

FEEDING STRATEGIES OF THE LITTLE BROWN BAT, *MYOTIS LUCIFUGUS*, IN SOUTHERN NEW HAMPSHIRE¹

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Abstract. Feeding strategies of the little brown bat, *Myotis lucifugus*, were investigated in southern New Hampshire USA from early May through late August 1974. Nightly food consumption was estimated by comparing mean prefeeding body weights with postfeeding weights taken as individuals returned to the roost from their first feeding period (at 2200 to 2400 h) and from a subsequent foraging period (at 0330 to 0500 h). Pregnant bats consumed an average of 2.5 g of insects (2.72 kJ/g prefeeding body weight) nightly, lactating females ate 3.7 g (4.23 kJ/g), and juveniles ingested 1.8 g (2.47 kJ/g). Increased food consumption in lactating bats accommodated reproductive energy demands and was facilitated by rising food availability. Increasing levels of independent food consumption in juveniles accompanied weaning.

Fecal analysis revealed that diets of individual bats were diverse. All available insects 3 to 10 mm in body length were accepted as food items. Nematoceran Diptera were by far the most common insects taken in light-trap samples, and constituted a major portion of the diet throughout the summer. Coleoptera, Trichoptera, Lepidoptera, Ephemeroptera, and Neuroptera were also consumed in appreciable numbers.

Comparison of dietary composition with prey availability indicates that pregnant bats consumed 3-10 mm prey in approximate proportions encountered during June, when insect availability was low and unpredictable. However, lactating, postlactating, and nonreproductive ♀♀ exhibited more selective feeding in July, when insects were more abundant. This increase in selectivity reflected exploitation of beetles and mayflies, which were uncommon in trap samples. In August, juveniles approximated random feeding patterns, as they learned to forage. We suggest that increased resource availability allowed selective feeding in adult bats during July, as predicted by prey selection models. However, reduced discriminatory abilities may prevent similar levels of prey selection in juveniles.

Key words: Chiroptera; food consumption; foraging strategies; insectivorous bat; *Myotis lucifugus*; New Hampshire; prey selection.

INTRODUCTION

Predator-prey interactions have been the focus of several recent theoretical models and mathematical treatments, all of which predict that predators should respond to rising prey density by increasing selectivity in their diets (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Cody 1974, Charnov 1976, and others). Field and laboratory tests have borne out this hypothesis in fishes (Ivlev 1961, Werner and Hall 1974), a mantid (Charnov 1976), and the Common Swift (Lack and Owen 1955). Emlen and Emlen (1975) presented evidence that the models correctly describe feeding habits of laboratory mice, and Turner (1975) demonstrated that foraging of vampire bats also conforms to these predictions. Bryant (1973), however, found that prey selection in House Martins does not become more intense as aerial insect abundance rises. Although the models attempt to describe foraging strategies under natural conditions, many tests of the theories have been conducted in the laboratory, where prey quantity and quality can be carefully controlled.

Among mammals, insectivorous bats are especially valuable subjects for field investigation of foraging models, since prey availability is readily monitored

and dietary items can be identified by fecal analysis. Furthermore, quantitative estimates of food consumption are possible, due to the relatively synchronous foraging habits and restricted feeding periods of these bats.

In this study we estimate daily energy intake and describe dietary composition of the little brown bat (*Myotis lucifugus*) in New Hampshire. Quantitative and qualitative variation in diet throughout the summer are related to changes in prey availability and energy requirements. Prey selection is investigated, and food preferences are compared with those reported for this species in other geographic areas.

MATERIALS AND METHODS

Field study.—Food consumption was estimated at three summer nursery colonies of *M. lucifugus* in southern New Hampshire (Hillsborough County): (1) Turpin barn, town of Hancock, maximum adult population of 150 bats, (2) Carr barn, town of Peterborough, maximum 500 adults, and (3) Miller barn, town of Amherst, maximum 500 adults. Each colony was visited at 9-day intervals from late May through early August 1974.

Bats were captured in a Tuttle trap (Tuttle 1974) upon emergence at dusk, and each individual was weighed to the nearest 0.1 g. This procedure was re-

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peated from 2200 to 2400 h (local time), as bats returned from their first feeding period. In order to avoid capturing individuals more than once within a sampling period, all bats were placed in a holding bag after weighing and were released when trapping was completed. Bats in both samples were grouped by sex, age, and reproductive condition. The change in mean weight for each group during the first foraging period was used as a measure of food consumption. We assume that the bats remain in H₂O balance during this period, with urinary and evaporative losses balancing intake by drinking.

In order to estimate food consumption in the predawn period, bats were trapped again from 0330 to 0500 h as they returned to their daytime roost. To establish a prefeeding weight for this period, we measured weight loss of bats captured on return from the first feeding. All individuals trapped between 2200 and 2400 h on 11, 20, and 29 July, and 7 August were retained in a large nylon net holding bag and reweighed during the predawn sampling. An average value of weight loss was obtained from these data (expressed as a percentage of weight gained in the first feeding), and was applied uniformly to all samples throughout the summer. For each trap night, the difference between the base weight calculated in this manner and the mean weight of bats returning to the day roost was used as a measure of food consumption after midnight.

A Burkard suction trap (Taylor 1951) was used to estimate insect availability on nights when bats were trapped at the Carr and Turpin barns. The trap was placed at the edge of Halfmoon Pond (a known feeding site at Boston University Sargent Camp, town of Hancock), with the mouth of the trap \approx 3 m above the ground. Aerial insects were sampled and automatically segregated into 50-min intervals from 2000 to 0510 h.

