

Night Roosting and the Nocturnal Time Budget of the Little Brown Bat, *Myotis lucifugus*: Effects of Reproductive Status, Prey Density, and Environmental Conditions

E.L.P. Anthony, M.H. Stack, and T.H. Kunz

Department of Biology, Boston University, 2 Cummington Street, Boston, Ma. 02215, USA

Summary. The insectivorous bat *Myotis lucifugus* typically apports the night into two foraging periods separated by an interval of night roosting. During this interval, many bats occupy roosts that are used exclusively at night and are spatially separate from maternity roosts. The proportion of the night which bats spend roosting, and thus the proportion spent foraging, vary both daily and seasonally in relation to the reproductive condition of the bats, prey density, and ambient temperature. A single, continuous night roosting period is observed during pregnancy. During lactation, females return to maternity roosts between foraging bouts, and night roosts are used only briefly and sporadically. Maximum use of night roosts occurs in late summer after young become volant. Superimposed upon these seasonal trends is day-to-day variation in the bats' nightly time budget. Long night roosting periods and short foraging periods are associated with cool nights and low prey density. This behavioral response may minimize energetic losses during periods of food scarcity.

Introduction

Optimal foraging theory states that natural selection acts upon feeding habits of predators in such a way that net energy yield per unit feeding time is maximized (Schoener 1971; Pyke et al. 1977). Foraging habits include many behavioral components (e.g., prey selection, habitat selection, and determination of the time of foraging and duration of feeding bouts), each of which may be modified to maintain maximal energetic efficiency under varying environmental conditions.

Information regarding feeding ecology of temperate zone insectivorous bats primarily relates to the types and quantities of prey taken (Kunz 1980), and the foraging habitats of many species are well known. However, temporal aspects of foraging behavior are not well understood in most bats. Activity patterns of several species have been investigated using mist nets (Cockrum and Cross 1964; Jones 1965; O'Farrell and Bradley 1970; Kunz 1973; Reith 1980) and ultrasonic bat detectors (Bell 1980). Detailed data on nocturnal time budgets have been difficult to obtain, primarily because the small size of most species precludes radiotracking. Only under rare circumstances can bat activity be directly observed throughout the night (as in Nyholm 1965); therefore, indirect methods such as those used by Swift (1980) must be used to establish time budgets for these animals.

Myotis lucifugus typically apports the time between dusk and dawn into two periods of foraging separated by an interval of night roosting. Because there is no evidence that this species

spends significant amounts of time in non-foraging activities while away from day or night roosts, variations in the time and duration of feeding bouts should be reflected in temporal aspects of night roosting behavior. Conditions that may influence the time and duration of foraging flights and night roosting periods include: 1) temporal aspects of prey activity, 2) prey abundance, 3) predator activity, and 4) energetic constraints. For these bats, energetic considerations are complex, as they include day-to-day variations in costs of flight and thermoregulation as well as seasonal changes in energy demands of reproduction. In this paper, we examine night roosting behavior of *M. lucifugus* to estimate the variability in nocturnal time budgets associated with season, reproductive condition, prey density, and environmental conditions.

Materials and Methods

Study Species

M. lucifugus is a hibernating vespertilionid bat that is widely distributed throughout North America. Females form summer maternity colonies of 100 to over 1,000 individuals, primarily in barns and attics, and cluster during the day in warm (> 32° C) maternity roosts along ridge poles, under metal roofs, in joist crevices, etc. Males usually day roost singly in cooler sites, but a few males are sometimes found roosting in buildings occupied by maternity colonies.

Foraging flights of *M. lucifugus* begin each night at dusk. After an initial flight of 1.5 to 3 h (Anthony and Kunz 1977), many bats retreat to buildings which house maternity colonies, and roost for variable periods of time in cavities which are used exclusively at night. These roosts are smaller and less exposed than maternity roosts. Bats typically leave the night roosts asynchronously for a second feeding period which ends at dawn.

Indirect Monitoring

Two night roosts used by *M. lucifugus* were studied in an abandoned barn (Merrill barn) in Hancock, Hillsborough County, New Hampshire. These roosts consisted of rectangular mortices or cavities (# 1 = 8 × 5 × 10.5 cm; # 2 = 15 × 5 × 12 cm) in the lower surface of horizontal beams, approximately 4 m from the floor. A thermocouple was inserted into each mortice to monitor roost occupancy; another thermocouple was placed adjacent to one roost to monitor barn temperature. All temperatures were continuously recorded from 19 April to 2 September, 1974, using two Foxboro recorders.

