1 OF/DE 1

MICROCOPY RESOLUTION TEST CHART
NATIONAL BUREAU OF STANDARDS
STANDARD REFERENCE MATERIAL 1010a
(ANSI and ISO TEST CHART No. 2)

National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service

Services des thèses canadiennes

Ottawa, Canada
K1A 0N4

CANADIAN THESES

THÈSES CANADIENNES

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

**THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED**

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

**LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE**

NON-SELECTIVE MATING IN THE LITTLE BROWN BAT, .

MYOTIS LUCIFUGUS (LeConte) .

by

Virginia Wai-Ping, 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, Carleton University

Ottawa, Canada

April 1986

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights; and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-29893-6

The undersigned hereby recommend to the Faculty of
Graduate Studies and Research acceptance of this thesis,
submitted by Virginia Wai-Ping, B.Sc., in partial fulfillment of the
requirements for the degree of Master of Science.

Chairman, Department of Biology

Supervisor

Carleton University

April 1986

ABSTRACT

The mating season of Myotis lucifugus has two phases. During the active phase females do not copulate selectively with the largest or heaviest available males; they appear to mate randomly but all matings are heterosexual. During the active phase there are no correlations between age, body size and body weight in adult males. During the torpid phase adult males select partners, but 35% of the time they choose males. The results of this study demonstrates that M. lucifugus mate randomly and promiscuously.

ACKNOWLEDGEMENTS

I would like to thank Dr. M.B. Fenton for financial, logistic and moral support through all phases of this study. I am particularly grateful for the freedom Brock gave me to explore my research interest.

Drs. P.J. Weatherhead and J. Picman made useful suggestions throughout this study and on earlier drafts of this thesis. Special thanks to Dr. B. Thomas for statistical advice that made this thesis possible.

I thank P. Chippindale, A. Rein, D. Krull and A. Westcott for their assistance in the field and not complaining when the weather was not the greatest. I thank the bat lab for tolerating my moods during the completion of this thesis. I am indebt to M. Stoneman for assistance whenever the trash 80 crashed.

The moral support of A. Westcott and my parents were invaluable throughout my stay at Carleton.

This study was financially supported by operating and equipment grants to Dr. M.B. Fenton from the Natural Science and Engineering Research Council and by Carleton University Fellowships to VWP.

TABLE OF CONTENTS

	page
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Tables	vii
List of Figures	viii
List of Appendices	ix
Introduction	1
The Study Animal	5
Study Sites	6
Material and Methods	
Matings	
Weight	7
Copulations	8
Presentation Experiments	9
Playback Experiments	12
Results	
Matings	
Weight	15
Copulations	17
Presentation Experiments	17
Playback Experiments	19
Discussion	20
Conclusions	31

Tables

page

32

Figures

39

Appendices

49

Literature Cited

52

List of Tables

	Page
1. Example of a presentation experiment data sheet.	32
2. Mean weight of the age-sex class at the start of the captive study	33
3. Weight change of the age-sex class during the captive study	34
4a. Correlation coefficients of forearm length and weight in 1984	35
4b. Correlation coefficients of forearm length and weight in 1985	35
5a. Comparison of copulating and non-copulating male weight	36
5b. Comparison of copulating and non-copulating male forearm length	36
6. Comparison of the male-female and male-male torpid matings to the proportion of females and males in the hibernating population	37
7a. Proportion of males and females hibernating in clusters of varying size and singly.	38
7b. Comparison of males and females hibernating in large a large cluster and in smaller clusters and singly	38

List of Figures

	Page
1. Floor plan of the Renfrew mine	39
2. Presentation apparatus	40
3. Cluster Analysis of adult male weight	41
4. Weight change during the captive study	42
5. Distribution of <u>M. lucifugus</u> weight	43
6. Forearm lengths of <u>M. lucifugus</u>	44
7. Proportion of free-flying individuals attracted to the live animal presentation	45
8. Proportion of free-flying individuals attracted to the other species	46
9. Proportion of free-flying individuals attracted to <u>M. lucifugus</u>	47
10. Proportion of adult females attracted to the echolocation signals of <u>M. lucifugus</u> at a nursery roost.	48

Appendices

	Page
I. Cluster Analysis	49
II. Log-linear Analysis	50

INTRODUCTION

Four ecological criteria can be used to predict whether animals mate polygynously, monogamously or randomly. They are:

- 1) the relative investments of the parents in rearing offspring (Trivers 1972),
 - 2) the ability of one sex to defend resources (e.g. roosting sites, food patches) required by the opposite sex (Orlans 1969, Bradbury and Vehrencamp 1977, Emlen and Oring 1977)
 - 3) the ability to prevent individuals of the opposite sex from mating with other individuals (Orlans 1969, Emlen and Oring 1977).
- and/or 4) the ratio of males and females in a population (Brosset 1976).

Of 850 species of bats, the mating system is known for 15 species. The most common mating system is polygyny, with males defending resources required by females (Bradbury and Emmons 1974, Brosset 1976, Dwyer 1970, Gerell and Lundberg 1985, Khajuria 1972, Kunz et al. 1983, McCracken and Bradbury 1981, Morrison 1979, Morrison and Morrison 1981, Nelson 1965, and Porter 1979) or restricting access to females (Kleiman and Racey 1968). Bradbury (1981) reported lekking behaviour in Hypsignathus monstrosus, and monogamy has not been demonstrated in bats (see Bradbury 1977).

In temperate bats, hibernation can separate insemination and fertilization by up to seven months (Hartman 1933, Wimsatt 1945). During hibernation "torpid" matings, which involve an active male and

2
a torpid individual occur. Since "torpid" matings are probably unpredictable, a male would be required to remain active throughout the winter to prevent "his" female from mating with other males. This mate guarding behaviour would be energetically costly. Temperate bats that hibernate appear to mate randomly and promiscuously and this is probably related to the temporal separation of insemination and fertilization (Thomas et al. 1979).

Regardless of the mating system adopted by animals, individuals must be able to locate mates, and they may use acoustic, olfactory, tactile and/or visual signals in this endeavour. To date the study of communication signals used by bats during mate location has been restricted to species that are easily observed, use vocalizations that are audible to the human ear, and visual displays in open, well-lighted, habitats (reviewed by Bradbury 1977, Fenton 1985). The communication modalities used by species relying on high frequency sounds and habitats that are not well illuminated have not been well studied.

The purpose of this study was to investigate mate choice and the communication signals used by Myotis lucifugus (LeConte), a temperate vespertilionid bat that is capable of producing high frequency signals, and uses dark mating sites. Myotis lucifugus has a reproductive cycle typical of most temperate bats (see above).

The mating season and the onset of hibernation in M. lucifugus overlap, producing a two-phased mating season (Fenton 1969). During the first or "active phase", females appear to locate active mates, while in

the second or "torpid phase", males locate torpid individuals with whom to mate (Thomas et al. 1979).

Before hibernation, males of varying weight (Carmody et al. 1971, Fenton 1969) comprise the population of bats visiting the hibernacula. Variations in body weight could reflect differences in body size or fat reserves. Manning (1985) suggested that females may mate with larger males when body size is correlated with age, and larger males are older. If large size is an indication of the relative amount of body fat it could reflect foraging success and represent another reason for females to mate with heavier males. If male foraging ability and longevity are heritable characteristics then one would expect females to mate with heavy males. During the "active phase" of the mating season I conducted a number of studies to determine whether females mated with the heaviest and/or largest (i.e, forearm length) males available, and whether differences in male weight were related to body size, age and/or fat reserves.

