ENERGETIC ADVANTAGES OF SLIGHT DROPS IN BODY TEMPERATURE IN LITTLE BROWN BATS, *MYOTIS LUCIFUGUS*

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Abstract—1. At constant ambient temperatures (T_a) below their thermal neutral zone (TNZ), little brown bats, *Myotis lucifugus*, maintain a wide range of steady-state body temperatures (T_b).

2. The relationship between oxygen consumption and T_b–T_a differential at constant T_as below the TNZ is curvilinear.

3. Small drops in T_b from high T_b levels result in significantly greater energy savings than subsequent T_b reductions of equal increments.

INTRODUCTION

Deep body temperature (T_b) and oxygen consumption (OC) as functions of ambient temperature (T_a) have been determined for a wide variety of mammals. Assuming that the organisms under consideration do not significantly utilize anaerobic energy producing metabolic pathways and T_b is constant during the period of measurement, the rate of OC is directly related, with little error, to metabolic heat production. Possible interrelationships between T_b, OC, and T_a have often been discussed and debated (Scholander *et al.*, 1950; Kleiber, 1961; King, 1964; Tucker, 1965; Porter & Gates, 1969; McNab, 1970; Strunk, 1971; Kleiber, 1972; Calder, 1972; Calder & King, 1972; Strunk *et al.*, 1973; McNab, 1980). Of particular interest is the relationship of OC and the T_b–T_a differential (T_b–T_a) in endotherms at T_as below the thermal neutral zone (TNZ). In mammals in which steady-state T_b is constant and independent of T_a, i.e. in homeothermic endotherms, T_b–T_a differential can be obtained only by varying T_a. It is, therefore, impossible to analyze the relation of OC to T_b–T_a at constant T_a in such species. Among heterothermic endotherms, however, some data are available (Studier & O'Farrell, 1972, 1976) for OC at a wide range of steady-state T_bs at constant T_a. This paper reports the relationships between OC and T_b–T_a at constant T_as below the TNZ in a heterothermic endotherm, the little brown bat, *Myotis lucifugus*, and comments on the energetic advantages of this thermoregulatory strategy.

MATERIALS AND METHODS

Data analyzed for the present study are taken from Studier & O'Farrell (1972). Details of materials and methods used appear in that paper and will be summarized here. Adult, female little brown bats of varying reproductive conditions (pregnant, lactating, post-lactating) collected throughout the summer from a maternity colony were studied. All laboratory studies were performed on the day of capture. Steady-state OC and T_b were recorded at T_as of 16–40°C at 4°C intervals. Laboratory controlled T_as were programmed to coincide with T_as in the natural roost.

RESULTS AND DISCUSSIONS

Steady-state T_bs of little brown bats at various controlled T_as (shown in Fig. 1) indicate the heterothermic pattern of thermoregulation exhibited by these bats when tested on the day of capture. Much of the variability in level of regulated T_b is a function of stage of pregnancy, stage of reproductive cycle, etc. (Studier & O'Farrell, 1972).