0029-8549/81/0051/0151/\$01.20

Roost occupancy was quantified in two ways: 1) The time that bats first entered the roost (indicated by a temperature increase relative to barn temperature) and the time that the last bat(s) exited (resulting in a rapid temperature decline) were used to calculate the length of time the roosts were used each night. 2) Feces produced by night-roosting bats were collected over 9-day intervals in aluminum pans placed beneath both roosts, dried for 12 h at 100° C, and weighed to the nearest 0.01 g. Dry mass of guano was converted to bat-hours of roost occupancy on the basis of guano production rates after the first feeding period. In three hours of roosting immediately after feeding, pregnant *M. lucifugus* produce an average of 0.018 g guano per bat per hour, lactating bats produce 0.025 g per bat-hour, and juveniles produce 0.011 g per bat-hour (Rumage 1979).

To determine whether patterns of night roost use are related to environmental conditions and/or prey availability, roost # 1 was monitored with a thermocouple in 1976. A Burkard suction trap (Taylor 1951) was used to estimate insect density each night from 30 May through 28 July. The trap was placed with its mouth approximately 3 m above the ground at the edge of Half-moon Pond, a known feeding site, 3 km from the night roost location. Insects were collected and automatically segregated into 50-min samples from 2000 to 0510 h (EDT).

Daily maximum and minimum temperatures and hourly precipitation data were obtained from the Army Corps of Engineers, MacDowell Dam, Peterborough N.H., 7 km from the study site. Cloud cover was estimated by personal observation, supplemented by records of the Silver Ranch Air Park, Jaffrey, N.H., 16 km from the study site. Times of sunset, moonrise, and moonset were taken from the Eldridge Tide and Pilot Book using appropriate correction factors for Hancock, N.H.

Direct Monitoring

In years when roost use was not continuously monitored by temperature sensing (1975, 1978, 1979), we removed bats from night roosts at various phases of the reproductive cycle to determine the number of bats using the roosts, as well as their sex, age, and reproductive condition. In addition to the previously described site (Merrill colony; pre-parturition flight count=300 bats), we censused mortice-type night roosts of *M. lucifugus* located in barns in Hancock (Turpin; 110 bats), Peterborough (Sargent; 900–1,000 bats), and Deering (Hunter; 470 bats), N.H. At all sites, the night roosts were used only at night and were spatially separate from the maternity roosts. All sampling was conducted between 2445 and 0300 h (EDT).

During the final year of the study (1979), night roosting behavior was observed at the Hunter colony using a Javelin night viewing device and a Justrite headlamp fitted with an Eastman Kodak Wratten # 87 infrared filter. Observations were made on three nights during pregnancy (25 May, 8 and 15 June), two nights during lactation (29 June and 6 July), and three nights after juveniles were fledged (20 July, 3 and 17 August). Observers were positioned behind a blind approximately 6 m from a night roost (24 × 5 × 11 cm). The numbers of bats entering and leaving the roost were tallied continuously and summarized over 15-min intervals from 2200 to 0600 h (EDT). Roost temperature was monitored concurrently using a thermistor and a Yellow Springs Instruments (YSI) telethermometer.

Direct observation and censuses of bats in night roosts were performed to supplement and verify information obtained by indirect monitoring. However, both activities were minimized to avoid undue disturbance to the colonies.

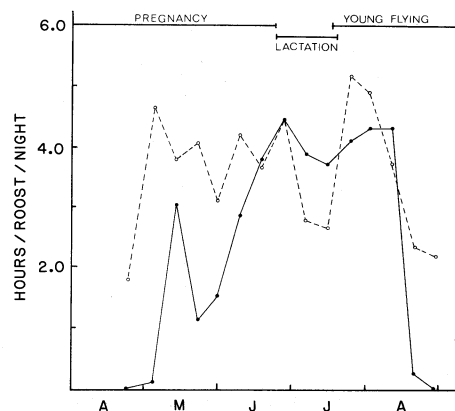


Fig. 1. Seasonal trends in mean lengths of night roosting periods. Means are calculated over 9-day intervals, averaging data from roosts # 1 and # 2 at Merrill barn in 1974 (dotted line); in 1976 only roost # 1 was monitored (solid line). Reproductive chronology is based on combined trapping data from several nearby colonies. The transition from pregnancy to lactation is shown when 50% of the reproductive females in emergence trap samples are pregnant and 50% are lactating. The bar indicating lactation ends when 50% of the reproductive females trapped are lactating and 50% are post-lactating. The juvenile population is considered volant when young constitute 50% of the trap samples