In the active phase, M. lucifugus mate at night in dark sites where visual signals are relatively unimportant during mate location. During the "active phase" females probably rely on acoustic, and/or olfactory signals when locating a mate. To assess the relative importance of acoustic and olfactory signals during mate location, I performed presentation experiments.

Thomas et al. (1979) suggested that during the "torpid phase" of the mating season active males do not selectively mate with torpid

females. Since arousal from hibernation is energetically expensive (Ewing et al. 1970) and spermatogenesis ceases prior to hibernation (Gustafson 1979) males arousing from torpor should mate with torpid females. To determine if this was true, I recorded the sex of the torpid individual involved in a "torpid phase" mating. Fenton (1969) reported that females usually hibernated alone or in small clusters which could facilitate male location of torpid females. To check this I recorded the number of males and females hibernating in clusters of varying size.

The mating season of M. lucifugus begin approximately six-weeks after the young become volant. After birth, one might expect adult females to become progressively more interested in adult males, and to explore this, I presented echolocation signals of various individuals to adult females at a nursery colony during parturition, lactation and weaning.

The Study Animal

In southern Ontario, female M. lucifugus leave hibernacula in the spring before males and congregate in roosts, such as attics, forming nursery colonies. Once females leave the hibernacula they ovulate and fertilization is achieved from sperm in their uterus (Hartman 1933, Wimsatt 1945). Females give birth to a single young between 7 June and 5 July (Barclay 1982, Fenton 1969, pers. obs.), and the young grow rapidly and are capable of limited flight when 19 days old. By 27 days of age their flight is indistinguishable from that of an adult (Buchler 1980a). Unlike females, adult males usually spend their spring and summer solitarily (Fenton and Barclay 1980).

From late July, adult males and nulliparous females congregate at hibernacula in nightly "swarms" (Fenton 1969), and when parous females and juveniles join in these nightly swarms the mating season begins. Hibernacula are also mating sites and the mating season begins about mid-August and continues throughout hibernation. Hibernation begins in mid to late September.

During the active phase, mating groups form on the walls of the hibernacula, around adult males (Thomas et al. 1979). During group formation adult males orient towards and land at mating sites if no other individual is present (Thomas et al. 1979). Subadults and adult females land only if other individuals are present (Thomas et al. 1979). Individuals at mating sites continuously produce vocalizations typical of echolocation signals (Barclay et al. 1979), and there are no obvious displays or aggressive interaction during group formation (Thomas et al.

1979).

STUDY SITES

I Renfrew Mine

The Renfrew mine (Renfrew County, ca. 150km west of Ottawa, Ontario) is abandoned and serves as a hibernaculum for Myotis lucifugus, M. septentrionalis, M. leibii, Pipistrellus subflavus and Eptesicus fuscus and as a mating site for M. lucifugus and E. fuscus. Myotis lucifugus make up 90% of the bats using the mine (Fenton 1969) which consists of approximately 300 meters of tunnels (Figure 1), with drill holes (ca 8cm in diameter) at 1m intervals along the wall-ceiling interfaces. The tunnel dimensions are approximately 1.5m x 2.5m (width x height), and most interactions between swarming M. lucifugus occur along the tunnels or at/in drill holes (Thomas et al. 1979). Experiments were conducted at the mine during the active and torpid phase of the mating season in 1984 and 1985 (1 August to 19 October).

II Burnstown

A nursery colony of at least 400 M. lucifugus was located in the attic of the Presbyterian Church in Burnstown (100km west of Ottawa, Ontario). This nursery colony was used from 1 June to 20 July 1985 for playback experiments (see below).

MATERIAL AND METHODS

During 1984 and 1985 I determined the reproductive condition and sex of each animal handled. Their body weights (using an OHAUS CM200 electronic scale, accurate to 0.1 gram) and forearm lengths (in 1984 I used a vernier caliper, accurate to 0.1mm, in 1985 I used a Helios dial caliper, accurate to 0.05mm) were recorded. In 1984 I did not always measure forearm length. Following the criteria of Racey (1974), males with fused epiphyseal joints and swollen testes were reproductively mature and classified as adults, while all other males were reproductively immature and classified as subadults. Reproductively mature females had fused epiphyseal joints and bare patches around their nipples indicating that they had nursed young were classified as adults. All other females were reproductively immature and were considered to be subadult (Racey 1974, Kunz and Anthony 1982).

Unless otherwise stated, whenever I refer to an individual's age I am referring to its reproductive condition (i.e., adult/subadult).

I Matings

Weight

To determine whether the differences in individual body weights influenced their ability to survive periods without food (e.g., hibernation), I conducted a captive study. The study involved taking animals as they arrived at the mine and within 30 min recording their age (see above), sex, weight and forearm length. Each animal was placed in a styrofoam cup which was then covered with gauze, and were kept in the shade and given water 4 times daily between 29

August and 4 September 1984. Because I expected their weight to change dramatically over the first 24h as they emptied their digestive tracts, I weighed them at 0h, 12h, 24h and every 24h thereafter.

From previous banding efforts by myself (in 1984), Thomas et al. (1979) and Fenton (1969), at the Renfrew mine, I captured some animals of known minimum age (years), and I made the usual measurements. These data were analysed to determine whether there were any relationships between age (years), weight and forearm length.

For individuals captured during 1984 and 1985 whose forearm length and body weight were recorded I analysed the data to determine if there was a relationship between body weight and body size.

Copulation

During 1984 and 1985 males mating with active individuals were captured, and the routine measurements recorded. To determine whether adult females mated with the heaviest (weight) or the largest (forearm length) available males, the weights and forearm lengths of males engaged in active matings were compared to those of active males, that were not mating, but were on the wall at the same time and in the same section of the mine.

Mohr (1945) reported the ratio of M. lucifugus males and females in three hibernacula in Pennsylvania remained constant over periods of five to thirteen years. Mohr returned to three hibernacula at the same time of year. Over a thirteen year period one hibernaculum was sampled on four occasions and the proportion of hibernating males

ranged from 54 to 56%. Over a seven and five year period two hibernacula were sampled on three occasions and the proportion of males ranged from 68 to 71.1%, and 58.4 to 66.6%, respectively. At the Renfrew mine the proportion of males and females in the hibernating population remained constant between 1967 to 1969 (Fenton pers. comm.). Since the proportion of males found in a hibernating population tends to remain constant over a number of years, I used the proportion of males in the hibernating population during August and September in the Renfrew mine as reported by Fenton (1970) to determine whether adult males randomly mated with torpid individuals. I also measured the incidence of females in the hibernating population by sampling solitary bats and those in clusters.

II Presentation Experiments

Presentation experiments were conducted to determine whether the reproductive maturity and sex of an individual influenced its attractiveness to conspecifics. I investigated the communication modalities that free-flying individuals could use during group formation and mate location.

Between 5 August and 6 September 1985, acoustic and olfactory presentations were performed using individuals of varying age, sex and species. Presentations were performed on evenings when bat activity at the mine was high. On warm ($>10^{\circ}\text{C}$) evenings that were not windy, rainy or foggy (Barclay 1982, pers. obs.), and bat activity was high (30-40 bats counted in a five min period one hour after dark), I

conducted the presentations. For the presentations I used individuals captured one hour after dark and none of them were kept for more than two hours before being used. The timing of the presentations varied, and depended upon the time that large numbers of bats started to arrive at the mine. I usually began presentations one and a half hours after the arrival of the first bat, and again just after midnight.

