Energetics of Pregnancy and Lactation in Free-ranging Little Brown Bats (Myotis lucifugus)

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Abstract
We combined field measurements of metabolic rate, made with doubly labeled water, with data from our previous studies to examine reproductive energetics in 24 female little brown bats (Myotis lucifugus). Including estimates of tissue or milk production, M. lucifugus required an average of 33.7 kJ d−1 of assimilated energy in pregnancy compared to 41.3 kJ d−1 during lactation. Predicted insect consumption was 5.5 g d−1 for a 9-g pregnant female and 6.7 g d−1 for a 7.9-g lactating female. About 2% of total energy assimilated during pregnancy was stored as new tissue, whereas lactating females exported 32% as milk. Estimated assimilated energy demand on the first day of lactation was 33.8 kJ d−1 and increased to 60.3 kJ d−1 at peak lactation. By subtracting laboratory measurements of roosting costs from observed metabolized energy expenditure, we calculated that foraging flight by 9-g pregnant M. lucifugus required 4.46 kJ h−1; this was 13% less than allometric predictions. Foraging flight accounted for the largest proportion of the daily metabolized energy budget during pregnancy (61%) and lactation (66%). The large amount of energy devoted to foraging by this aerial-feeding bat may partially explain the low proportion of energy it allocates to tissue production and milk export.

Introduction

Although mammalian reproduction has many components, most theoretical and empirical work has concentrated on gestation and lactation (Gittleman
and Thompson 1988). Energetic costs associated with pregnancy and lactation are well documented in laboratory-maintained species (McClure 1987) and domesticated livestock (Brody 1945). Although studies under rigidly controlled laboratory conditions are valuable, their results may not be applicable to free-ranging animals. In the wild, mammals must contend with predator avoidance and evasion, daily and seasonal changes in environmental parameters (temperature, moisture, radiation, etc.), and daily and seasonal changes in the quantity and quality of available food. In addition, many mammals actively pursue their prey and incur large energetic expenses associated with foraging. Captive studies eliminate the need for foraging and often disregard this potentially large component of the energy budget. The uncertainties involved with extrapolating laboratory data to the field situation make it imperative to assemble data on the energetics of reproduction in free-ranging mammals.

Despite the taxonomic and ecological diversity of the Chiroptera, bats have seldom been used in studies of reproductive energetics. These flying mammals, however, are well suited for field studies because of their small body size, accessibility, high reproductive rates, and small, often invariant litter size. In addition, their energetically expensive mode of locomotion contrasts sharply with that of the relatively sedentary, but more frequently studied, rodents and insectivores. In this article we will describe energy expenditure by free-ranging little brown bats, *Myotis lucifugus*, a widely distributed Nearctic species.

Although *M. lucifugus* is a small mammal (7-11 g), it has a relatively long gestation period (60 d) and produces only a single offspring each year (Barbour and Davis 1969). The young are functionally altricial at birth, but they are extremely large, weighing 30% of the mother’s postpartum mass; the single newborn weighs slightly more than the entire litter mass predicted for a similar-sized terrestrial eutherian (Kurta and Kunz 1987). Young *M. lucifugus* do not begin to forage until they reach 84% of the mother’s mass (Burnett and Kunz 1982) but are totally weaned after only 26 d. Adults are completely insectivorous and capture their prey while in continuous flight. Unlike most small terrestrial mammals, these bats are long-lived and may survive up to 30 yr in the wild (Keen and Hitchcock 1980).

A number of techniques exist for estimating daily energy expenditure of mammals in the field (Kunz and Nagy 1988). Perhaps the most direct and reliable of these is the doubly labeled water (DLW) technique, a method which measures CO₂ production (described below). Although this technique has been used with a variety of mammals in recent years, most studies have focused on nonreproductive individuals (Nagy 1987). In the present study, we used doubly labeled water to measure the metabolic rate of 24
free-ranging *M. lucifugus* during pregnancy or lactation. Previous work by our laboratory has examined various energy-related parameters in this species, including roosting metabolic rates, time/activity budgets, adult and juvenile body composition, milk composition, and milk output. On the basis of our previous work and the results of the present study, we can now calculate average daily energy expenditure in free-ranging *M. lucifugus* and determine the relative importance of roosting requirements, foraging expenses, tissue production, and milk-energy export.