Results

Seasonal Patterns of Night Roost Occupancy

Seasonal trends of night roost use in the Merrill colony are depicted in Figs. 1 and 2. Bats first occupy night roosts in late April, and roost use subsequently increases during early May, as bats arrive from hibernacula. Mean lengths of night roosting periods (Fig. 1) rise sharply at this time, whereas mean nightly guano production (Fig. 2) rises more gradually. This discrepancy may be explained by long nights and low insect density early in the season, which may promote long roosting intervals, while guano production is minimal subsequent to unproductive foraging efforts.

Night roosting activity declines briefly in late May, but during late pregnancy night roosts are used more extensively (Figs. 1 and 2). Sampling from night roosts in May showed that they are used exclusively by pregnant females at this time (Table 1). The number of bats occupying each night roost during pregnancy varied from 2 to 17. Although adult males constitute a significant proportion of bats trapped upon emergence at these colonies early in summer (up to 43% at Turpin, <10% at other sites; unpublished data), they apparently do not night roost with females.

Following parturition in late June, night roost use declines (Figs. 1 and 2). At Merrill barn, where indirect monitoring was conducted, we found only non-reproductive females in the mortices in early July (Table 1). However, at two other locations, night roosts were occupied not only by non-reproductive females, but also by lactating females (some with young) and a few pregnant females. The number of bats per roost varied from 1 to 23. Juveniles removed from these roosts ranged in age from 1 day (forearm = 14.9 mm) to 8 days (forearm = 27.6 mm; Kunz and Anthony in press). Since *M. lucifugus* is incapable of sustained flight at this age (Buchler 1980), these bats must have been transported to the night roosts by their mothers.

In late July, when most juveniles can fly and forage independently, night roost use reaches its maximum (Figs. 1 and 2),

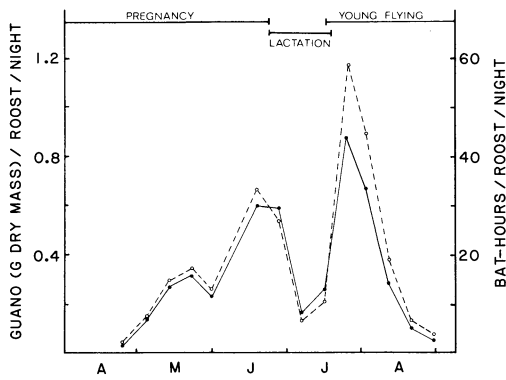


Fig. 2. Seasonal trends in guano production during night roosting periods, 1974. Dry weight of guano collected beneath roosts is indicated by the solid line; the numbers of bat-hours of roost occupancy calculated from these measurements are indicated by the dotted line. The conversion factor for pregnant females (see text) was applied from April through 22 June, that for lactating females was used from 2 July through 20 July, and 0.022 g per bat-hour was used in the intervening period when roosts were occupied by both pregnant and lactating individuals (see Table 1). After 20 July, 0.015 g per bat-hour was used as a conversion factor, reflecting use of roosts by juveniles and adult females. Although no data are available on guano production of post-lactating females, we have assumed that their guano output would approximate that of pregnant females. Means are calculated over the same 9-day intervals as in Fig. 1, averaging data from roosts # 1 and # 2 at Merrill barn, and are plotted on day 5 of each interval

reflecting occupancy by both adults and volant young (Table 1). The number of bats per mortice ranged from 1 to 32. Night roost utilization declines in late August when bats begin to depart for hibernacula.

