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SPATIAL PARTITIONING BY TWO SPECIES OF SYMPATRIC BATS,
MYOTIS CALIFORNICUS AND MYOTIS LEIBII -)

by

Gregory Charles Woodsworth, B.Sc.

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

Department of Biology
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September, 1981

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September 21, 1981

ABSTRACT

The spatial and temporal patterns of foraging behaviour of two pairs of species of sympatric, insectivorous bats, Myotis californicus/M. leibii and M. lucifugus/M. yumanensis, were examined in the Okanagan Valley of British Columbia. Bats were banded with reflective tags, and a powerful spotlight was used to identify foraging bats at five sites throughout the summer of 1980. Myotis leibii and M. californicus spatially partition food resources with M. leibii feeding over areas over or adjacent to rocky bluffs, and M. californicus over water close to the river bank. Patterns of temporal activity were similar in their respective foraging areas. Feces analysis shows similarities in their diets which may be a factor in maintaining the observed patterns of resource division. Myotis lucifugus and M. yumanensis did not partition food resources spatially to the same extent as M. californicus and M. leibii and may compete with each other along another resource axis.

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TABLE OF CONTENTS

	Page
Abstract.....	iii
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	viii
Introduction.....	1
Study animals.....	4
Methods and Materials.....	7
Study sites.....	8
Experimental design.....	11
Trapping.....	11
Sampling procedure.....	13
Response to patchy prey.....	16
Feces analysis.....	16
Insect sampling.....	17
Results.....	18
Trapping.....	18
General patterns of activity.....	18
Effect of the spotlight.....	19
Response to patchy prey.....	21
<u>M. leibii</u> / <u>M. californicus</u>	23
<u>M. yumanensis</u> / <u>M. lucifugus</u>	25
Foraging behaviour.....	26

Insect availability.....	29
Feces analysis.....	30
Discussion.....	32
Prey selection.....	38
Assessment of the reflective tag- spotlight technique.....	39
Conclusions.....	44
References.....	45
Tables.....	51
Figures.....	61

LIST OF TABLES

Table	page
1. Number of mist-net and Tuttle trap hours.....	51
2. Species and numbers of bats banded.....	52
3. Number of bats banded at study sites.....	53
4. Reduced level of feeding activity with use of the spotlight.....	54
5. Bat response to insect swarm induced above UV light.....	55
6. Increased buzz:pass ratio over UV light.....	56
7. Response to patchy prey above UV light.....	57
8. Number of tagged <u>M. leibii</u> / <u>M. californicus</u> and <u>M. lucifugus</u> / <u>M. yumanensis</u> observed per site.....	58
9. Orders and numbers of insects caught over UV light.....	59
10. Relative abundance and percent frequency of insects in fecal pellets.....	60

LIST OF FIGURES

Figure	Page
1. Profile of <u>M. leibii</u> and <u>M. californicus</u>	61
2. Map of study area.....	62
3. Photographs of the five study sites.....	63
4. Graphs showing the average patterns of nightly bat activity.....	64
5. Species average nightly activity patterns.....	65
6. Insect distribution in relation to the UV light.....	66
7. Number of tagged bats observed relative to to numbers captured and tagged.....	67

INTRODUCTION

Many authors consider competition an important evolutionary force leading to niche separation, specialization, and diversification (MacArthur, 1958; Hardin, 1960; Miller, 1967; Pianka, 1974). However, the notion that community structure is determined predominantly by competition through a series of 'assembly rules' (Diamond, 1975) has been increasingly subject to criticism (e.g. Connor and Simberloff, 1979). The structure of the community is determined largely by the species diversity which has been correlated to niche restriction through competition (Dobzhansky, 1950; MacArthur and Wilson, 1967). Studies examining the consequences of species interactions have assumed a priori that the concept of competitive exclusion in nature can occur in communities that are at competitive equilibrium. It is unlikely that competitive exclusion occurs other than in the laboratory (e.g. Gause, 1934) as competitive equilibrium is rarely achieved in natural systems (Grubb, 1977; Sale, 1977; Wiens, 1977).

The question of random vs. non-random communities and the role competition plays in either model is far from resolved. Competition is difficult to demonstrate and quantify in nature but the fact that it exists is not in contention. Competition may exert strong selective

pressure in areas of geographic overlap between two similar species (Mayr, 1963) and could lead to coexistence within the same habitat by occupation of different niches (Lack, 1949). When two or more species compete for a limiting resource it is advantageous to minimize the level of competitive interaction (Pianka, 1974)

Niche separation implies that members of the community partition available resources, and the mechanisms by which they do so are central to understanding the ecology and evolution of the sympatric species. Resource partitioning has been clearly demonstrated for many groups of animals including barnacles (Connell, 1961), marine snails (Kohn, 1959), sunfish (Werner, 1977), desert lizards (Pianka, 1966, 1969; Schoener, 1968) and birds (MacArthur, 1958; Cody, 1968; Keast, 1968; Partridge, 1976). There is no reason to suspect a priori that bats are not subject to competitively mediated selective pressures and subsequently adopt various strategies by which competition is reduced among members of the community.

Bats are nocturnal and it is difficult to observe their habits. For this reason descriptions of the strategies and mechanisms by which bats reduce competitive interactions are not abundant. As food relations appear to be one of the most important aspects of community systems (Hutchinson, 1959), much effort has been directed to determining which insects are eaten by bats through

analysis of stomach contents (Ross, 1967; Pine, 1969; Easterla and Whitaker, 1972; Kunz, 1974; Whitaker and Black, 1976; Buchler, 1976), feces (Hamilton, 1933; Black, 1972, 1974; Coutts et al., 1973; Husar, 1976; Belwood and Fenton, 1976), and culled insect fragments (Poulton, 1929; Ross, 1961; Hill and Morris, 1971; Fenton, 1975). The results show a great deal of overlap in the diets of bats and the evidence does not strongly support the hypothesis that bats specialize on particular taxa of insects. Insectivorous bats may prove to be opportunistic feeders, quick to exploit swarms of insects found in patchy distribution (Fenton and Morris, 1976; Gould, 1978; Vaughan, 1980).

Other mechanisms that reduce competition include morphological adaptations and temporal and spatial partitioning of resources. Several authors (Rosenzweig, 1966; McNab, 1971; Fenton, 1972; Freeman, 1979) have examined various differences in morphological characters of bats in a community and suggested that these differences may reflect dietary specialization. However, the degree of overlap of morphological characters among sympatric bats (Findley, 1976) would not make this an effective mechanism by which resources could be divided. Other studies (e.g. Brown, 1968; Hooper and Brown, 1968; Kunz, 1973;) have shown that temporal activity varies among bats and may serve to reduce competition for

4

resources. Evidence of temporal partitioning depends largely on mist-net captures and the capture site of a bat may not be synonymous with its feeding area (Fenton, pers. comm.). With the exception of Nyholm's work (1965), evidence for spatial partitioning is questionable for the same reason or has been based on impressions (e.g. Wallin, 1969). Bell (1980) used ultrasonic sensing equipment to identify bat species by their echolocation calls in various habitats and showed a high degree of species overlap in the spatial and temporal components of their foraging behaviour in Arizona.

The purpose of this study was to determine if and how two species of sympatric bats, Myotis leibii and M. californicus, minimize competition. Bats banded with reflective tape were monitored each night at different sites with a spotlight to determine the spatial and temporal patterns of their foraging behaviour.