Data on OC and T_b–T_a at various controlled T_as from 16–32°C were analyzed by both stepwise polynomial regression and by least squares regression analysis of eleven possible power, root, and reciprocal transformations of both OC and T_b–T_a together and independently to determine the best statistical descriptions of the relationships between these variables. Regression coefficients for the independent variable (T_b–T_a) as a squared term or squared transformation were invariably significant, except at a T_a of 32°C. Based on comparing coefficients of determination (r^2) for maximal values, the best uniform regression analysis, except at 32°C, were curvilinear equations of the form $y = bx^2 + a$, where y is OC in cc/g per hr and x is T_b–T_a in °C. Equations are given in Table 1 and illustrated in Fig. 2. The relationship of OC to T_b–T_a becomes progressively less curved as T_a rises until at a T_a of 32°C, which is the thermal neutral temperature for this species (Stones & Wiebers, 1965), the relationship is linear. Since thermal conductance (McNab, 1980) is represented by the slopes of the lines in Fig. 2, at T_as below the TNZ, thermal conductance is not a constant. Linear regression analysis of these variables (OC and T_b–T_a) will, therefore, underestimate actual thermal conductance when T_b–T_a is large and overestimate thermal conductance when T_b–T_a is small. As stated earlier, in homeothermic endotherms, the only method of obtaining T_b–T_a is by modifying T_a. For such species, thermal conductance is characteristically estimated by analyzing the slope of the relationship of OC to T_a at T_as below the TNZ. Since T_b is constant in such species, the abscissa is related to T_b–T_a and resultant figures show a negative slope since T_b–T_a decreases as T_a rises. Such graphic representations are,
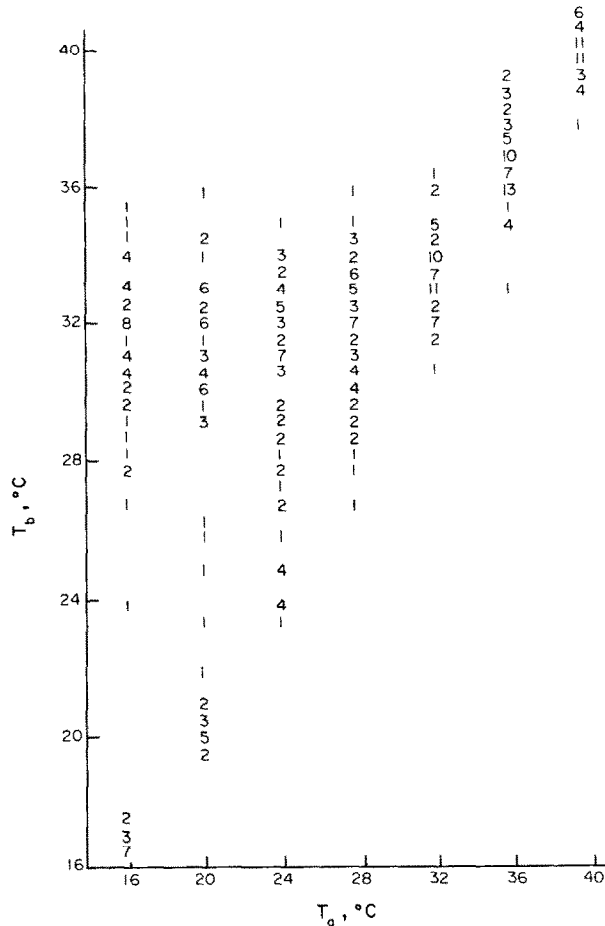
Fig. 1. Steady-state body temperatures (T_b) of adult female *Myotis lucifugus* of varying reproductive condition at constant ambient temperatures (T_a). Numbers indicate the number of data points at that position.

therefore, inverted left to right in comparison to Fig. 2. Inspection of some published figures depicting OC as a function of T_a in homeothermic endotherms

Table 1. Reduced statistical data for the relationship of oxygen consumption (*y*, in cc/g per hr) to body temperature to ambient temperature differential (*x*, in °C) at various ambient temperatures (T_a) in *Myotis lucifugus*. Regression coefficients are for equations of the form $y = bx^2 + a$. $P < 0.0005$ in all cases. Values in parentheses are standard errors.

| T_a (°C) | Regression coefficients | | F | d.f. | r^2 |
	b	a			
16	0.0192 (0.0013)	0.268 (0.154)	203.4	1,29	0.875
20	0.0194 (0.0014)	0.149 (0.120)	182.8	1,23	0.888
24	0.0263 (0.0020)	0.558 (0.077)	166.8	1,33	0.835
28	0.0430 (0.0062)	0.480 (0.096)	48.6	1,29	0.627
32*	0.441 (0.081)	0.271 (0.158)	29.4	1,32	0.487

* Regression coefficients are for the linear equation: $y = bx + a$.

shows relationships which appear to be curvilinear although they are often analyzed in rectilinear fashion (e.g. Banholzer, 1976; Grant & Dawson, 1978; Kamau *et al.*, 1979; Degabriele & Dawson, 1979; Rübsamen & Kettembeil, 1980). The rectilinearity of this relationship has been questioned previously (Tracy, 1972). Furthermore, when thermal conductance is calculated on individual measurements of T_b and OC, it is apparent for many species that thermal conductance is not constant (McNab, 1980). Since methods are available for curvilinear (polynomial) regression analysis, such analysis should be performed to determine the best descriptive statistics of data such as OC as a function of T_a in homeothermic endotherms. Such analysis would yield more accurate estimates of minimal standard metabolism and thermal neutral temperature (Studier *et al.*, 1975).