Whenever possible a full sequence of animals and stimuli were used in each set of presentations. A full sequence of presentations involved presenting acoustic, olfactory, acoustic and olfactory simultaneously, and the live animal for individuals of varying age, sex and species (see Table 1). Each stimulus was presented for two minutes followed by two minutes of no stimulus. The sequence of individual and stimulus were randomized for each presentation sequence.

To observe bat activity around the presentation cage (see Figure 2), I used a headlamp equipped with a Kodak Wratten Red Filter #29 ($>600\text{nm}$). This illumination should not have affected the bats since their eyes do not detect long wavelengths (Thomas *et al.* 1979). At a distance of two metres from the cage a circle of light 120cm in diameter was illuminated by these headlamps. The number of free-flying individuals attracted and not-attracted to the cage during each presentation was recorded. An individual was considered to be attracted if it changed its flight path and flew in towards the speaker and/or flew within 30cm of the presentation cage. All other

individuals within the 120cm² circle of light were scored as not-attracted. I could not determine the age, sex and species of an individual responding to the presentation stimuli.

The acoustic presentation involved broadcasting the vocalizations of an individual from an empty cage. A broadband capacitance microphone and a mylar speaker (flat 5 kHz to 140 kHz) coupled with an ultrasonic power amplifier were used to broadcast the vocal signals of a specific individual (Simmons et al. 1979). These instruments were calibrated using a Bruel and Kjaer sound level meter (Model 2209), so that at a distance of 10cm the intensity of the presentation stimulus matched the output of the bat. The speaker broadcasting an individual's vocal signals was placed in an empty cage at the presentation site while the individual was kept at least 15m away from the presentation site (see Figure 1).

The olfactory stimulus was an empty cage that had previously held an animal for at least 10 min. During an olfactory presentation an individual was removed from its cage and the now empty cage was presented. After the two minute presentation the individual was put back into its cage. Between each presentation sequence, all cages were cleaned using 95% Ethanol, and by labelling cages I consistently used the same cage to house individuals of the same age, sex and species. Some cages were never used to house a bat and these cages were presented to the free-flying population as an empty cage control.

On several evenings presentation cages, each housing a single bat were left in the mine over night, and I presented marked individuals

of varying age, sex and species in the cages. The presentation cages trapped individuals that entered the cage, and I recorded the age and sex of the trapped individual.

III Playback Experiments

To determine whether adult females became progressively more interested in the vocalizations of conspecifics as they gave birth, lactated and their young became volant I conducted playback experiments at a nursery colony during the period of parturition, lactation and weaning.

On a single evening, a full sequence tape of echolocation signals including an adult male, an adult female, a subadult male and a subadult female, at least one other species (E. fuscus or Lasiurus cinereus), or synthesized echolocation signals (Omni bat) and tape noise was presented at the nursery roost (see Table 1). The order of stimuli presentation was randomized and each stimulus was presented for two minutes followed by a one minute period of no stimuli. The number of free-flying individuals attracted and not-attracted to the presentation stimulus were recorded. A bat was considered to have been attracted if changed its flight path and flew towards the speaker and/or flew within 30cm of the speaker. Bats flying within one and a half metres (limit of my peripheral vision) of the speaker were scored as not-attracted.

The bats' responses were determined by lying underneath the speaker and watching as the bats flew over the speaker. In this position I used the sky as a light background onto which I could count the

number of bat silhouettes. The individual scoring the response of the adult females as they flew by the speaker was not aware of the age, sex or species of the vocalizations being broadcast.

Recordings of M. lucifugus were made in 1984 using individuals caught at the Renfrew mine. These individuals were allowed to fly in a 4m x 4m canvas tent. Echolocation signals were recorded using a broadband capacitance microphone attached to a Racal Store 4D Tape-recorder (operated at 76 cm/s). The echolocation signals of the other species and the Omni bat were obtained from the library of vocalization tapes of Dr. M.B. Fenton, Carleton University.

To facilitate the playback of echolocation signals at the nursery colony, full sequence tapes were pre-recorded. Playbacks were performed using a Racal Store 4D Tape-recorder (operated at 76cm/s.), a mylar coated speaker (flat 5kHz to 140 kHz) driven by an ultrasonic power amplifier, (both built by the Carleton University Science Workshop after the specifications of Simmons et al. 1979). The speaker was placed in the path that most bats used when leaving the roost. The speaker was positioned approximately 1m above the ground and 1m from the height that most bats flew.

Presentations were performed at dusk, as the bats left their roosts. Presentations were not performed as the bats returned to the roost because there was insufficient natural light to see the bats clearly.

It was not possible to determine whether all individuals visiting the mine or leaving the nursery colony were exposed to all

presentation stimuli, therefore sample sizes of the number of bats responding to the presentation experiments does not necessarily represent the entire population at the mine or at the nursery colony.

All statistical analyses were 2-tailed.

RESULTS

I Matings

Weight

A total of 77 M. lucifugus was used in the weight change study (22 adult males, 10 adult females, 26 subadult males and 19 subadult females). There were significant weight differences between the age and sex classes (ANOVA $F=5.2$ $p<0.05$). This difference was due to the large variation in adult male weight, and a cluster analysis (see Appendix D) was used to separate the adult male class into two groups (Figure 3). A cluster analysis was performed to remove some of the subjectivity involved in subdividing the adult male class into groups with lower weight variations. Although this captive study indicates that there are two classes of adult males, based on body weight, in fact adult male weight is continuously distributed (see Figure 5). At the start of the study adult males in Group 2 were significantly heavier than all other age-sex classes (Table 2). During the first 24h the absolute weight change between all age, sex and weight categories were equal (see Figure 4 and Table 3). However, for the remainder of the study period the heavy adult males (Group 2) lost significantly more weight than the other classes (Table 3). Ewing et al. (1970) reported that during August and September adult males have 0.18 grams and 0.38 grams of fat/ gram of lean dry weight, respectively, this suggests that the difference in adult male weight was due to differences in fat reserves. Visual inspection of the animals at the start of this study showed that the individuals

classified as heavy adult males (Group 2) showed signs of having a larger amount of body tissue in their abdominal region. At the end of the captive study heavy adult males were still very active (i.e., moving about in the styrofoam cup), whereas individuals from the other classes were not as active or were torpid.

During 1984 and 1985 the forearm and weight of 319 and 869 individuals, respectively, were recorded. There were significant differences in the weight between each age and sex class but not between years (Figure 5). There were significant differences in forearm length between all age and sex classes and years (Figure 6). This difference in forearm length of each age-sex class between the two years was less than 1.0mm and was probably due to the change in the measurement recorded between the two years. In 1984 forearm measurement included the length of the carpals, whereas in 1985 the length of the carpals was excluded (see van Zyll de Jong 1985).

Since there were significant differences in the forearm length between the age-sex classes and year, I performed correlation analyses keeping the age-sex classes separated by year. The result show no significant relationship between adult male weight and forearm length (Table 4a, b). However, there was a positive correlation between forearm length and weight in the subadults. This was not surprising since the subadult classes included individuals that were less than one year old. The relationship observed is probably related to increases in size and weight as the juveniles attained adult size (see Carmody et al. 1971 and Ewing et al. 1970).