**Material and Methods**

*Doubly Labeled Water Technique*

The DLW technique indirectly measures metabolic rate through the differential turnover of hydrogen and oxygen isotopes (\(^3\)H and \(^18\)O) in the body water pool. After labeled water has been injected into an experimental animal, the concentration of each isotope declines over time. Tritium is lost from the body as water; \(^18\)O is lost both as water and as \(\text{CO}_2\). The difference in isotope turnover rates can be used to calculate \(\text{CO}_2\) production. The theory behind this technique and potential errors associated with it are described by Nagy (1980, 1983).

*Field and Laboratory Protocol*

After leaving hibernation, *Myotis lucifugus* females form maternity colonies in man-made structures such as barns or attics. Fieldwork was carried out at five such colonies in southern New Hampshire and northern Massachusetts between May 9 and July 23, 1986. Individual bats were gathered from their maternity roosts at approximately 1300 hours. After capture, each bat was weighed to the nearest 0.01 g and marked with a numbered plastic band. We injected each bat intraperitoneally with 0.024 mL of sterile water containing 95 atom % of \(^18\)O and 32 μCi of \(^3\)H/\(\mu\)L. We allowed 1 h for equilibration of isotopes with the body water pool (Kunz and Nagy 1988) before taking a small (ca. 60 μL) blood sample from a vein in either the wing or tail membrane. Each bat was released inside its home roost after bleeding. Ambient temperature (\(T_a\)) inside the roost was continuously monitored with a recording hygrothermograph; minimum and maximum \(T_a\)'s outside the roost were obtained from the nearest weather station. Approximately 9% of all injected bats were recaptured 1 or 2 d after injection; mean deviation from exactly 1 or 2 d was \(-0.03 \pm 0.01\) d (SE; \(n = 26\)). Upon recapture, each bat was weighed and bled a second time; mean change in body mass was
−1.9 ± 0.7%. Blood samples were flame-sealed in heparinized glass capillary tubes and transported on ice to the laboratory. The blood was vacuum-distilled, and the resulting water was analyzed for isotope activity. Tritium was measured by liquid scintillation counting and $^{18}$O by proton activation analysis. Laboratory procedures and equations for calculating CO$_2$ production are detailed by Nagy (1983).

Preliminary analysis indicated that two pregnant bats had much lower CO$_2$ production rates (31% and 63% of the mean) than the others. These low rates were associated with the lowest overnight $T_a$'s (4° and 7°C) recorded during our study and suggested that these bats had become torpid in response to a temperature-induced food shortage. *Myotis lucifugus* does not use torpor as an everyday strategy during late pregnancy or lactation (Kurta, Johnson, and Kunz 1987); hence, we excluded these two animals from our analysis of daily energetic patterns.

**Conversion Factors and Diet Composition**

We converted measured CO$_2$ production into equivalent energy units on the basis of the composition of an average insect diet. We obtained the nitrogen, fat, ash, and H$_2$O content of insects from Redford and Dorea (1984). To calculate protein content, we assumed that chitin made up 12.8% of insect dry mass and that chitin was 6.9% nitrogen (Wigglesworth 1965). After subtracting chitinous nitrogen from total insect nitrogen, we calculated crude protein on the basis of a 16% nitrogen content of a typical protein (Brody 1945). Carbohydrate was obtained by subtracting the mass of chitin, protein, fat, ash, and water from the total. Thus, a typical diet of insects consists of 70% water, 17.8% protein, 4.6% fat, and 2.2% carbohydrate. One gram of protein, fat, or carbohydrate contains 23.6, 39.5, or 17.7 kJ of energy, respectively (Robbins 1983); chitin contains 21.2 kJ g$^{-1}$ (calculated from Karasov 1982). We assumed that 95% of ingested protein, fat, and carbohydrate was assimilated and that chitin was totally indigestible (Altman and Dittmer 1968). Almost 15% of assimilated protein energy is lost as urea (Brafield and Llewellyn 1982). Thus, one gram of fresh insects provides *M. lucifugus* with 7.25 kJ of ingested energy, 6.12 kJ of assimilated energy, or 5.51 kJ of metabolized energy. Our calculated energy density of 7.25 kJ g$^{-1}$ wet mass (24.17 kJ g$^{-1}$ dry mass) is similar to values obtained by bomb calorimetry (Kunz 1988). If we assume that one gram of metabolized protein, fat, or carbohydrate yields 862, 1,400, or 830 mL CO$_2$ g$^{-1}$, respectively (Brafield and Llewellyn 1982; Robbins 1983), each liter of CO$_2$ produced represents 24.5 kJ of metabolized energy or 27.2 kJ of assimilated energy.
Field Metabolic Rate

