METABOLIC PHYSIOLOGY OF EUTHERMIC AND TORPID LESSER LONG-EARED BATS, *NYCTOPHILUS GEOFFROYI* (CHIROPTERA: VESPERTILIONIDAE)

DAVID J. HOSKEN AND PHILIP C. WITHERS

Zoologisches Museum der Universität Zürich-Irchel, Winterthurerstr 190, 8057 Zürich, Switzerland (DJH)

Department of Zoology, The University of Western Australia, Nedlands, Western Australia 6907, Australia (PCW)

Thermal and metabolic physiology of the Australian lesser long-eared bat, *Nyctophilus geoffroyi,* a small (ca. 8 g) gleaning insectivore, was studied using flow-through respirometry. Basal metabolic rate of *N. geoffroyi* (1.42 ml O_2 g^{-1} h^{-1}) was 70% of that predicted for an 8-g mammal but fell within the range for vespertilionid bats. *N. geoffroyi* was thermally labile, like other vespertilionid bats from the temperate zone, with clear patterns of euthermy (body temperature >32°C) and torpor. It was torpid at temperatures ≤25°C, and spontaneously aroused from torpor at ambient temperatures ≥5°C. Torpor provided significant savings of energy and water, with substantially reduced rates of oxygen consumption and evaporative water loss. Minimum wet conductance (0.39 ml O_2 g^{-1} h^{-1} $°C^{-1}$) of euthermic bats was 108% of predicted, and euthermic dry conductance was 7.2 J g^{-1} h^{-1} $°C^{-1}$ from 5–25°C. Minimum wet and dry conductances of bats that were torpid at an ambient temperature of 15–20°C (0.06 ml O_2 g^{-1} h^{-1} $°C^{-1}$ and 0.60 J g^{-1} h^{-1} $°C^{-1}$) were substantially less than euthermic values, but conductance of some torpid bats increased at lower ambient temperatures and approached values for euthermic bats. Metabolic rates of bats torpid at ambient temperatures >10°C and bats euthermic in the thermoneutral zone indicated a metabolic Q_{10} of 3.9. That high Q_{10} suggested that there may have been an intrinsic reduction in metabolic rate during torpor, in addition to down-regulation of thermoregulation (which accounted for most of the reduction in metabolic rate) and the normal Q_{10} effect.

Key words: *Nyctophilus geoffroyi,* lesser long-eared bat, torpor, euthermy, metabolism, water loss, conductance, Q_{10}

Energetic costs of endothermy are high (French, 1992), and endotherms living in temperate climates are faced with a two-fold problem, seasonally cold temperatures and a concurrent reduction in availability of food (McNab, 1982). These problems are especially relevant for small mammals with their high ratio of surface area to volume and small reserves of fat (French, 1985).

One way to survive periods of decreased productivity and cold is to decrease energetic expenditure by daily or seasonal torpor, during which body temperature is lowered and often approaches ambient temperature. Routine reduction in metabolic rate and body temperature in response to decreased ambient temperature and activity has been recorded in many bats inhabiting temperate latitudes (e.g., Kurta and Kunz, 1988; McNab, 1982; Webb et al., 1993). Torpor can reduce metabolic expenditure by >90% (Hosken, 1997; Hosken and Withers, 1997; Morris et al., 1994; Thomas et al., 1990). Although most studies of the metabolic physiology of microchiropteran bats have investigated species from Europe and North America (Findley,

1993), there has been recent interest in the physiology of Australian bats, especially vespertilionids (Geiser et al., 1996; Hosken, 1997; Hosken and Withers, 1997; Morris et al., 1994).

We investigated the thermal and metabolic physiology of an Australian vespertilionid, the lesser long-eared bat, *Nyctophilus geoffroyi* in the laboratory. This is a small (ca. 8 g) gleaning insectivore (Hosken et al., 1994), found throughout most of mainland Australia (Maddock and Tidemann, 1995). Kulzer et al. (1970) reported that *N. geoffroyi* maintained a body temperature ca. 2–4°C above ambient temperature at 24°C when torpid, and Maddock and Tidemann (1995) reported it to enter torpor, but there are no detailed studies of its metabolic physiology. We compare here rates of oxygen consumption and carbon dioxide production, respiratory exchange ratio, rate of evaporative water loss, and thermal conductance for euthermic or torpid bats over a range of ambient temperatures.

Materials and Methods

Animals.—Body temperature and metabolic rate were investigated for eight adult *N. geoffroyi*, two males and six non-pregnant females. Bats were captured near the Perrup Research Centre (34°10′S, 116°50′E), ca. 350 km S of Perth, Western Australia. They were housed in outdoor flight-cages (5 by 2 by 2.2 m) at the University of Western Australia, under regimes of natural light and temperature. Bats were fed mealworms (*Tenebrio molitor*), with occasional crickets (*Teleogryllus*) and bushcrickets (*Requena verticalis*). Mealworms were dusted with powdered milk, and a vitamin supplement (Pentavite, Roche Consumer Health, Dee Why, New South Wales, Australia) was added. Fresh water was supplied ad lib. Metabolic investigations in autumn and winter 1996, began after animals had been in captivity for ca. 3 weeks. All bats appeared healthy and maintained a stable body mass between ca. 6–10 g, averaging 8.0 ± 0.1 (*SE*) g.