Direct observation confirmed these seasonal trends and provided additional information regarding night roosting behavior. Most activity at the night roost occurred between 2400 and 0400 h. Bats generally entered the roost after exhibiting repeated "checking" behavior (Vaughan and O'Shea 1976). This behavior consisted of flying toward the roost entrance, stalling or alighting briefly at the edge of the mortice, and quickly falling away into flight. When entering the roost, bats initially landed on the beam near the mortice and then crawled in. Once inside, they formed a tight cluster at the highest point. Bats did not appear to enter torpor, as ear movements, scratching, self-grooming, and changes in position within the roost were commonly

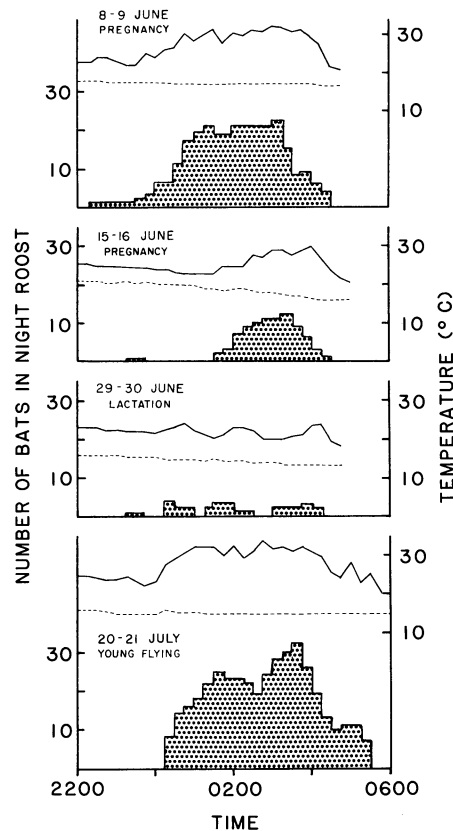


Fig. 3. Results of direct observation of night roosts, 1979. Stippled areas indicate total number of bats present in the night roost every 15 min, as calculated from a running tally of entrances and exits. The upper solid line plots the temperature record obtained from a thermistor located in the roost; the dotted line traces outdoor ambient temperature. The area under the curve represents 69.00 bat-hours of roost occupancy on 8-9 June, 20.50 bat-hours on 15-16 June, 7.75 bat-hours on 29-30 June, and 100.25 bat-hours on 20-21 July (when observation began at 2430 h). Nights with incomplete entrance and exit data are omitted

observed. When leaving, bats simply dropped from the roost and took flight.

Using a continuous tally of entrances and exits, we calculated the number of bats occupying the roost for every 15-min interval throughout the night (Fig. 3). During pregnancy (8 June), the

Table 1. Results of night roost censuses. Preg = Pregnant, Lact = Lactating, PL = Post-lactating, NR = Non-reproductive females, Juv = Juvenile males and females

Date	Site	No. of Roosts	No. of Bats	% Preg	% Lact	% PL	% NR	% Juv
15 May 1975	Merrill	2	5	100				
19 May 1979	Turpin	2	13	100				
19 May 1979	Merrill	3	25	100				
24 May 1975	Merrill	1	3	100				
25 May 1975	Turpin	3	33	100				
1 July 1978	Merrill	2	9				100	
1 July 1978	Turpin	2	18	11	39		22	28
1 July 1978	Sargent	1	23	26	26		17	30
21 July 1979	Turpin	4	6		33	17		50
29 July 1978	Merrill	4	42		5	81	2	12
29 July 1978	Sargent	1	23		22	17		61
29 July 1978	Hunter	3	68		10	28		62

Table 2. Summary of correlation analyses. Sets of control variables are as follows: a=Tmin, weather (cloud cover and precipitation), moon phase (0=new, 15=full), % moonlight (% of time between sunset and midnight that the moon is up), insects >2 mm in body length; b=date, Tmin, weather, moon phase, % moonlight, reproductive condition; c=date, weather, moon phase, % moonlight, insects >2 mm, reproductive condition; d=date, Tmin, weather, insects >2 mm, reproductive condition; e=date, Tmin, insects >2 mm, reproductive condition; f=Tmin, weather, insects >2 mm, moon phase, % moonlight, reproductive condition; g=date, Tmin, weather, moon phase, % moonlight, insects >2 mm, reproductive condition; h=Tmin, weather, moon phase, % moonlight; i=date, weather, moon phase, % moonlight; j=date, Tmin, weather; k=date, Tmin, moon phase, % moonlight. Lunar index=(moon phase) × (% moonlight) × (1 if clear, 0.5 if partly cloudy, 0.1 if overcast). Night length=sunset time to sunrise time in minutes. A= multiple-partial correlation, F= 5.29