Fig. 1. Relationship between body mass and daily CO₂ production by pregnant and lactating Myotis lucifugus.

Results

We measured the CO₂ production rates of 10 pregnant and 14 lactating Myotis lucifugus (fig. 1). Carbon dioxide production during pregnancy averaged $1,224 \pm 47.3$ (SE) mL d⁻¹ compared to $1,036 \pm 59.5$ mL d⁻¹ during lactation. Mean body mass averaged $9.02 \pm 0.28$ g for pregnant bats and $7.88 \pm 0.14$ g during lactation. Mass-specific rates of CO₂ production, as well as assimilated and metabolized energy equivalents, are given in table 1. The observed metabolic rates of pregnant and lactating M. lucifugus exceeded that predicted for an 8–9-g nonreproductive eutherian by over 40% (Nagy 1987). Metabolic rate during pregnancy was greater than during lactation on a whole-animal basis ($t = 2.32$; df = 22; $P = 0.03$), but mass-specific metabolic rate did not differ between reproductive conditions ($t = 0.65$; df = 22; $P = 0.52$). It is important to emphasize, however, that metabolic rates obtained with DLW do not include chemical energy stored as new tissue or exported as milk (see Discussion).

We used standard parametric correlation analyses to investigate the relationship between observed metabolic rate and eight methodological and
Table 1

Daily carbon dioxide production and metabolized and assimilated energy equivalents for free-ranging Myotis lucifugus

<table>
<thead>
<tr>
<th></th>
<th>Late Pregnancy</th>
<th>Lactation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon dioxide production:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mL d⁻¹)</td>
<td>1,224 (47.3)</td>
<td>1,036 (59.5)</td>
</tr>
<tr>
<td>(mL g⁻¹ d⁻¹)</td>
<td>137 (6.6)</td>
<td>131 (6.3)</td>
</tr>
<tr>
<td>Metabolized energy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(kJ d⁻¹)</td>
<td>29.9 (1.2)</td>
<td>25.3 (1.5)</td>
</tr>
<tr>
<td>Assimilated energy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(kJ d⁻¹)</td>
<td>33.2 (1.3)</td>
<td>28.1 (1.7)</td>
</tr>
</tbody>
</table>

Note. SEs are given in parentheses. Carbon dioxide production and energy equivalents are based only on field measurements using DLW; production and milk export are not included. Mean body mass was 9.0 g in late pregnancy and 7.9 g in lactation.

Environmental variables—body mass, percent change in body mass, time between injection and recapture, date, minimum and maximum roost $T_a$, and minimum and maximum external $T_e$. When pregnant and lactating groups were examined separately, metabolic rate was not significantly correlated with any of the variables (all $P > 0.08$). To enhance the probability of detecting small effects, we combined the data from pregnant and lactating females, and we statistically corrected for the obvious intergroup differences in reproductive condition and body mass by using partial correlation analysis. After we corrected for reproductive condition and body mass, maximum roost $T_a$ was the only significant variable, explaining 19% of the residual variation in metabolic rate (partial $r = -0.44$; $P = 0.02$). The lack of a correlation between metabolic rate and change in body mass or time between injection and recapture suggested that our methods did not unduly influence energy expenditure by the bats. The explanatory power of environmental variables in the present study was quite low and was similar to that reported for free-ranging birds (Bryant, Hails, and Prys-Jones 1985); environmental effects in our study were probably minimized by the bats' habit of clustering within protected wooden cavities (Kurta 1985). Together, body mass, reproductive condition, and maximum roost $T_a$ accounted for only 39% of the total variation in metabolic rate ($R = 0.62$; $P = 0.02$). Factors that might explain some of the remaining variation but could not be quantified in this study include individual differences in body temperature (Kurta et al. 1987), stage
of lactation, and/or length of the energetically expensive foraging period (see Discussion).