In 1985 I captured individuals that were at least 18 ($n=21$), 7 ($n=18$) and 1 ($n=16$) years old. There were no significant difference in the weight of the individuals in each of these age classes (ANOVA $F=2.09$ $p>0.05$), but there were significant differences in forearm length (ANOVA $F=3.34$, $p<0.05$). This difference in forearm length did not increase with increasing age (SNK $p<0.05$). The lack of a relationship between age and forearm length and weight may be attributed to the fact that the exact ages of the individuals in each age class was not known.

Copulations

During the "active-phase" of the mating season adult females were not selecting to mate with the heaviest or largest (forearm length) available male (Table 5a, b) and all active matings were heterosexual and with conspecifics. During the "torpid phase" of the mating season, active adult males mated with torpid females more frequently than expected at random (Table 6), however 35% of all torpid matings were homosexual. Hibernating females tended to occur in small clusters and singly, as reported by Fenton (1970) (Table 7).

Presentation Experiments

The response of 7472 individuals to 212 presentations of various stimuli was recorded and I used log-linear analysis (see Appendix II) to determine whether there were significant differences in the proportion of individuals attracted to each of the stimuli (acoustic, olfactory, acoustic and olfactory and live animal stimulus for animals of varying age, sex and species). The results of these

experiments indicated that the free-flying bats were equally attracted to the live animal presentations regardless of the age, sex and species of the individual being presented (Figure 7). However, the presentation of acoustic, olfactory, and acoustic and olfactory stimuli of the other species did not attract more individuals than the empty cage control (Figure 8). The M. lucifugus presentations showed a number of interesting things (Figure 9). Free-flying individuals were significantly more attracted to the adult male acoustic and acoustic and olfactory stimuli than the empty cage control, and there were no significant differences in the proportion of individuals attracted to the adult male acoustic and the adult male acoustic and olfactory presentations. These results suggest that, at a distance, olfactory signals are not important during mate location and group formation. This is further supported by the fact that all other stimuli, including the adult male olfactory stimuli, were not significantly different from the empty cage control.

A total of 20 individuals (9 adult males, 3 adult females, 3 subadult female, 3 subadult male, and 2 other species) was left in the mine over night. Only one individual was placed in each cage. The adult male was the only age-sex that was successful in catching free-flying animals ($n=6$ and 3 individuals respectively). Eight of the 9 individuals captured were conspecifics and supports the assumption that the majority of individuals responding to the presentation stimuli were M. lucifugus. The age, sex and species of the individuals responding to the presentation experiments were unknown.

III Playbacks Experiments

Log-linear analyses (see Appendix II) showed that females are equally attracted/not-attracted to the echolocation signals of individuals of varying age, sex and species (Figure 10). The proportion of free-flying individuals attracted to each of the vocalizations decreased after the young became volant. This could be related to the departure of adult females and young from the roost for the rest of the active season as the young became volant.

DISCUSSION

The results of this study show a number of interesting things. During parturition, lactation and weaning, adult females do not appear to be interested in the vocalizations of adult males. During the "active phase" of the mating season, free-flying individuals are attracted to the vocalizations of adult males, however they are equally attracted to live animals of varying age, sex and species. Adult females do not mate with the heaviest or the largest available males, and there are not apparent relationships between male age, weight and/or body size. During the "torpid phase" adult males mate with torpid females more frequently than with torpid males, however 35% of all torpid matings are homosexual.

Gould (1971) suggested that the nocturnal habit of bats would result in vocalizations replacing visual signals used by diurnal animals. In bats, vocalization have been shown to be important during mother-young recognition (e.g. Antrozous pallidus Brown 1976, Noctilio albiventris Brown et al. 1983, Rhinolophus ferrumequinum Matsumura 1979, 1981, M. lucifugus Thomson et al. 1985); interactions at feeding sites (Euderma maculatum Leonard and Fenton 1984, M. lucifugus Barclay 1982), mate pacification (Barclay and Thomas 1979), and repelling predators (e.g. Peromyscus maniculatus Martin and Fenton 1978). The use of vocalizations, typical of echolocation, in individual recognition has been proposed by a number of researchers (Avery et al. 1984, Bradbury 1977, Thomas et al. 1979). The range of frequencies that any one individual is capable of producing is

probably large enough to allow unique vocal signatures (Fenton 1977). The results of this study suggests that during the mating season vocalizations (typical of echolocation see Barclay 1982) may allow individuals to recognize adult males from other individuals.

Olfactory communication is also important to bats in recognition when individuals are in close proximity (Quay 1970, e.g. Tadarida brasiliensis Gustin 1984). In retrieval experiments T. brasiliensis identify their young using olfactory signals. Buchler (1980b) identified a scent post used by newly volant M. lucifugus. These individuals landed at the scent post, a tree, before flying off towards their roost or foraging sites. During group formation M. lucifugus have naso-nasal contact with females and other group members, prior to mating (Thomas et al. 1979). Pearson et al. (1952) reported that prior to copulation, male Plecotus townsendii "vigorously rub their snout over the face, neck, forearms and ventral surface of the female". Davis and Herreid (1960) reported distinct differences in the odours of male and female Noctilio albiventer and T. brasiliensis. These studies show that olfactory signals are important not only in mother-young recognition but possibly in mate location.

I did not expect a difference in the proportion of individuals attracted to the live animal and the simultaneous presentation of acoustic and olfactory stimuli. I expected the individual whose acoustic and olfactory stimuli was most attractive to the free-flying population to be maintained when the live animal was presented. However, the age, sex and species of the live animal did not influence the proportion of

free-flying individuals attracted. The difference in response to the live animal and the simultaneous presentation of acoustic and olfactory stimuli maybe attributed to low frequency sounds (5 kHz) associated with the animal moving about in the cage. These low frequency sounds may be the stimulus that attract free-flying bats to the live animal regardless of age, sex and species (see below).

Thomas et al. (1979) found that a live adult male was most attractive to the free-flying individuals. The lack of consistency between my results and those of Thomas et al. (1979) may be related to the duration of each presentation, and structural differences in the presentation sites used. Thomas et al. (1979) and I used presentation sites that had different ceiling heights (10m and 2m respectively). The larger the distance between the ceiling, where bats concentrated their activity, and the presentation cage the more an individuals has to assess the individual being presented. The distance between my presentation cage and the free-flying bats was approximately 1m. This distance may not have been large enough for the bats to assess the individual being presented and behave appropriately. I suspect the lack of discrimination in my live animal presentation is the result of free-flying bats being initially attracted to a trapped individual (see below).

While trapping animals, for various purposes, I noticed an increase in activity level around the trap as the number of bats trapped increased and as the number of bats flying around the trap increased. The movement of bats in the trap produced low frequency sounds (see

above). Therefore, the longer a caged individual is presented the more likely the stimulus, that the free-flying population is responding to, will change (i.e., after awhile the individuals attracted to the presentation site may be attracted to the free-flying bats around the cage and not the initial stimulus). The five minute presentation period used by Thomas et al. (1979) may have been long enough for the stimulus attracting free-flying bats to change.