Prey selection was investigated concurrently at Sargent Camp. The most suitable site for simultaneous collection of foraging bats and insect samples was the Nubanusit River, which winds through secondary mixed coniferous-deciduous forest. At the collection site, the river is \approx 15 m wide and 1 m deep. Previous monitoring of this site in 1973, using ultrasonic detectors (unpublished), revealed consistent patterns of bat activity, including feeding buzzes, throughout the summer. Collections were made at 9-day intervals, from 29 May to 25 August 1974. Two 12-m Japanese mist nets were set over the water in either a "V" or "T" configuration. Net positions were alternated each time in an effort to maximize capture efficiency (Kunz and Brock 1975). On a few nights, one 6-m net was used to channel bats into the longer nets or to catch individuals which altered their flight paths to avoid the 12-m nets.

Bats arrived at the net site from the east within 20 min after the start of emergence. Although the origin of bats foraging in the area is unknown, the closest nursery roosts are the barn at Sargent Camp, 1.2 km

northeast of the river, and the Rice barn, 1.5 km southeast of the collecting site. Bats from either colony must fly through wooded terrain before arriving at the river. On most nights, the animals remained in the vicinity of the nets for $<$ 30 min. Most captures occurred as individuals flew low along the water to drink.

Each bat removed from the net was placed in a covered paper cup until morning in order to collect feces. Before release at Sargent barn (between 1100 and 1300 h), the sex, age, and reproductive condition of each bat were determined, and a 1B lipped bat band (U.S. Fish and Wildlife Service) was applied to the right forearm. Feces were transferred from paper cups to glass vials and stored in a desiccator until analyzed in the laboratory. Sixty-two samples were collected during the course of the study.

A New Jersey light-suction trap was suspended at the edge of the river, \approx 2 m above the surface of the water, in order to sample aerial insects at a height at which bat activity was consistently observed. Insects were collected for 1 h, starting at the time the first bat left the day roost. Bat activity at the net site had ceased when insect sampling was terminated.

Laboratory study.—Fecal samples were dried at 80°C for 24 h, and were weighed to the nearest 0.1 mg on an analytical balance. A solution of 4 parts Photo-flo,[®] 1 part 70% isopropyl alcohol, and 1 part distilled H₂O was used to soften the feces overnight. To isolate identifiable insect remains, each fecal pellet was placed in a petri dish of 70% ethyl alcohol and was teased apart under a dissecting microscope (45 \times). Fragments of wings, legs, tarsi, and antennae were compared with reference material for identification. Diptera, Trichoptera, Hymenoptera, Homoptera, and Neuroptera were consistently classified to family. Coleoptera, Lepidoptera, and Ephemeroptera were identified to order only.

Quantification of prey types in the diet was facilitated when fecal pellets remained intact. Coutts et al. (1973) determined that each pellet of an insectivorous bat contains the remains of either 1 large insect or a number of smaller ones. Thus, for each pellet of a sample, the presence of scales or numerous hairs indicated that the bat had eaten at least 1 moth or caddisfly, respectively. This number was increased according to the number and types of tarsi and antennae encountered. For other taxa, a minimum of 1 individual per pellet was assumed unless the number of eyes, legs, or wings recovered exceeded 2, 6, or 4, respectively (although only 2 wings were allowed for Diptera). This minimum estimate was increased if morphological differences in wing or leg fragments assigned to a single taxon indicated consumption of more than 1 individual. Relative importance of each taxonomic group in the diet of individual animals was then expressed as percent by number encountered in the fecal sample. Overall frequency of occurrence of major dietary items was expressed as: (number of samples contain-

TABLE 1. Food consumption estimates (g) during the first (I) and second (II) feeding periods, and summary of total nightly intake. Values for the first feeding period are based on increases in mean weights of bats during this interval. Between midnight and dawn, a weight loss of 80% of the initial meal in adults and 70% in juveniles was expected if no feeding occurred (see text). Thus, values for the second foraging period represent the difference between this base weight and mean weights of bats returning to the roost at dawn. *N* is the number of bats in prefeeding/midnight/predawn samples. Letters in parentheses indicate colonies at which bats were collected (T = Turpin barn, C = Carr barn, M = Miller barn). Asterisks denote a rainy morning. Total intake represents the sum of means for both feeding periods

Date	<i>N</i>	Pregnant		Lactating		Juveniles	
		I	II	I	II	I	II
9 May (T)	10/17/...	1.5	...				
18 May (T)	7/ 3/19	1.9	1.2				
27 May (T)	13/15/14	1.4	0.3				
27 May (C)	21/ 5/...	0.3	...				
5 Jun (T)	3/ 4/29	1.9	0.8				
5 Jun (C)	20/ 9/14	2.4	2.1				
8 Jun (M)	30/ 7/42	0.8	1.5				
14 Jun (T)	10/16/25	1.8	0.9				
14 Jun (C)	19/ 9/26	2.6	0.5				
17 Jun (M)	13/14/ 8			2.4	1.7		
23 Jun (C)	8/ 5/ 7	1.6	0.1				
23 Jun (C)	27/10/ 5			2.5	1.1		
27 Jun (M)	36/28/16			2.3	2.4		
2 Jul (T)	4/ 7/10			2.4	0.7*		
2 Jul (C)	20/ 6/ 6			2.4	0.9*		
5 Jul (M)	32/15/17			2.2	1.5		
11 Jul (T)	7/ 5/ 1					0.7	0.8
14 Jul (M)	12/ 4/ 5			1.8	1.7		
20 Jul (T)	17/16/ 3					0.8	1.1
20 Jul (C)	43/15/16					1.4	0.9
29 Jul (T)	5/ 5/ 9					1.1	0.0
7 Aug (T)	6/ 3/11					1.5	0.7
	\bar{x}	1.6	0.9	2.3	1.4	1.1	0.7
	SD	0.65	0.66	0.22	0.58	0.32	0.42
Total intake (g)		2.5		3.7		1.8	
Energy intake (kJ)		21.75		32.19		15.66	
Intake after midnight (%)		36.0		37.8		38.9	

ing the food item/total number of samples) $\times 100$. Bats were also grouped by date of capture and reproductive condition, and dietary composition was re-computed as percent by number.