THE STUDY ANIMALS

Myotis californicus (Audubon and Bachman) and Myotis leibii (Audubon and Bachman) are sympatric in southern British Columbia, much of western United States and Mexico (Hall and Kelson, 1959). Both belong to the subgenus Selysius and Findley (1972) has placed both bats within the "leibii group". Bats in the subgenus Selysius are characterized as small, short-rostrumed, and short-jawed

with relatively small feet and broad plagiopatagia. Bogan (1974) noted that there are no two bats more similar than M. californicus and M. leibii in temperate North America and it is difficult to use external morphology to identify them accurately over much of their sympatric range, particularly in the south-west U.S. Bogan (1974) used multivariate analysis to distinguish them, relying on simultaneous consideration of 14 external and internal characteristics. This technique is obviously not useful in the field and the difficulties of field identification have precluded any studies concerning patterns of behaviour and interspecific relations.

Two subspecies, Myotis californicus californicus (Audubon and Bachman) and Myotis leibii melanorhinus (Merriam), are sympatric in the Okanagan Valley of British Columbia where they are sufficiently different in three external characters to permit accurate and consistent identification and separation (Figure 1). The most obvious difference is the colour of the dorsal pelage which ranges from a pale blonde to an orange-yellow in M. leibii and from a glossy chestnut to a rich brown in M. californicus. This contrasts with Bogan's findings (1974) in New Mexico where M. leibii was darker than M. californicus. This was the most important traditional character used to separate the two species initially for subsequent character analysis. Second, the distance from

the tip of the nostril to the hairline is always greater in M. leibii than M. californicus. Finally, the braincase of M. californicus is more rounded than that of M. leibii. This difference is subtle and, in this study, was used only to confirm identification by the more readily visible external characteristics.

The spatial and temporal components of their foraging behaviour was compared to those of another complex of bats, M. lucifugus and M. yumanensis, which are morphologically similar to each other (but not to M. leibii and M. californicus). There is a large amount of overlap in some of the characteristics traditionally used to separate these two species in the field, particularly the length of the toe hairs and the length and texture of the pelage. Although a large percentage of the members this complex is easily identifiable as one species or the other, there is still no reliable feature to distinguish the remaining percentage displaying intermediate characteristics which may be a result of hybridization (Harris, 1974; Parkinson, 1979).

METHODS AND MATERIALS

Field work for this study was conducted between 5 May and 15 August 1980. All study sites were located between the towns of Okanagan Falls ($49^{\circ}21'N$, $119^{\circ}36'W$) and Oliver ($49^{\circ}10'N$, $119^{\circ}37'W$), about 20 km apart, in the Okanagan Valley of British Columbia (Figure 2).

The Okanagan Valley is one of several deep trenches of the Nechako Plateau, which is rolling upland developed on a mixed assemblage of rocks in which intrusive and volcanic rocks of the Tertiary age predominate. Only a very few rounded hills exceed 1700 m and the major part of the area is at 800 m (Bird, 1972). The plateau is in the rainshadow of the Coast-Cascade mountains and the study area, in the southern portion of the valley is in the driest part, receiving less than 30 cm of precipitation annually. The summers are hot with the mean maximum temperature ranging from 26° to 32° C and 150-175 days remain frost-free throughout the year.

This inter-montane physiographic region with its dry climate results in a biotic region atypical of Canada and is more akin to the semi-arid areas of the southwest U.S. The vegetation is characteristically open. Grassy patches alternate with stands of trees. Ponderosa Pine (Pinus ponderosa) is dominant in the drier areas, with its greatest distribution at elevations between 500 and 1000 m

(from the edges of the valley floor to the tops of most hills). It is often found in association with Lodgepole Pine (Pinus contorta). Engelmann Spruce (Picea engelmanni) and Alpine Fir (Abies lasiocarpa) dominate the forest cover between 1200 m and timber line. Where the forest is replaced by grassland, xerophytes such as sagebrush (Artemisia, 7 species), Antelope brush (Purshia tridentata), Rabbit brush (Chrysothamnus nauseosus), cactus (Opuntia fragilis, O. polyacantha), milkweed (Asclepias speciosa), stickseed (Lappula squarrosa), greasewood (Sarcobatus vermiculatus) and sumac (Rhus glabra, Toxicodendron rybergii) are common. Along the streams willows (Salix, 7 species) and Black Hawthorn (Crataegus douglasii) predominate and the underbrush is composed of Snowberry (Symphoricarpos spp.) and rose bushes (Rosa spp) (Harshberger, 1958).

STUDY SITES

Five sites were selected in May based on several criteria, namely 1) Myotis californicus or M. leibii were captured consistently or observed to feed at that site, 2) the site was sufficiently different from the other sites in its physical and biotic components such as topography, proximity to water, and vegetation, and 3) the site was located on the valley floor. Sites with the same elevation were chosen as intraspecific patterns of foraging

behaviour may vary with elevation.

The five sites meeting these criteria fell into three categories based on their topographical features, namely open water situation, rocky bluff situation or a combination of the two (Figure 3).

The Okanagan River (O.K. River), adjacent to a provincial camp-ground, was the only truly open water situation. The river is part of an irrigation system that is the sole source of water for the intensive agriculture of the valley. The river widens from 20 m at a dam 600 m upstream to 60 m at the study site. Consequently the water flow is slower and less turbulent and the depth of the river at its midpoint is 1.5 m. A footbridge spans the river at this point and this enabled me to position monitoring equipment at mid-stream. The river is bordered by willows and cottonwoods upstream and by cattails (Typha sp.) at the study site. The nearest steep hills or bluffs are 150 m west of the study site.

Okanagan Bluff (O.K. Bluff) and Gallagher Bluff fell into the rocky bluff category. O.K. Bluff is a 60° - 80° slope 120 m high and 200 m wide. The slope is a mosaic of rocky outcrops, bunchgrass, sagebrush and small Ponderosa Pines. The study site was at the side of the road which was cut into the steep hillside 20 m above the Okanagan River. The river at this point is 15 m wide and

fast-flowing. O.K. Bluff is approximately 500 m upstream from the O.K. River site.

Gallagher Bluff is a large rock slide area; its 40° slope extends 300 m up the hillside and is 400 m wide. It is made up of loosely packed, large boulders, 1-5 m in diameter, and supports no vegetation. The perimeter of the bluff is fringed by sagebrush and Ponderosa Pine. A portable version of the monitoring equipment was carried up the slope to the study site. This site was approximately 250 m from a large body of water (Gallagher Lake) and 100 m up the slope from an irrigational flume, some 3 m wide.

McIntyre Bank and Gallagher Lake were the remaining two sites at which steep cliffs were immediately adjacent to bodies of water. An extension of Gallagher Bluff falls sharply into Gallagher Lake, a circular body of water 350 m in diameter. The study site was by the water's edge and adjacent to a field of bunchgrasses and sagebrush.

The study site at McIntyre Bank was in a clearing among Ponderosa Pines, cottonwoods, and willows beside the bank of the Okanagan River. The river at this point was 20 m wide and fast-flowing. The river ran at the base of a wooded rocky slope dominated by a vertical rock face 500 m high and 600 m wide.

EXPERIMENTAL DESIGN

At each of the five sites I monitored the level of bat feeding activity to determine the spatial and temporal patterns of the feeding behaviours of M. californicus and M. leibii. I also measured the responses of bats to artificially induced patches of prey and attempted to determine whether either species preyed selectively upon the available insect population.

Bats were captured every night of the study period except for three days on either side of the full moon, in mist-nets and Tuttle traps (Tuttle, 1974). I set mist-nets for a total of 250 h and trapped 438 h at 16 locations, 14 of which were within 500 m of a study site. Trapping and netting sites were close to or over water, and at the entrances to abandoned mine adits, caves, or buildings that were known to contain colonies of bats.

