ENERGETICS AND WATER FLUX OF FREE-RANGING BIG BROWN BATS 
(EPTESICUS FUSCUS) DURING PREGNANCY AND LACTATION

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ABSTRACT.—We used doubly labeled water to measure carbon dioxide production and water 
flux during pregnancy and lactation in free-ranging big brown bats, Eptesicus fuscus. Mean (±SE) 
carbon dioxide production was 1.749 ± 144 ml/day during pregnancy (n = 16) and 2.770 ± 351 
ml/day during lactation (n = 5). Including estimates of tissue production and milk export, we 
calculated that the average requirement for assimilated energy was 48.9 and 105.1 kJ/day for 
pregnant and lactating females, respectively. About 2% of the total energy required during 
pregnancy was placed into fetal tissue; milk energy accounted for 28% of the energy assimilated 
during lactation. Daily water flux was 8.47 and 17.07 ml/day for pregnant and lactating females, 
respectively. We calculated that E. fuscus obtained >66% of its water preformed in the diet, but 
20–22% of daily water intake was from drinking. Urinary water was the largest component of 
water efflux during pregnancy (72%) and lactation (56%); water exported in milk represented 
22% of daily water efflux during lactation. Calculated evaporative losses for free-ranging E. fuscus 
were half those predicted from laboratory measurements.

Water and energy are factors contributing to the timing and success of mammalian repro-
duction. Consequently, the physiological literature is replete with measurements of various 
energy- and water-related costs associated with pregnancy and lactation. However, the potential 
contribution of each cost to the life-history evolution of a species must be examined within the 
context of total daily or seasonal flux. For example, a maximal milk output of 5 kJ/day is a 
significant energy drain if the mother’s intake is only 10 kJ/day, but of relatively little consequence 
if intake is 100 kJ/day. Although energy expenditure and water turnover often are quantified 
in the laboratory (Coutts et al., 1973; Holleman and Dietrich, 1973), such measurements may 
not apply to free-ranging animals (Nagy and Peterson, 1988). In the wild, mammals must contend 
with predators, competitors, elusive prey, and fluctuating environmental conditions. The demands 
of reproduction should be considered within this complex ecological framework and not solely 
within a rarified laboratory environment.

In recent years, several investigators have used the doubly labeled-water technique to measure 
water and energy flux simultaneously in free-ranging mammals (Bell et al., 1986). Most, however, 
have used only males or nonreproductive females. In the present study, we used doubly labeled 
water to examine daily expenditure of energy and water turnover, during pregnancy and lac-
tation, in 21 free-ranging big brown bats, Eptesicus fuscus. This insectivorous bat was well suited 
for such a study because of its low body mass (15–24 g), small litter size (two), colonial habits, 
and strong roost-fidelity (Barbour and Davis, 1969). In addition, we chose E. fuscus because of 
the extremely large ecological and physiological data base available for this species (Kurta and 
Baker, in press). Our intent was to measure daily energy expenditure and water flux by pregnant 
and lactating females and to partition daily budgets into various components by use of data from 
our previous studies and from the literature.

METHODS

The doubly labeled-water technique provides an indirect measure of metabolic rate through the differential 
turnover of hydrogen and oxygen isotopes (H and O) in body water of an animal. After injection of labeled 
water into an experimental animal, the concentration of each isotope declines over time. Tritium is lost from 
the body as water, whereas O is lost both as water and carbon dioxide. The difference in turnover rate
between the isopes is used to calculate the amount of CO₂ produced (Nagy, 1980). The initial dilution of ¹⁸O in the body-water pool is used to calculate total water content of the body, and the decline in tritium levels is used to calculate water influx and efflux (Nagy and Costa, 1980).