Data analysis.—Stepwise regression analysis (BIOMED BMDP2R, Dixon 1975) was used to determine whether dietary composition was highly correlated with insect availability (a condition of random

feeding), or whether a significant amount of prey selection was exercised by the predator. The percent of each taxonomic group represented in the diet of individual bats was the dependent variable. Percentages encountered in the light-trap sample served as an independent variable. In addition, 6 classes of bats were designated as "dummy" variables, whose variates were 0 or 1: pregnant, lactating, postlactating,

TABLE 2. Feces production of bats captured at the Nubanusit net site within 20 min after emergence. Values represent mean dry weight (g) of guano produced by each group, ± 1 SD. Where no SD is given, the sample size is 1. *N* for other groups is given in parentheses

Date	Pregnant	Lactating	Post lactating	Nonreproductive ♀ ♀	♂ ♂	Juvenile
29 May	.0143 \pm .0060 (2)					
7 Jun	.0123 \pm .0091 (9)			.0091	.0116	
27 Jun	.0182 \pm .0106 (7)	.0219 \pm .0073 (4)		.0036		
4 Jul		.0290 \pm .0107 (2)		.0193 \pm .0018 (2)		
22 Jul		.0550 \pm .0206 (2)			.0289	
31 Jul			.0104 \pm .0030 (2)	.0263 \pm .0092 (3)	.0282	.0271 \pm .0018 (4)
9 Aug			.0248	.0304		.0208 \pm .0123 (10)
18 Aug				.0383 \pm .0016 (2)		.0315 \pm .0120 (5)
25 Aug						.0053
\bar{x}	.0148	.0320	.0152	.0237	.0229	.0239
SD	.0092	.0165	.0070	.0015	.0080	.0117

Analysis of variance was run on pregnant, lactating, nonreproductive ♀ ♀ and juveniles. $F = 4.10$; $P < .05$.

and nonreproductive females, males, and juveniles. This step allows the relationship between diet and trap sample to be analyzed, eliminating variation in feeding habits due to reproductive condition on any given night. A regression was computed separately for each date of collection.

RESULTS

Food consumption in the first feeding period

Food consumption estimates for *M. lucifugus*, based on differences in prefeeding and postfeeding weights, are given in Table 1. In the first feeding period, lactating females consumed an average of 2.3 g of insects (0.301 g/gram prefeeding body weight), whereas pregnant females ingested an average of 1.6 g (0.203 g/gram body weight). A Mann-Whitney *U*-test (Siegel 1956) revealed a significant difference between these means ($U = 14.00$; $P = .05$). Juvenile bats tended to consume less than adults in the same foraging period ($\bar{x} = 1.1$ g; 0.175 g/gram body weight). However, juveniles were captured only on a small number of nights. Thus, statistical comparison of these data with consumption estimates for adults was not attempted.

Relative levels of food consumption can also be inferred from dry weights of feces. Table 2 summarizes mean weights of feces collected from bats captured at the Nubanusit net site within 20 min after emergence. After this brief period of foraging, lactating bats produced more feces than other adult females and juveniles, implying a higher level of food consumption. Analysis of variance demonstrated a significant difference among groups ($F = 4.10$; $P < .05$), and the Student-Newman-Keuls multiple comparisons test revealed that the difference lay between pregnant and lactating females ($Q = 1.71$; $P < .01$). The relatively high level of food consumption exhibited by lactating bats is consistent with results reported above.

Wet weight of food consumed was subsequently calculated from mean dry weights of feces collected, assuming 88% assimilation efficiency and 60% H₂O content of insects eaten (T. H. Kunz, W. T. Rumage III, and E. L. P. Anthony, *personal observation*). These estimates were compared with those derived from weight changes over a 2- to 3-h period (Table 1). Within 20 min after emergence, pregnant bats consumed 18.5% (0.296 g; $N = 18$) of the total meal estimated for the first feeding period, lactating bats 27.8% (0.640 g; $N = 8$), and juveniles 43.4% (0.478 g; $N = 20$).

These high percentages indicate that field estimates of food consumption over a 2- to 3-h period may be extremely low. Buchler (1975) has shown that food may begin to pass through the digestive tract of *M. lucifugus* in <1 h. Thus, rapid food passage may be responsible for underestimation of consumption when weight change or feces production is measured over a foraging period >1 h.