TRAPPING

Mist-nets (9 m x 2 m, 38 mm mesh) and Tuttle traps were set from dusk to 1-2 h after sunset. When mist-nets were placed in open areas it was advantageous to elicit an audible 'distress' call to attract other bats, not necessarily of the same species. This greatly increased the chance of capturing a bat that would have otherwise avoided the net. Bats captured and confined in the holding bag of the Tuttle trap similarly attracted other bats into

the bag with their audible calls. Tuttle traps proved to be more versatile than mist-nets as they could be erected at any time of the night and left until the following morning. It is generally difficult to capture bats in mist-nets in their feeding grounds as they can easily use echolocation to detect the nets. A bat captured in a mist net may be using that location as part of a flyway (Fenton, pers. comm.) which is not synonymous with its feeding area. This is also true of Tuttle traps which are, however, easier to position and appear to be more effective in trapping bats within their foraging area.

I trapped and mist-netted a total of 452 h which were divided roughly equally among the five study sites (Table 1) with the exception of Gallagher Lake, which was selected as a study site on 16 July, relatively late in the summer. The geography of Gallagher Lake did not lend itself to favorable placement of mist-nets and Tuttle traps as natural flyways were not evident. Furthermore, Gallagher Lake is an open area subject to strong winds which adversely affect the chances of capturing bats. For these reasons, extensive trapping at this site seemed unwarranted.

Captured M. yumanensis and M. lucifugus were tagged immediately and released at the same site. Myotis leibii and M. californicus were held overnight in order to collect fecal samples. They were then tagged and released

at the site of capture the following night. Bats were banded with size XB split celluloid bands (A.C.Hughes, England) covered with coloured reflective tape (3M Co.) and then secured onto the left or right forearm according to sex, left for female and right for male. Different colours were used for different species. The species and sex of a tagged bat in flight could be determined accurately up to distances of 250 m with the aid of a hand-held, seal-beam spotlight (approximately 200000 candle-power).

SAMPLING PROCEDURE

The activity of bats is influenced by the lunar cycle for reasons that are still unclear (Fenton, pers. comm.). Activity appears to be depressed during the full moon and for this reason I suspended field work for three days before and three days after the full moon. I arbitrarily divided the time from sunset to sunrise into three equal periods; early, middle, and late. Within the remaining block of nights in the lunar cycle, each site was sampled with equal frequency with respect to the period of the night.

Sampling

I sampled a total of 388 0.5-h periods at the five study sites throughout the summer. When analyzing the

temporal foraging of bats, it is more critical to divide the night into smaller temporal units such as hourly intervals. Although the three periods, i.e., early, middle, and late, were sampled with equal frequency at each site, 1-h intervals within each period were not. An average of 9.7 half-hour samples ($s=4.19$) were conducted within each 1-h interval. The data for temporal partitioning were standardized for each 1-h interval by dividing the dependent variable (activity or the number of tag observations) by the independent variable (number of 0.5 h sample periods obtained for each 1-h interval).

Each sample consisted of measuring the feeding activity of the bats for 0.5 h. I measured the level of feeding activity by recording the number of bat passes (sensu Fenton, 1970) and the feeding buzzes (Griffin, 1958) with a narrow band (40 kHz) ultrasonic sensor or 'leak detector' (Simmons et al., 1979). After a 5 min 'control' period i.e., an interval in which I obtained a measure of the undisturbed feeding state, an ultraviolet light (15 inch, 120 V, G.E F15T8-BL, unfiltered) placed in a central part of the feeding area, was turned on. The light attracted a cloud of insects within 1-2 min (see Fenton and Morris, 1976; Bell, 1980) and the degree to which the bats responded to this aggregation of insects by a measurable increase of passes and buzzes allowed me to measure the differential response by bats to patchy prey

at different sites.

The number of sequential 5-min periods that the UV light was left on depended on the level of bat activity during the initial 5-min control period and the latency of bat response to the UV light. For example, at Gallagher Bluff it was common to record zero activity during both the control period and a number of successive 5 min periods with the UV light on. In this case the UV light was left on until I was able to measure bat response to the insect aggregation. At the other four sites it was more common to record some activity during the 5-min control period. The UV light was then turned on for 10 min and off for 5 min and then on for another 10 min. This pattern would vary with the number of 0.5-h periods sampled sequentially. No more than three 0.5-h periods were sampled consecutively at one site at any time.

The technique of identifying bats in flight with a spotlight is new and its effect upon the feeding activity of the bats was unknown at the onset of the study. For this reason, the amount of time the spotlight was used during any 0.5-h sample varied from 15% - 66% throughout the summer. However, the amount of time the spotlight was used was equal from site to site for any one night; therefore, each site was affected to the same degree by the spotlight. The colour and placement of bands and thus the species and sex of the observed banded bats were

recorded and characteristics of their feeding behaviour were noted. Techniques of using the spotlight effectively, with minimal disturbance to the bats, will be described in the Discussion.

RESPONSE TO PATCHY PREY

To determine the general response by bats to patchy prey, I compared the total number of passes and buzzes recorded during the control periods (UV light off) to the numbers recorded when the light was on. Species response was measured by counting the numbers of tagged bats inside the circle of influence of the UV light i.e., the diameter of an insect swarm above the UV light, when the light was on and the same area when the light was off.

FECES ANALYSIS

To determine if bats were feeding selectively within their feeding areas, I compared the relative abundance of various taxa of free flying insects available to the bats at the time of capture to the relative proportion found in their feces.

Feces collected from bats held overnight were soaked in a solution of four parts Photo-flo to one part 70% isopropanol (Black, 1972; Belwood and Fenton, 1976). After 12 h of soaking, five pellets from each bat were teased apart individually and examined under a dissecting

microscope.

The chitinous fragments of insects were identified to the ordinal level. Coleoptera are easily identified by the large fragments of the elytra and appendages, Lepidoptera by the presence of wing scales, Diptera by their distinctive compound eyes, and Trichoptera by their characteristic bead-like antennae. Fragments were compared to slides of identified insect fragments from Ontario prepared by Karen Strong.

INSECT SAMPLING

To estimate prey availability I used a sweep-net to catch insects after an aggregation had formed over the UV light. The number of sweeps (15) was standardized for each sample. I was forced to estimate the insect population visually when the insects congregated too high above the UV light to be caught with a sweep net.

Two voucher specimens of M. californicus and M. leibii were collected and deposited in the British Columbia Provincial Museum in Victoria.

RESULTS

TRAPPING

A total of 958 bats of 12 species was captured, including one shot, at 16 locations between Okanagan Falls and Gallagher Lake (Table 2). Of these bats 477 (48.8%) were Myotis yumanensis, 257 (26.3%) M. lucifugus, 80 (8.2%) M. leibii, and 64 (6.5%) M. californicus. A total of 878 (90%) of the captured bats was banded with coloured reflective bands; 654 (67%) were trapped at the five study sites (Table 3).

GENERAL PATTERNS OF ACTIVITY

I compared the temporal component of the foraging behaviour of the two pairs of bats, M. leibii/M. californicus and M. lucifugus/M. yumanensis, to those displayed by the general bat population. Some data on their foraging behaviour were calculated by recording the number of tagged bats observed with the spotlight. General activity patterns at different sites were determined simply by monitoring echolocation calls (number of passes and buzzes) at each site throughout the night. Numbers of echolocation calls were also used to determine the effect of the spotlight on the foraging behaviour and the response to patchy prey by the general bat population.

The level of feeding activity as measured by the number

of buzzes is closely related to the general activity as measured by the number of passes. However, the feeding success, measured by the number of buzzes per pass, does not increase proportionally at peak times of activity (Figure 4a-e) resulting in a flatter curve for the buzzes than for the passes.