Laboratory methods.—The rate of oxygen consumption ($\dot{V}O_2$; ml O_2 g^{-1} h^{-1}) and carbon dioxide production ($\dot{V}CO_2$; ml CO_2 g^{-1} h^{-1}) were measured using flow-through respirometry. Bats were weighed to the nearest 0.1 g before each experiment. They had not been fed for 12 h, which was sufficient for them to be post-absorptive (Kovtun and Zhukova, 1994). Each bat was placed in a 0.8l glass chamber fitted with a cone of wire mesh from which the bat could hang. The chamber was placed in a controlled-temperature room (±2°C) at ambient temperatures (T_a) from 5–40°C at five degree intervals. Ambient temperature was measured in outflowing air (Model HMP35B probe and HMI36 humidity data processor, Vaisala OY, Helsinki, Finland). Air flow into the chamber ($\dot{V}I$) was controlled at 100 ml/min using a mass-flow meter (Model 5871-A, Brooks Instrument B. V., Veenendaal, Holland). This rate ensured that excurrent air had a content of $O_2 > 20\%$. Air entered at the base of the chamber and exited at the top, near the apex of the wire cone and the bat. Time required to reach 90% of a change in O_2 concentration was ca. 5 min, reflecting the unidirectional flow of air and location of the bat near the outlet of the chamber.

Excurrent air was dried using anhydrous calcium sulphate (Drierite) before passing through one channel of a paramagnetic oxygen analyzer (Model OA184, Servomex Ltd., Crowborough, United Kingdom) and an infrared CO_2 analyzer (Model Binos C, Hereus-Leybold G. M. B. H., Hanau, Germany). A GWBASIC program and Promax XT personal computer recorded the differential output of the O_2 analyzer (ambient air minus excurrent air) and the analog output of the CO_2 analyzer via a RS−232 interface with a digital multimeter (Model 1905, Thurlby Electronics Ltd., Cambridge, United Kingdom). $\dot{V}O_2$ and $\dot{V}CO_2$, corrected to standard temperature and pressure for dry air, were calculated using single-point samples taken every 30 s (torpid bats) or every 5–30 s (euthermic bats). The faster rate of sampling for euthermic bats facilitated determination of steady-state $\dot{V}O_2$ and $\dot{V}CO_2$ because those bats tended to become torpid quickly at lower T_a. Absolute humidity of ambient and excurrent air was measured using two humidity probes (Model HMP35B probe and HMI36 humidity data processor, Vaisala OY, Helsinki, Finland), and the rate of evaporative water loss (EWL; mg g^{-1} h^{-1}) was calculated.

Calculations of steady-state $\dot{V}O_2$, $\dot{V}CO_2$, and EWL are based on principles outlined by Withers (1977):

$$\dot{V}_{O_2} = [(\dot{V}_I \cdot F_{IO_2}) - (\dot{V}_E \cdot F_{EO_2})] \cdot 60/M,$$

$$\dot{V}_{CO_2} = (\dot{V}_E \cdot F_{ECO_2}) \cdot 60/M, \quad \text{and}$$

$$EWL = [(\dot{V}_I \cdot \chi_{EO_2}) - (\dot{V}_I \cdot \chi_{IO_2})] \times 60/(1000 \cdot M),$$

where $\dot{V}_E$ was the flow of dry air out of the chamber (ml/min), F_{IO_2} and F_{ICO_2} were the fractional O_2 and CO_2 concentrations of ambient air, F_{EO_2} and F_{ECO_2} were the fractional O_2 and CO_2 concentrations of air out of the chamber, χ_{IO_2} and χ_{EO_2} were the absolute humidity (mg/l) of ambient and excurrent air, and M was the body mass of the bat. $\dot{V}_E$ was calculated as $\dot{V}_I \cdot (1 - F_{IO_2} - F_{ECO_2})/(1 - F_{EO_2} - F_{ECO_2})$. The O_2 and CO_2 analyzers were calibrated to 0.2095 and 0 respectively using ambient air.

Data for torpid bats were collected during the day, but data for euthermic bats at low T_a were usually collected at dusk. Bats were kept in the metabolic chamber until a steady state of $\dot{V}O_2$, $\dot{V}CO_2$, and EWL had been reached (ascertained visually from graphs displayed by the computer). This was ≥2 h for torpid bats and ≥20 min for euthermic bats. It was essential to ensure that bats had attained a steady state of $\dot{V}O_2$, $\dot{V}CO_2$, and EWL, because body temperature (T_b) was recorded at the end of each experiment, and it was assumed that that represented the actual T_b when other data were collected. At least 40 min of sampling for torpid bats in steady-state $\dot{V}O_2$, $\dot{V}CO_2$, and EWL, and ≥10 min of sampling for euthermic bats, were used to calculate the $\dot{V}O_2$, $\dot{V}CO_2$, and EWL. The T_b of each bat was recorded ≤45 s of removal from the chamber by inserting a fine thermocouple 1 cm into the animal's rectum. Data were discarded if insertion of the thermocouple took ≥45 s, if the bat had urinated or defecated in the chamber, or if the bat remained active.

