BIOLOGY OF *MYOTIS THYSANODES* AND *M. LUCIFUGUS* (CHIROPTERA: VESPERTILIONIDAE)—II. BIOENERGETICS OF PREGNANCY AND LACTATION

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Abstract—Through bomb calorimetry of known-age young bats, we have determined the energy cost of pregnancy and lactation in *Myotis thysanodes* and *M. lucifugus* finding that:
1. Energy demand during pregnancy is hyperbolic.
2. A very rapid increase in energy involved in embryo growth occurs during late pregnancy when the mothers are no longer homeothermic.
3. This increased energy demand occurs earlier pre-partum in *M. thysanodes* than in *M. lucifugus*.
4. Energy utilized during late embryo growth in *M. lucifugus* (130 cal/day) is significantly greater than in *M. thysanodes* (78 cal/day).
5. Lactation in *M. thysanodes* requires at least 346 cal/day and is much more energy demanding than is pregnancy.

INTRODUCTION

ALTHOUGH energy requirements of pregnancy and lactation have been studied in humans, domestic cattle and several common laboratory rodents (see, for example Brody, 1945; Nelson & Evans, 1961), only recently have data on energetic demands of reproduction been reported for any feral species (Kaczmarski, 1966; Migula, 1969).

Our recent studies have shown that thermoregulatory performances of *Myotis lucifugus* and *M. thysanodes* are significantly affected by reproductive stages (Studier & O'Farrell, 1972). Like other chiropterans, these bats exhibit extremely rapid pre- and postnatal growth (O'Farrell & Studier, 1972). This study presents data on the energy demands of pregnancy and lactation in the two species and includes a further analysis of previous work.

MATERIALS AND METHODS

Known-age embryos with attached placentae from bats used in previous studies (O'Farrell & Studier, 1972; Studier & O'Farrell, 1972) were dried to constant weight,

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crushed and pelleted in mixture with benzoic acid (6318 cal/g). A total of thirty-one pellets were then burned in a Parr oxygen bomb calorimeter (Model 1300) and energy contents of embryos were calculated (see O'Farrell *et al.*, 1971). Additionally, data on postnatal growth and development (O'Farrell & Studier, 1972) were reanalyzed as discussed subsequently in connection with energy cost of lactation. All data were subjected to statistical analyses using an IBM 360, Model 22.

RESULTS AND DISCUSSION

Previous studies concerning bioenergetics of pregnancy and lactation in feral species of mammals (Kaczmarski, 1966; Migula, 1969) have used food consumption as a parameter indicative of calories above maintenance levels required for growth and development of embryos. That method is, of course, valid if the pregnant females are homeothermic throughout the period of pregnancy and extends through lactation if those females also regulate their body temperature at the same levels as do pregnant females. The present method of bomb calorimetry alleviates that requirement and, since the bats studied are not homeothermic throughout pregnancy and lactation (Studier & O'Farrell, 1972), it is specifically useful in this case. This method requires reasonably accurate information on the age of embryos or neonates which may preclude its usefulness in some studies. The study of caloric content of embryos and neonates provides an estimate of the minimum energy which must be daily devoted to growth and is strictly comparable to similar studies using food consumption as a measure only if the excess food ingested is totally assimilated and used exclusively for foetal growth or milk production. Since previous studies of these species (O'Farrell *et al.*, 1971) and other bats and small rodents (Brisbin, 1966; Barrett, 1969; Neuhauser & Brisbin, 1969), show food utilization in excess of 90 per cent of total ingested available calories, both methods of estimating energetics of pregnancy and lactation appear to be approximately equal measures.

Pregnancy

Energy content of embryos with attached placentae are plotted against days prior to birth in Fig. 1. The relationships depicted in Fig. 1 are obviously hyperbolic. Since we are not able to calculate least squares lines for best fit as a hyperbola, we have settled for the best fit polynomial regression lines as given in Table 1. Additionally, Table 1 gives the straight line equations for the last linear segments of the data shown in Fig. 1. During all of early pregnancy, very few calories are devoted to foetal growth. We have shown previously (Studier & O'Farrell, 1972) that during this time span, pregnant females are homeothermic. From the same study, we can calculate the approximate days at which females of both species stop regulating their body temperatures. Those days are at $-37 \cdot 4$ days for *M. thysanodes* and $-18 \cdot 0$ days for *M. lucifugus*. From the data in Table 1, the switch to rapid embryo growth (where $Y = 0$) occurs on $-33 \cdot 6$ days for *M. thysanodes* and $-15 \cdot 7$ for *M. lucifugus*. The loss of homeothermy, therefore, occurs as an immediate prerequisite to rapid foetal growth in both species.
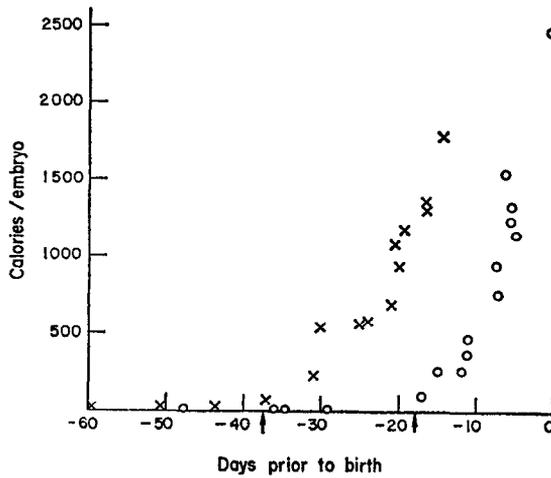
FIG. 1. Energy content (cal/embryo) of known-age embryos with attached placentae of *Myotis thysanodes* (×) and *M. lucifugus* (○). Arrows on abcissa mark last calculated days that pregnant bats would be homeothermic.