Correlated variables		Partial <i>r</i>	Control variables	Simple <i>r</i>
Length of night roosting period	Reproductive condition	A**	a	0.40*
	Insects >2 mm	-0.35*	b	NS
	Tmin	-0.38*	c	NS
	Moon phase	NS	d	NS
	Lunar index	NS	e	NS
Time from sunset to beginning of night roosting period	Reproductive condition	NS	a	NS
	Insects >2 mm	0.33*	b	0.35*
	Tmin	NS	c	NS
	Moon phase	NS	d	NS
	Lunar index	NS	e	NS
Total insects 2000–2410 h	Date	0.36*	h	0.31*
	Tmin	0.30*	i	0.34*
	Moon phase	-0.33*	j	-0.33*
Insects >2 mm 2000–2410 h	Weather	NS	k	NS
	Date	0.31*	h	NS
	Tmin	NS	i	NS
	Moon phase	-0.33*	j	-0.32*
Length of night roosting period	Weather	NS	k	NS
	Night length	-0.70***	g	-0.67***

NS= $p > 0.05$; *= $p < 0.05$; **= $p < 0.01$; ***= $p < 0.001$ (two-tailed)

night roost was used extensively, and bats were present throughout a single, continuous roosting period. Turnover of individuals was low (0.7 total entrances (=exits)/total bat-hours of occupancy). A week later (15 June), when a few juveniles were present in the day roost, the night roost was used less extensively, later in the evening, and turnover was slightly higher (0.9). During lactation (29 June), few bats used the night roost, occupancy was intermittent, and turnover of individuals was high (4.1). In late summer when young were weaned (20 July), the number of bats using this roost was markedly increased, a single continuous period of occupancy was again observed, and turnover of individuals was moderate (1.5). These seasonal trends parallel those described by indirect monitoring. Fig. 3 shows that temperature records accurately represent temporal patterns of roost occupancy, and mean bat-hours of use calculated from guano collection (Fig. 2) are similar to those obtained from areas under the curves in Fig. 3 (see legend).

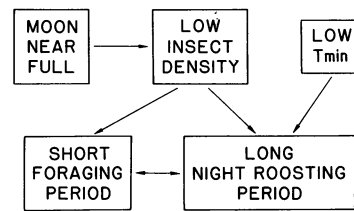


Fig. 4. Relationships of bat activity, prey density, and environmental conditions in June and July, 1976, as revealed by partial correlation analysis. Arrows represent statistically significant correlations, but do not necessarily imply direct causality. Insect density refers only to size classes eaten by *M. lucifugus*

Daily Patterns of Night Roost Occupancy

Superimposed on seasonal changes in night roosting behavior are nightly fluctuations in the length of night roost occupancy and in the length of the interval between sunset and entry into the night roost. Relationships between these fluctuations and environmental conditions, prey density, and other variables were examined by partial correlation analysis. The objective of this analysis is to evaluate the strength of the linear relationship between two variables, while removing the effects of one or more other variables (Kleinbaum and Kupper 1978). Dummy variables were used to code for reproductive condition (pregnant, lactating, post-lactating) and weather factors (cloud cover and rain). Multiple-partial correlation analysis was used when either of these sets of dummy variables was tested for correlation with another variable. Correlation coefficients and control variables for each analysis are reported in Table 2.

The amount of time the night roost is occupied is most closely associated with the reproductive condition of females, as would be expected from seasonal trends discussed above. In addition, there is an inverse relationship between night roosting time and the number of insects >2 mm in body length trapped during the bats' first feeding period (2000–2410 h). This suggests that when the effects of reproductive condition are removed, bats spend less time in the night roost (and presumably more time foraging) when prey density is high. Insects <2 mm in body length were excluded from these analyses because they are not included in the diet of *M. lucifugus* (Anthony and Kunz 1977). Minimum temperature is also negatively correlated with night roost use, indicating that the roosts are occupied for relatively longer periods on cooler nights.

The time from sunset until the first entry into the night roost reflects the length of the first feeding period, as the bats' emergence time does not vary significantly relative to sunset between late May and late July (unpublished data). Length of this interval is correlated with density of insects >2 mm, indicating that bats delay entry into the night roost when prey are abundant. A highly significant negative correlation was found between length of night roost occupancy and length of the sunset-to-entry interval, indicating that the night roost is occupied for less time when the first foraging period is extended.