Wet thermal conductance (C_{wet}; ml O_2 g^{-1} h^{-1} $°C^{-1}$) was determined as $\dot{V}O_2/\Delta T$, where $\dot{V}O_2$ was measured in ml O_2 g^{-1} h^{-1} and ΔT was ($T_a - T_b$). We retained fundamental units of measurement of $\dot{V}O_2$ (ml O_2) for wet thermal conductance. Dry conductance (C_{dry}; J g^{-1} h^{-1} $°C^{-1}$), in contrast, was calculated as (MHP − EHL)/ΔT, where MHP was metabolic heat production (J g^{-1} h^{-1}; calculated from $\dot{V}O_2$ assuming 20.1 J/ml O_2) and EHL was evaporative heat loss (J g^{-1} h^{-1}; calculated from EWL assuming a latent heat of vaporization of 2,300 J/g). Calculation of dry thermal conductance required conversion of ml O_2 and g H_2O to a common unit of joules.

Eight bats were used throughout this investigation, and each bat was measured once to obtain euthermic data and once to obtain torpid data at each temperature. However, final sample sizes varied because some data were excluded, due to problems in obtaining euthermic data at low T_a and torpid data at high T_a.

Means are given with ±1 *SE*. Data were analysed using *t*-tests, least-squares linear regression and analysis of variance (ANOVA) with the Student-Newman-Keuls (SNK) multiple comparison test. We used Bartlett's test for homogeneity of variance, and only mention in the text where it was significant, indicating heterogeneity of variance. ANOVA is robust even if there is heterogeneity of variance, especially if sample sizes are nearly equal (Zar, 1984). A significance level of 0.05 was used. For regression analyses when there were two different relationships of the Y value on X, a critical breakpoint (X value) was calculated by dividing the data into two sets; those were regressed separately to minimize residual sum of squares pooled for two regressions (Withers, 1980; Yeager and Ultsch, 1989).

Results

Bats adjusted well to the experimental protocol and were typically at rest during experiments, perched in their normal roosting posture at the apex of the wire cone near the outlet. There were no significant differences in T_b of torpid or euthermic male and female bats at any T_a for which comparisons were possible. As a result, data from both sexes were combined in subsequent analyses.

Body temperature.—Nyctophilus geoffroyi is thermally labile with a clear dichotomy in T_b of euthermic and torpid bats at low T_a (Fig. 1a). The distinction between T_b of euthermic and torpid bats is less clear at higher T_a, but Speakman's (1988) criterion of $T_b < 26°C$ for torpor separated torpid and euthermic bats, except for one torpid bat with a T_b of 26°C at a T_a of ca. 24°C. There was considerable variation at most T_a in T_b of bats that were euthermic (Fig. 1a). Nevertheless, below a T_a of 29.5°C, the crit-

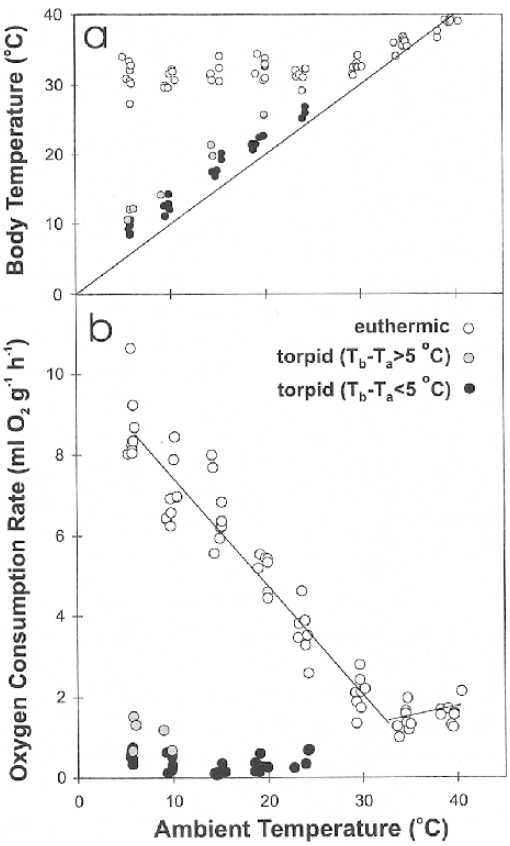

FIG. 1.—The relationship between a) body temperature and ambient temperature and b) metabolic rate and ambient temperature, of *Nyctophilus geoffroyi* when euthermic, torpid but thermoregulating ($\Delta T > 5°C$), and passively torpid ($\Delta T < 5°C$).

ical point for separate regressions of T_b at low and high T_a, the T_b of euthermic bats (31.6 ± 0.2°C) was independent of T_a (slope of 0.034 was not significantly different from zero; $r^2 = 0.03$; $n = 40$ measurements of eight bats). T_b was elevated at higher T_a of 35°C (T_b = 35.9°C ± 0.3, n = 8) and 40°C (T_b = 38.7 ± 0.3°C, n = 8).