In the mine the level of bat activity varied between areas and over the course of an evening. Although Thomas et al. (1979) did not compare the number of individuals attracted to a presentation with the level of bat activity (e.g., number of bats in the area), the individual most attractive to the free-flying population in my experiment was the same as theirs (i.e., adult male).

Adult male behaviour (i.e., orienting and landing at unoccupied mating sites, see above), coupled with the ability of individuals to discriminate between the vocalizations of adult males and other individuals, are probably important distal signals during group formation and mate location. When individuals are in close proximity olfaction may be important in confirming the age and sex of an individual (see above). Visual signals do not appear to be important during mate location by M. lucifugus (Thomas et al. 1979, personal observation). The importance of tactile stimuli may be important to M. lucifugus during mating but is obscured because physical contact occurs during olfactory communication, e.g., naso-nasal, and with the act of mating.

During parturition, lactation and weaning, females are not

attracted to the echolocation signals of conspecific adult males. In fact they do not appear to respond differentially to the echolocation signals of M. lucifugus and other species. This may be the result of females not being interested in the vocalizations being presented, a difference in the attractiveness of vocalizations associated with an echolocating individual and those of a stationary individual, and/or females not being able to distinguish the calls of individuals because of the "acoustic clutter" associated with bats leaving the roost. It is difficult to test the first possibility. However, one can test the second possibility by presenting echolocation signals and vocalizations of stationary individuals to adult females during parturition and weaning. By presenting vocalization associated with echolocation and those of stationary individuals at foraging sites, where Barclay (1982) was successful in obtaining responses of free-flying individuals to M. lucifugus signals, one could address the latter possibility. It would be interesting to compare the response to playbacks, of the type just described, at nursery colonies and foraging sites.

The phenomenon of delayed ovulation and fertilization in temperate vespertilionids and rhinolophids (Hartman 1933, Wimsatt 1945, Fenton 1984) gives rise to a number of interesting questions. In insects where females have multiple mates, sperm competition has been studied (for a review see Parker 1970). Sperm competition involves sperm from different males competing to fertilize a females' ova(ovum). Sperm competition in M. lucifugus is possible since females probably copulate with a number of males (Thomas et al. 1979) and sperm from a number

of males is probably present in the female at the time of fertilization. Racey (1973) has shown that sperm remain viable after seven months of storage in a hibernating bat. Hartman (1933) suggested that sperm viability may be enhanced by hibernating because the uterine fluids coagulate with decreasing body temperature, and presumably decrease sperm mobility and metabolism (Hartman 1933). Crichton et al. (1981) suggested that secretions from the uterine epithelia may provide energy for vital sperm metabolism which may also increase sperm viability.

If sperm competition occurs in M. lucifugus one should observe a number of trends. Males should attempt to mate with as many females as possible (see Thomas et al. 1979). During the "active phase" females do not appear to mate selectively with males that are heavier or larger. However, M. lucifugus males copulate with torpid females during hibernation (Thomas et al. 1979), and the advantage of being a heavy male may be expressed during the "torpid phase" of mating because males must arouse from hibernation, which is energetically expensive (Ewing et al. 1970). Therefore males with greater fat reserves would be able to arouse more frequently and engage in "torpid phase" matings, which may increase their fitness.

On the other hand, females may mate with as many males as possible to ensure that they have viable sperm in their uterus at the time of fertilization. One interesting feature of the mating system of M. lucifugus is that the sex of the individual locating mates changes between the "active" and "torpid" phase of mating. During the "torpid phase" males locate females, and in the "active phase" females locate

males. If females are only interested in obtaining enough sperm to ensure fertilization then it would be just as easy for males to locate females during the "active" phase, unless, females are choosing their mates. The results of this study show that females do not choose their mates base on weight or forearm length. However, there may be other criteria that females use when selecting a mate (e.g., age). If sperm competition does occur then females have no control over which males' sperm will fertilize her. However, during the "active phase", females may select their mate(s) to increase the possibility of being fertilized by sperm from a male they chose.

Male age may be a criterion that females use when selecting a mate. However, the number of copulations that involved an individual of known minimum age was very low ($n=1$). The low recapture rates (in 1985 ca 2% of the animals marked in 1984 were recaptured) precludes the study of age and the number of matings obtained. In this study male age does not appear to be related to forearm length or body weight. However, the individuals in each of the age classes were of known minimum age and the overlap in age between the groups may be vast, hence obscuring any trends.

Thus far the importance of sperm competition has not been investigated in bats. The spatial separation of hibernacula and nursery colonies and the temporal separation of insemination and fertilization makes it difficult to study sperm competition in bats (Fenton 1985). However, reproductive dormancy may play a significant role in the mating system that an animal employs. For example in M. lucifugus the

combination of delayed ovulation, "torpid phase" matings, and the vast quantity of energy required for female defence throughout the winter results in a random and promiscuous mating system (Thomas et al. 1979). Hibernation is not a characteristic that is restricted to temperate vespertilionids, some tropical vespertilionids enter extended periods of torpor (see Gustafson 1979, Fenton 1985). Members of the genus Miniopterus, found in both temperate and tropical habitats, are known to hibernate. Miniopterus spp. differ from M. lucifugus in that fertilization occurs prior to hibernation and males do not engage in "torpid phase" matings (Medway 1971, Richardson 1977). These two reproductive strategies has been classified by Gustafson (1977), as follows:

- 1) Type 1: In males spermatogenesis ceases prior to hibernation and there are no mating throughout hibernation. The females of these species do not store sperm and are fertilized prior to hibernation (Miniopterus spp. strategy)
- 2) Type 2: In males spermatogenesis ceases prior to hibernation and mating continues throughout hibernation. The females store sperm and ovulation is delayed (M. lucifugus strategy)

It would be very interesting to investigate the mating systems adopted by Type 1 vespertilionids (e.g. M. schreibersii) since female defence throughout hibernation is not necessary to ensure paternity.

Although parental investment in offspring rearing (Trivers 1972), resource defence (Orians 1969, Bradbury and Vehrencamp 1977, Emlen and Oring 1977), female defence (Orians 1969, Emlen and Oring

1977) and the ratio of females to males in a population (Brosset 1976) are important factors in predicting the mating strategy adopted by animals, including bats (see Bradbury 1977), I suggest that the reproductive cycle of an animal, whether or not they hibernate, will also influence the mating system adopted.

Biologists assume that during the mating season individuals can locate and identify mates that are reproductively mature, of the opposite sex and of the same species. The results of this study indicate that during the "active phase" all matings are heterosexual, involving conspecifics. During the "torpid phase" 35% matings are homosexual. These results support the suggestion of Thomas *et al.* (1979) that *M. lucifugus* mate randomly and promiscuously and that active males often do not correctly identify the sex of a torpid individual.

As with most studies the process of answering one question gives rise to numerous other questions. This study is no different in that respect. Since I have shown that free-flying individuals can determine the age and sex of an individual by its vocalizations, it would be interesting to determine whether we can detect structural differences using sound spectrum analysis techniques (see Barclay 1982, Thomson *et al.* 1985). During the active mating season it would be interesting to conduct choice experiments using adult females to determine whether there are male vocalizations that are more attractive than others. If vocalizations of males have varying attractiveness then one may be able

to identify the features of male vocalizations that make one male more attractive than another. It would be interesting to determine if there are any relationship between vocal attractiveness and male age, weight and forearm length.

