22 Post-natal growth and energetics of suckling bats

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Abstract
There are several practical limitations associated with the study of post-natal growth and energetics of free-ranging bats. However, when these limitations are compared to the biases introduced by research on captive bats, the advantages of studying free-ranging bats outweigh the disadvantages. A recent development in methods used to age field-captured bats during the post-natal period makes it possible to conduct age-specific analyses of body mass, body composition, thermoregulation, milk energy intake and field metabolic rates. Results from such analyses can reveal indexes of physiological maturity, rates and efficiencies of accretionary growth, estimates of energy budgets of sucklings and estimates of energy requirements and maternal investment by lactating females.

Age-specific increases of body mass in free-ranging bats are linear or nearly linear during the preflight period. In some species the maximum preweaning body masses of sucklings approach adult levels before the onset of flight. Sucklings from a litter size of one often exhibit high relative and absolute growth rates and experience a loss of body mass during the early flight and weaning period. Sucklings from a litter of two usually grow more slowly and achieve a lower relative body mass at the onset of flight. Total body water decreases from a high near 80 % of body mass at birth to 67-73 % (adult levels) by the age of early flight. Protein and fat are both deposited during the preflight period and, in some species, it appears that fat is mobilized during the early flight and weaning period. Mobilization of fat, and the related decrease in body
mass, in the early night and weaning period may help to ensure the successful transition of sucklings from a diet of milk to one of insects.

Suckling bats are poikilothermic in the early post-natal growth period and appear to allocate little of their metabolizable energy to thermoregulation. Deferred development of thermoregulation in insectivorous bats (as in altricial birds) may allow the maximum amount of metabolizable energy and material to be allocated to growth before the onset of flight and weaning. Maternity roosts are often located at sites that are warmed by solar radiation during the day roosting period or they become altered by the entrapment of metabolic heat. These conditions appear to promote rapid post-natal growth, minimize heat loss from sucklings and reduce the maintenance cost to females during the energetically costly period of lactation. Based on rates of accretionary growth and estimates of metabolizable energy available from daily milk energy intake, gross growth efficiency during peak lactation is 0.20 and 0.16 for Myotis lucifugus and Eptesicus fuscus, respectively. Total energy requirements and maternal investment of lactating females were estimated from measurements of milk energy intake by sucklings and knowledge of the gross efficiency of milk production by females.

Introduction

Growth and energy allocation in suckling mammals are important aspects of reproduction. While bats share many features of gestation, lactation and pelage development with other mammals, they also share several developmental and locomotor characteristics with aerial feeding insectivorous birds. Suckling bats are flightless and are totally dependent upon their mothers during the early post-natal period. Before young bats are able to achieve independence from this maternal influence, they must learn how to fly and capture food on the wing. This requires that wing structure, flight musculature and vocal and auditory (echolocation) characteristics be sufficiently developed before the onset of flight.

There are few reported studies on the energetics of suckling bats. This contrasts with a growing literature on the energetics of nesting birds (see reviews by O'Connor 1983, Ricklefs 1984). Although the energetics of post-natal growth have been more extensively studied in terrestrial mammals, most reports have been on domestic (see, for example, Brody 1945), laboratory-reared (Drozdz, Gorecki & Sawicka-Kapusta 1972; Sawicka-Kapusta 1974; Fedyk 1975; Gebezyński 1975; McClure & Randolph 1980; Gebezyński & Gebezyńska 1984), or captive wild animals (Sadlier 1969, Oltedal 1984). The limited research on post-natal growth and energetics in small, free-ranging, terrestrial mammals largely reflects the difficulty of finding nests that contain suckling young. For many species, young animals are seldom trappable until they are weaned. Moreover, when suckling mammals are found, the lack of suitable aging techniques (Petrusewicz & Macfadyen 1970, Morris, 1972) limits meaningful analyses of age-specific development and behaviour of free-ranging individuals.

Colonial insectivorous bats offer distinct advantages over many other free-ranging mammals for the study of post-natal growth and energetics of sucklings. Young bats of several species are accessible at maternity roosts, individuals can be marked and recaptured repeatedly from birth through weaning, and reliable aging techniques have been developed (Kunz & Anthony 1982). To date, studies on the energetics of suckling bats have included analyses of body composition (O'Farrell & Studier 1973, Stack 1985, Fujita 1986, E.D. Pierson & T.H. Kunz unpublished results), thermoregulation (Bartholomew, Leitner & Nelson 1964; Herreid 1967; Weigold 1972; Noll 1979; Fujita 1986), milk energy intake, and field metabolic rate (T.H. Kunz & K.A. Nagy unpublished results). Few investigators have considered environmental factors that influence patterns and rates of post-natal growth in bats (Tuttle 1975, 1976; Hoying 1983).