To investigate possible effects of captivity on the ability of euthermic bats to thermoregulate, we used two linear regressions of ΔT and time after capture (range = 25–110 days) at T_a of 30 and 35°C. These ambient temperatures were chosen because they included data measured soon after capture, as well as after >3.5 months. The slope of neither regression line was significantly different from zero ($r^2 < 0.43$, $P > 0.11$, $n = 8$).

Nyctophilus geoffroyi became torpid at T_a of 24.2°C (T_b = 26.0°C) down to 5.7°C (T_b = 8.5°C; Fig. 1a). Bats were able to rewarm spontaneously from the lowest experimental temperatures. The T_b of torpid bats was significantly related to T_a ($r^2 = 0.94$; n = 33 measurements of eight bats): $T_b = 4.9$ (±0.57) + 0.95 (±0.04) T_a. At all experimental temperatures, the range in T_b of torpid bats was high, ca. 5°C, and this variation was partly mirrored in the data for $\dot{V}O_2$ (Fig. 1b), for which bats with $\Delta T > 5°C$ generally have a higher $\dot{V}O_2$. There was no consistent relationship between the pattern of T_b for individual bats when euthermic or torpid over the whole range of T_a, i.e., bats with the highest T_b at one T_a may have had the lowest T_b at another T_a.

Metabolic rate.—The $\dot{V}O_2$ varied with T_a and also displayed a clear euthermic-torpid dichotomy (Fig. 1b). Data for euthermic bats are typical of an endothermic homeotherm, with a linear increase in $\dot{V}O_2$ as T_a decreases below 34°C (the critical point for the two regressions), with variation in T_a accounting for 91% of the variation (r^2 = 0.91; n = 56 measurements of eight bats): $\dot{V}O_2 = 10.14$ (±0.24) − 0.268 (±0.012) T_a. The slope of that line, 0.268 ml O_2 g^{-1} h^{-1}, was an approximate measure of C_{wet} but should be interpreted with caution because of large variation in T_b and non-Newtonian effects (McNab, 1980); for example, the line below the critical point intercepts the Y-axis at 37.9°C not the euthermic T_b of 31.6°C. The $\dot{V}O_2$ of euthermic bats significantly differed between 30°C (2.1 ± 0.2) and 35°C (1.4 ± 0.1 ml O_2 g^{-1} h^{-1}) and 30°C and 40°C (1.6 ± 0.1) but not between 35 and 40°C ($F = 8$, $d.f. = 2, 21$; $P < 0.05$). We consider $\dot{V}O_2$ at 35°C to be the best estimate of basal metabolic rate (BMR), because it is the lowest mean value at a T_a close to the breakpoint temperature.

The $\dot{V}O_2$ of torpid bats was always well

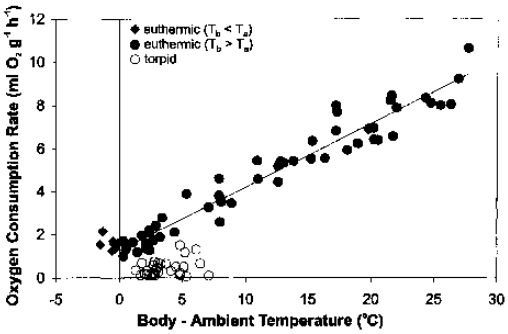

FIG. 2.—The relationship between $\dot{V}O_2$ and ΔT of euthermic and torpid *Nyctophilus geoffroyi*.

below the corresponding value for euthermic bats (Fig. 1b). There was considerable variation in the $\dot{V}O_2$ of torpid bats at all T_a, hence the lack of significance in most comparisons. Although the lowest $\dot{V}O_2$ for torpid bats was at a T_a of 15°C (0.26 ± 0.11 ml O_2 g^{-1} h^{-1}, n = 7), this was only significantly different from $\dot{V}O_2$ at 5°C and 20°C (F = 5, $d.f.$ = 4,29; $P < 0.05$; significant heterogeneity of variance with B_4 = 11). Bats with a higher ΔT tended to have a higher $\dot{V}O_2$ (Fig. 1b).

Torpor substantially reduced energetic expenditure. On average, the lowest $\dot{V}O_2$ of torpid bats was 0.26 ml O_2 g^{-1} h^{-1} at 14.5°C, whereas the greatest absolute saving of energy was 7.9 ml O_2 g^{-1} h^{-1} at 5°C; the greatest proportional saving was 96.5% of euthermic $\dot{V}O_2$ at 15°C.