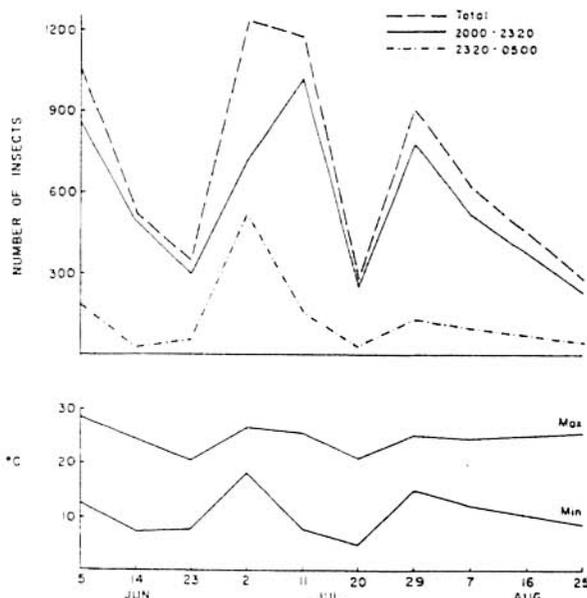
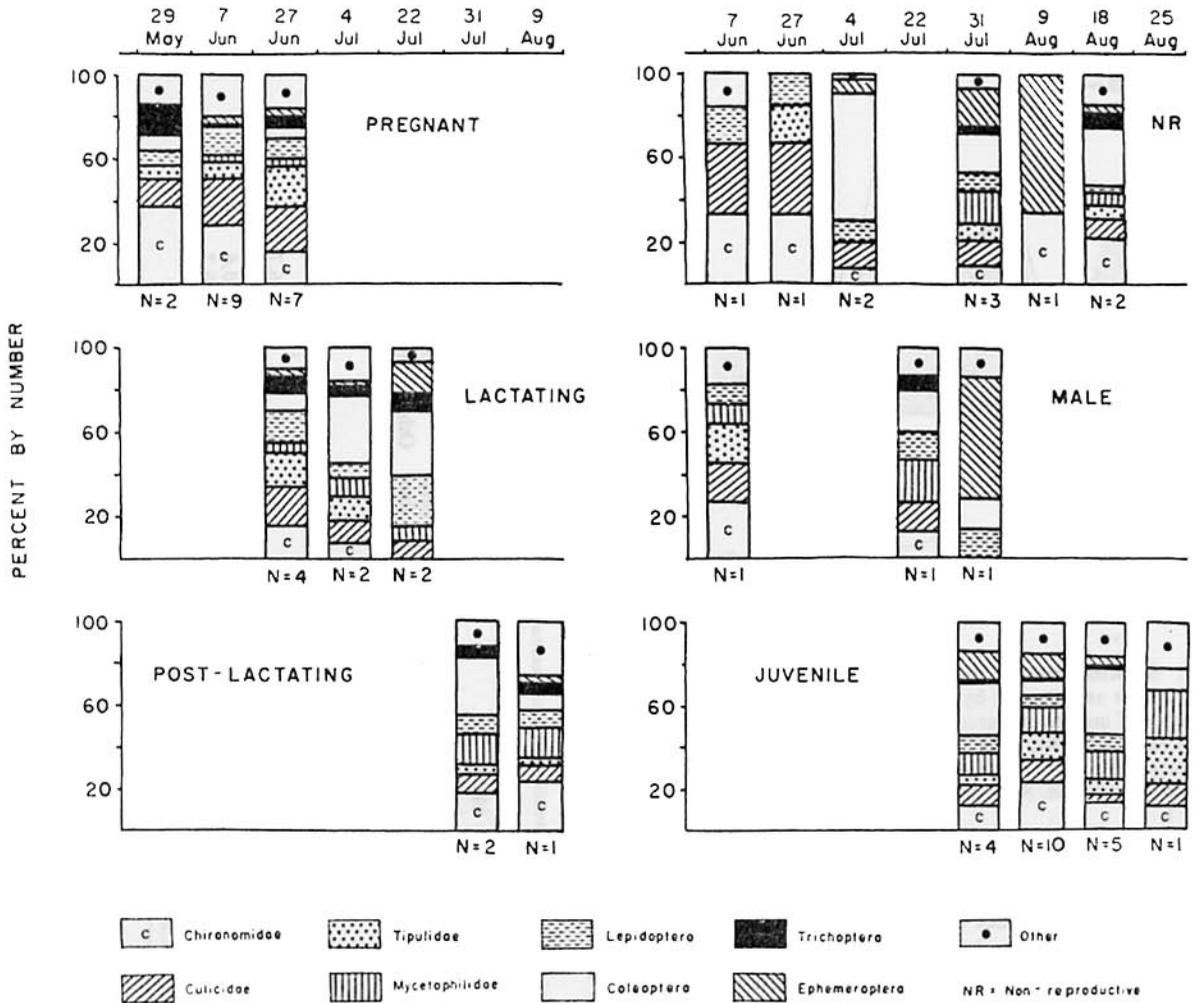


FIG. 1. Seasonal trends in insect availability at Halfmoon Pond as revealed by suction-trap samples. Total number of insects captured between 2000 and 0510 h is plotted for each trap night, as well as the number of insects captured during the first feeding period (2000–2320 h) and the second feeding period (2320–0510 h). Maximum temperatures for netting days ($^{\circ}\text{C}$) and minimum temperatures recorded the next morning are also included.

Food consumption after midnight

Food intake after midnight was generally less than during the first foraging period (Table 1). On the average, pregnant females consumed 0.9 g during this interval, lactating individuals ate 1.4 g, and juveniles ingested 0.7 g. Summing estimates of mean food consumption for both feeding periods reveals a minimum nightly intake of 2.5 g in pregnant bats, 3.7 g in lactating females, and 1.8 g in juveniles. Assuming the energy equivalent of stomach contents to be 8.70 kJ/g wet weight (Kunz et al., *personal observation*), corresponding nightly energy intakes average 2.72 kJ/g prefeeding body weight during pregnancy, 4.23 kJ/g during lactation, and 2.47 kJ/g during postflight growth and development of young.

Over 60% of the total nightly intake occurred before midnight, when insect availability was highest (Fig. 1). We assume all bats fed at this time, since none remained in the roost after emergence. Food eaten after midnight represented 36.0% of the total nightly catch in pregnant bats, 37.8% in lactating individuals, and 38.9% in juveniles (Table 1). Although emergence and return activity during this interval is asynchronous, we assume in our calculations that most bats leave the roost for a single foraging flight between midnight and dawn. Lactating bats deviate from this pattern, however, since feeding of young requires periodic return to the roost during this period (E. L. P. Anthony and T. H. Kunz, *personal observations*).

FIG. 3. Dietary composition of *M. lucifugus*.

Ephemeroptera, Homoptera, and Hymenoptera were often collected, but constituted only a small percentage of the total fauna (Fig. 2, Table 3).