The purpose of this paper is to review studies on post-natal growth and energetics of suckling bats. Brief consideration is given to captive studies, but emphasis is placed on results from field studies of known-age individuals. The post-natal growth period is here defined as the time from birth until the epiphyses of long bones become visibly closed (Kunz & Anthony 1982). This period may extend from several weeks in some species to months in others. Operationally, post-natal growth can be divided into three distinct periods: preflight, early flight and weaning, and post-weaning. For insectivorous bats, the preflight period is distinguished by a diet consisting exclusively of milk. The early flight and weaning period is characterized by a gradual transition from a diet of milk to one of milk and insects, whereas the post-weaning period is marked by a diet consisting exclusively of insects.

Post-natal growth curves and age estimation

Growth curves

Many qualitative and analytical approaches have been used to describe post-natal growth in insectivorous bats. Some workers (see, for example, Dymond 1936; Sigmund 1964; Hayward 1970; Krátky 1970, 1981; Yokoyama, Uchida & Shiraiishi 1975) have used various kinds of

Reasons for selecting a particular method of study have varied with the objectives, the species being considered, the accessibility of suckling bats to the investigator and the number of bats present in the maternity roost. Although allometric analysis is a convenient way of comparing relative growth rates, it completely avoids the age issue. Growth curves plotted from average measurements of bats by date of capture invariably underestimate post-natal growth rates (Tuttle 1975, T.H. Kunz unpublished results), and these cannot be used to age bats. Post-natal growth curves of bats derived from captive studies seldom, if ever, are comparable to growth curves derived from field studies (figure 1). Young bats reared in captivity often weigh more than bats of a similar age in the field and many show signs of stunted bone growth (Orr 1954, Jones 1967, Maeda 1972). Thus, measurements taken on known-age individuals in the field provide the most reliable information for quantifying age-specific growth and developmental processes. The most serious limitation of the latter approach is the inability to recapture enough known-age individuals, after young have become volant, to describe complete growth curves. Other limitations of post-natal growth studies on captive and free-ranging bats are discussed by Krátký (1981).

Age estimates
Most studies on post-natal growth of free-ranging bats have assumed that individuals with attached umbilical cords range in age from 0 to 24 h (see, for example, Davis 1969, Krátký 1970, Rakhmatulina 1972;

Figure 1. Comparisons of post-natal growth in free-ranging and captive (a) Antrozous pallidus and (b) Pipistrellus pipistrellus.
Kunz 1973, 1974; Tuttle 1975; Yokoyama & Uchida 1979; Kunz & Anthony 1982; Burnett & Kunz 1982; Hoying 1983). This assumption, however, may not be valid for bats that roost in extremely humid environments (Krátky 1981). Some individuals may retain the umbilicus for periods exceeding 24 h.

Because forearm length can be measured easily and consistently, it has become the character of choice in most studies on post-natal growth. This character, however, has limited use for age estimation, since it usually reaches the lower range of adult size early in the post-natal period (figure 2a), and often before bats are capable of flight (see, for example, Pearson et al. 1952, Davis 1969). Despite this limitation, forearm length is invariably the most reliable character for aging bats in the preflight period (Kunz & Anthony 1982). Body mass is not a good character for estimating age because of its sensitivity to nutritional input, energy expenditure and water flux. Additionally, body mass may show little or no measurable increase during and immediately following the weaning period (see, for example, Anthony 1982, Burnett & Kunz 1982, Hoying 1983, Stack 1985). Other measurements such as total length, tail length and finger length, often recorded from preserved bats (Krátky, 1970, 1981), cannot be taken accurately enough under field conditions to be useful for aging purposes. Ideally, the most appropriate characters for age determination are those that change continuously throughout the post-natal period.