Discussion

Assimilated Energy Demands during Late Pregnancy

Energy required during pregnancy includes that indicated by DLW (table 1) as well as chemical energy stored in the fetus and maternal reproductive structures. Previous studies by our laboratory provide reasonable estimates of these additional costs and allow us to determine their importance in the overall energy budget. Newborn *Myotis lucifugus* in New Hampshire weigh 2.3 g (Burnett and Kunz 1982) and consist of about 18% protein and 3% fat (Stack 1985; Fujita 1986). If we assume negligible carbohydrate, total energy content is 12.5 kJ per neonate. About 78% of the energy stored in the fetus, placenta, uterus, and mammary glands is in the fetus itself (Migula 1969; Kurtz and Kunz 1987). Thus, total production during gestation is about 16.0 kJ.

Although one might expect energy demand to change significantly as the fetus approaches term, the lack of a correlation between metabolic rate and body mass during pregnancy (fig. 1) suggests that stage of gestation is not important in determining energy expenditure in the field. Capture dates (May 22 to June 9) and body masses (7.7–10.1 g) indicate that these bats were in the last half of their 60-day pregnancy and ranged from about mid-gestation to just before parturition. Based on only the DLW measurements (table 1), assimilated energy requirements in late pregnancy consist of 30 d at 33.2 kJ d⁻¹, or 996 kJ. Almost all eutherian production occurs in late gestation (Robbins 1983); therefore, we included total production (16 kJ) as part of expenses incurred in late pregnancy. Thus, total energy required in late gestation is 1,012 kJ; on average, 33.7 kJ of assimilated energy, or 5.5 g of insects, would be needed each day (table 2). Fetal tissue represents only 1.2% of all energy assimilated in late pregnancy. Despite the large size of *M. lucifugus* neonates, this proportion is one-quarter to one-half that reported for other small mammals over their entire gestation (e.g., Migula 1969; McClure 1987).

Assimilated Energy Demands during Lactation

Analyses of stomach contents show that young *M. lucifugus* consume only milk from birth to day 18 and then combine milk and insects until day 27, when weaning is complete. On the basis of field measurements of juvenile
of lactation, and/or length of the energetically expensive foraging period (see Discussion).

Discussion

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Table 2

Average assimilated energy requirements of Myotis lucifugus during late pregnancy and lactation

<table>
<thead>
<tr>
<th></th>
<th>Late Pregnancy</th>
<th>Lactation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maintenance energy per day (kJ d⁻¹)</td>
<td>33.2</td>
<td>28.1</td>
</tr>
<tr>
<td>Total maintenance energy (kJ)</td>
<td>996.0</td>
<td>730.6</td>
</tr>
<tr>
<td>Production energy per day (kJ d⁻¹)</td>
<td>0.5</td>
<td>13.2</td>
</tr>
<tr>
<td>Total production energy (kJ)</td>
<td>16.0</td>
<td>342.7</td>
</tr>
<tr>
<td>Production + maintenance (kJ d⁻¹)</td>
<td>33.7</td>
<td>41.3</td>
</tr>
<tr>
<td>Production + maintenance (kJ)</td>
<td>1,012.0</td>
<td>1,073.3</td>
</tr>
<tr>
<td>Insects required per day (g d⁻¹)</td>
<td>5.5</td>
<td>6.7</td>
</tr>
<tr>
<td>Predicted foraging rate (g h⁻¹)</td>
<td>1.3</td>
<td>1.7</td>
</tr>
</tbody>
</table>