The diet

The diet of *M. lucifugus* remained diverse throughout the summer and included Diptera, Coleoptera, Lepidoptera, Trichoptera, Ephemeroptera, Neuroptera, Homoptera, and Hymenoptera (Fig. 3, Table 4). Food items ranged from 3 to 10 mm in body length (Fig. 4). Emlen's diversity index (Emlen 1973) was calculated for the dietary composition of groups of bats (classified by age, sex, and reproductive condition) captured on each net night (Table 5). These values ranged from 0.581 to 0.883, revealing a high diversity in diet which was maintained throughout the summer. Quantitative diversity of food items was similar in all groups, regardless of sex, age, or reproductive condition, and no seasonal trends in diversity measures were evident. Although these indices were

calculated for groups of bats, diets of individuals were also diverse (some sample sizes of one are included in Table 5).

Qualitative changes in diet were observed, however, during the summer (Fig. 3). Although dipterans re-

TABLE 4. Frequency of occurrence of insect taxa in the diet: (number of samples in which food item was encountered/total number of samples) \times 100

Taxa	%
Chironomidae	85.5
Lepidoptera	85.5
Culicidae	77.4
Tipulidae	67.7
Coleoptera	59.7
Mycetophilidae	54.8
Ephemeroptera	51.6
Hymenoptera (Braconidae)	33.9
Trichoptera	32.3
Neuroptera (Hemeroibiidae)	19.4

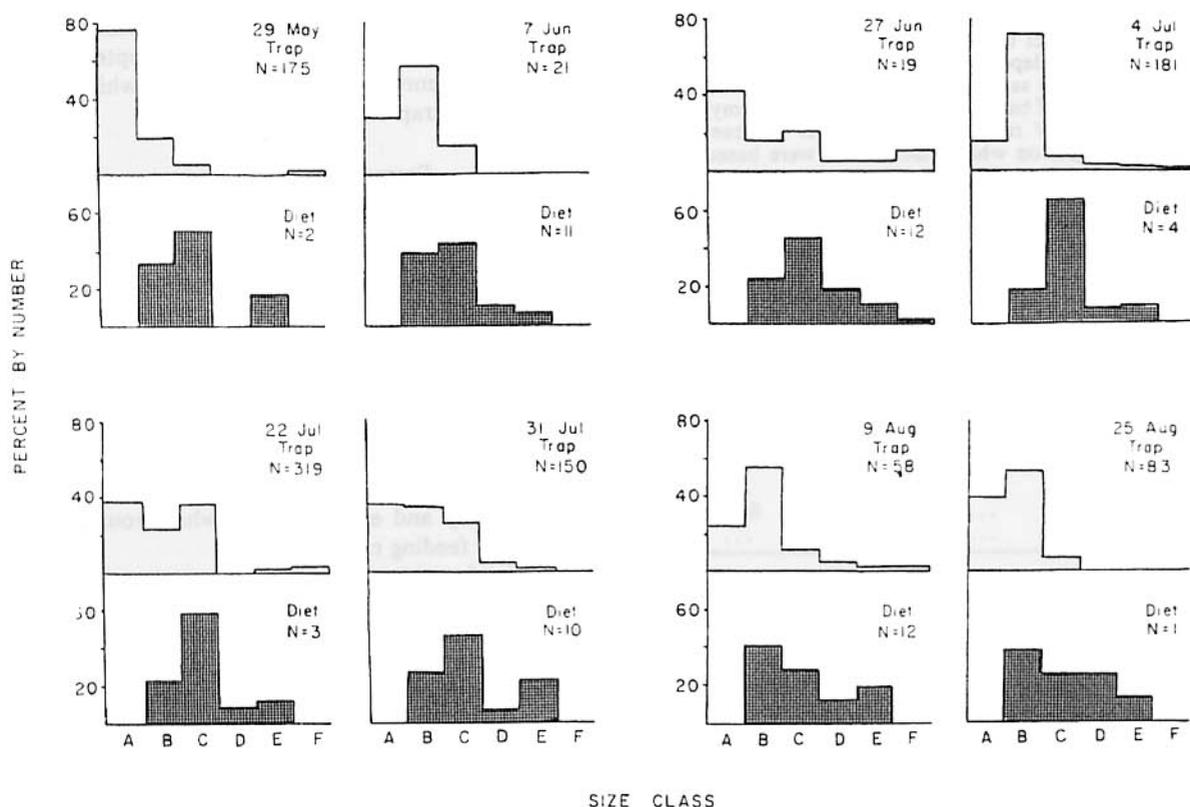


FIG. 4. Frequency distributions of insect size classes in trap samples and in the diet of *M. lucifugus*. Size class A = 0.1–2.0 mm body length; B = 2.1–4.0 mm; C = 4.1–6.0 mm; D = 6.1–8.0 mm; E = 8.1–10.0 mm; F = > 10 mm. All bats captured on each net night were included in this calculation, regardless of sex, age, or reproductive condition. Sample size for trap data represents total number of insects captured within the 1-h sampling period (except 29 May, when the trap was run for 2 h). *N* in diet graphs represents total number of bats analyzed.

mained major dietary items in all groups of bats, utilization of Coleoptera and Ephemeroptera increased notably in July and August. Consumption of these insects rose when they were first recorded in light-trap samples.

Prey selection

We made the following assumptions in assessing the degree of prey selection exercised by *M. lucifugus*: (1) insect samples collected in the light-suction trap are

considered accurate representations of prey availability. Positively phototactic insects, notably moths and midges (Borror et al. 1976), may in fact be overrepresented in the samples, and beetles may be underrepresented. Biases cannot be avoided, however, in sampling insect faunas. The light-suction method was chosen in this study for practical reasons. (2) If individuals consumed insects in proportions encountered (random feeding), percentages of taxa included in the diet would be highly correlated with percentages observed

TABLE 5. Diversity of diet in *M. lucifugus*. Diversity indices were calculated according to Emlen (1973): $\sum p_i e^{-p_i}$. Calculations were based on taxonomic categories for which positive identification in fecal material was possible: families of Diptera, Trichoptera, Hymenoptera, Homoptera, and Neuroptera; orders for other insects. Minimum and maximum values of the index are 0.37 and 1. Asterisks indicate sample sizes of 1; other sample sizes are given in Table 2.