Metabolic rate and (ΔT).—For euthermic bats, there was a linear relationship between $\dot{V}O_2$ and ΔT (Fig. 2). For bats with $T_b > T_a$, the relationship was $\dot{V}O_2$ = 1.25 (±0.15) + 0.30 (±0.01) ΔT, with r^2 = 0.94 and n = 53. The intercept (1.25 ml O_2 g^{-1} h^{-1}) reflected the intrinsic metabolic rate of bats when $T_b = T_a$, i.e., when there was no thermoregulatory requirement, and that value was within the 95% *CI* of BMR (1.16–1.64 ml O_2 g^{-1} h^{-1}). The slope of this relationship, 0.30 ml O_2 g^{-1} h^{-1} °C^{-1}, was another measure of thermal conductance. It closely corresponded to the value obtained from the regression of $\dot{V}O_2$ and T_a of 0.27 ml O_2 g^{-1} h^{-1} °C^{-1}. When bats were heat-stressed and $T_b < T_a$, $\dot{V}O_2$ tended to increase (by a Q_{10} effect), so those data were not included in the regression.

For torpid bats, $\dot{V}O_2$ was clearly lower than for euthermic bats at equivalent ΔT but the relationship between $\dot{V}O_2$ and ΔT was not significant (F = 3, $d.f.$ = 1,27; r^2 = 0.05; n = 29): $\dot{V}O_2$ = 0.18 (±0.18) + 0.08 (±0.05) ΔT. Nevertheless, the lower slope than for euthermic bats (0.08 versus 0.30) was expected because torpid bats had a lower thermal conductance, and the lower intercept (0.18 versus 1.25) reflected the intrinsically lower $\dot{V}O_2$ of torpid bats, because they had a lower T_b than euthermic bats.

Respiratory exchange ratio.—$\dot{V}CO_2$ of bats closely paralleled $\dot{V}O_2$ and, hence, were not shown or analyzed separately. The respiratory exchange ratio (RER = $\dot{V}CO_2$/$\dot{V}O_2$) of euthermic bats had a slight, but significant, positive linear relationship with T_a (r^2 = 0.38; n = 63 measurements of eight bats), increasing from 0.76 (±0.006) at T_a = 5°C (with the highest $\dot{V}O_2$) to 0.82 (±0.01) at T_a = 40°C. There was no significant relationship between RER and T_a for torpid bats (r^2 = 0.08; n = 25 measurements of eight bats); RER was 0.80 ± 0.01.

Evaporative water loss.—For euthermic bats, a critical T_a of 34°C separated two regressions of EWL on T_a. There was no significant dependence of EWL on T_a from 5 to 34°C (r^2 = 0.0004; n = 42 measurements of eight bats), with a mean EWL of 2.48 (±0.09) mg H_2O g^{-1} h^{-1}. At T_a > 34°C, EWL increased steeply (Fig. 3a) and, at ca. 40°C, was significantly higher than at all other T_a. Torpid bats usually had a lower EWL than euthermic bats. The EWL of torpid bats was slightly but significantly elevated at 25°C (1.2 mg g^{-1} h^{-1}; n = 2) compared with other torpid values (F = 3.7, $d.f.$ = 4,27).

Thermal conductance.—Wet thermal conductance was not calculated for bats at T_a >30°C (Fig. 3b), because ΔT was small at high T_a, and this made accurate determination of conductance difficult. There

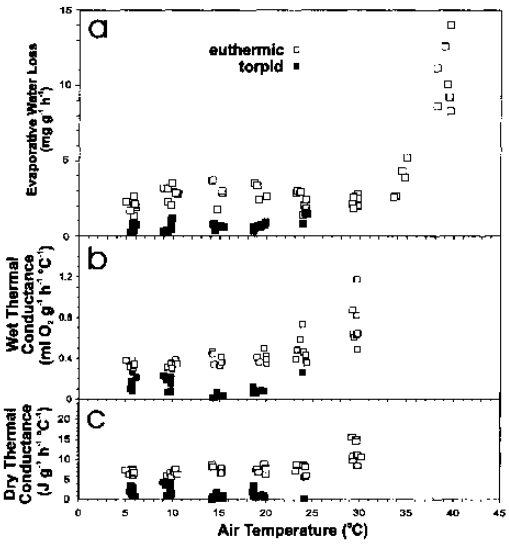

FIG. 3.—The relationship between a) evaporative water loss and ambient temperature, b) wet thermal conductance and ambient temperature, and c) dry thermal conductance and ambient temperature, of euthermic and torpid *Nyctophilus geoffroyi*.

were significant differences in C_{wet} of euthermic bats from T_a 5 to 30°C ($F = 17.3$, *d.f.* = 5,38; significant heterogeneity of variance with $B_5 = 20$), with C_{wet} at 30°C significantly different from that at all other T_a, and C_{wet} at 25°C greater than at 5 and 10°C.

