance from B. H. Colony
36	SURF	Surfaces, land, water
37	TR/S	Surfaces within Transects, land
38	Y38	land transect
39	Y39	land transect
40-50	Y-40 - Y-50	Water Transects
51	Y*SR	Interaction of Years and Surfaces
52-69	Y-52 - Y-69	Interaction of Weeks within each Year
70	NIPE)	Night period Time Slots
71	Y71)	
72	LOCN)	Locations
73	Y73	
74	DIWN)	Wind direction
75	Y75)	
76	INSC	Insect Abundance
77	INSZ)	Insect Size >4 mm
78	Y78)	<3 mm
79-84	ASSN-Y84	Assistants
85-86	Y85-Y86	Angles from M. M. Colony
87-88	Y87-Y88	Angles from B. H. Colony
89	Y89	Wind direction (always equals 1.0)

APPENDIX 4: Summary of Multiple Regression Analysis of passes and buzzes.

BAT ACTIVITY AND FEEDING NATURAL LOGARITHM BUZZ AND PASS *log_e (λ+1)*

STEP NUMBER	1	SIMULTANEOUS ADDITION OF VARIABLES	YEAR	SURF	TR/S	Y38	Y39	Y40	Y41	Y42	Y43	Y44	Y45	Y46
			Y47	Y48	Y49	Y50	LOCN	Y73	INSC	ASSN	Y80	Y81	Y82	Y83
REG YEAR	Y84	212.65110		8	50604									
RESIDUAL		903.48093		1	01287									
TOTAL		1116.13203		1	21716									

19 05 PER CENT REDUCTION IN TOTAL SS

REGRESSION EQUATION																
PASS =	2.114	+	0.21098	YEAR	+	0.18158	SURF	+	0.13848	TR/S	-	0.28849	Y38	-	0.05852	Y39
		-	0.09922	Y40	+	0.24108	Y41	+	0.02028	Y42	-	0.11744	Y43	+	0.37619	Y44
			0.37653	Y45	+	0.19075	Y46	-	0.23625	Y47	-	0.04727	Y48	-	0.11975	Y49
		-	0.08306	Y50	-	0.15705	LOCN	+	0.26182	Y73	+	0.08672	INSC	+	0.24371	ASSEN
		-	0.34827	Y80	+	0.09074	Y81	+	0.06153	Y82	+	0.40007	Y83	+	0.19049	Y84

BAT ACTIVITY AND FEEDING NATURAL LOGARITHM BUZZ AND PASS

STEP NUMBER	1	SIMULTANEOUS ADDITION OF VARIABLES	YEAR	SURF	TR/S	Y38	Y39	Y40	Y41	Y42	Y43	Y44	Y45	Y46
			Y47	Y48	Y49	Y50	LOCN	Y73	INSC	ASSN	Y80	Y81	Y82	Y83
REG YEAR	Y84	114.01647		4	560358									
RESIDUAL		576.096670		0	645848									
TOTAL		690.11317		0	752577									

16 52 PER CENT REDUCTION IN TOTAL SS

REGRESSION EQUATION																
BUZZ	0.5819	+	0.109621	YEAR	+	0.207392	SURF	+	0.107997	TR/S	-	0.113503	Y38	-	0.026515	Y39
		+	0.091124	Y40	+	0.345019	Y41	-	0.072379	Y42	-	0.218290	Y43	+	0.053975	Y44
		-	0.232252	Y45	+	0.259887	Y46	-	0.124205	Y47	-	0.058413	Y48	-	0.001904	Y49
		-	0.075959	Y50	-	0.042871	LOCN	+	0.125970	Y72	+	0.101987	INSC	+	0.173219	ASSN
		-	0.319053	Y80	+	0.001121	Y81	-	0.135925	Y82	+	0.096250	Y83	-	0.120182	Y84

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END

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