Note. The term “maintenance energy” refers to energy expenditures indicated by DLW measurements (table 1); “production” represents chemical energy stored as new tissue during pregnancy or exported as milk during lactation (see text). Energetic costs during late pregnancy were calculated only for the last 30 d of gestation; costs for lactation were based on the entire 26-d lactation period. Mean body mass was 9.0 g for pregnant bats and 7.9 g for lactating individuals.

metabolic rate using DLW and the composition of M. lucifugus milk (Kunz, Stack, and Jenness 1983; T. H. Kunz, unpublished data), daily milk-energy production during the first 17 d can be predicted by:

\[ E_{m} = 10.34 + (\text{age}) 0.50, \]  

where \( E_{m} \) is milk energy in kJ, and age is in days. If we assume that milk-energy output is 10.8 kJ on day 1, 19.3 kJ on day 18, and zero on day 27, then M. lucifugus exports 342.7 kJ in the form of milk during the entire lactation period.

Our field measurements indicate an average assimilated energy demand of 28.1 kJ d⁻¹ (table 1), not including milk; over a 26-d lactation period, this amounts to 730.6 kJ. Including milk, the assimilated energy requirement is 1,073.3 kJ, or 41.3 kJ d⁻¹. A 7.9-g M. lucifugus must consume 6.7 g of insects in order to meet this average daily energy demand (table 2).

The Use of Body Stores during Lactation

During pregnancy, many mammals store fat that later subsidizes the high cost of lactation (Sadleir 1984). Myotis lucifugus loses 0.54 g of body mass
during lactation (Burnett and Kunz 1982). If this loss consists entirely of fat, it could provide 21.3 kJ, or 2.0%, of total energy required during lactation (table 2). Thus, stored energy (21.3 kJ) equals only 52% of the average daily demand (41.3 kJ; table 2). The 9-g bat *Plecotus auritus* is similar in that body stores can supply less than 1 day’s average energy requirement (Speakman and Racey 1987).

*The Gross Efficiency of Lactation*

The gross efficiency of lactation (GEL) is the percentage of total assimilated energy that is exported as milk (Brody 1945). A milk-energy export of 342.7 kJ and a total requirement of 1,073.3 kJ yields a GEL of 32%. This is lower than values reported for most other mammals, which range from 30% to 60% (Brody 1945; Dryden and Anderson 1978; Fedak and Anderson 1982; Costa et al. 1986). The estimates for other mammals, however, were based on animals that did not actively forage during lactation. Any energy spent on foraging should reduce the observed GEL, and foraging is the largest component of the daily energy budget for lactating *M. lucifugus* (see below).

*Predicting Changes in Energetic Parameters during Lactation*

The energy demands of a growing mammal require increasing maternal investment until the start of weaning. For example, lactating *Peromyscus maniculatus* increase daily food intake by 96%, 136%, and 194% over nonreproductive levels in the first, second, and third weeks of lactation, respectively (Stebbins 1977). Although we were not able to monitor *M. lucifugus* with known-age pups in this study, we can predict the magnitude of changes that occur using the GEL. Milk-energy output by *M. lucifugus* can be calculated with equation (1); dividing milk-energy output by the GEL (0.32) provides an estimate of total assimilated energy required by the mother. Predicted energy demand increases from 33.8 kJ d⁻¹ on day 1 to 60.3 kJ d⁻¹ at peak lactation (table 3). Insect consumption would increase from 5.5 to 9.9 g d⁻¹.

Our predictions are quite reasonable in terms of observed CO₂ production. Subtracting 19.3 kJ of milk energy at peak lactation from the total of 60.3 kJ (table 3) yields 41.0 kJ of assimilated energy (36.9 kJ of metabolized energy); this is equivalent to 191 mL CO₂ g⁻¹ d⁻¹. The highest metabolic rate actually measured in our study was 187 mL CO₂ g⁻¹ d⁻¹. Similarly, predicted CO₂ production on day 1 was within 7% of our lowest observed value.