Because insect density is closely related to the bats' nocturnal time budget, we examined environmental factors which may affect insect activity. The total number of insects captured between 2000 and 2410 h is positively correlated with date, as is the number of insects >2 mm, indicating a seasonal trend in insect abundance, the maximum occurring in July. When this seasonal effect is removed, minimum temperature shows a positive relationship with total insect density, but not with density of insects

> 2 mm, indicating that the relationship with temperature is due primarily to the small insect component. Both measures of insect density are significantly correlated with moon phase, the lowest densities occurring during bright portions of the lunar cycle. A diagrammatic summary of all partial correlation analyses is presented in Fig. 4.

Discussion

Occupation of night roosts between foraging flights is a common habit of temperate zone insectivorous bats (Dalquest 1947; Krutzsch 1954; Cross 1965; Hirshfeld et al. 1977), but little attention has been paid to behavioral and ecological aspects of night roost use. Our data indicate that night roosting is a flexible component of the nocturnal time budget in *M. lucifugus*, and that nightly and seasonal variation in night roost use is related to the bats' reproductive activity and foraging success.

The seasonal trends we observed, characterized by a reduction in night roosting during lactation and maximum night roost use after young become volant, are consistent with seasonal patterns reported by Davis et al. (1968) in *Eptesicus fuscus*. Similarly, O'Shea and Vaughan (1977) observed that night roosts are seldom used by *Antrozous pallidus* during the active maternity period. Another aspect of seasonal variation observed in both *M. lucifugus* and *A. pallidus* (O'Shea and Vaughan 1977) is extensive night roosting during periods of cool weather. Our temperature data show that the roosts are occupied for long periods in early May, but the amount of guano collected beneath the roosts is not commensurate with this amount of use. This evidence suggests that extended spring roosting periods occur in response to the long nights and poor foraging conditions encountered when bats first arrive at summer habitats. Energetic advantages are probably derived from night roosting when cool ambient temperatures and low insect densities prevent net energy gains from foraging.

Night-to-night time budget variability in midsummer can also be explained on an energetic basis. During June and July, night length is relatively constant (mean = 531 min, SE = 1.5, range = 39 min), and nocturnal insect density in southern New Hampshire is high. However, insect resources remain spatially and temporally variable, and bats spend less time foraging and more time roosting when insect density is low or cool ambient temperatures prevail. This relationship implies that bats cease foraging when poor foraging success and/or high costs of flight and thermoregulation prevent maintenance of a positive energy balance. Satiation may motivate return to a night roost when foraging is more successful.

These behavioral responses are consistent with Rosenzweig's (1974) prediction that inactivity within a shelter may be more profitable to an animal than foraging when food is limited or ambient temperature is low. This should occur only when the animal cannot derive as much long-term benefit from foraging as from remaining in the burrow or roost, where it is safe from predators and energy expenditure is minimal. In bats, the metabolic expense of foraging is particularly great due to the high cost of flight (Thomas 1975). Therefore, high energy returns must be maintained to obtain a net profit while feeding. When prey availability precludes high capture rates, *M. lucifugus* apparently retreats to night roost in small cavities. Although this response eliminates energy input for the duration of the roosting period, energy expenditure of clustered bats in these confined spaces is low (Kunz et al., in preparation). By minimizing energy output in this way, overall energy balance for the night is probably more favorable than if foraging were continued.

The alternative to minimizing energy expenditure by night roosting when foraging conditions are poor is extending the foraging period to scour the habitat for as many prey as possible. Norberg (1977) states that minimal feeding time should be inversely related to prey density for predators that must gather a fixed minimum amount of energy per day. Rosenzweig (1974) also predicts that reductions in prey density or ambient temperature which are less severe than those considered above will result in increased foraging time. This response to reduced food supply would only be expected over the range of prey densities at which it is possible for the predator to derive a net profit from foraging. This range may be particularly restricted in bats, due to the large energy investment required for foraging. Furthermore, temperate zone insectivorous bats probably do not have a fixed daily food requirement, as the capability of daytime torpor may confer flexibility in the time scale over which energy balance can be averaged. Thus, a "wait-it-out" response to reduced food supply and cold temperatures is more likely to be observed in heterothermic bats than in strict homeotherms with lower foraging costs.