We conducted field work at three E. fuscus maternity colonies in eastern Massachusetts between May and July 1985 and 1986. Individual bats were gathered from their maternity roosts between 1300 and 1500 h. After capture, each bat was weighed to the nearest 0.01 g (Ohaus, Model 1010-10) and marked with a numbered plastic band (A. C. Hughes, Ltd.). We used a calibrated glass syringe (Hamilton) to inject each bat intraperitoneally with 0.05 ml of sterile water containing 95 atom % of ¹⁸O and 32 microcuries (1.184 × 10¹⁵ Bq) of ³H/µl. We allowed 1 h for equilibration of isotopes with the body-water pool (Kunz and Nagy, 1988). During equilibration, bats were housed in small wooden cages that simulated the roost environment and minimized physiological and psychological stress (Kunz and Kurta, 1988). After equilibration, we obtained a small blood sample from a vein in the wing or tail membrane (Kunz and Nagy, 1988) before releasing the bat inside its home roost. Injected bats were recaptured 1 or 2 days after injection. Mean deviation from exactly 1 or 2 days was −0.06 ± 0.03 days (n = 21); this negative deviation may lead to an underestimate of daily costs by 3–6% (Speakman and Racey, 1988). Upon recapture, each bat was weighed and bled a second time; mean change in body mass was +0.2 ± 0.6%. Between captures, minimum and maximum ambient temperatures were recorded inside each roost; occasional equipment failure prevented us from obtaining roost temperatures on all days. Minimum and maximum ambient temperatures outside the roosts were obtained from on-site measurements or the nearest weather station.

Blood samples were flame-sealed in heparinized glass capillary tubes and transported on ice to the laboratory. Each sample was vacuum distilled, and the resulting water was analyzed for isotope activity. Tritium was measured by liquid-scintillation counting; ¹⁸O was measured by proton-activation analysis (Wood et al., 1975). Carbon dioxide production, total water content of the body, and water flux were calculated by use of the equations of Lifson and McClintock (1966) as modified by Nagy (1975).

We calculated water and energy budgets based on average insect composition. Insects typically contain 70% water, 17.8% protein, 4.6% fat, 2.2% carbohydrate, 3.8% chitin, and 1.5% ash (Kurta et al., 1989a). We assumed that 95% of ingested protein, fat, and carbohydrate was assimilated and that chitin was totally indigestible (Altman and Dittmer, 1968). Thus, 0.07 g of dry feces are produced from each gram of ingested insects. Assimilated protein, fat, or carbohydrate (glycogen) contains 23.6, 39.5, or 17.7 kJ/g, respectively (Robbins, 1983); chitin contains 21.2 kJ/g (calculated from Karasov, 1982). Approximately 15% of assimilated protein energy is not metabolized but is excreted as urea (Braithwaite and Llewellyn, 1982). One gram of fresh insects, therefore, provides E. fuscus 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 wet mass (24.17 kJ/g dry mass) is similar to values obtained with bomb calorimetry (Kunz, 1988). If 1 g of metabolized protein, fat, or carbohydrate yields 862, 1,400, or 830 ml CO₂, respectively (Braithwaite and Llewellyn, 1982; Robbins, 1983), then each liter of CO₂ produced represents 24.5 kJ of metabolized energy or 27.2 kJ of assimilated energy. In addition, each liter of CO₂ produced indicates that 0.75 g of protein has been metabolized. When calculating water budgets, we assumed that metabolism of 1 g of protein, fat, or carbohydrate produced 0.425, 1.08, or 0.556 ml H₂O/g, respectively (Braithwaite and Llewellyn, 1982; Robbins, 1983). Based on these equivalents and typical insect composition, we calculated that 0.583 ml of metabolic water results for each liter of CO₂ produced.