Three of the sites, O.K. Bluff, O.K. River and Gallagher Bluff, showed bimodal patterns of activity with peaks of activity one hour either side of midnight and a second peak before dawn (Figure 4a, b, e). McIntyre Bank showed a distinct unimodal pattern of activity with a peak between 02:00 and 03:00 (Figure 4c). The reason for this is unclear as there appeared to be an abundance of insects throughout the night. Gallagher Lake showed an unusual activity pattern in that the periods of peak activity occurred between 24:00-01:00 and in the first and last hours of the night (Figure 4d). Only three 0.5-h samples were taken in the first 1-h period at that site, which may not be representative of the true level of activity for that time interval.

EFFECT OF THE SPOTLIGHT

To determine the effect of the spotlight on the feeding activity of bats, I totaled the number of passes and buzzes when the spotlight was on and off in 26 0.5-h samples, controlling for the UV light. The total amount

of time for each of the four combinations, i.e., spotlight on, UV light on; spotlight off, UV light on, etc., was equal in each case. The UV light, therefore, did not bias any activity changes when testing for the effect of the spotlight in these 26 trials. The decrease in both the numbers of passes and buzzes when the spotlight is on is significant at all sites (Table 4). The activity is reduced by approximately 40% but the rate of attempted capture (number of passes: number of buzzes) is only marginally reduced (6.2 to 5.7). The degree of impact of the spotlight varied from site to site, and appears to be correlated with the spatial distribution of the insects. Bats showed the greatest aversion to the light at O.K. River and McIntyre Bank where the insects appeared to be evenly distributed over the water's surface. At O.K. River and especially Gallagher Bluff, insects seemed to be localized in discrete patches and the tolerance to the spotlight was proportional to the degree of insect patchiness, which was assessed visually.

The negative effect of the spotlight was temporary as the bats left the immediate area of the intense beam of the spotlight and returned to feed at the UV light 30 s to 2 min after the spotlight was turned off. This was pattern repeated over 10 times in 17 samples with the same results each time and was constant from night to night.

Bats seemed to associate the spotlight with the UV

light at least at Gallagher Bluff, where unlike my other sites, there was usually (ca 90% of samples) no bat activity in the initial control period and therefore no cause to turn the spotlight on to identify bats. However, when the UV light was turned on and a cloud of insects had formed above the light, I needed to use the spotlight to identify the foraging bats. After monitoring Gallagher Bluff for three weeks in this fashion, I found that the bats waited until the UV light was turned off and then fed on the dispersing insects. Presumably this association would be made only after repeated trials and thus supports the hypothesis that some bats feed in the same area every night.

RESPONSE TO PATCHY PREY

1. Bats in general

Bats showed a significant increase ($p < 0.001$) in the numbers of both passes and buzzes to patches in insects above the UV light (Table 5) at all sites with the exception of the number of passes at O.K. River. The data from Gallagher Lake also showed low overall response, as measured by the change in the level of feeding activity during the control period and the periods in which the UV light was turned on. The low level of response was possibly a result of the constant strong winds that prevailed, preventing the formation of clumps of insects

above the light. The presence of the bats was in response to the insects and not to the light itself as I recorded no bat response when the UV light did not attract insects. The increases in the numbers of passes and buzzes is not indicative of more feeding attempts measured by the ratio of buzzes to passes at all sites. At O.K. River, McIntyre Bank, and Gallagher Lake, the increased concentration of insects over the UV light attracted a greater number of bats than were feeding in the area before the UV light was turned on. The increase in the number of feeding bats probably reduced the potential insect returns for any one individual bat and thus the increase in insect capture rate, remained marginal. At O.K. Bluff and Gallagher Bluff, however, there appeared to be a superabundance of insects relative to the number of bats able to exploit the cloud of insects above the light. This is reflected by the significantly higher buzz:pass ratio at these sites when the light was turned on (Table 6).

The degree of response by bats to the insect patches was proportional to the insects' response to the light which in turn is a function of their spatial distribution during the control period. If the spatial distribution (assessed visually) remained relatively uniform after the UV light was turned on, the increase in bat activity over the UV light was small as at O.K. River (Figure 6). The relative increase in bat activity was greatest at

Gallagher Bluff where I saw few flying insects before the light was turned on.

2. Response by M. lucifugus/M. yumanensis,
and M. leibii/M. californicus

Reflective tagged M. yumanensis showed a significant positive response to the light ($p < 0.001$) only at O.K. River (Table 7) as did M. lucifugus at McIntyre Bank ($0.05 > p > 0.01$). Myotis lucifugus, however, was negatively associated with the UV light at O.K. River. Barclay (1981) has shown that some bats 'eavesdrop' on the echolocation calls of other bats and use this information to locate and exploit patches of insects. Therefore, bats may be attracted to an area of increased feeding activity from adjacent areas when the UV light was turned on. All of the M. leibii and M. californicus I observed were at least 20 m from the UV light, whether it was on or off. All tagged bats observed during the summer were actively feeding at the sites unless otherwise stated.

M. leibii/M. californicus

1. Temporal Partitioning

The temporal activity of these two bats overlapped 60.7%. The peak activities for both bats occurred between 22:00-23:00 and 01:00-02:00 (Figure 5 a). M. californicus was more active in the second peak of activity than was M.

leibii. M. leibii was more active in the last hour than the preceeding 2 h, although the percentage of activity was roughly equal to that of M. californicus.

2. Spatial Partitioning

There was a highly significant difference in the proportions of M. leibii and M. californicus observed at three sites ($p < 0.001$). M. leibii was recorded in significantly greater proportion to M. californicus at both O.K. Bluff and Gallagher Lake whereas M. californicus was observed 82 times at O.K. River compared to four times for M. leibii (Table 8). I was able to monitor two sites simultaneously with two sets of monitoring equipment and the help of an assistant. On three different nights M. leibii was observed at O.K. Bluff at the same time to an observation of M. californicus at O.K. River. Although 17.5% and 35.9% of M. leibii and M. californicus, respectively, were captured at McIntyre Bank, the numbers of observed tags were very low at this site (3 M. leibii; 2 M. californicus). Neither M. leibii nor M. californicus was recorded at Gallagher Bluff although evidence other than tag observations indicates that either, or both species was active there. On the last three nights of the study I used an oscilloscope-period meter combination to identify foraging bats by their echolocation calls. Although many species are easily distinguishable by their calls, M. leibii and M. californicus are not (Fenton and

Bell, 1981). However, the calls of these two species can be separated as a unit from those of other species in the Okanagan Valley; thus I was able to determine that one or both species fed at Gallagher Bluff.

M. leibii also forages above water (Fenton et al., 1980; this study) but does not appear to do so in association with M. californicus. I observed M. leibii feeding over the Okanagan River on 12 July and 8 August when it was cool ($T = 10^{\circ}\text{C}$). I found no bats, which were normally active at this time, along the nearby bluff and only 15 bats active over the river. These observations suggest that M. leibii was displaced from its preferred feeding area to one at which insects were more abundant. On both of these occasions M. leibii foraged 3-5 m over midstream while M. californicus fed by the banks of the river at a height of 5-10 cm.

M. lucifugus/M. yumanensis

1. Temporal Partitioning

In contrast to those of M. leibii and M. californicus, the temporal activities of M. lucifugus and M. yumanensis differed in their times of peak activity (Figure 5 b). M. lucifugus showed three peaks of activity, viz., between 21:00-22:00, 24:00-01:00 and 04:00-05:00. M. yumanensis activity was bimodal with peaks between 23:00-24:00 and 02:00-03:00. However, on the basis of the 78% overlap of

their foraging times, these two species did not temporally partition their resources to the same extent as M. leibii and M. californicus.