Moon phase is the only environmental parameter related to density of prey (insects > 2 mm in body length) in our partial correlation analysis. The effect of the moon on nocturnal insect activity has been a subject of considerable debate (Williams 1936, 1940; Williams and Singh 1951; Williams et al. 1956; el-Ziady 1957; Bidlingmayer 1964; Bowden and Church 1973). Our results indicate, however, that the number of flying, trappable insects is reduced during bright portions of the lunar cycle in open areas frequented by foraging *M. lucifugus*. Bell (1980) reported similar observations in feeding sites of insectivorous bats in Arizona. Population effects, such as lunar emergence rhythms of aquatic insects, and behavioral changes related to moonlight may contribute to these fluctuations in prey availability.

Although moon phase is related to nocturnal insect density in our study, this variable is not correlated with lengths of foraging or roosting periods of the bats. A lunar index reflecting the amount of moonlight experienced by foraging bats before midnight also showed no correlation with bat time budgets (see Table 2). Therefore, we conclude that *M. lucifugus* does not exhibit "lunar phobia" of the type described in neotropical frugivorous bats (Erkert 1974; Morrison 1978). Moonlight avoidance in these bats is considered an adaptive response to predation pressure (Morrison 1978). In temperate North America, some predators include bats in their diets opportunistically (Gillette and Kimbrough 1970; Fenton and Fleming 1976), but there are no known temperate zone predators which regularly prey on bats; thus, selection pressure for simple avoidance of bright moonlight may not exist. Moon phase may, however, influence the activity of *M. lucifugus* more indirectly, acting through changes in behavior, abundance, or availability of prey. Lunar influences on prey behavior have been reported to affect temporal foraging patterns of vampire bats; resting cattle are the preferred prey, and cattle rest primarily when the moon is down (Turner 1975). Similarly, Trillmich and Mohren (1981) attribute fur seals' tendency to spend less time at sea at full moon to lunar effects on the vertical distribution of their aquatic prey.

The large maternity colonies formed by *M. lucifugus* facilitate study of nocturnal time budgets by allowing the overall responses of a population to be evaluated. In comparing bat time budgets on different nights, we assume only that inter-animal variation in time of entry into night roosts and in duration of stay within the roosts remains constant. Information on the activity of individuals would further test the hypotheses proposed in this study.

Improvements in animal marking techniques, night-viewing devices, and other monitoring methods may permit these data to be obtained without disturbing the animals' normal behavior patterns.

Acknowledgements. We are grateful to Charles Merrill, Beatrice Trum Hunter, and Charles Turpin, who permitted us to conduct field work on their property. We thank W.T. Ramage, III, J.G. Hallett, N.A. Murray, and S. Scutaro for field assistance, and P.V. August and C.D. Burnett for statistical and editorial advice. This study was supported by a Sigma Xi Grant-in-Aid of Research (ELPA), a National Science Foundation Graduate Fellowship (ELPA), a Theodore Roosevelt Memorial Grant from the American Museum of Natural History (ELPA), a Boston University Faculty Research Grant (THK), and the National Science Foundation (GY11245; SER 78-14984; THK).