**Results**

**Metabolic rate**.—We measured the CO₂ production rates of 16 pregnant and five lactating E. fuscus. Mean (±SE) production of carbon dioxide was 1.749 ± 0.144 ml/day during pregnancy and 2.770 ± 0.351 ml/day during lactation. Assimilated energy equivalents are 47.6 ± 3.92 and 75.3 ± 9.54 kJ/day during pregnancy and lactation, respectively. Mean body mass was 20.84 ± 0.77 g for pregnant females and 17.57 ± 0.38 g in lactation. Mass-specific metabolic rate was 85.3 ± 6.8 ml CO₂ g⁻¹ day⁻¹ during pregnancy and 160.4 ml ± 22.1 ml CO₂ g⁻¹ day⁻¹ during lactation. Carbon dioxide production during lactation was significantly greater than during pregnancy on both a whole-animal basis (t = 3.18, d.f. = 19, P = 0.005) and on a mass-specific basis (t = 4.40, d.f. = 10, P = 0.0003).

During pregnancy or lactation, mass-specific CO₂ production was not correlated with absolute length of the measurement period, deviation of the measurement period from 24 or 48 h, body
mass, percent change in body mass, minimum and maximum external ambient temperature, or minimum and maximum ambient temperature within the roost (product-moment correlations; all \( P > 0.10 \)). The lack of a significant correlation between metabolic rate and absolute measurement period, deviation of the measurement period, or change in body mass suggests that our methods had little influence on energy expenditure by the bats. The low explanatory power of environmental (temperature) variables is similar to that seen in free-ranging little brown bats, *Myotis lucifugus* (Kurta et al., 1989a) and in some birds (Bryant et al., 1985). Although maternal energy demand might be expected to change significantly as the fetus approaches term, the lack of a significant correlation between metabolic rate and maternal body mass during pregnancy suggests that stage of gestation is not a major determinant of energy expenditure by free-ranging bats. Similar results were reported for *M. lucifugus* (Kurta et al., 1989a). Presumably, most variation in CO2 production by *E. fuscus* is related to differences in length of the energetically costly foraging period (Brigham and Fenton, 1986) or differential use of torpor (Audet and Fenton, 1988). Prolonged torpor obviously occurred in two pregnant *E. fuscus* and resulted in metabolic rates (27.9 ± 11.7 ml CO2 g⁻¹ day⁻¹) <50% of the mean value. Excluding these two animals from the correlation analyses did not result in significant relationships.

**Body water content and water flux.**—A small amount of labeled water leaked from the injection site of five pregnant *E. fuscus*; consequently, we could not calculate total body water based on 18O dilution for these bats. Total body water measured as 18O-dilution space was 67.6 ± 0.7% for the other 11 pregnant bats and 69.5 ± 1.2% for the five lactating females. These values are not significantly different (t = 1.48, d.f. = 14, \( P = 0.16 \)) and are similar to those reported by Stack (1985) based on desiccation. Combining both pregnant and lactating females yielded a mean body-water content of 68.2 ± 0.6% (n = 16). Water influx averaged 406 ± 29 ml H2O kg⁻¹ day⁻¹ (8.47 ± 0.67 ml/day) during pregnancy and 997 ± 194 ml H2O kg⁻¹ day⁻¹ (17.13 ± 3.03 ml/day) during lactation. Water efflux was 407 ± 26 ml H2O kg⁻¹ day⁻¹ (8.47 ± 0.60 ml/day) for pregnant females and 989 ± 189 ml H2O kg⁻¹ day⁻¹ (17.00 ± 2.95 ml/day) for lactating *E. fuscus*. Mass-specific rates of influx (t = 3.02, d.f. = 42, \( P = 0.04 \)) and efflux (t = 3.06, d.f. = 41, \( P = 0.04 \)) were significantly greater, and more variable (F-tests, \( P < 0.0001 \)), for lactating bats than for pregnant individuals. The greater flux during lactation probably is related to milk export.

Mass-specific influx and efflux did not differ significantly during pregnancy (paired t = 0.21, d.f. = 15, \( P = 0.84 \)) or lactation (paired t = 0.92, d.f. = 4, \( P = 0.41 \)) indicating that water budgets were balanced on a daily basis. Daily water flux, therefore, was taken to be the mean of influx and efflux rates, or 406 and 993 ml H2O kg⁻¹ day⁻¹ for pregnant and lactating *E. fuscus*, respectively. These mean rates are equivalent to 8.47 ml/day during pregnancy and 17.07 ml/day during lactation.