2. Spatial Partitioning

There is a significant difference in the numbers of M. lucifugus and M. yumanensis observed at any site ($p < 0.05$) with the exception of O.K. Bluff ($0.1 > p > 0.05$) (Table 8). Each species frequented certain sites more than others, with M. yumanensis found in significantly greater proportion at O.K. River ($\chi^2 = 1240$, d.f.=1, $p < 0.001$) than all other sites combined. Although observed in significantly different numbers from site to site ($\chi^2 = 45.8$, d.f.=3, $p < 0.001$), M. lucifugus was more evenly distributed among sites.

FORAGING BEHAVIOUR

My observations in the Okanagan Valley suggest that bats use 'foraging beats'. One striking example of space fidelity occurred every night for a two week period at the beginning of the study. At O.K. River I observed a tagged M. yumanensis at the same time (22:00- 2300) every night within the same 40 m² area, foraging 5-20 cm above the water's surface. As the bat was highly regular in time and space and because few bats had been banded up to that time, I suspect it was the same individual.

Similar observations were made for unidentified individuals at Gallagher Bluff where it was unusual to see any more than five bats at any time. Based on repeated patterns such as size and colour, time of arrival, feeding characteristics etc., it was my strong impression that the same individuals returned to the same foraging area every night.

Many observations within one or two or more consecutive samples indicated that some bats foraged within a defined but undefended space of the general feeding area. One M. yumanensis at McIntyre Bank flew a 25 m diameter loop starting at the river bank at a height of 2 m, flying to a height of 8 m over the middle of the river and returning to the starting point. This circuit was repeated consecutively over 40 times. I used trees as markers to assess flight path deviation and it appeared the bat deviated from this path only to capture an insect. This circular foraging behaviour was noted almost every night at different sites. On 8 August at Gallagher Bluff, a bat was observed to maintain a circular foraging pattern above the UV light. This circle was 6 m in diameter when the light was turned on and the insects were tightly packed above it. However, when the UV light was turned off the insects began to disperse and the bat continuously increased the diameter of its feeding circle to accommodate the changing spatial distribution of its prey.

This flexible behaviour can be adaptive under adverse environmental conditions. On 11 July at McIntyre Bank, bats, ceased foraging in intermittent rain and left the study area. One enterprising individual, however, remained active by maintaining a circular flight path beneath the canopy of a coniferous tree. The bat deviated from its path only to capture an insect. In one 5 min period this bat accounted for 88 passes (one loop of the flight path) and 18 buzzes (100% of the recorded activity).

Ninety two percent of the observed M. californicus at O.K. River foraged within 10 m of the river bank and usually among the passages through the emergent vegetation that bordered the river. When the number of feeding bats was small almost all species fed close to the bank. As the density of foraging bats increased, individuals were forced into the more marginal feeding areas of midstream.

M. leibii followed a predictable 'foraging beat' at Gallagher Lake. At least one individual patrolled 200 m of the shore-line at a height of 5 m on four consecutive nights. At O.K. Bluff M. leibii predictably flew into a wide V-shaped cut in the bluff wall and reversed its direction at this turn-around point. I took advantage of this stereotyped behaviour by placing a Tuttle trap in the notch. The trap sustained a high capture rate throughout the summer.

I noted at the two bluff sites that the bats foraged in groups of three or four. At Gallagher Bluff insects gathered within 1-2 min over the UV light as soon as it was turned on in 80% of the samples. In 80% of the samples the bats did not locate the swarm for at least 5 min and in 50% of the samples the swarm was located by two or more individuals at precisely the same time often flying in from the same direction. Bats arriving shortly after the swarm had been located by the first individual may have been 'eavesdropping' on the feeding activity of the finder (Barclay, 1981).

INSECT AVAILABILITY

Lepidoptera, Diptera, and Trichoptera were the three most abundant orders of insects available to the bats as a source of prey at all sites throughout the summer (Table 9). Diptera ($n = 562-3340$) accounted for 66-98.3% of all insects sampled at each site, significantly more than all other insects combined at each site ($p < 0.001$). Lepidoptera was more abundant than Trichoptera at O.K. River, Gallagher Lake, and Gallagher Bluff but the reverse was true at O.K. Bluff. However, the proportions of insects (Table 9) found at each site are not indices of the true proportion of insects found at any site from night to night. These proportions vary enormously with the occurrence of breeding swarms or on nights of high insect emergence. The availability of insect taxa to the bats

also varied with the time of the night. Surprisingly, no Coleoptera were found in any of the sweep-net samples and the eight beetles recorded at Gallagher Bluff were probably too large (30-40 mm long) for the bats under study.

The spatial distribution of the insect population varied from site to site. Insects were more uniformly distributed at sites associated with water, possibly a result of insect emergence at these sites. The distribution was patchy at other sites to an extreme at Gallagher Bluff where the only patches of insects were recorded over the UV light.

FECES ANALYSIS

I collected 18 and 7 samples of five pellets each of feces from M. leibii and M. californicus, respectively, from four sites. The results of the feces analysis from the four sites combined indicate that both species fed predominantly on Trichoptera (Table 10) and that the proportions of beetles and moths found in the feces of both species are roughly equal. M. leibii may have fed preferentially on Diptera at O.K. Bluff. This may account for the greater overall importance of Diptera in the diet of this species as compared to M. californicus. Based on the small sample sizes of analyzed feces, conclusions cannot be made concerning feeding patterns or whether M. californicus and M. leibii selectively consume certain

taxa of insects. However, the results indicate that both species of bats ate the same four insect orders in roughly equal proportions.

DISCUSSION

This study shows that two species of sympatric, insectivorous bats, Myotis leibii and M. californicus, spatially partition available resources. Whereas the temporal patterns of foraging activity are virtually identical, M. leibii foraged in areas of rocky bluffs and M. californicus over open-water situations. These observations agree with those of Fenton et al. (1980), which were based on trapping data. The trapping data from this study supports the hypothesis that M. leibii is the more common of the two species at bluffs ($\chi^2=34.4$, d.f.=1, $p < 0.001$) and M. californicus more common over open water ($\chi^2=16.0$, d.f.=1, $p < 0.001$). It is interesting that at McIntyre Bank, a bluff associated with water, there was no significant difference between the number of M. leibii and M. californicus trapped ($\chi^2=1.84$, d.f.=1, $p > 0.1$).

Fenton and Bell (1979) found M. californicus in Arizona feeding along the margins of clumps of trees or around the edges of the tree canopies. They noted, however, that open stretches of water were not common but where they did occur, M. californicus fed over the water. Krutzsch (1954) found M. californicus close to water in the Sonoran desert but also foraging near vegetation close to the ground.

The nature of the feeding areas of M. leibii is not well documented as some studies have treated M. leibii and

M. californicus as a unit (e.g. Black, 1974) because of the difficulty of identifying live specimens in the field. Although Findley et al. (1975) found M. leibii in the desert it was more common in mesic habitats such as grasslands, oak-pine woodland, Ponderosa Pine, and mixed coniferous and spruce-fir communities.

Most species of bats are dependent on free water for metabolic requirements (Carpenter, 1969). M. californicus' status as a common arid land dweller (Findley et al., 1975) is reflected by its renal structure, which is similar to that of other desert-dwelling bats. M. californicus has a greater urine-concentrating ability than M. leibii (Geluso, 1978). On this basis one might expect M. leibii to feed closer to water than M. californicus which is not the case. Although arid-adapted species such as M. californicus are able to conserve water efficiently they will drink when water is available (Geluso, 1978). Furthermore, water does not appear to be a limiting factor in the distribution of bats in the narrow Okanagan Valley ;therefore, the fact that M. leibii forages further from the water than M. californicus need not be regarded as anomalous. It is likely M. leibii frequent the river to drink.