*Comparing the Energetics of Pregnancy and Lactation*

During gestation, 16.0 kJ are stored in the fetus and maternal reproductive structures; during lactation, 342.7 kJ are exported as milk. Milk-energy out-
Table 3
Predicted energy demand on various days of lactation for Myotis lucifugus

<table>
<thead>
<tr>
<th>Day of Lactation</th>
<th>Milk-Energy Output (kJ d⁻¹)</th>
<th>Total Energy Required (kJ d⁻¹)</th>
<th>Insects Required (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.....</td>
<td>10.8</td>
<td>33.8</td>
<td>5.5</td>
</tr>
<tr>
<td>7.....</td>
<td>13.8</td>
<td>43.1</td>
<td>7.0</td>
</tr>
<tr>
<td>13.....</td>
<td>16.8</td>
<td>52.5</td>
<td>8.6</td>
</tr>
<tr>
<td>18.....</td>
<td>19.3</td>
<td>60.3</td>
<td>9.9</td>
</tr>
</tbody>
</table>

Note. Milk-energy output is calculated with equation (1). Predictions of total energy requirements are based on the gross efficiency of lactation (see text). Total energy represents assimilated energy. Day 18 is peak lactation.

put, therefore, exceeds production energy during gestation by a factor of 21.4. Average daily requirements during lactation (41.3 kJ d⁻¹; table 2) exceed those of late pregnancy (33.7 kJ d⁻¹) by a factor of 1.2. Considering the large ratio of milk export to tissue production, one might expect larger differences in average daily expenditure. The smaller body size of lactating females, however, leads to lower maintenance requirements than in pregnant *M. lucifugus*. Roost *Tₜ* is often 2°–5°C higher during lactation and should decrease resting metabolic rate by 10%–30% (Stones and Wiebers 1967). Relative foraging costs are also presumably lower for lactating females; insect densities are greater during lactation (Anthony and Kunz 1977) and should lead to an increase in foraging efficiency (see below).

The Energetic Cost of Foraging during Pregnancy

Most attempts to estimate the energetic cost of foraging flight in bats have relied on the allometric equation of Thomas (1975) that is based on wind-tunnel studies of three bird and two bat species. Using our field measurements of daily metabolized energy expenditure (table 1) and our recent measurements of roosting costs (Kurta et al. 1987), we calculated the energetic cost of the foraging period for *M. lucifugus* by subtraction. The daily metabolized energy budget (*Eₐ*) of a free-living bat is divided into three main components such that:

\[ Eₐ = P₃ₐ (t₃ₐ) + P₅ₐ (t₅ₐ) + P₇ₐ (t₇ₐ), \]
where the subscripts DR, NR, and F represent the day-roosting, night-roosting, and foraging periods, respectively; \( P\) and \( t\) represent the power requirement and duration, respectively, of those periods. Time and power requirements of day and night roosting by pregnant \( M.\) lucifugus are shown in table 4. Rearranging equation (2) to solve for \( P\) indicates that foraging flight by 9 g \( M.\) lucifugus requires 4.46 kJ h\(^{-1}\); this is 13% lower than predicted by equation (36) of Thomas (1975). Birds that fly continuously while foraging, such as swifts and swallows, also have flight costs that are lower than predicted by wind-tunnel-generated allometric equations (Hails 1979).