For pregnant and lactating females, correlations of mass-specific rates of influx and efflux with length of measurement, minimum external ambient temperature, minimum roost ambient temperature, and body mass were not significant (all \( P > 0.05 \)). Influx (t = 0.81, d.f. = 5, \( P = 0.03 \)) and efflux (t = 0.77, d.f. = 5, \( P = 0.04 \)) were correlated with maximum ambient temperature of the roost during pregnancy but not during lactation (both \( P \geq 0.30 \)). Influx (t = -0.90, d.f. = 3, \( P = 0.04 \)) and efflux (t = -0.91, d.f. = 3, \( P = 0.03 \)) were correlated with maximum external ambient temperature during lactation but not during pregnancy (both \( P \geq 0.30 \)). Small sample sizes and border-line probabilities indicate the need for further work in clarifying the relationship between water flux and environmental temperature in this species.

In addition, rates of influx (t = 0.72, d.f. = 14, \( P = 0.002 \)) and efflux (t = 0.62, d.f. = 14, \( P = 0.01 \)) of pregnant females were correlated with percent change in body mass. These correlations suggest that pregnant bats that gained weight had slightly greater fluxes than those that did not; such correlations are common in free-ranging animals (Bell et al., 1986; Nagy et al., 1978). Regressions of influx and efflux on change in body mass intersect the y-axis at about 410 ml H2O kg⁻¹ day⁻¹. This flux is essentially identical to the previously calculated 406 ml H2O kg⁻¹ day⁻¹; consequently, we ignored the slight difference when analyzing water budgets.
Energetics.—In addition to energy expenditure measured by doubly labeled water, the cost of pregnancy includes chemical energy stored in the fetus and maternal reproductive structures. Using bomb calorimetry, Stack (1985) showed that the energy density of neonatal E. fuscus is 4.54 kJ/g. Newborn E. fuscus weigh 3.3 g (Burnett and Kunz, 1982); therefore, the average E. fuscus litter contains 30.0 kJ of energy at birth. In E. fuscus, 78.7% of the energy stored in the fetus, uterus, placenta, and mammary glands during pregnancy is in the fetus itself (Stack, 1985). Thus, we calculate that total production by pregnant E. fuscus is 38.1 kJ.

Eptesicus fuscus has a gestation period of about 60 days (Barbour and Davis, 1969). The capture dates (14 May–11 June) and body masses (16.8–25.9 g) of our pregnant bats indicated that these females ranged from about midgestation to near parturition; thus, our field measurements provide a reasonable estimate of average assimilated energy demands during the last half (30 days) of gestation. Measurements with doubly labeled water indicated that requirements for assimilated energy during late pregnancy consist of 30 days at an average of 47.6 kJ/day, or 1,428 kJ. For simplicity, we assumed that all production occurred during the last half of pregnancy (Robbins, 1983). Therefore, total energy expenditure in late pregnancy is 1,466 kJ, or an average of 48.9 kJ/day; E. fuscus needs 8.0 g of fresh insects to meet this daily energy demand. Energy placed into fetal tissue (30 kJ) represents only 2.0% of the total; this proportion is lower compared with that of small terrestrial mammals (McClure, 1987; Migula, 1969) but slightly greater than that reported for M. lucifugus (1.4%—Kurta et al., 1989a).