The most promising ‘externally visible’ characters for quantifying growth and for aging bats are the cartilaginous epiphyses of long bones. Cartilaginous ‘windows’ or unfused epiphyses of wing bones have long been used to distinguish between young and adult bats in the field (reviewed by Anthony 1986). Rybář (1969a, 1969b, 1971) was among the first to quantify the changes in the length of epiphyseal plates of wing elements during post-natal growth in bats. Some investigators have used the degree of closure of the epiphyses to assign relative ages to individuals in field captured animals (see, for example, Geluso et al. 1976, Buchler 1980). Others have quantified changes in the length of the epiphyseal cartilages of the metacarpal-phalangeal joints of the fourth digit (referred to as the ‘total gap length’), during the post-natal period, and have used these to derive age-predictive equations (Kunz & Anthony 1982, Burnett & Kunz 1982, Hoying 1983). These equations have been used in several recent studies to estimate the age of young bats (Stack 1985, Fujita 1986, T.H. Kunz & K.A. Nagy unpublished results).

The total gap length of the fourth metacarpal-phalangeal joint increases linearly during the early preflight period (figure 2b). Before or

Figure 2. (a) Age changes in total (epiphyseal) gap length $T$ and (b) forearm length in *Eptesicus fuscus*. (After Burnett & Kunz 1982.)
near the time that the forearm length reaches adult size (figure 2a), the total gap length begins to decrease linearly (figure 2b). The period over which growth can be quantified and age can be accurately predicted will vary for a given species (Burnett & Kunz 1982, Hoying 1983). Generally, age can be determined from measurements of the total cartilaginous gap length as long as the distal plate of the gap remains visible (as viewed with a dissecting microscope and ocular micrometer). Age-predictive equations can be derived from regression analyses of field data (Kunz & Anthony 1982), after reversing the axes so that either forearm length or total gap are independent variables and age is the dependent variable. Such a regression analysis for the total gap length is shown in figure 3.

Energetics of growth

Body mass

Relative growth curves of body mass for eight species of insectivorous bats are shown in figure 4. Visual inspection of these curves

Figure 3. Regression method for estimating ages of juvenile *Epitesicus fuscus* from total gap length $T$. (After Burnett & Kunz 1982.)

Figure 4. Relative post-natal growth curves of free-ranging (a) *Myotis velifer* (Kunz 1973), (b) *Myotis lucifugus* (Kunz & Anthony 1982), (c) *Pipistrellus pipistrellus* (Rakhmatulina 1972), (d) *Myotis grisescens* (Tuttle 1975), (e) *Pipistrellus subflavus* (Hoying 1983), (f) *Antrozous pallidus* (Davis 1969), (g) *Epitesicus fuscus* (Burnett & Kunz 1982) and (h) *Rhinolophus cornutus* (Yokoyama, Uchida & Shirashi 1975).
reveals that growth in body mass is linear, or nearly so, during the preflight period. Linear rates of mass increase, during the preflight period, have been used in interspecific comparisons of post-natal growth in bats (reviewed Tuttle & Stevenson 1982) and in comparisons with other vertebrates (Case 1978).

Body mass decreases following the onset of flight in at least three species of insectivorous bats (Myotis velifer, M. lucifugus and Pipistrellus pipistrellus) that have been studied in the field (figure 4a–c). Similar losses in body mass have been observed near the time of weaning in some captive bats (see, for example, Kleiman 1969, Krátký 1970, Maeda 1972, Funakoshi & Uchida 1980). Loss of mass during the weaning period suggests that nutritional conditions and energy expeditures at this time may be important. Kunz (1973) postulated that reduced milk consumption associated with weaning, inefficient insect capture in the early days of flight and the added costs associated with flying may lead to the mobilization of fat reserves and loss of body mass in insectivorous bats. Since losses in body mass occur in captive as well as free-ranging bats, reduced milk intake at the time of weaning may be a major factor. Explanations put forward to account for similar mass losses in young birds at the time of fledging include mobilization of body fat and a decrease in water content of the integument as individuals progress toward maturity (Lack 1968, O’Conner 1983, Ricklefs 1984). The suggestion of Bryant & Hails (1983) that fat stores deposited during early growth in aerial feeding insectivorous birds provide ‘insurance’ against unpredictable food supplies may equally apply to some insectivorous bats.