Date	Pregnant	Lactating	Post lactating	Nonreproductive		Juvenile
				♀♀	♂♂	
29 May	.835					
7 Jun	.844			.760*	.844*	
27 Jun	.876	.880		.760*		
4 Jul		.867		.693		
22 Jul		.825			.859*	
31 Jul			.860	.883	.695*	.846
9 Aug			.881*	.581*		.881
18 Aug				.851		.851
25 Aug						.851*

TABLE 6. Summary of results of stepwise regressions. Percentages of each insect taxon represented in diets of individual bats was the dependent variable. Percentages encountered in light-trap samples served as an independent variable. Six classes of bats were designated as "dummy" variables (see text). *N* represents the number of observations (percentages) on which calculations were based. *r* = partial correlation coefficient (trap sample vs. dietary composition); *R*² = proportion of the variation in diet explained by the trap sample

Date	All taxa			Taxa < 2 mm excluded		
	<i>N</i>	<i>r</i>	<i>R</i> ²	<i>N</i>	<i>r</i>	<i>R</i> ²
29 May	14	0.73*	0.54	12	0.73*	0.53
7 Jun	62	0.43*	0.19	51	0.53*	0.28
27 Jun	105	-0.07	...	83	0.36*	0.13
4 Jul	57	-0.01	...	53	0.00	...
22 Jul	38	-0.14	...	32	-0.11	...
31 Jul	137	-0.04	...	118	0.02	...
9 Aug	129	0.07	...	107	0.29*	0.08
25 Aug	12	-0.07	...	10	0.03	...

* *P* < .05.

in trap samples. Thus, in a regression, composition of trap samples would explain a significant amount of variation in diet. (3) If bats fed selectively, representation of various taxa in trap samples would not be significantly correlated (or would be negatively correlated) with dietary composition. Therefore, in a regression, the taxonomic distribution of trap samples would not be a good predictor of dietary composition.

When all insect taxa encountered were entered into stepwise regressions, the percentages observed in trap samples were significantly correlated with proportions consumed on 29 May and 7 June (Table 6). Thus, although feeding approached a random condition on two nights, a significant amount of selection was exercised at all other times. Since diets never included insects < 2 mm in length (Cecidomyiidae and Ceratopogonidae), much of the selectivity revealed in this analysis may reflect avoidance of these taxa. Although *M. lucifugus* can detect wires as small as 0.12 mm in diameter in the laboratory (Curtis 1952 cited in Griffin 1958), insects < 2 mm long may be difficult to detect under field conditions (see Discussion). Thus, if detection of these insects is limited, they may contribute little to the bats' effective environment and should therefore be eliminated from the analysis.

When these taxa were removed from the regression, composition of trap samples explained a significant amount of variation in dietary composition on 29 May, 7 June, 27 June, and 9 August (Table 6). Thus, pregnant bats (and other adults) fed somewhat randomly within the 3–10 mm prey size range early in summer, when insect availability was low and variable. Juveniles, which constituted the majority of the sample on 9 August (10 out of 12), also approached a condition of random feeding. Lactating, postlactating, and nonreproductive females fed more selectively in July, when prey were most abundant. This increase in

selectivity reflected exploitation of Coleoptera, Ephemeroptera, and to a lesser extent Hymenoptera (Braconidae) and Neuroptera (Hemerobiidae), which were uncommon in trap samples.

DISCUSSION

Food consumption

Seasonal trends of food consumption described in this study are consistent with those reported by Kunz (1974) in a field study of *Myotis velifer*. In late spring and early summer, foraging success of pregnant bats was highly variable (Table 1), and consumption was generally lower at that time than during lactation. Juvenile bats exhibited a low level of food consumption during the first feeding period in mid-July, soon after they became volant, but ingestion levels increased in late July and early August, when young approximated the feeding rate of adults.

Variability in foraging success during pregnancy may be related to resource availability. In May and June, insect abundance was lower than in midsummer, and fluctuated with changes in environmental conditions, especially temperature (Figs. 1 and 2). Assuming that prey were temporally and spatially patchy, more successful bats may have exploited local swarms of insects, whereas less successful individuals failed to locate patches that provided equivalent energy returns. The large difference in foraging success exhibited by bats at Turpin and Carr barns on 27 May indicates that local insect availability may greatly influence hunting success.

Lactating bats increased food consumption in late June and early July, maintaining a relatively constant level until young were weaned. Since beetles are more heavy-bodied than dipterans, increase in the proportion of Coleoptera consumed may account for greater consumption without assuming a higher capture rate. However, capture rate may increase in lactating bats, relative to pregnant ones, due to lower wing loading (Kunz 1974) and greater prey density. Despite peak prey abundance in July, juveniles exhibited poor foraging success at that time. Since females continue to feed their young as they learn to forage, milk in the stomach upon emergence may reduce total capacity, thus lowering insect consumption (Kunz 1974). Increased food intake of juveniles after weaning contributes to growth and fat deposition which must precede migration to hibernacula.

Direct comparison of our data with laboratory estimates of food consumption is difficult, since two studies conducted with captive *M. lucifugus* reported only wet weight of food consumed and failed to indicate caloric value. Coutts et al. (1973) reported an average consumption of 0.93 g of mealworms per day in 6 postlactating *M. lucifugus* and 1.22 g/day in 3 males, all maintained in outdoor cages. Pregnant females, maintained at a thermoneutral temperature of 92°F

(33°C) by Stones and Wiebers (1965), consumed an average of 3.28 g of mealworms per day, whereas lactating individuals ate 2.81 g/day under the same conditions.