The foraging areas of M. leibii and M. californicus may not be necessarily related to the location and proximity of their day roosts. M. californicus is primarily a

crevice-dweller in the southwest U.S. but will roost in almost any available site e.g., houses, mine adits, bridges, hollow trees, etc. (Krutzsch, 1954). M. leibii has been noted as a crevice-dweller in any rugged terrain such as canyons and bluffs (Robbins et al., 1977; Tuttle and Heaney, 1974). There appears to be no lack of suitable day roosts for either species in any part of the topographically diverse Okanagan Valley. As both species may roost in similar areas it seems unlikely that O.K. River, for example, was any closer to the roosting site of M. californicus than to that of M. leibii and that the location of the foraging area thereby determined its preferred foraging area. The two sites at which the two species were strongly partitioned, O.K. River and O.K. Bluff, were less than 500 m apart. In light of the fact that certain insectivorous bats commute up to 80 km from the day roosts to feeding sites (Barbour and Davis, 1969; Davis et al., 1962), and ignore seemingly potential feeding grounds en route, it is difficult to imagine that spatial partitioning over a matter of 500 m reflects the location of the day roosts.

Night roosts are used for digestion and permit bats to remain close to food resources before returning to their day roost. Hirshfeld et al. (1977) found that M. californicus night-roosts primarily in vegetation and I found two M. leibii night-roosting in small caves in the

rocky bluffs in this study.

Although 35.9% (n=23) of M. californicus and 17.5% (n=14) of M. leibii were trapped at McIntyre Bank, only two and three tags, respectively, of these species were observed there throughout the entire summer. Twelve of the M. leibii and all of the M. californicus were trapped or netted shortly after sunset in the rocky bluff adjacent to the study site. This may simply reflect the proximity of their day roosts to the trapping site and not their foraging area. It is possible that these bats commuted to foraging areas elsewhere, perhaps even 12 km upstream to the O.K. River site.

As noted previously, water associated feeding areas appeared to support a more uniformly distributed insect (prey) population than bluffs. The feeding strategies of some birds depend on the distribution of their food, feeding in groups in a patchy environment and defending a feeding area when the food becomes concentrated enough to more than repay the energy expended in its defence (Horn, 1968). M. californicus, which feeds in a non-patchy environment, is a more aggressive animal than M. leibii, at least when handled (personal observation), and this characteristic can almost be used to separate the two species taxonomically (Bogan, 1974). However, no instances of aggressive interactions or active defence of a feeding area by M. californicus were observed in this study. M.

leibii and M. californicus may partition resources vertically at times when insects are not available to M. leibii in its preferred feeding area on colder nights. Myotis daubentoni and M. mystacinus in Scandinavia hunt, respectively, in the zone next to the water and in the space higher up close to tree canopies (Wallin, 1961; Nyholm, 1965). Myotis velifer and Pipistrellus hesperus have been observed to occupy different altitudes at peak feeding times (Vaughan, 1959). Thus it may be that M. californicus and M. leibii habitually occupy separate areas in the horizontal plane and separate vertically in contact zones.

Sonograph and fast Fourier transform (FFT) analysis of the echolocation calls of M. californicus and M. leibii does not indicate any significant difference in the time-frequency components, intensity, or prey-detection distance (Fenton and Bell, 1981). Such differences may allow one species to be better adapted for feeding above water or along bluffs.

The evidence that two other species of similar, sympatric bats, M. lucifugus and M. yumanensis, spatially or temporally partition their resources is not as conclusive as that for Myotis leibii and M. californicus. Fenton et al. (1980) found both species feeding over fast-flowing water but M. yumanensis fed mainly by the banks and M. lucifugus over midstream. Horizontal

separation of these two species over water was not observed in this study. Their temporal activities overlap by 78.8% and therefore, temporal partitioning does not appear to be an important mechanism for reducing competition between these two species.

Myotis lucifugus and M. yumanensis may not be subject to the same selective pressures as M. leibii and M. californicus and do not partition resources on other than the food resource axis. Species interactions and the resulting community structure may be influenced by historical events rather than apparent selective forces such as competition (Wiens, 1977). Bell (1980) found no evidence of spatial or temporal partitioning of feeding areas among 11 species of insectivorous bats in Arizona.

Parkinson (1979) and Harris (1974) found limited hybridization between M. lucifugus and M. yumanensis in the interior of southwestern North America. Parkinson (1979) found them to be "ecologically similar" in northern California and southcentral Oregon and suggested that this may have effected morphological convergence. Certainly in the Okanagan Valley these two species are ecologically similar in their foraging and roosting behaviours. I found mixed colonies in the attics of two houses 500 m away from the closest study site. However, this extreme morphological similarity in the Okanagan Valley may have resulted in incorrect identification in many cases.

Ironically, the problems of field separation of M. lucifugus and M. yumanensis in the Okanagan Valley presents the same situation faced by the students of M. leibii and M. californicus in most other areas. The nature of the interspecific relationship of these two bats will remain obscure until the extent of the hybridization is determined and they can be separated accurately in the field.

PREY SELECTION

Black (1974) investigated the food habits and food partitioning in an insectivorous bat community in New Mexico. All species were classified as moth strategists or beetle strategists. Black pooled his data for M. leibii and M. californicus but suggested that if the two species had been separable, one might be a beetle strategist and the other a moth strategist. Krutzsch (1954) speculated that M. californicus fed on oak moths as this bat often foraged around live oak trees. The results of this study do not support Black's (1974) hypothesis as both species fed on Diptera and Trichoptera to a greater degree than on Lepidoptera or Coleoptera. However, the relative energetic value of each prey species is an unknown factor in a species' foraging strategy. Obviously a large, soft-bodied moth provides a greater caloric return than a small chironomid but the relative abundance of these prey items adds another dimension to the bats' foraging strategy. I

often watched bats which were probably fighting over large moths when other smaller prey items were far more abundant and were known to have been taken by the bats on other nights. These observations support a number of other studies (Vaughan, 1980; Bell, 1980; Fenton and Morris, 1976) suggesting that bats are largely opportunistic feeders.

I did not examine the diets of M. lucifugus and M. yumanensis and these two species could partition resources along the food axis. Two other similar insectivorous bats, Myotis evotis and M. auriculus, differ in food preferences when sympatric (Black, 1974) but have similar food habits when allopatric (Husar, 1976).

ASSESSMENT OF REFLECTIVE TAG-SPOTLIGHT TECHNIQUE

The use of capture data from mist-nets and Tuttle traps as an indirect method of studying the spatial and temporal aspects of bat foraging behaviour is not without notable bias. Studies by O'Farrell and Bradley (1970), Jones (1965), and Cockrum and Cross (1964) showed peak periods of activity shortly after sunset and diminishing levels of activity thereafter. As Bell (1980) noted, the capture data may reflect the drinking times of the bats more than their foraging times. By the same token, they may also reflect the drinking sites more than the foraging areas. As noted previously, foraging bats are not particularly

susceptible to capture and thus a bat captured at one site may forage in another.

Kunz (1973) proposed that in Iowa Eptesicus fuscus and Lasiurus borealis partitioned resources by having significantly different patterns of temporal activity, and that others, i.e., Lasiurus borealis and L. cinereus, did so by having spatially separated foraging areas. His conclusions were based on results of mist-net capture data and therefore subject to the aforementioned biases. Further error was introduced in the interpretation of his data by using an inappropriate statistical test, the Mann-Whitney U test, to determine if the temporal foraging patterns of five species of bats were significantly different. The Mann-Whitney U test will test only for differences in the medians of activity and not for differences in the overall pattern. For example, one species that shows a bimodal pattern with peaks of activity before and after midnight would have the same median of peak activity as another species that showed a unimodal pattern of activity with a normal distribution curve peaking at midnight or another with a peak after dusk but heavily skewed to the right. In all cases the period of median activity is not significantly different but the temporal patterns vary considerably.