Based on analysis of stomach contents from known-aged juveniles, we determined that lactation lasts approximately 34 days and that young E. fuscus consume only milk for the first 26 days. Based on field measurements of metabolic rate of juveniles and the composition of E. fuscus milk (Kunz et al., 1983), we calculated that milk energy export for 34 days represents 1,014 kJ, or 29.8 kJ/day. Our field measurements of lactating females in the present study indicate that average requirement for assimilated energy, not including milk, is 75.3 kJ/day; for 34 days, this adds to 2,560 kJ. Including milk export, total costs become 3,574 kJ or 105.1 kJ/day. Average daily expenditure during lactation is more than double that of pregnancy. A lactating E. fuscus needs 17.2 g of fresh insects, 99% of maternal mass, to supply its daily energy requirement; this proportion is slightly greater than that reported for lactating M. lucifugus (85% of maternal mass—Kurta et al., 1989a). During lactation, E. fuscus exports 28% of total assimilated energy as milk. Myotis lucifugus, with a smaller litter size and a shorter lactation period (26 days), devotes 32% of total expenditure of energy during lactation to milk export (Kurta et al., 1989a). We caution that our calculations for lactating E. fuscus are preliminary. Our sample size is small (five) and includes only two capture dates; consequently, our measured maintenance costs may not be representative of all of lactation. Our “average” value, however, is 24% lower than the 138 kJ/day predicted by Kunz (1987) for peak lactation in E. fuscus.

Eptesicus fuscus females lose an average of 14–15% of their postpartum body mass during lactation (Burnett and Kunz, 1982; Stack, 1985). This decline in body mass represents 47 kJ (Stack, 1985), or 1.3% of our calculated total cost (3,574 kJ), and is similar to percentages reported for 8-g M. lucifugus (2.0%—Kurta et al., 1989a) and 9-g Plecotus auritus (<5%—Speckman and Racey, 1987). The entire amount of energy withdrawn from stores during lactation would not provide an E. fuscus with enough energy to meet the average requirement for one day. Although many mammals store significant quantities of fat during pregnancy to later subsidize lactation (Sadleir, 1984), this strategy apparently is not used by small insectivorous bats (Racey and Speckman, 1987). The small body size of E. fuscus may preclude storage of large amounts of fat in a pregnant female already accommodating a large litter mass (40% of maternal postpartum mass—Burnett and Kunz, 1982).

Water flux.—Field measurements of water flux, by isotope-dilution techniques, exist for only four species of bats including E. fuscus. In two previous studies, only nonreproductive individuals were used. Bell et al. (1986) reported a mean flux of 200 ml kg⁻¹ day⁻¹ in the 13-g insectivorous Macrotrus californicus, and von Helversen and Reyer (1984) reported 1,165 ml kg⁻¹ day⁻¹ for
the 11.5-g nectarivorous *Anoura caudifer*. Both measurements are considerably different from those we obtained for pregnant (406 ml kg⁻¹ day⁻¹) and lactating (939 ml kg⁻¹ day⁻¹) *E. fuscus*. Differences among *E. fuscus*, *A. caudifer*, and *M. californicus* may be related to differences in diet, habitat (for *M. californicus*, tropical for *A. caudifer*), or reproductive condition.

The fourth bat species, *M. lucifugus*, apparently is the only small eutherian that has had flux quantified in the field during pregnancy and lactation (Kurta et al., 1989b); in this temperate insectivorous species, flux rates were 696 and 888 ml kg⁻¹ day⁻¹ during pregnancy and lactation, respectively. During pregnancy, the lower mass-specific turnover of water in *E. fuscus*, compared to that of *M. lucifugus*, probably is related to the lower surface-area:body-mass ratio of the larger *E. fuscus*, but the generally cooler roosting environment of *E. fuscus* also may be a factor. During lactation, however, *E. fuscus* actually has a higher mass-specific water flux than the smaller *M. lucifugus*. The higher flux is presumably related to the greater milk output needed by *E. fuscus* to raise a litter of two compared to a single offspring in *M. lucifugus*.