There is little evidence of post-flight losses of body mass in species that give birth to two young (figure 4d–f). Increases in body mass occur steadily throughout most of the early post-natal period in Antrozous pallidus, Eptesicus fuscus and Pipistrellus subflavus, but at lower rates following the onset of flight. Pipistrellus pipistrellus (which typically gives birth to two young) experiences a post-flight loss in body mass, and is an apparent exception to this pattern (figure 4c). Failure to observe a post-flight loss of body mass in other species may simply be an artefact of the methods used for data collection and analysis (see discussion below). Notwithstanding, a common feature among species that give birth to two young is that individual sucklings achieve a lower body mass (relative to adults) at the onset of flight and weaning. By contrast, species that produce a single young (M. velifer, M. lucifugus, M. grisescens and Rhinolophus cornutus) grow rapidly in both absolute and relative terms and usually approach adult masses late in the preflight period.

The above observations are consistent with Case’s (1978) conclusion that slow post-natal growth rates in mammals tend to be associated with larger litter sizes (see also Burnett & Kunz 1982). If milk is a limited resource to suckling bats, then sibling competition may be a factor that lowers the relative rates of mass increase in bats from a litter of two or more. If maternal care during early flight and weaning is prolonged, as appears to be the case in Eptesicus fuscus (Burnett & Kunz 1982), Antrozous pallidus (Vaughan & O’Shea 1976, O’Shea & Vaughan 1977) and R. cornutus (Yokoyama & Uchida 1979), then deposition of major fat reserves in the preflight period may not be important for the support of early flight. By contrast, in those species where maternal care during early flight and weaning is relatively short (e.g. Myotis), fat stores deposited in the preflight period may be essential to support the cost of early foraging flights, when young bats are learning how to fly and capture insect prey.

Interpretation of inter- and intraspecific differences in rates and patterns of body mass change during the post-natal period can be masked by such variables as capture interval, sample size, methods of curve fitting and the geographic location and/or thermal environment of maternity roosts. For example, comparisons of post-natal growth curves for body mass in E. fuscus, based on three different methods of data collection and curve-fitting, reveal similar although qualitatively different patterns of growth of body mass (figure 5a–c). Long recapture intervals, relative to the period of growth (figure 5a) may obscure small but energetically important losses in body mass (figure 5b), particularly in the early flight and weaning period. Similarly, when original data are summarized with curvilinear regressions (figure 5c) without including individual data points, short term but important variations in body mass are likely to be obscured. This can be seen when two methods were used to plot changes in body mass during the post-natal period in M. velifer (Kunz 1973).

Differences in slopes and shapes of growth curves between years and study sites also may reflect metabolic responses to contrasting thermal environments at maternity roosts (Tuttle 1975, Hoying 1983), different colony sizes (Tuttle 1975), food resources available to lactating females (Hoying 1983), and the energy cost of food acquisition by post-flight young (Tuttle 1976). Post-natal gains in body mass in banded cohorts of M. grisescens were significantly different at two maternity caves of contrasting thermal environments (Tuttle 1975). Similarly, Hoying (1983) reported differences in post-natal growth rates in Pipistrellus subflavus during two years of study, characterized by differences in ambient (and roost) temperature and insect availability.
Body composition and energy density

Post-natal changes in the percentage of total body water (TBW) can provide indexes of physiological maturity (Adolph 1970, Adolph & Heggeness 1971). Of the species that have been examined during the post-natal growth period (Myotis thysanodes, M. lucifugus and E. fuscus), young bats are born with a TBW content approaching 80% (O’Farrell & Studier 1973, Stack 1985, Fujita 1986, E.D. Pierson & T.H. Kunz unpublished results). The percentage of TBW decreases throughout the early, linear period of post-natal growth and ceases to change toward the end of the preflight period (figure 6). Thereafter, the percentage of TBW stabilizes near adult levels (67–73%). High rates of decrease in per cent water have been associated with rapid growth rates in birds (Austin & Ricklefs 1977), but too few data are available to test this hypothesis with bats.