**Predicting Foraging Time during Lactation**

Although the length of the foraging period is not known for lactating \( M.\) lucifugus, its mean duration may be calculated by the method of Helversen and Reyer (1984). As in pregnancy, the daily metabolized energy budget during lactation is divided into three compartments as shown in equation (2). Total metabolized energy expenditure \( (E_D)\) is 25.3 kJ (table 1). Day- and night-roosting power requirements for a 7.9-g lactating bat are 0.37 and 0.67 kJ h\(^{-1}\), respectively (Kurta et al. 1987). On the basis of aerodynamic theory and the morphology of \( M.\) lucifugus, Aldridge (1988 and personal communication) suggests that flight costs for a 7.9-g \( M.\) lucifugus during lactation are 7% less than for a 9-g pregnant bat; therefore, we assume that flight costs \( (P_f)\) during lactation are 4.15 kJ h\(^{-1}\). Although the duration of day roosting \( (t_{DR})\) is known (15.8 h), the duration of night roosting \( (t_{NR})\) and foraging \( (t_f)\) are unknown. One unknown, however, is defined in terms of the other \( (t_{NR} = 8.2 - t_f)\), and equation (2) may be rearranged to solve for \( t_f\). Our calculated duration of the mean foraging period is 4.0 h (table 4). Within this period, lactating \( M.\) lucifugus would have to ingest 6.7 g of insects at a rate of 1.7 g h\(^{-1}\) (table 2); capture rates up to 2.1 g h\(^{-1}\) have been observed in the field (Anthony and Kunz 1977). A greater rate of prey capture during lactation than during pregnancy (table 2) is expected because of higher insect densities during lactation (Anthony and Kunz 1977) and the direct effect of insect densities on feeding rates (Racey and Swift 1985).

**The Impact of Foraging Costs**

In a recent paper, Garland (1983) developed an allometric equation that predicts the cost of foraging, as a percentage of daily metabolized energy expenditure, for terrestrial mammals. The Garland equation predicts that an 8-9-g mammal should use about 1% of its daily energy budget on foraging.
<table>
<thead>
<tr>
<th>Activity</th>
<th>Late Pregnancy</th>
<th></th>
<th></th>
<th>Lactation</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Power Required (kJ h⁻¹)</td>
<td>Time (h)</td>
<td>Percent of Total Time</td>
<td>Energy Required (kJ)</td>
<td>Percent of Total Energy</td>
<td>Power Required (kJ h⁻¹)</td>
<td>Time (h)</td>
<td>Percent of Total Time</td>
</tr>
<tr>
<td>Day roosting</td>
<td>.52</td>
<td>15.6</td>
<td>65.0</td>
<td>8.1</td>
<td>27.0</td>
<td>.37</td>
<td>15.8</td>
<td>65.8</td>
</tr>
<tr>
<td>Night roosting</td>
<td>.82</td>
<td>4.3</td>
<td>17.9</td>
<td>3.5</td>
<td>11.7</td>
<td>.67</td>
<td>4.2</td>
<td>18.8</td>
</tr>
<tr>
<td>Foraging</td>
<td>4.46</td>
<td>4.1</td>
<td>17.1</td>
<td>18.3</td>
<td>61.2</td>
<td>4.15</td>
<td>4.0</td>
<td>15.4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>24.0</td>
<td>100.0</td>
<td>29.9</td>
<td>100.0</td>
<td></td>
<td>24.0</td>
<td>100.0</td>
</tr>
</tbody>
</table>

Note: Total metabolized energy is from Table 1. Power requirements while roosting were based on Kurta et al. (1987); power requirements while foraging were calculated (see text). The length of the foraging period during lactation was also calculated (see text), but the duration of other periods was based on previous studies in New Hampshire (Kurta et al. 1987) and Ontario (Barclay 1982). Body mass was assumed to be 9.0 g in late pregnancy and 7.9 g in lactation.
costs. Minimum power requirements for flying bats, however, are extremely high—almost double the maximum metabolic capabilities of exercising terrestrial mammals (Thomas 1975). Consequently, even though the foraging period accounts for only 15%–17% of the daily time budget of *M. lucifugus*, foraging is the largest component of the average daily metabolized energy budget—61% in late pregnancy and 66% in lactation (table 4). Previous studies of insectivorous and nectarivorous bats have estimated that foraging requires 38%–74% of daily energy expenditure (Studier and O’Farrell 1980; Burnett and August 1981; Helversen and Reyer 1984; Stack 1985; Bell, Bartholomew, and Nagy 1986; Speakman and Racey 1987). Although foraging costs may be energetically unimportant for nonvolant mammals (Garland 1983), this is clearly not the case for aerial-foraging bats. The high cost of aerial foraging may be one reason that the proportion of energy allocated to tissue or milk production by *M. lucifugus* is low compared to the proportion allocated by small terrestrial mammals.

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