References

- Anthony ELP, Kunz TH (1977) Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58:775-786
- Bell GP (1980) Habitat use and response to patches of prey by desert insectivorous bats. *Can J Zool* 58:1876-1883
- Bidlingmayer WL (1964) The effect of moonlight on the flight activity of mosquitoes. *Ecology* 45:87-94
- Bowden J, Church BM (1973) The influence of moonlight on catches of insects in light-traps in Africa. Part II. The effect of moon phase on light-trap catches. *Bull Ent Res* 63:129-142
- Buchler ER (1980) The development of flight, foraging, and echolocation in the little brown bat (*Myotis lucifugus*). *Behav Ecol Sociobiol* 6:211-218
- Cockrum EL, Cross SP (1964) Time of bat activity over water holes. *J Mammal* 45:635-636
- Cross SP (1965) Roosting habits of *Pipistrellus hesperus*. *J Mammal* 46:270-279
- Dalquest WW (1947) Notes on the natural history of the bat, *Myotis yumanensis*, in California, with a description of a new race. *Amer Midland Nat* 38:224-247
- Davis WH, Barbour RW, Hassell MD (1968) Colonial behavior of *Eptesicus fuscus*. *J Mammal* 49:44-50
- el-Ziady S (1957) A probable effect of the moonlight on the vertical distribution of Diptera. *Bull Soc Entom Egypte* 41:655-662
- Erkert HG (1974) Der einfluß des Mondlichtes auf die Aktivitätsperiodik nachtaktiver Säugetiere. *Oecologia (Berl)* 14:269-287
- Fenton MB, Fleming TH (1976) Ecological interactions between bats and nocturnal birds. *Biotropica* 8:104-110
- Gillette DD, Kimbrough JD (1970) Chiropteran mortality. In: BH Slaughter, DW Walton (eds), *About bats: a chiropteran symposium*. Southern Methodist Univ Press Dallas p 262-283
- Hirshfeld JR, Nelson ZC, Bradley WG (1977) Night roosting behavior in four species of desert bats. *Southwestern Nat* 22:427-433
- Jones C (1965) Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. *Tulane Studies Zool* 12:93-100
- Kleinbaum DG, Kupper LL (1978) *Applied regression analysis and other multivariable methods*. Duxbury Press North Scituate, Massachusetts
- Krutzsch PH (1954) Notes on the habits of the bat, *Myotis californicus*. *J Mammal* 35:539-554
- Kunz TH (1973) Resource utilization: temporal and spatial components of bat activity in central Iowa. *J Mammal* 54:14-32
- Kunz TH (1980) Daily energy budgets of free-living bats. In: DE Wilson, AL Gardner (eds), *Proceedings: Fifth International Bat Research Conference*. Texas Tech Press Lubbock p 369-392
- Kunz TH, Anthony ELP (in press) Age estimation and post-natal growth in the bat *Myotis lucifugus*. *J Mammal*
- Kunz TH, Stack MH, Anthony ELP (in preparation) Energy of bats conserved by night roosting in small cavities.
- Morrison DW (1978) Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Anim Behav* 26:852-855
- Norberg RÅ (1977) An ecological theory on foraging time and energetics and choice of optimal food-searching method. *J Anim Ecol* 46:511-529
- Nyholm ES (1965) Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). *Ann Zool Fenn* 2:77-123
- O'Farrell MJ, Bradley WG (1970) Activity patterns of bats over a desert spring. *J Mammal* 51:18-26
- O'Shea TJ, Vaughan TA (1977) Nocturnal and seasonal activities of the pallid bat, *Antrozous pallidus*. *J Mammal* 58:269-284
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Quart Rev Biol* 52:137-154
- Reith CC (1980) Shifts in times of activity by *Lasionycteris noctivagans*. *J Mammal* 61:104-108
- Rosenzweig ML (1974) On the optimal aboveground activity of banner-tail kangaroo rats. *J Mammal* 55:193-199
- Rumage WT III (1979) Seasonal changes in dispersal pattern and energy intake of *Myotis lucifugus*. MA Thesis, Boston University
- Schoener TW (1971) Theory of feeding strategies. *Ann Rev Ecol Syst* 2:369-404
- Swift SM (1980) Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *J Zool, Lond* 190:285-295
- Taylor LR (1951) An improved suction trap for insects. *Ann Appl Biol* 38:582-591
- Thomas SP (1975) Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. *J Exp Biol* 63:273-293
- Trillmich F, Mohren W (1981) Effects of the lunar cycle on the Galápagos fur seal, *Arctocephalus galapagoensis*. *Oecologia (Berl)* 48:85-92
- Turner DC (1975) The vampire bat: a field study in behavior and ecology. Johns Hopkins Univ Press Baltimore
- Vaughan TA, O'Shea TJ (1976) Roosting ecology of the pallid bat, *Antrozous pallidus*. *J Mammal* 57:19-42
- Williams CB (1936) The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Phil Trans Roy Soc Lond B* 226:357-389
- Williams CB (1940) An analysis of four years captures of insects in a light trap. Part II. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. *Trans Roy Ent Soc Lond* 90:227-306
- Williams CB, Singh BP (1951) Effect of moonlight on insect activity. *Nature* 167:853
- Williams CB, Singh BP, el-Ziady S (1956) An investigation into the possible effects of moonlight on the activity of insects in the field. *Proc Roy Ent Soc Lond A* 31:135-144

Received in June 1981