Other methods of assessing bat activity which are able to identify positively actively foraging bats reflect a

more accurate interpretation of the activity patterns. Bell (1980) used a combination of oscilloscope and zero-crossing period meter and found continuous activity throughout the night with peaks of activity 2.5-4.5 h after sunset. He also found no evidence of resource partitioning among species. Unfortunately, the extreme similarity of the echolocation calls of M. leibii and M. californicus precluded the use of the oscilloscope-period meter in this study.

Nyholm's (1965) study on the ecology of Myotis mystacinus and M. daubentoni is perhaps the most definitive evidence of spatial partitioning in bats. Unlike traps used in other studies, Nyholm's ingenious bat trap, baited with insects, ensured the capture of bats that were actively foraging. Overland this trap could be set at different heights and bats feeding over the water were captured by knocking them into the water with sand. The results show that these bats fed in the same area but vertically partitioned resources.

Banding bats with light-reflective tags, as done in this study, does not necessitate the subsequent capture of tagged bats to determine behavioural patterns. Observation of a tagged bat allows species identification, sexing, and assessment of the bat's mode of behaviour, i.e., foraging or transitory, as indicated by a characteristic zig-zag, erratic path or a straight, uninterrupted one,

respectively. This method is direct and accurate but two disadvantages are evident.

First, it is probable that one tagged individual can account for a number of recorded observations. It was sometimes possible to compensate for this by not recording the tagged bat if it was obviously the same one observed moments before. The other disadvantage is the strong inhibitory effect of the spotlight on the normal foraging behaviour of bats. A bat invariably left an area if the light beam was placed directly on it for more than a few seconds. There are two ways to minimize this effect. First, the beam should not be placed directly on the bat for any longer than it takes to identify it, usually less than a second. Second, the peripheral light of the beam is powerful enough to observe foraging behaviour, once the bat's identity has been established, for distances up to 40-50 m. This peripheral light does not appear to affect the bat's behaviour, especially if the main beam follows, rather than precedes, the flight path of the bat.

Two different coloured tags should not be placed on either the same or different forearms of a bat for in-flight identification. Red and yellow tags together on the beating wing of a bat appears orange and can be confused for either red or yellow at a distance.

It is difficult to estimate the minimum number of bats

to be tagged before one is able to observe predictably one tag in the spotlight within a 0.5-h sample period. The estimate ranges from 50 (female M. lucifugus) to 70 (female M. yumanensis) individuals (Figure 7). The males of all species were both trapped and observed in significantly lower numbers.

Despite these limitations, this simple technique is powerful in providing information on the behavioural patterns of bats that is not assessable by other methods.

CONCLUSIONS

1. Myotis leibii and M. californicus reduce interspecific competition in the Okanagan Valley by spatial partitioning of resources. The similarity of their diets may reinforce this behaviour. The temporal foraging patterns of these two bats are not substantially different..

2. Evidence of competition and resource partitioning is not conclusive for Myotis yumanensis and M. lucifugus. Accurate separation of these two species is a prerequisite to future behavioural studies regarding the nature of their relationship.

3. Bats showed variable response to insect swarms above the UV light at different sites related to the spatial distribution of the insect population.

4. The reflective tag-spotlight technique is a direct method of studying bat activity and circumvents interpretational biases of mist-net capture data.

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TABLES

Table 1

Number of mist-net and Tuttle trap hours
per study site, 5 May to 15 August, 1980

	Mist-net	Tuttle trap	total
O.K.Bluff	30	108	138
O.K.River	60	30	90
McIntyre Bank	36	54	90
Gallagher Lake	28	0	28
Gallagher Bluff	38	68	106
	<hr/>	<hr/>	<hr/>
Total	192	260	452

Table 2

Species and numbers of bats captured
between Okanagan Falls and Gallagher
Bluff, 5 May to 15 August 1980

	male	female	total
<u>Myotis yumanensis</u>	90	387	477
<u>M. lucifugus</u>	79	178	257
<u>M. leibii</u>	18	62	80
<u>M. californicus</u>	6	58	64
<u>Antrozous pallidus</u>	6	18	24
<u>M. volans</u>	10	8	18
<u>M. evotis</u>	3	5	8
<u>M. thysanodes</u>	2	4	6
<u>Eptesicus fuscus</u>	2	4	6
<u>Lasionycteris noctivagans</u>	-	1	1
<u>Plecotus townsendii</u>	1	-	1
<u>Euderma maculatum</u>	-	1	1
Unidentified	3	12	15
	<hr/> 220	<hr/> 738	<hr/> 958

...Table 8 cont.

n = # of half-hour periods sampled

T = # of bats trapped (see Table 2)

o = # of observed tagged bats feeding

e = expected # of tagged bats observed, based on T

; e.g. M. leibii at O.K. Bluff $e = \frac{80}{80 + 64} \times 61$

n.s. = not significant; * $p < 0.001$; ** $0.1 > p > 0.05$

Table 4

Numbers of bat passes and buzzes recorded over equal periods (390 min) with spotlight on and off (χ^2 tests the null hypothesis that there is no significant difference between the numbers of passes and buzzes when the spotlight is off or on)

	Passes	Buzzes
Spotlight off	o = 5171 e = 4212.5	o = 906 e = 720
Spotlight on	o = 3245 e = 4212.5	o = 534 e = 720
	$\chi^2 = 436.18$ *	$\chi^2 = 96.1$ *

o = recorded number of passes or buzzes

e = expected number of passes or buzzes

* $p < 0.001$

Table 5

Bat response to induced clouds of insects over UV light as measured by the number of passes and buzzes recorded during the total number of periods with the UV light on vs UV light off

(χ^2 tests the null hypothesis that there is no significant difference between the number of passes (buzzes) with the UV light off or on)

O.K.Bluff O.K.River McIntyre B. Gallagher L. Gallagher B.

number of bat passes

UV light on

o = 12811 o = 9820 o = 20582 o = 5673 o = 9464
e = 12234.8 e = 9998.9 e = 19496.6 e = 5378.1 e = 8514.4

UV light off

o = 8163 o = 7350 o = 12782 o = 3724 o = 3388
e = 8739.2 e = 7170.9 e = 13867.3 e = 4018.8 e = 4337.5
 $\chi^2 = 65.09$ $\chi^2 = 7.67$ $\chi^2 = 145.58$ $\chi^2 = 37.79$ $\chi^2 = 317.7$

*

**

*

*

*

55a

continued...