In the only study presenting daily energy requirements for *M. lucifugus*, O'Farrell et al. (1971) reported a value of 0.53 kcal/g body weight (2.22 kJ/g) in one captive postreproductive female. Assuming an assimilation efficiency of 88%, adult females in our study exhibited slightly greater energy utilization (2.39 kJ·g⁻¹·day⁻¹ in pregnancy, 3.72 kJ·g⁻¹·day⁻¹ in lactation). Numerous factors contribute to a higher consumption level in the field: (1) energy demands of reproduction, (2) costs associated with flight and foraging, and (3) use of more than one feeding period (since laboratory data were based on one daily feeding). Comparison is further complicated by the tendency of captive bats to overeat (Rasweiler, *In press*). Because the bat maintained by O'Farrell et al. (1971) deposited fat during the course of their study (gaining weight from 7.57 to 8.20 g), this laboratory estimate may be artificially inflated.

In a field study similar in design to ours, Kunz (1974) estimated food consumption of 0.3 g/gram body weight in female *M. velifer* during lactation. Assuming energy value of stomach contents to be 8.70 kJ/g, as in *M. lucifugus*, energy intake of *M. velifer* is less than that reported here for the little brown bat (2.61 kJ/g vs. 4.23 kJ/g), possibly reflecting differences in energetics of lactation and/or weight-specific metabolic rates.

Our data indicate that food consumption by *M. lucifugus* increases by ≈10.5 kJ/day (2.5 kcal/day) during lactation, relative to the pregnancy period. Although this increase is consistent with the findings of Studier et al. (1973) that the energy cost of lactation is greater than that of pregnancy, the magnitude of increase is larger than expected on the basis of their data. These authors reported an investment of 77.6 cal/day (0.32 kJ/day) for fetal growth in *M. thysanodes*, compared with 346.0 cal/day (1.45 kJ/day) for nourishment of neonatal young. Since energy demands imposed upon female bats increase during the period of juvenile dependency (Jenness and Studier 1976), energy costs averaged over the entire lactation period would be somewhat higher than 1.45 kJ/day. Similar data are unavailable for *M. lucifugus*. However, an increase in energy requirements of the same order of magnitude would be expected during lactation, relative to pregnancy, since the two species are similar in body size.

To assert that the difference in food intake between pregnant and lactating individuals (10.5 kJ/day) represents energy expended in milk production, one must assume that the cost of pregnancy is negligible with respect to the total energy budget of the animal. Studier et al. (1973) demonstrated an average investment of only 129.7 cal/day (0.54 kJ/day) for fetal growth in *M. lucifugus*, which is indeed small in com-

parison to total consumption of 5.2 kcal/day (21.75 kJ/day) during pregnancy.

Furthermore, to make this comparison, one must assume that energy costs associated with activity and thermoregulation are similar in pregnancy and lactation. However, various observations lead us to believe that this assumption is invalid. (1) Monitoring of flight activity (unpublished) at maternity roost entrances reveals that lactating bats travel to and from feeding sites more often during the night than pregnant animals, since they must periodically return to feed the young. Thus, more energy may be expended in flight during lactation due to increased travel time, even though wing loading is lower than during pregnancy. (2) Care of young requires greater alertness and higher activity levels throughout the day than during pregnancy. (3) A reduction in controlled body temperature occurs in *M. lucifugus* during lactation (Studier and O'Farrell 1976), indicating decreased energy requirements for thermoregulation. The possibility that additional physiological and behavioral changes influence the cost of maintenance during the lactation period must be investigated before a fully detailed energy budget can be developed.

Feeding rate

The present study reveals that pregnant females consume 18.5% (0.296 g) of the estimated initial meal within 20 min after emergence, and lactating females eat 27.8% (0.640 g) of the total in that time. These data suggest that capture rate is lower for pregnant animals, requiring that they forage throughout the early feeding period in order to fill their stomachs. However, lactating animals feed more rapidly and may not need to fly for 2–3 h in order to gather a full meal. Part of this time may be spent roosting in foraging areas. Alternatively, the bats may continue to feed, passing food quickly through the digestive tract throughout this period. If this is the case, food consumption estimates over a 2- to 3-h period may be extremely low.

Juvenile bats ate 43.4% (0.478 g) of the total insect meal within 20 min after emergence. Although wet weight of food consumed during this period is comparable in adults and young, the total insect meal of juveniles is smaller than that of adults. Thus, the percent of total consumption occurring soon after emergence is higher in young bats. This comparison suggests that juveniles are incapable of sustaining efficient foraging flight throughout a 2- to 3-h period, and may roost for part of this time.

Feeding efficiency in this 20-min period was impressive, both in juveniles and adults. Pregnant and post-lactating females consumed ≈0.3 g of insects between the time of emergence and time of capture. Assuming average prey to be the size of a mosquito—2.2 mg (Griffin et al. 1960)—a feeding rate of 140 insects in 20 min, or 7 insects/min is indicated. This rate is very close to that estimated for *M. lucifugus* by Gould

(1955, 1959), both by this method and by direct observation of foraging flights (8 insects/min), and higher than that observed by Griffin et al. (1960) in the laboratory (1.5 to 5.7 insects/min). Lactating bats consumed ≈ 0.6 g and juveniles 0.4 g in the same amount of foraging time. The diet of these groups included a greater proportion of beetles, which are heavier than dipterans. Thus, feeding rate, expressed as number of insects captured per min, was probably roughly equivalent in all bats.