TABLE 1—EQUATIONS FOR MINIMUM PRENATAL AND POSTNATAL ENERGY REQUIRED FOR GROWTH IN *M. lucifugus* AND *M. thysanodes*

M. lucifugus—prenatal equations

(1) calories $= 129 \cdot 7 X_b + 2039$ $N = 12$
$\quad\quad (0 \cdot 3030) \quad (196 \cdot 9)$

(2) calories $= 2 \cdot 396 X_b{}^2 + 148 \cdot 1 X_b + 2007$ $N = 16$
$\quad\quad (0 \cdot 2621) \quad (163 \cdot 5)$

M. thysanodes—prenatal equations

(3) calories $= 77 \cdot 62 X_b + 2614$ $N = 11$
$\quad\quad (0 \cdot 3062) \quad (132 \cdot 9)$

(4) calories $= 1 \cdot 025 X_b{}^2 + 114 \cdot 0 X_b + 2909$ $N = 15$
$\quad\quad (0 \cdot 05798) \quad (104 \cdot 4)$

M. thysanodes—postnatal equations

(5) g live wt. $= -0 \cdot 00994 X_a{}^2 + 0 \cdot 409 X_a + 2 \cdot 95$ $N = 138$
$\quad\quad (0 \cdot 00071) \quad (0 \cdot 083)$

(6) g organic wt. $= -0 \cdot 00115 X_a{}^2 + 0 \cdot 0920 X_a + 0 \cdot 546$ $N = 138$
$\quad\quad (0 \cdot 00012) \quad (0 \cdot 0155)$

(7) kcal/individual $= -0 \cdot 00559 X_a{}^2 + 0 \cdot 458 X_a + 2 \cdot 73$ $N = 138$
$\quad\quad (0 \cdot 00063) \quad (0 \cdot 073)$

X_b is the number of days prior to birth; X_a is the number of days after birth. Numbers in parentheses are standard errors of the means.

The period of rapid growth requires 77·6 cal/day in *M. thysanodes* which is significantly less than the 129·7 cal/day required by *M. lucifugus* ($t = 121·2$; $N = 21$; $P < 0·001$). Additionally, the initiation of rapid growth in *M. thysanodes* at 34 days prior to birth occurs earlier than the 16 days prior to birth that such rapid growth is initiated in *M. lucifugus*.

Approximate energetic demand of pregnancy during the period of rapid growth in these bats plus energetic requirements of some rodents are given in Table 2.

TABLE 2—ESTIMATED ENERGY DEMAND OF PREGNANCY AND LACTATION FOR LITTERS AND INDIVIDUAL EMBRYOS AND YOUNG

Species	cal/day per litter	Litter size	cal/day per embryo	Reference
		Pregnancy		
M. thysanodes	77·6	1	77·6	Present study
M. lucifugus	129·7	1	129·7	Present study
Microtus arvalis	255·6–305·6	4–5	51·1–76·4	Migula (1969)
Clethrionomys glareolus	344·4	5	68·8	Kaczmarski (1966)
		Lactation		
M. thysanodes	346·0	1	346·0	Present study
Microtus arvalis	1700·0–1750·0	4–5	340·0–438·5	Migula (1969)
Clethrionomys glareolus	1188·9	5	237·8	Kaczmarski (1966)

From the studies of Kaczmarski (1966) and Migula (1969), energetic costs of pregnancy in rodents appear to be linear rather than hyperbolic as in these vespertilionids. It appears, however, that extra cal/day per embryo are quite similar except for very high values in *M. lucifugus*. Since daily feeding periods of bats are quite restricted due to nocturnal feeding habits and since flight becomes increasingly more difficult and awkward as embryos approach term, it is altogether possible that the energy demands of pregnancy are such as to preclude the development of more than one offspring per female in all but the strongest flyers among chiropteran insectivorous species. Also, it would appear imperative that bats must become conformers as they approach term.

Lactation

From our previous studies (O'Farrell & Studier, 1972), we have calculated the rates of live weight gain and rates of gain of total organic weight of neonates (Table 1). Daily theoretical minimum energy cost of lactation was then calculated from these data by multiplying original data by mean kcal/g organic weight of term embryos (Table 1). This value, 5·001 kcal/g organic weight, compares well with values for several small rodents given by Gorecki (1967). During the 3-week postpartum lactation and growth period, *M. thysanodes* require a daily minimum average

of 346 extra calories above maintenance for milk production. Lactation, then, obviously requires significantly more daily energy than pregnancy; therefore, regulation of body temperature during lactation would be even more harmful than during pregnancy. The mother's ability to remain heterothermic post-partum is of even more value than during late pregnancy (Studier & O'Farrell, 1972). In association with the extreme change in wing loading after delivery (Davis, 1969), lactating bats are much more agile than are pregnant bats and would, therefore, be able to capture insects more readily and be able to devote considerably more energy to reproductive functions. As discussed previously, however, in relation to energy costs and ability to feed during pregnancy, it is quite possible again that the inter-relationships of cost of energy for milk production and ability to feed efficiently may preclude the development of more than one young in most bats.

As seen in Table 2, absolute energy costs of milk production in rodents are much higher than in *M. thysanodes*; however, again, bioenergetic demands of lactation per neonate are quite similar.

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Key Word Index—Bioenergetics; pregnancy; lactation; bats; *Myotis thysanodes*; *Myotis lucifugus*; thermoregulation; growth; development.