The behaviour of mothers after retrieving their young (i.e., licking) suggests that they scent marking their offspring. Hence, offspring identification may be achieved by the mother recognizing her offspring as smelling like herself. The observations reported by Davis and Herreid (1960) suggests that it would be possible for females, and males, to identify the sex of an individual by just their body odour. It would be fascinating to determine whether there are some male odours that are more attractive than others.

From this study and Fenton (1970) it appears that female hibernation behaviour may facilitate male mate location. However, during this study there were a large number of male-male matings. It would be interesting to determine whether cluster size influences the frequency of male-male matings. As mentioned above, differences in female odours may also play a role in male mate location during the torpid phase.

During the hibernation period adult males are responsible for locating and identifying mates which is energetically expensive. Therefore one would expect males to selectively mate with torpid females. However 35% of these torpid matings are homosexual. It would be interesting to determine whether there are energetic costs involved with being the torpid partner. If females have viable sperm

in their uterus prior to hibernation and there are costs to the recipient of torpid matings, then it would be to the females advantage to avoid torpid phase matings. Adult male and female M. lucifugus are morphologically very similar, with females being slightly larger (Fenton and Barclay 1980), this may allow females to hide their sexuality identity.

CONCLUSIONS

1. During the active phase females do not preferentially choose larger or heavier males for copulations and all copulations are heterosexual and involve adult conspecifics.
2. During the torpid phase adult males try to copulate with other males 35% of the time.
3. During the active phase free-flying bats are equally attracted to individuals of varying age, sex and species.
4. There is no correlation between body size (forearm length) and body weight in males of known minimum age.
5. During swarming, heavy males are capable of surviving extended periods without food, and show no signs of distress.

Table 1. An example of a presentation experiment data sheet.

During a single presentation sequence each of these cells were filled. For example in a 2 min period 6 free-flying individuals were attracted to the adult male A stimuli and 16 were not attracted (N).

	A ⁺		O		AO		LA ⁺	
	R	N	R	N	R	N	R	N
Adult male	6	16						
Adult female								
Subadult male								
Subadult female								
Other Species								
	R	N						
empty cage								

⁺ Stimuli presented, A (acoustic), O (olfactory), AO (acoustic and olfactory) and LA (live animal) presentations (see text). Only the acoustic (A) were presented at the nursery colony.

Table 2. Mean weights of all five classes.

Class		Weight (g) ($\bar{X} \pm \text{S.E.}$)	(n)
Adult male	Group 1	7.5 ± 0.25	(16)
	Group 2	$11.7 \pm 0.3^{***}$	(6)
Adult female		7.68 ± 0.12	(10)
Subadult male		7.05 ± 0.11	(26)
Subadult female		7.28 ± 0.16	(19)

*** $p < 0.05$ ANOVA $F = 59.44$,

$p < 0.001$ SNK

Table 3. Weight ($\bar{X} \pm 1S.E.$) change during the captive study.

Class		29 Aug - 30 Aug	30 Aug - 3 Sept
Adult male	Group 1	0.96 ± 0.07	0.78 ± 0.1
	Group 2	1.04 ± 0.1	$1.47 \pm 0.23^{***}$
Adult female		0.99 ± 0.11	$0.67 \pm 0.1 (9)^{+}$
Subadult male		0.96 ± 0.07	0.59 ± 0.04
Subadult female		1.00 ± 0.13	$0.67 \pm 0.07 (18)^{+}$

*** $p < 0.005$ ANOVA $F=14.8$

$p < 0.001$ SNK

⁺ Sample sizes in brackets are those different from Table I as a result of animals escaping.

Table 4a Correlation coefficients (r) of forearm length
and weights in 1984

Class	Before ⁺		After ⁺	
	n	r	n	r
Adult males	73	.06	22	.09
Adult females	42	.07	9	.4
Subadult male	81	.3***	26	.14
Subadult female	47	.03	19	.04

⁺ Before and after the first forpid bat in mine, August
17 1984

p<0.001

Table 4b Correlation coefficients (r) of
forearm length and weight in 1985.

Class	n	r
Adult male	252	-0.06
Adult female	251	0.064
Subadult male	141	0.29***
Subadult female	225	0.26*

p<0.001

*
p<0.05

Table 5a Comparison of copulating and
non-copulating male weight.

	1984 O	1985 O	1984+1985 O ⁺⁺ E ⁺⁺	
+	65	50	115ns	106
-	50	47	97	106

+ copulating male weight greater (+) or less
than (-) non-copulating male

ns $p > 0.1$ $\chi^2 = 1.53$

Table 5b Comparison of copulating and
non-copulating male forearm length.

	1984 O	1985 O	1984+1985 O ⁺⁺ E ⁺⁺	
+	74	50	124*	110.5
-	51	46	97	110.5

+ copulating male forearm longer (+) or
shorter (-) than non-copulating male.

++ Observed(O) frequencies were compared
using a Chi-squared analysis assuming
an expected frequency (E) of 1:1

* $p > 0.05$ $\chi^2 = 3.299$

Table 6 Comparison of the proportion of male-female and male-male torpid matings to the proportion of females and males in the hibernating population.

	September		October		Sept + Oct	
	O	E ⁺	O	E ⁺	O	E ⁺
male-female	10	7.98	5	1.26	15	9.24
male-male	4	6.02	4	7.74	8	13.76*

* $p < 0.05$ $\chi^2 = 6.0$

+ Observed proportions (O) are compared with the expected proportions (E) reported by Fenton (1970).

Table 7a Proportion of males and females
hibernating in clusters of various sizes.

Sex	Large Cluster	Small Cluster	Single
male	74	30	11
female	8	7	4

Table 7b Comparison of females hibernating in a
large cluster and in small clusters and singly.

Sex	Large Cluster (Observed)	Large Cluster ⁺ (Expected)
male	74	64.6
female	8	17.3

* $p < 0.025$ $\chi^2 = 6.3672$

⁺ Expected proportions are calculated using the
proportion of males and females found in
small clusters and singly.

Figure 1: Floor plan of the Renfrew mine, the study area (////) was visited regularly each night. During presentations, experimental animals not being used were kept at least 15m away (X) from the presentation site (P). Animals were caught at various locations (——) including the entrance (E) for various experiments.

Figure 2: Presentation apparatus. The cage was made of 1/4" hardware cloth, the inner tube was a store bought plastic funnel. The dimensions of the cage and funnel are shown on the figure.

12.5

3.1

20.5 cm

2.5

15.0 cm

Figure 3: Cluster analysis of adult male weight at the start of the captive study. The weight of the adult males at the beginning of the weight change experiment is shown at the top of the graph. Horizontal lines connect weights of two males, or two groups of males that are similar. The smaller the Degree of Relatedness value the closer the weights of the two males, or groups.

Figure 4: Weight change ($\bar{X} \pm 1S.E.$) during the captive study. The weight change of the heavy adult males ($\bullet-\bullet$), normal adult males ($\blacksquare-\blacksquare$), adult females ($\square-\square$), subadult males ($\blacktriangle-\blacktriangle$) and subadult females ($\triangle-\triangle$) during the weight change experiment.