Torpid bats had a significantly higher C_{wet} at 5, 10, and 25°C than at 15 and 20°C, and C_{wet} was also higher at 25°C than at 5 and 10°C ($F = 11.3$, *d.f.* = 4,24). Mean minimum C_{wet} at T_a from 15 to 20°C was 0.060 (±0.010) ml O_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 13$ measurements of eight bats). C_{wet} of torpid bats was generally lower than the corresponding value for euthermic bats, especially at 15 and 20°C (Fig. 3c).

The C_{dry} followed the same general pattern as C_{wet} (Fig. 3c). It did not vary significantly for euthermic bats at T_a from 5 to 25°C (7.2 ± 0.2 J g^{-1} h^{-1} $°C^{-1}$; $n = 32$), but was significantly elevated at 30°C (12.0 ± 0.9 J g^{-1} h^{-1} $°C^{-1}$; $n = 8$). The only significant difference in C_{dry} of torpid bats was at 15°C (0.60 ± 0.21 J g^{-1} h^{-1} $°C^{-1}$; $n = 7$) compared with 10°C. The C_{dry} of torpid bats was generally lower than the corresponding value for euthermic bats, especially at 15 and 20°C (Fig. 3c).

DISCUSSION

The lesser long-eared bat is thermally labile and can be either euthermic or torpid at low T_a, although there is a high metabolic cost to euthermy at low T_a. This thermolability is typical of microchiropteran bats in temperate areas (e.g., Hosken, 1997; Hosken and Withers, 1997; Kurta and Kunz, 1988; Lyman, 1977; McNab, 1982; Morris et al., 1994; Speakman, 1988; Studier, 1981; Webb et al., 1993). The day-to-day variability in thermal and metabolic data might be due, in part, to daily variation in reserves of body fat (Audet and Thomas, 1997).

Body temperature and metabolic rate.—The T_b of *N. geoffroyi* displayed clear patterns of euthermy, with T_b ca. 32°C, and torpor, with T_b usually within 1–5°C of T_a. Mean euthermic T_b is low by eutherian standards but typical of microchiropteran bats (e.g., Genoud, 1993; Hosken, 1997; Hosken and Withers, 1997). Even slight depression of euthermic T_b leads to significant metabolic savings. For example, *Plecotus auritus* affect an energetic saving of >40% by reducing T_b from 38 to 31°C at a T_a of 25°C (Webb et al., 1993), and such a reduction reflects a trade-off between benefits of remaining active (such as avoiding predators) and energetic economy (Studier, 1981; Webb et al., 1993).

Torpid *N. geoffroyi* generally have T_b within 1–5°C of T_a, although the T_b of torpid bats was extremely variable (present study; Kulzer et al., 1970). This is typical of microchiropteran bats (Beer and Richards, 1956; Bell et al., 1986; Hock, 1951; Speakman and Racey, 1989; Studier, 1981). At low T_a (5–10°C), *N. geoffroyi* maintain a high T_b (ca. 10°C) and correspondingly high $\dot{V}O_2$, similar to other Australian vespertilionid bats (Hosken, 1997; Hosken and Withers, 1997; Morris et al., 1994). The rel-

atively high T_b and $\dot{V}O_2$ reported for torpid vespertilionids from Australia compared with values for bats from the northern hemisphere may be related to differences in experimental conditions, climatic factors, and effects of captivity or reproductive condition. In this study, length of captivity (25–110 days) did not influence thermoregulation, but bats may acclimate ≤3 days of captivity (*Artibeus jamaicensis*—Studier and Wilson, 1979).

The BMR of *N. geoffroyi* was ca. 70% of that predicted for an 8-g mammal (Kleiber, 1961) but fell within the range reported for vespertilionid bats, which typically have a lower BMR than predicted (McNab, 1982). The T_a at which BMR was recorded, 35°C, also is similar to that reported elsewhere (Bell et al., 1986; Hosken and Withers, 1997; Morris et al., 1994; Stones and Weibers, 1967), with a lower critical temperature of ca. 33.5°C.

Torpor led to significant energetic savings of ca. 96% at all T_a. This is similar to that reported for other Australian bats (Hosken, 1997; Hosken and Withers, 1997; Morris et al., 1994). Minimum $\dot{V}O_2$ during torpor was ca. 17% of BMR, which is within the range of reduction reported for hibernators and daily heterotherms, although at the upper end of the former and lower end of the latter (Geiser and Ruf, 1995). Studier and O'Farrell (1980) reported that the $\dot{V}O_2$ of euthermic and torpid *Myotis lucifugus* and *M. thysanodes* were indistinguishable at T_a of 20 and 24°C, respectively, and similarly, *P. subflavus* cannot enter torpor at T_a above ca. 18°C (McNab, 1974). This is not the case for *N. geoffroyi,* which had a substantial energetic savings through torpor at T_a up to ca. 25°C.