Based on our isotope-dilution measurements and data from the literature, we partitioned daily water flux into its major components. Pregnant *E. fuscus* ingests an average of 8.0 g of insects each day, and a lactating female, 17.2. If insects are 70% water, then preformed water intake is 5.60 and 12.04 ml/day during pregnancy and lactation, respectively. If 0.583 ml of metabolic water are produced for each liter of CO₂ produced, then production of metabolic water is 1.02 ml/day during pregnancy and 1.61 ml/day during lactation. Total daily flux measured by tritium turnover is 8.47 ml/day for pregnant *E. fuscus* and 17.07 ml/day for lactating females. Subtracting preformed and metabolic water from total flux provides an estimate of the volume of drinking water required. During pregnancy, females obtain 1.85 ml/day from drinking, whereas lactating females require 1.61 ml/day.

Preformed water represents >66% of daily influx, but 20-22% of daily influx is obtained by drinking. A similar reliance on drinking water (20-26% of daily influx) was reported for free-ranging *M. lucifugus* in New England (Kurta et al., 1989b). The extent to which *E. fuscus* relies on drinking water in mesic Massachusetts (<22%) is considerably lower than predicted by Carpenter (1969) for *E. fuscus* in desert regions (42%).

We also partitioned daily water efflux into urinary, fecal, and evaporative components based on our field measurements and data from the literature. Carpenter (1969) studied the urine-concentrating ability of *E. fuscus* from Arizona and California with captive bats maintained on a diet of insects, bananas, and cottage cheese. He reported that *E. fuscus* needs 4.63 ml H₂O to excrete the urea resulting from metabolism of 1 g of protein. If 0.75 g of protein are metabolized for each liter of CO₂ produced from an insect diet, then protein metabolism by *E. fuscus* in the present study is 1.31 and 2.08 g/day during pregnancy and lactation, respectively. Assuming that Carpenter’s (1969) data on urea production apply to free-ranging bats, we calculated that the resulting urea requires 6.07 and 9.63 ml H₂O for excretion. These volumes probably are conservative, because urine-concentrating ability of bats from the arid Southwest may be greater than that of *E. fuscus* in Massachusetts (Bassett, 1982). If 0.07 g of dry feces are produced from each gram of ingested insects and if fresh bat feces contain 60% water (Bassett and Studier, 1988; Rumage, 1979), then *E. fuscus* loses 0.84 and 1.81 ml H₂O as fecal water during pregnancy and lactation, respectively. For lactating females, daily milk water averages 3.83 ml (Kunz et al., 1983). Subtracting urinary, fecal, and milk water from total daily flux provides an estimate of water loss by pulmocutaneous evaporation. During pregnancy, evaporative losses equal 1.52 ml and, during lactation, 1.80 ml.

Calculated evaporative losses are considerably less than expected from laboratory studies. Carpenter (1969), for example, indicated that evaporative water loss of *E. fuscus* in flight equals 3.10% of body mass per hour and that evaporative water loss during roosting is 0.57% of body mass per hour. If these rates apply, then our 20.8-g pregnant bats should lose 4.01 ml through evaporation, or 2.6 times more than we calculated. Laboratory measurements, such as Carpenter’s (1969), probably overestimate evaporative losses while roosting because laboratory workers generally use solitary bats exposed to dry air. In the field, *E. fuscus* consistently clusters with conspecifics in relatively moist environments (40-90% relative humidity); these behaviors should
reduce evaporative losses by decreasing exposed surface area and by decreasing metabolic rate. In addition, Carpenter’s (1969) measurement of water loss during flight was made at an ambient temperature of 25°C. Ambient temperatures encountered by foraging *E. fuscus* in New England generally are 10–20°C. The lower air temperature during foraging flight leads to a lower body temperature (O’Farrell and Bradley, 1977) which decreases the vapor-pressure deficit and lessens water loss by evaporation (Studier and O’Farrell, 1980). The predominance of urinary over evaporative losses by *E. fuscus* in the present study is similar to that reported for free-ranging *M. lucifugus* (Kurta et al., 1989b).

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