Changes in ash-free lean dry mass (AFLDM) and fat content during the post-natal period provide the basis for analyzing and interpreting energy accretion and gross growth efficiency. During the preflight period, AFLDM accumulates at a rate of approximately 0.07 g/day both in M. lucifugus and E. fuscus (E.D. Pierson & T.H. Kunz unpublished, Stack 1985). Although the rate of gain in AFLDM may decrease in the early flight and weaning period, it is noteworthy that this compartment continues to increase during the postweaning period (Stack, 1985, Fujita 1986, E.D. Pierson & T.H. Kunz unpublished results). The rapid gain in energy during the preflight period in M. lucifugus (E.D. Pierson & T.H. Kunz unpublished results) and E. fuscus (Stack 1985) largely reflects increases in fat content. Young M. lucifugus are born with approximately 0.10 g of fat and accumulate an additional 0.05 g/day in the preflight period. By the time sucklings of M. lucifugus begin to fly, they have accumulated a total fat mass of 0.7 g (10.8%). Similarly, young E. fuscus are born with approximately 0.24 g of fat and accumulate a maximum fat mass of 0.88 g (8.3%) in the preflight period. On the basis of an average energy density of 22.2 kJ/g for AFLDM and 39.3 kJ/g for fat, and of the mass increments of these two compartments, rates of energy accretion during the preflight period average 3.67 kJ/day for M. lucifugus (E.D. Pierson & T.H. Kunz unpublished results) and 3.56 kJ/day for E. fuscus (Stack 1985).

Figure 5. Post-natal growth curves of Eptesicus fuscus based on different methods of collecting and plotting field data. (a) Davis et al. (1968), (b) T.H. Kunz & K.A. Nagy (unpublished results) and (c) Kunz (1974).
When lean dry mass and total body fat of young *M. lucifugus* are plotted against body mass, it is clear that both compartments increase linearly, spanning the post-natal growth period from birth to weaning. The high variability of total body fat (figure 7a), relative to the lean dry mass (figure 7b) for individuals that exceed 5.5 g (minimum preflight mass), lends support to the hypothesis that fat is mobilized during the early flight and weaning periods.

**Ontogeny of thermoregulation**

The ontogeny of thermoregulation in *M. lucifugus* (Fujita 1986) is similar to that reported for other bat species (see, for example, Noll 1979, Weigold 1973), altricial birds (Marsh 1979) and some small, terrestrial mammals (Hill 1976, Scheck 1982). Young insectivorous bats (and altricial birds) are essentially poikilothermic in the early preflight period. This is followed by a rapid transition to an effective thermoregulatory stage. Fujita (1986) suggested that the sharp increase in thermoregulatory ability in *M. lucifugus* late in the preflight period may be related to the accumulation of brown adipose tissue and the completion of hair growth. As suggested for some birds and rodents, the delayed onset of active thermoregulation may be an important adaptation to permit rapid growth (McClure & Randolph, 1980, O’Conner 1983).

**Thermoregulation and the maternity roost environment**

Developmental changes in thermoregulatory ability of bats are facilitated by the increasing capacity of the young to produce heat and by aggregate changes in their ability to retain heat (larger mass, increased insulation and improved locomotor ability). Moreover, facultative
torpor, behavioural roost selection and clustering each contribute to reduced thermoregulatory costs of sucklings. Following the departure of females from roosts to feed at night, some sucklings may enter torpor, depending upon their mass and developmental stage and the thermal environment of the maternity roost. Facultative torpor may be an important energy saving strategy for young bats, especially when the roost temperatures drop below thermoneutrality and before their pelage is fully developed. When roost temperatures approach thermoneutrality, energy expenditure of suckling bats should also be minimal. The physical structure of maternity roosts and the gregarious roosting behaviour of several colony species (reviewed by Kunz 1982) should help to maintain roost microclimate and body temperatures of suckling bats at normothermic temperatures (figure 8). Maternity roosts located at sites where individuals are subjected to direct and indirect solar heating (see, for example, Kunz 1973, Humphrey, Richter & Cope 1977) may prompt bats to move along thermal gradients to seek out optimal roost conditions (Licht & Leitner 1967). This behaviour should help to minimize energy expenditure and water loss during the roosting period.

Energy budgets of suckling bats

Compartment model

A simple compartment model of an energy budget for suckling bats is shown in figure 9, where $E_i$ represents ingested milk energy, $E_{fu}$, faecal and urinary energy, $E_{me}$, metabolizable energy and $E_g$ energy accretion during growth (protein and fat). Metabolizable energy $E_{me}$ is calculated by multiplying ingested energy $E_i$ by the metabolizability of milk. Metabolizable energy can be subdivided into (1) the energy fraction retained in the body through accretionary growth $E_g$ and (2) energy expended for maintenance, biosynthesis, thermoregulation, rest and

![Diagram of energy budget](image-url)
activity can be derived, where \( E_m = E_{me} - E_g \). Gross growth efficiency \( e_{eg} \) is determined as the ratio of accretionary growth energy to metabolizable energy: \( e_{eg} = E_g / E_{me} \).