The diet

Extensive use of Diptera by *M. lucifugus* in southern New Hampshire is not surprising, since these insects constitute a major portion of the available prey within the size range appropriate for this species. A high level of predation on dipterans was also reported by Belwood and Fenton (1976) for *M. lucifugus* in Ontario, where foraging over water is common, and midges and other Nematocera are by far the most abundant insects throughout the summer. Buchler (1976) reported that Diptera comprised only a minor portion of the diet of *M. lucifugus* in New York state, because most of the flies available were < 2 mm in body length. In Indiana, *M. lucifugus* consumed Lepidoptera most frequently, and preyed upon Trichoptera, Diptera, and Homoptera in fewer numbers (Whitaker 1972). This variation in feeding habits indicates that *M. lucifugus* feed as "selective opportunists" (*sensu* Fenton and Morris 1976), exploiting local insect faunas to their best advantage by preying upon the most abundant and diverse insect taxa within the appropriate size range. Since dietary flexibility is the adaptive strategy espoused by this species, it is not surprising that most bats remain food generalists, taking a variety of prey. However, individuals occasionally specialize on one insect type which is locally abundant (e.g., mayflies in Buchler (1976), and mayflies and beetles in this study).

An acceptable prey size range of 3 to 10 mm body length is consistent with Buchler's (1976) estimate of 4 to 9 mm. Diets reported for this species by Belwood and Fenton (1976), Whitaker (1972), and Gould (1955) are also composed of insects within this range. Although taxonomic identity of prey varies geographically, size of insects selected remains relatively constant. Thus, size of a prey item must be an important criterion used by this species to decide whether to pursue an insect once it is detected. Hespeneide (1971) similarly stressed the importance of prey size, rather than taxonomic identity, in the feeding strategy of insectivorous birds. However, other prey characteristics detectable by echolocation (shape, texture, flight pattern, etc.) may also be utilized by bats under natural foraging conditions (Simmons et al. 1974, 1975). For example, Buchler (1976) noted that although moths and mayflies were similar in size and abundance in his study area, only the latter were preyed upon by *M. lucifugus* in appreciable numbers.

The lower limit of the prey size range may be determined by the nature of pulses utilized for echolocation and dictates of cost/benefit ratios. While searching for insects, *M. lucifugus* emits FM pulses sweeping from 120 to 40 kHz, representing approximate wavelengths of 3 to 8 mm (Gould 1955, Griffin et al. 1960). Since echo quality is highest when the size of a target equals the wavelength of emitted sound, detection of insects in the 3- to 8-mm size range is facilitated by the frequency spectrum of the pulse. However, insects < 3 mm in body length and/or wingspan (Cecidomyiidae and Ceratopogonidae) are undoubtedly more difficult to locate, and the cost of capture may outweigh energy returns. Buchler (1976) noted that cecidomyiids were eaten by *M. lucifugus* when offered in a feeding dish. Therefore, he inferred that avoidance is related to reduced capture success rather than unpalatability.

The upper limit of the prey size range may be imposed by the increase in capture and handling time required to utilize large insects, and by competition with the only other common bat in the area, *Eptesicus fuscus* (16–22 g). *Myotis keenii* is the only species similar in size to *M. lucifugus* which is frequently found in nursery roosts in New Hampshire. Since this bat occurs only in small numbers, lack of intense competition may allow little brown bats to remain diverse in feeding habits, utilizing all available prey within the appropriate size range.

Prey selection

This study reveals that adult female *M. lucifugus* are selective in their diet in July, when insects are most abundant, and a constant, predictable energy source is assured. In contrast, pregnant bats feed more randomly when absolute abundance of insects is low, and availability is unpredictable in space and time. To this point, the data support theoretical predictions of Emlen (1966), MacArthur and Pianka (1966), and others.

The situation is complicated, however, by rising energy demands of lactation (and fat deposition in non-reproductives) during the period of peak prey density. Two responses to this increased requirement can be envisioned: (1) formation of a "search image" to improve foraging efficiency (Tinbergen 1960), which would increase apparent selectivity, or (2) a tendency toward greater generalization, maximizing energy intake/unit foraging time by rejecting fewer potential prey items (Schoener 1971). The first strategy would exaggerate effects of increased prey density, whereas the latter would cancel them, partially or entirely.

Although *M. lucifugus* adults become more selective in their diet in July, taking fewer midges and a greater proportion of beetles and mayflies, no significant tendency toward specialization is evident. Thus, while increased resource availability allows selectivity to be exercised, this effect is counterbalanced by a trend toward generalization dictated by increased en-

ergy demands (the second strategy outlined above). Absence of intense competition may further reduce tendencies toward specialization at this time.

Prey selection requires ability on the part of the predator to discriminate among available food items. When beetles are available to the bats, they may be easily discriminated from all others by echolocation, due to their highly-sclerotized, hard-bodied form. However, differentiation among Diptera may be much more difficult. Thus, selectivity in favor of beetles in July may be influenced by ease of discrimination. Lack of strong preference among dipterans, especially in June, may indicate that discrimination among these groups is not worth the necessary investment of time and energy. Nonselective feeding in juveniles suggests that they are unable to differentiate among different prey types as effectively as adults. Lack of selectivity in the foraging habits of young *M. lucifugus* was also documented by Belwood and Fenton (1976).

Due to simultaneous changes in prey availability and energy requirements of predators, the present study does not provide a rigorous test of prey selection models. Their predictions are used to explain changes in feeding habits observed; thus, their validity is proven only in a tautological fashion. Although the models were developed to explain predator-prey interactions in the field, natural communities may be too complex to provide convenient test arenas. In most cases, controlled conditions or resource modifications are required to test responses to single environmental or physiological variables. For insectivorous bats, manipulation of prey density in outdoor flight cages (Gustafson 1975) may provide the proper balance between controlled and natural conditions to yield data more rigorously assessing the validity of prey selection models.

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