Figure 5: Distribution of M. lucifugus weight prior to hibernation

(1 August to 19 September 1984 and 1985). There were significant differences in weight between adult males, adult females, subadult males and subadult females (ANOVA $F=195.63$ $p<0.001$) but not between years (ANOVA $F=3.4$, $p>0.05$)

WEIGHT (GMS)

Figure 6: Forearm lengths ($\bar{X} \pm 1\text{S.E.}$) of M. lucifugus caught prior to hibernation 01 August to 19 September in 1984 ( ) and 1985 ( ). There were significant differences in the forearm lengths between adult males, adult females, ~~subadult males and subadult females~~ (ANOVA $F=18.78$, $p<0.001$) and between the two years (ANOVA $F=105.56$, $p<0.001$).

Figure 7: Proportion of free-flying individuals that were attracted to the live animal and the empty cage presentations. Sample sizes are shown above each histogram. The proportion of free-flying individuals attracted to the live animal presentations were significant greater than that attracted to the empty cage ($Z > 2.0$, $p < 0.001$). There were no significant differences in the proportion of free-flying individuals attracted to each of the other classes presented ($Z < 1.77$, $p > 0.05$).

Figure 8: Proportion of free-flying individuals that were attracted to the acoustic (▨), olfactory (▩), acoustic and olfactory (▧), and the live animal (▦) stimuli of other species and the empty cage (■). Sample sizes are above each histogram. There were no significant differences between the proportion of individuals attracted to the acoustic, olfactory and acoustic and olfactory stimuli of the other species and the empty cage ($Z < 1.8$, $p > .05$). There was a significant difference in the proportion of free-flying individuals attracted to the live animal and the empty cage ($Z = 6.3$, $p < 0.0001$).

Figure 9: Proportion of free-flying individuals attracted to Myotis lucifugus acoustic (▨), acoustic and olfactory (▩) and olfactory (▧) stimuli. Sample sizes are shown above each histogram. The proportion of individuals attracted to the olfactory stimuli was not significantly different from the empty cage (■, $p > 0.05$). The proportion of free-flying individuals attracted to the adult male acoustic and adult male acoustic and olfactory stimuli were significantly greater than the empty cage control ($Z > 2.0$, $p < 0.001$). There were no significant differences between the proportion of individuals attracted to the adult male acoustic and the adult male acoustic and olfactory presentations ($Z = 1.94$, $p > 0.05$). The proportion of the free-flying population attracted to all other stimuli were not significantly different from the empty cage control ($Z < 1.7$, $p > 0.05$).

Figure 10: Proportion of adult females attracted to the echolocation signals of Myotis lucifugus, other species and tape noise during lactation (□) and once the young start flying (▨). There were significant differences in the proportion of individuals attracted during lactation and when the young started to fly ($Z=2.8$, $p<0.05$). There were no significant differences in the proportion of individuals attracted to the vocalizations of all individuals and the blank tape presentation ($Z=1.5$, $p>0.05$).

Appendix I

Single level cluster analysis (see Lehner 1979) allows one to separate individuals into natural groups or clusters based on a single variable (e.g. weight). An index

$$D = \frac{xy}{x+y}$$

where x and y are the weight of individual x and y, is determined. The value of D indicates the relationship of two weights, that is lower values of D indicate a closer relationship.

In this study the initial weight of males and their weight throughout the captive study period were used to calculate D.

Appendix II

Log-linear analysis is very similar to a multi-dimensional Chi-square (see Colgan 1978 and Norusis 1983, 1985), in that expected cell frequencies are calculated using a mathematical model. The model that is used to generate the expected cell frequencies is tested against the observed cell frequencies. In a matrix ($i \times j$) with i rows and j columns a Pearson statistic

$$\chi^2 = \sum_i \left(\sum_j (x_{ij} - m_{ij})^2 / m_{ij} \right)$$

or a log-likelihood ratio statistic

$$G^2 = 2 \sum_i \sum_j x_{ij} \log(x_{ij} / m_{ij})$$

where x_{ij} is the observed cell frequency and m_{ij} is the expected cell frequency of the i^{th} row and j^{th} column. A model is accepted ($p > .05$), or rejected ($p < .05$) based on the Pearson χ^2 and/or the log-likelihood ratio statistic. If a model is rejected a number of alternate models are tested against the observed cell frequencies until a model that produces expected cell frequencies that are statistically acceptable. A model that generates expected values that match those observed is essential since, the expected values are used in comparisons between various groups (Z-statistic).

The data collected in the presentation and playback experiments are categorical and therefore non-normally distributed.

Log-linear analysis does not require data to be normally distributed. This procedure transforms the data by taking the natural logarithm. The advantage of using a log-linear model to analyse proportional data is two fold. First of all this procedure allows one to use proportional data, unlike analysis of variance techniques, and allows multiple-comparisons, unlike Chi-squared analyses.

The model that match my data set was a saturated model, since the age, sex, species and the stimuli type influenced the proportion of free-flying individuals attracted to the presentiaon stimuli.

Literature Cited

- Avery, M.L., P.A. Racey, and M.B. Fenton. 1984. Short distance location of hibernaculum by little brown bats (Myotis lucifugus). Mammal. Soc., 49:588-590.
- Barclay, R.M.R. 1982. Interindividual use of echolocation calls: Eavesdropping by bats. Behav. Ecol. Sociobiol. 10:271-275.
- Barclay, R.M.R., M.B. Fenton, and D.W. Thomas. 1979. Social behavior of the little brown bat, Myotis lucifugus. II. Vocal communication. Behav. Ecol. Sociobiol. 6:137-146.
- Barclay, R.M.R., and D.W. Thomas. 1979. Copulation call of Myotis lucifugus: A discrete situation-specific communication signal. J. Mammal. 60(3):632-634.
- Bradbury, J.W. 1977. Social organization and communication In (ed. W.A. Wimsatt) Biology of bats, vol III. Academic Press, New York, ppl-72.
- Bradbury, J.W. 1981. The evolution of leks. In (R.D. Alexander and D.W. Tinkle, eds.) Natural selection and social behaviour. Chirion Press, New York. pp.138-169.
- Bradbury, J.W., and L.H. Emmons. 1974. Social organization of some Trinidad bats. I. Emballonuridae. Z. Tierpsychol. 36:137-183.
- Bradbury, J.W., and S.L. Vehrencamp. 1977. Social organization and foraging in Emballonurid bats. III. Mating systems. Behav. Ecol. Sociobiol. 2:1-17.
- Brosset, A. 1976. Social organization in the African bat, Myotis bocagei. Z. Tierpsychol. 42:50-56.
- Brown, P. 1976. Vocal communication in the pallid bat, Antrozous pallidus. Z. Tierpsychol. 41:34-54.
- Brown, P., 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. 1980a. The development of flight, foraging, and echolocation in the little brown bat (Myotis lucifugus). Behav. Ecol. Sociobiol. 6:211-218.
- Buchler, E.R. 1980b. Evidence for the use of a scent post by Myotis lucifugus. J. Mammal. 61:535-538.
- Carmody, G.R., M.B. Fenton, and D.S.K. Lee. 1971. Variation in body