...Table 5 cont.

number of buzzes

UV light on

o = 2099	o = 2313	o = 4294	o = 1507	o = 2659
e = 1789.6	e = 2603.7	e = 3835.1	e = 1326.6	e = 2128.6

UV light off

o = 969	o = 2158	o = 2269	o = 811	o = 634
e = 1278	e = 1867.3	e = 2727.8	e = 991.3	e = 1111.4

$\chi^2 = 128.1$ *

$\chi^2 = 77.6$ *

$\chi^2 = 132.22$ *

$\chi^2 = 57.32$ *

$n^+ = 308$

297

182

318

$n^- = 220$

213

202

136

162

$n^+ =$ # 5 min periods UV light on
 $n^- =$ # 5 min periods UV light off

expected values determined as follows:

* $p < 0.001$; ** $0.01 > p > 0.001$

e.g. expected # of passes,

$$\text{UV light on} = \frac{n^+}{n^+ + n^-} \times (\text{Total \# passes})$$

Table 6

Comparison of the number of buzzes per pass when UV light on/vs. UV light off for each half-hour sample (paired sample t-test and associated probabilities indicate that the buzz:pass ratio is significantly lower when the UV light is off, except at O.K.River and Gallagher Lake)

Site	n	$\sum_1^n \text{RBP1} - \text{RBP2}$	t	p
O.K.Bluff	89	3.598	3.594	p < .001
O.K.River	87	1.602	1.14	n.s.
McIntyre Bank	81	1.606	1.709	0.1 > p > 0.05
Gallagher Lake	53	1.048	0.72	n.s.
Gallagher Bluff	80	7.974	5.719	p < 0.001

n = # of paired samples at each site

RBP1 = Ratio of buzzes to passes with UV light on

RBP2 = Ratio of buzzes to passes with UV light off

t = t test value

p = probability value for t test

Table 7

Number of tagged M. lucifugus and M. yumanensis observed

feeding over UV light, 10 June to 15 August, 1980

(Where sample size is adequate for statistical analysis

χ^2 values and associated probabilities show significantly

higher proportion of bats feeding above UV light when on)

	O.K. Bluff	O.K. River	McIntyre Bank	Callagher Lake
<u>M. lucifugus</u>				
UV light on	1	2	22	3
UV light off	0	13	9	6
χ^2 value	-	-	5.451 **	-
<u>M. yumanensis</u>				
UV light on	8	388	14	4
UV light off	5	152	7	1
χ^2 value	n.s.	103.0 *	n.s.	-

n.s. = not significant; * $p < 0.001$; ** $0.01 > p > 0.05$

Table 8

Number of tagged M.leibii/M.californicus and
M.lucifugus/M.yumanensis observed per site,
 10 June to 15 August, 1980

(χ^2 tests the null hypothesis that there is
 no significant difference in the numbers of
 observed M.leibii and M.californicus (or
M.lucifugus and M.yumanensis) observed per site)

		O.K.Bluff	O.K.River	McIntyre Bank	Gallagher Lake
		n = 89	n = 90	n = 82	n = 53
<u>M.leibii</u>	80	o = 60 (20)	4 (94)	3 (66)	52 (66)
(<u>M.lucifugus</u>)	257	e = 33.8 (14.5)	47.4 (592.5)	— (51.6)	31.3 (45.1)
<u>M.californicus</u>	64	o = 4 (36)	82 (1948)	2 (132)	4 (108)
(<u>M.yumanensis</u>)	477	e = 27.4 (41.7)	38.2 (125.7)	— (147.4)	24.8 (128.8)
χ^2		45.4 (2.86)	90.2 (483.8)	— (5.6)	30.1 (13.05)
		* n.s.	*	**	* *
					continued...

...Table 8 cont.

n = # of half-hour periods sampled

T = # of bats trapped (see Table 2)

o = # of observed tagged bats feeding

e = expected # of tagged bats observed, based on T

$$e = \frac{o \cdot T}{n} \quad \text{e.g. } M. \text{leibii} \text{ at V.K.Bluff } e = \frac{80}{80 + 64} \times 61$$

n.s. = not significant; * $p < 0.001$; ** $0.1 > p > 0.05$

Table 9
Orders and numbers of insects
caught over UV light

	O.K.Bluff n = 12	O.K.River n = 11	McInt Bank n = 9	Gllghr L. n = 7	Gllghr Bluff n = 10
Lepidoptera	109 (12.9)	61 (8.3)	156 (5.4)	40 (1.1)	112 (12.2)
Diptera	562 (66.6)	603 (82.5)	2544 (88.3)	3340 (98.3)	736 (80.1)
Trichoptera	173 (20.5)	2 (.3)	173 (6.0)	17 (.5)	60 (6.5)
Coleoptera	—	—	—	—	8 (.9)
Ephemeroptera	—	65 (8.9)	6 (.2)	—	2 (.2)
Total	849	731	2879	3397	918

n = # of nights insect population sampled

() = % of column total

Table 10

Relative abundance and per cent frequency
of insects in fecal pellets

	O.K.Bluff n = 13	O.K.River n = 0	McIntyre Bank n = 2	Gallagher L. n = 3	Total n = 18
<u>M.leibii</u>					
Lepidoptera	36 (13)	—	6 (7.0)	5 (10.9)	47 (11.5)
Diptera	100 (35.8)	—	13 (15.3)	8 (17.4)	121 (29.5)
Trichoptera	107 (38.3)	—	62 (73.0)	31 (67.4)	200 (48.9)
Coleoptera	36 (13.0)	—	4 (4.7)	2 (4.3)	42 (10.2)
total	279	0	85	46	410
<u>M.californicus</u>	n = 3	n = 3	n = 0	n = 1	n = 7
Lepidoptera	29 (54.7)	1 (1.8)	—	4 (4.6)	34 (15.6)
Diptera	1 (1.9)	13 (24.5)	—	4 (4.6)	18 (8.2)
Trichoptera	16 (30.2)	34 (64.1)	—	98 (88.2)	148 (68.2)
Coleoptera	7 (13.2)	5 (9.4)	—	5 (4.5)	17 (7.8)
total	53	53	0	111	217

n = # of fecal pellets analyzed

() = % of column total

FIGURES

Figure 1

Profiles of Myotis leibii (left) and
M. californicus (right).

Note the differences in the colour of the
pelage and the distance from the tip of the
nostrils to the hairline.

Figure 2

Map of study area.

Study sites are shown by a star (☆),

1 - O.K.Bluff; 2 - O.K.River;

3 - McIntyre Bank; 4 - Gallagher Lake;

5 - Gallagher Bluff. Town site is shown

by (●). Bodies of water are shown by (///)

and bluffs by contour lines (///)

Inset: location of study area.

Figure 3

Photographs of the five study sites.

- (a) O.K.Bluff, rocky bluff, some vegetation.
- (b) O.K.River, open water. (c) McIntyre Bank, river adjacent to bluff. (d) Gallagher Lake, open water adjacent to bluff. (e) Gallagher Bluff, rocky bluff, no vegetation.

a O.K. Bluff

b O.K. River

c McIntyre Bank

d Gallagher Lake

e Gallagher Bluff

Figure 4

Graphs showing the average patterns of
nightly bat activity.

(a) O.K.Bluff. (b) O.K.River. (c) McIntyre Bank.
(d) Gallagher Lake. (e) Gallagher Bluff.

Solid line (——) represents the percentage mean
number of passes in each hour for that site.

Dashed line (----) represents the percentage
mean number of buzzes in each hour for that site.

Vertical bars give the 95% confidence limits for
each point. $n(p)$ = mean number of passes recorded.
 $n(b)$ = mean number of buzzes recorded.

Figure 5

Species average nightly activity patterns

Graphs represents the percent mean number of observed tagged bats, by species, in each hour for all sites combined.

Figure 6 .

Insect distribution in relation to UV light
at (a) O.K.River and (b) Gallagher Bluff.

UV light off is represented by closed box.

UV light on is represented by open box.

Figures are based on visual assessment
of insect distribution.

O.K. River

Gallagher Bluff

Figure 7

Numbers of observed tagged bats in
relation to numbers tagged.

Cumulative number of M.yumanensis (a) and
M.lucifugus (b) females represented by an
open box (□); males represented by a
closed box (■). Observed number of
tagged M.yumanensis (a) and M.lucifugus (b)
females represented by open triangle (▽);
males represented by closed triangle (▼).

END

0 7 H 0 9 H 8 2

FIN