Respiratory exchange ratio.—The positive relationship between RER and T_a for euthermic *N. geoffroyi* has been noted for other bats (Hosken, 1997; Hosken and Withers, 1997). RER values for torpid *N. geoffroyi,* which were not related to T_a, also are similar to values for other bats (Hosken, 1997; Hosken and Withers, 1997).

Evaporative water loss.—Evaporative water loss (EWL) of euthermic bats had no thermal dependence from 5 to 30°C, despite the significant positive relationship between T_a and $\dot{V}O_2$ over the same range of temperature. This is probably due to the counteracting effects of T_a on $\dot{V}O_2$ and the gradient in water vapor pressure driving EWL. A similar result was reported by two other studies that used the same flow-through system (Hosken, 1997; Hosken and Withers, 1997).

Daily water loss of euthermic *N. geoffroyi* was ca. 6% of body mass at T_a of 5–30°C and 10% RH, and 25% of body mass at 40°C and 15% relative humidity. This bat occupies roosts with T_a as high as 40°C (Maddock and Tidemann, 1995), but RH of their roost is unknown. The EWL of euthermic *N. geoffroyi* was similar to that of other Australian bats under the same experimental conditions, 4–7% of body mass at 5–30°C and 10% RH, and 20–25% of body mass at 40°C and 15% RH, respectively (Hosken, 1997; Hosken and Withers, 1997). Webb et al. (1995) reported that bats lose ≤30% of body mass per day at low RH (<20%), a figure similar to that reported here for *N. geoffroyi,* which inhabits extremely arid areas of Australia where high water loss seems problematic. Daily water loss of bats is generally high compared with other mammals (Studier and O'Farrell, 1980). Nevertheless, a water loss of 23–32% of body mass is lethal for some bats (Studier et al., 1970).

Conditions within the roost can reduce EWL significantly, with reported water loss in natural roosts of 15–16% of body mass over 12 h (Studier et al., 1970). Although some bats occupy roosts of high RH (Studier and Ewing, 1971), they are in negative water balance at RH less than ca. 99% (Thomas and Cloutier, 1992). As a result of high EWL, selection apparently has favored renal adaptations for high urinary concentration as a means of conserving water (Geluso, 1980).

In mammals with limited access to water,

low BMR and torpor are sometimes considered a strategy for conservation of water (Bonaccorso et al., 1992; MacMillen, 1972). Torpor reduces EWL of bats to a fraction of euthermic levels (Carpenter, 1969; Hosken and Withers, 1997; Webb et al., 1995; this study). For *N. geoffroyi*, torpor reduces water loss to ca. 25% of euthermic values from 10–25°C, which is similar to other studies (Morris et al., 1994).

Thermal conductance.—For euthermic *N. geoffroyi*, both wet and dry conductance were independent of T_a from 5–25°C. Conductance (C) measured over this range of temperature (0.39 ml O_2 g^{-1} h^{-1} $°C^{-1}$, 7.2 J g^{-1} h^{-1} $°C^{-1}$) is our best estimate of minimum euthermic conductance. Thermal conductance (C) is typically constant below the thermoneutral zone (TNZ) (Aschoff, 1981), and the temperature range over which we reported a constant C is not unusual (Bonaccorso et al., 1992). Minimum euthermic C_{wet} for *N. geoffroyi* is 108% of that predicted by Herreid and Kessel (1967) and is typical for bats in general (Bonaccorso et al., 1992; Genoud et al., 1990). However, C of *N. geoffroyi* is high compared with some other Australian bats (Hosken, 1997; Hosken and Withers, 1997). This may be related to the potentially high temperature of their roosts (Maddock and Tidemann, 1995), because high C facilitates loss of heat. Thermal conductance of bats is related to characteristics of their roost (Kurta, 1985), and solitary tree-roosting bats typically have lower C than colonial species roosting in more sheltered environments (Shump and Shump, 1980). Interestingly, *N. geoffroyi* is generally a solitary tree-roosting bat (Hosken, 1996; Lumsden, 1995), yet has high conductance.

Torpor not only decreases $\dot{V}O_2$ and EWL but also C. Minimum C_{wet} of torpid bats is only 16% of that predicted for an 8-g mammal (Herreid and Kessel, 1967), and both C_{wet} and C_{dry} were lowest at a T_a of 15°C for torpid bats. A lower C has been noted for other bats when torpid (Genoud, 1993; Hosken and Withers, 1997; Morris et al., 1994) and other small mammals (Snyder and Nestler, 1990). Although there are diurnal differences in C (Aschoff, 1981), and we measured euthermic and torpid C at different times during the day, the differences in C of euthermic and torpid *N. geoffroyi* are much greater than the 50% circadian difference reported by Aschoff (1981). The C_{wet} of torpid bats was ca. 15% of euthermic C_{wet}. The C_{dry} has less diurnal variation than C_{wet} (Aschoff, 1981), but differences for C_{dry} of euthermic and torpid *N. geoffroyi* were as apparent as differences for C_{wet}. Reasons for differences in C of euthermic and torpid bats are not clear. Postural, respiratory, and circulatory changes during torpor could produce a poorly perfused, hypothermic periphery that acts as additional insulation and reduces C (cf. Hosken and Withers, 1997; Snyder and Nestler, 1990; Withers and Jarvis, 1980). The hypothesis that peripheral hypothermic tissue provides additional insulation is supported by the observation that C increases for torpid bats with elevated T_b and $\dot{V}O_2$, presumably because this hypothermic insulative layer is disrupted by the increased respiration and circulation required for elevated $\dot{V}O_2$ (cf. McNab, 1980) or the subcutaneous location of thermogenic brown fat (Dawson and Olson, 1987). The increase in $\dot{V}O_2$ of torpid bats at low T_a is not reflected necessarily by a correspondingly substantial increase in ΔT, because C_{dry} and especially C_{wet} also increase. Thus, the thermogenic response of these torpid bats at low T_a is not very effective.