Estimates of the amount of metabolizable energy available to suckling bats (and other mammals) can be determined directly by knowing the amount of milk energy intake, corrected for metabolizability (T.H. Kunz & K.A. Nagy unpublished). Isotope dilution methods and estimates of energy density of milk are required to make direct measurements of milk energy intake (Oftedal 1984, Kunz & Nagy 1986). Several allometric equations for estimating milk energy yield (= intake) at peak lactation have been published (see, for example, Brody, 1945, Linzell 1972, Hanwell & Peaker 1977, Oftedal 1984). Use of these equations requires knowledge either of maternal body mass, mass of mammary glands, mass of suckling at peak lactation, and/or the energy density of milk.

**Milk energy intake at peak lactation**

Estimates of milk energy intake (= output) derived from measurements of daily water flux (using isotope dilution methods) in sucklings and estimates made from two published allometric equations are compared in table 1. Direct measurement of milk energy intake in *M. lucifugus* is comparable to the estimate derived from equation (2) of Hanwell & Peaker (1977), although it exceeds the estimate derived from Oftedal’s (1984) equation by 24.1%. By contrast, measured milk energy intake in suckling *E. fuscus* is 32.6% greater than the estimate derived from Hanwell & Peaker’s equation, but it exceeds the estimate from Oftedal’s equation by only 6.7%. Given the biases of allometric equations derived from average values reported for different species (Heusner 1982), and the potential errors associated with estimating water flux from isotope dilution (Nagy & Costa 1980, Oftedal 1984, Kunz & Nagy 1986), the values given for milk energy intake in table 1 should be regarded as preliminary. Nonetheless, direct measurements of water flux and chemical analysis of milk should provide the most accurate estimate of milk energy intake. A potential complicating factor in use of isotope dilution methods for making direct measurements of water flux in suckling mammals is the possibility that lactating females may recycle water by ingesting urine and/or faeces from sucklings (Baverstock & Green 1975, Baverstock, Watts & Spencer 1979). If this indeed occurs, milk energy intake (= output) as determined by this method may be under-estimated. Studies are presently underway to investigate the possibility that water recycling occurs between mother and infant bats.

### Table 1. Comparison of energy budgets and gross growth efficiencies of suckling *Myotis lucifugus* and *Eptesicus fuscus* at peak lactation. Units are in kJ/day unless otherwise indicated.

<table>
<thead>
<tr>
<th></th>
<th><em>Myotis lucifugus</em></th>
<th><em>Eptesicus fuscus</em></th>
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</thead>
<tbody>
<tr>
<td>body mass</td>
<td></td>
<td></td>
</tr>
<tr>
<td>lactating female</td>
<td>7.7 g</td>
<td>16.1 g</td>
</tr>
<tr>
<td>suckling</td>
<td>6.5 g</td>
<td>10.5 g</td>
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<tr>
<td>accretionary growth ( E_g )</td>
<td>3.67</td>
<td>3.56</td>
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<tr>
<td>isotope dilution method</td>
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<tr>
<td>milk energy intake ( E_i )</td>
<td>18.98</td>
<td>22.87</td>
</tr>
<tr>
<td>metabolizable energy ( E_{me} )</td>
<td>18.03</td>
<td>21.73</td>
</tr>
<tr>
<td>gross growth efficiency ( e_{eg} )</td>
<td>20 %</td>
<td>16 %</td>
</tr>
<tr>
<td>Hanwell &amp; Peaker’s (1977) method</td>
<td></td>
<td></td>
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<tr>
<td>milk energy output (= intake ( E_i ))</td>
<td>18.52</td>
<td>15.41</td>
</tr>
<tr>
<td>metabolizable energy ( E_{me} )</td>
<td>17.59</td>
<td>14.63</td>
</tr>
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<td>gross growth efficiency ( e_{eg} )</td>
<td>21 %</td>
<td>22 %</td>
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<tr>
<td>Oftedal’s (1984) method</td>
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<tr>
<td>milk energy intake ( E_i )</td>
<td>14.40</td>
<td>21.45*</td>
</tr>
<tr>
<td>metabolizable energy ( E_{me} )</td>
<td>13.68</td>
<td>20.37</td>
</tr>
<tr>
<td>gross growth efficiency ( e_{eg} )</td>
<td>27 %</td>
<td>17 %</td>
</tr>
</tbody>
</table>