The curvilinearity of the relationship of OC to T_b-T_a at constant T_as in *M. lucifugus* (Fig. 2) would not appear to be related to changes in the bats' physical environment but probably reflects some animal-regulated property. Possibilities include animal regulated differences in metabolic heat production and/or in heat flow through changes in conductivities of the shell (King & Farner, 1961) or in peripheral blood flow, etc. The relatively linear, upper portions of the OC to T_b-T_a relations (Fig. 2) may well be parallel
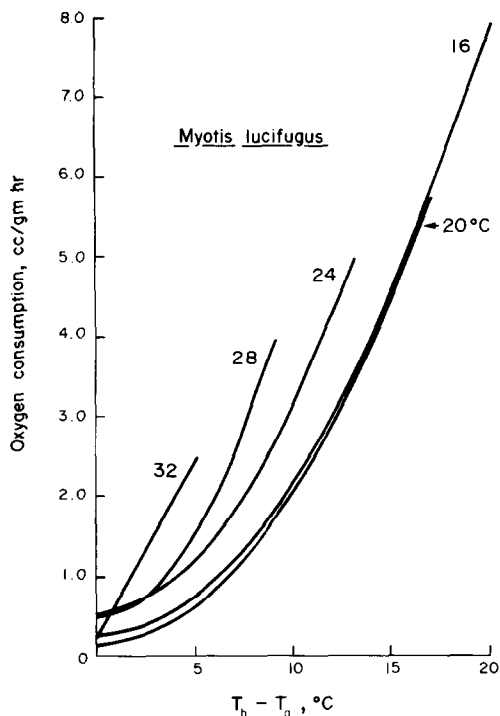
Fig. 2. Regression equations at various ambient temperatures for the relationship of oxygen consumption to body temperature to ambient temperature differential (T_b-T_a) in *Myotis lucifugus*.

and indicate uniform energetic responses at various T_as when T_b-T_a differential exceed a critical level. The lowering of r^2 values as T_a increases indicates that T_b-T_a differential explains progressively less of the variability in OC.

While a statistically significant rectilinear relationship exists between OC and T_b-T_a at all T_as analyzed, the relationship is best described by a curvilinear equation except at a T_a of 32°C. Use of a rectilinear equation predicts equal reductions in OC for any incremental reduction in T_b whereas the curvilinear equations show larger reductions in OC when T_b is reduced in equal increments from a high set point. As an example, at a T_a of 20°C a drop in T_b from 37°C (5.76 cc/g per hr) to 33°C (3.43 cc/g per hr) results in a reduction of OC of 2.33 cc/g per hr. Using 4.8 cal/cc of oxygen as an energy equivalent, this is a savings of 11.2 cal/g per hr. A further drop in T_b from 33°C to 29°C (1.72 cc/g per hr) results in a considerably reduced energy savings of only 8.2 cal/g per hr.

It is also useful to consider energy requirements for raising T_b. At a T_a of 16°C, minimum OC in *M. lucifugus*, when $T_b-T_a = 0$, is 0.268 cc/g per hr. A doubling of OC, to 0.536 cc/g per hr, yields a T_b-T_a of 3.7°C; a tripling of OC yields a T_b-T_a of 5.3°C; and, a quadrupling of minimal OC gives a T_b-T_a of 6.5°C. From this perspective, the curvilinearity of the relation of OC to T_b-T_a supports the hypotheses that homeothermy evolved gradually (Dawson *et al.*, 1979) or in stepwise intervals (Crompton *et al.*, 1978) rather than as a single major jump (Dawson & Hulbert, 1970), since the intermediate set points for controlled T_b require

disproportionately less energy than a very high T_b set point.

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