- weight and proteins in three Ontario populations of hibernating Myotis lucifugus (LeConte) (Chiroptera: Vespertilionidae). Can. J. Zool. 49(12):1535-1540.
- Colgan, P.(ed.) 1978. Quantitative ethology. John Wiley, New York.
- Crichton, E.G., P.H. Krutzsch, and W.A. Wimsatt. 1981. Studies on prolonged spermatozoa survival in Chiroptera. I. The role of uterine free fructose in the spermatozoa storage phenomenon. Comp. Biochem. Physiol. 70A:387-395.
- Davis, D.E., and C.F. Herreid. 1960. Comments on the odors of bats. J. Mammal. 41:396.
- Dwyer, P.D., 1970. Social organization in the bat Myotis adversus. Science 168:1006-1008.
- Emlen, S.T., and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.
- 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. 1959. Summer activity of Myotis lucifugus (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec: Can. J. Zool. 47:597-602.
- Fenton, M.B. 1970. Population studies of Myotis lucifugus (Chiroptera; Vespertilionidae) in Ontario. Life Sciences Contributions ROM No. 77.
- Fenton, M.B. 1977. Variation in the social calls of little brown bats (Myotis lucifugus). Can. J. Zool. 55:1151-1157.
- Fenton, M.B. 1984. Sperm competition? The case of vespertilionid and rhinolophid bats. IN (ed. Smith) Sperm competition and the evolution of animal mating systems. Academic Press, Toronto. pp.573-587.
- Fenton, M.B. 1985. Communication in the Chiroptera. Indiana University Press, Bloomington. ppl61.
- Fenton, M.B., and R.M.R. Barclay. 1980. Myotis lucifugus. Mammalian Species No. 142. ppl-8.
- Gerell, R., and K. Lundberg: 1985. Social organization in the bat Pipistrellus pipistrellus. Behav. Ecol. Sociobiol., 16:177-184.
- Gould, E. 1971. Studies of maternal-infant communication and

- development of vocalizations in the bats Myotis and Eptesicus. Comm. Behav. Biol., 5:263-313.
- Gustafson, A.W. 1979. Male reproductive patterns in hibernating bats. J. Reprod. Fert. 56:317-331.
- Gustin, K. 1984. Scent recognition between mother and young Tadarida brasiliensis mexicana. Bat Research News 25:44.
- Hartman, C.G. 1933. On the survival of spermatozoa in the female genital tract of the bat. Quart. Rev. Biol. 8:185-193.
- Khajuria, H. 1972. Courtship and mating in Rhinopoma h. hardwickei Gray (Chiroptera: Rhinopomatidae). Mammalia 36:307-309.
- Kleiman, D.G., and P.A. Racey. 1968. Observations on noctule bats (Nyctalus noctula) breeding in captivity. Lynx 10:65-77.
- Kunz, T.H., and E.L.P. Anthony. 1982. Age estimation and post-natal growth in the bat Myotis lucifugus. J. Mammal. 63(1):23-32.
- Kunz, T.H., P.V. August, and C.D. Burnett. 1983. Harem social organization in cave roosting Artibeus jamaicensis (Chiroptera: Phyllostomidae). Biotropica 15:133-138.
- Lehner, P.N. (ed.) 1979. Handbook of ethological methods. Garland STPM Press, New York. pp403.
- Leonard, M., and M.B. Fenton. 1984. Habitat use by the spotted bat (Euderma maculatum, Chiroptera: Vespertilionidae) roosting and foraging behaviour. Can. J. Zool. 61:1487-1491.
- Manning, J.T. 1985. Choosy females and correlates of male age. J. theor. Biol. 116:349-354.
- Martin, K.A., and M.B. Fenton. 1978. A possible defensive function for calls given by bats (Myotis lucifugus) arousing from torpor. Can. J. Zool. 56(6):1430-1432.
- Matsumura, S. 1979. Mother-infant communication in a horseshoe bat (Rhinolophus ferrumequinum nippon): development of vocalization. J. Mammal. 60:78-84.
- Matsumura, S. 1981. Mother-infant communication in a horseshoe bat (Rhinolophus ferrumequinum nippon): Vocal communication in three week old infants. J. Mammal. 62:20-28.
- McCracken, G.F., and J.W. Bradbury. 1981. Social organization and kinship in the polygynous bat, Phyllostomus hastatus. Behav. Ecol. Sociobiol. 8:11-34.

- Medway, L. 1971. Observations of social and reproductive biology of the bent-winged bat Miniopterus australis in northern Borneo. J. Zool. Lond. 165:261-273.
- Mohr, C.E. 1945. Sex ratios of bats in Pennsylvania. Proc. Penna. Acad. Sci., 19:65-69.
- Morrison, D.W. 1979. Apparent male defense of tree hollows in the fruit bat, Artibeus jamaicensis. J. Mammal. 60:11-15.
- Morrison, D.W., and S.H. Morrison. 1981. Economics of harem maintenance by a neotropical bat. Ecology 62(3):864-866.
- Nelson, J.E. 1965. Behavior of Australian Pteropodidae (Megachiropteran). Anim. Behav. 13:544-557.
- Norusis, M.J. 1983. SPSS^X Introductory statistics guide. M^CGraw-Hill, Toronto.
- Norusis, M.J. (ed.). 1985. Log-linear analysis. IN SPSS^X Advanced statistics guide. M^CGraw-Hill, Toronto. pp329-361.
- Orians, G.H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589-603.
- Parker, G.A. 1970. Sperm competition and its evolutionary consequences in insects. Biol. Rev., 45:525-567.
- Pearson, O.P., M.R. Koford, and A.K. Pearson. 1952. Reproduction of the lump-nosed bat (Corynorhinus rafinesquiei) in California. J. Mammal. 33:273-320.
- Porter, F.L. 1979. Social behavior in the leaf-nosed bat, Carollia perspicillata. Z. Tierpsychol. 50:1-8.
- Quay, W.B. 1970. Integuments and derivatives. In (W.A. Wimsatt, ed.) Biology of bats. Academic Press, New York. pp2-57.
- Racey, P.A. 1973. The viability of spermatozoa after prolonged storage by male and female European bats. Period. Biol. 75:201-205.
- Racey, P.A. 1974. Ageing and assessment of reproductive status of pipistrelle bats, Pipistrellus pipistrellus. J. Zool. (London) 173:264-271.
- Racey, P.A. 1979. The prolonged storage and survival of spermatozoa in Chiroptera. J. Reprod. Fert. 56:391-402.
- Richardson, E.G. 1977. The biology and evolution of the reproductive

cycle of Miniopterus schreibersii and M. australis (Chiroptera: Vespertilionidae). J.Zool., 183:353-375.

Simmons, J.A., M.B. Fenton, M. Jutting, and J. Palina. 1979. Apparatus for research on animal ultrasonic signals. R. Ont. Mus. Life Sci. Misc. Publ.

Thomas, D.W., M.B. Fenton, and R.M.R. Barclay. 1979. Social behavior of the little brown bat, Myotis lucifugus. I. Mating behavior. Behav. Ecol. Sociobiol. 6:129-136.

Thomson, C.E., M.B. Fenton, and R.M.R. Barclay. 1985. The role of infant isolation calls in mother-infant reunions in the little brown bat, Myotis lucifugus (Chiroptera: Vespertilionidae). Can. J. Zool. 63:1982-1988.

Trivers, R.L. 1972. Parental investment and sexual selection. In (B. Campbell, ed.) Sexual selection and the descent of man. Aldine, Chicago, pp. 139-179.

Tuttle, M.D. 1974. An improved trap for bats. J. Mammal. 55:475-477.

van Zyll de Jong, C.G. 1985. Handbook of Canadian Mammals, vol. 2, Bats. National Museum of Natural Sciences. pp212.

Wimsatt, W.A. 1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. J. Mammal. 26:23-33.

END

FIN

3 04 87