**Energy budgets of sucklings and growth efficiencies**

Partial and complete energy budgets for suckling *M. lucifugus* and *E. fuscus* at peak lactation are summarized in table 1. Estimates of accretionary growth during the prefight period are based on body composition analysis and calorimetry (Stack 1985, E.D. Pierson & T.H. Kunz unpublished results). Metabolizable energy was estimated from...
daily milk energy intake by assuming a value of 0.95 for the metabolizability of milk (Sadlier 1980). Assuming that measured values of ingested milk energy (based on isotope dilution methods) are closest to the true values, gross growth efficiencies for M. lucifugus (0.20) and E. fuscus (0.16) at peak lactation are essentially identical. These estimates of gross growth efficiency are of the same order of magnitude (0.12 to 0.37) as reported for five species of small, terrestrial mammals (McClure & Randolph 1980). Judging from post-natal growth studies on domestic livestock (see, for example, Brody 1945), gross growth efficiency in bats should be high in the early post-natal growth period, and it should decrease as sucklings progress toward maturity. No studies have reported gross or net growth efficiencies for bats or other free-ranging small mammals over the entire post-natal period.

Maternal investment and energy requirements of lactating females

To estimate maternal investment at peak lactation, I have assumed that the milk energy intake of sucklings is equal to the milk energy yield of lactating females. I have further assumed that milk energy yield represents the major component of maternal investment by lactating females. Energy invested by lactating females in other activities (e.g. social contacts and grooming) should represent a relatively small part of maternal investment. Thus, for a female M. lucifugus, which has a litter size of one, the estimated maternal investment at peak lactation is 18.98 kJ/day (table 1). For female E. fuscus, which has a litter size of two, the expected maternal investment during peak lactation is equal to twice the energy intake of a single bat (2 x 22.87 kJ/day = 45.74 kJ/day).

By using the above estimates of maternal investment and an assumed value of 0.33 for the gross efficiency of milk production (Kunz & Nagy 1986), the daily energy requirements for female M. lucifugus and E. fuscus at peak lactation should be 57.51 kJ/day, respectively. The estimated daily energy requirement of lactating M. lucifugus calculated from milk energy intake of sucklings is 37.5 % greater than the amount (35.98 kJ/day) estimated from nightly food intake on 27 June (40.89 kJ/day), as corrected for digestibility (0.88; Anthony & Kunz 1977). This discrepancy suggests either that nightly food intake of field-captured bats was underestimated (Anthony & Kunz 1977), that the assumed value for the gross efficiency of milk production (0.33) is too low or that the estimate of milk energy is too high. Even when the maximum reported value (0.40) for gross efficiency of milk production is used (Dryden & Anderson 1978), the calculated energy requirement of lactating females (47.45 kJ/day) still exceeds the value based on nightly food intake by 17.5 %. This suggests that our estimates of nightly food intake by lactating M. lucifugus (Anthony & Kunz 1977) may be underestimated by as much as 17.5 to 37.5 %. No independent estimates of nightly food intake are available for free-ranging E. fuscus to undertake similar comparisons.

Environmental factors

The relations between food supply, ambient and roost temperatures and the energetics of post-natal growth in bats are complex. Tuttle & Stevenson (1982) suggested that environmental conditions affecting prefight growth of bats could be divided into roost and non-roost factors. Roost factors affect sucklings and lactating females directly, whereas non-roost factors exert their effects on growing young indirectly by influencing the energy acquisition and milk yield of lactating females. Roost temperatures clearly have a major influence on the metabolic and water economy of sucklings and their mothers. Growth rates may be depressed when sucklings become torpid or when maintenance costs are elevated at low roost temperature. The most important non-roost factor affecting post-natal growth of bats is the availability of food to lactating females. Inclement weather (e.g. cold temperatures, rainy periods, prolonged drought) can have a direct inhibiting effect on insect activity, and this will indirectly influence the net energy intake by foraging bats. Low milk yield from lactating females can directly lead to depressed growth rates of growing young and/or increased suckling mortality (Tuttle & Stevenson 1982, Hoying 1983). Lactating females may sacrifice fat reserves and some lean mass to support the growth of sucking bats (Burnett & Kunz 1982, Stack 1985), but there is a limit to how much fat and lean mass can be given up by a female without reducing her own fitness. Obviously, a fruitful area for further study would be to examine the effects of roost temperature, ambient temperature and food availability on the growth and energetics of free-ranging insectivorous bats.

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