Metabolic depression during torpor.—Mechanisms responsible for reduced metabolic rate of torpid mammals and birds have been debated (Geiser, 1988; Heldmaier and Ruf, 1992; Snyder and Nestler, 1990). Two major factors contributing to reduced metabolic rate during torpor are abandonment of thermoregulation (or more correctly, a lowering of the thermoregulatory set-point) and a reduced metabolic rate as a consequence of lowered body temperature and a concomitant Q_{10} effect (Geiser, 1988; Sny-

der and Nestler, 1990; Withers, 1992). Metabolic rate during torpor might be depressed further intrinsically, for example, by changes in acid-base status (Malan, 1980, 1986, 1988).

We suggest a major role of down-regulation of the thermoregulatory set-point and a Q_{10} effect in reducing metabolic rate of *N. geoffroyi*. The $\dot{V}O_2$ at a T_a of 15°C could immediately decline at the onset of torpor from ca. 6.0 ml O_2 g^{-1} h^{-1} to BMR, a difference of 4.6 ml O_2 g^{-1} h^{-1}, by down-regulation (Fig. 1b). A consequence of this down-regulation is that T_b declines, so there is a further reduction in $\dot{V}O_2$ below BMR due to a Q_{10} effect. This Q_{10}-related reduction in $\dot{V}O_2$ is ca. 1.14 ml O_2 g^{-1} h^{-1} (from 1.4 to 0.26 ml O_2 g^{-1} h^{-1}). At a T_a of 15°C, the relative importance of down-regulation and a Q_{10} effect is about 4:1 (4.6/1.14). At higher T_a, the decrease in $\dot{V}O_2$ due to down-regulation is less ($\dot{V}O_2$ of euthermic bats is lower), as is the Q_{10} decrease (torpid T_b is higher); at 25°C, the ratio is 2.4:1. At lower T_a, the decrease in $\dot{V}O_2$ due to down-regulation is greater ($\dot{V}O_2$ of torpid bats increases but not as much as for euthermic bats), and the Q_{10} decrease is greater (T_b is lower); at 5°C, the ratio is 3.6:1. Thus, down-regulation of the thermoregulatory set-point and the consequent Q_{10} effect are both contributors to metabolic reduction in torpid *N. geoffroyi* over a wide range of T_a, although the down-regulation effect is always greater.

Heldmaier and Ruf (1992) suggested that the metabolic rate of torpid Djungarian hamsters (*Phodopus sungorus*) was explained solely by down-regulation. Their evidence was an identical linear relationship between $\dot{V}O_2$ versus ΔT for euthermic and torpid hamsters (cf. our Fig. 2). The slope of this relationship is C_{wet}, which is apparently the same for euthermic and torpid hamsters. Absence of a difference in elevation of $\dot{V}O_2$ for euthermic and torpid hamsters indicates the surprising absence of a Q_{10} effect. Results for Djungarian hamsters are very different from ours for *N. geoffroyi*, for which C changes markedly during torpor and there is a substantial Q_{10} effect.

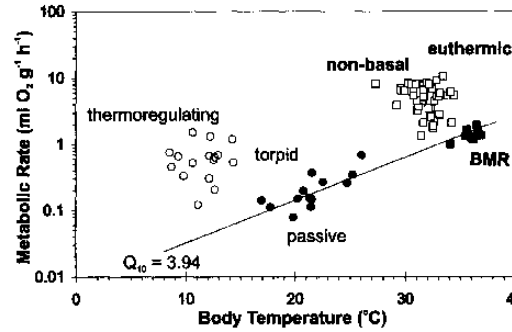

FIG. 4.—The relationship between $\dot{V}O_2$ and body temperature of euthermic (BMR and non-basal) and torpid (passive and thermoregulating) *Nyctophilus geoffroyi*. The regression line for $\dot{V}O_2$ of bats when passively torpid and euthermic at BMR is equivalent to a Q_{10} of 3.94.

Finally, is there evidence for intrinsic metabolic depression in torpid *N. geoffroyi*? Unfortunately, the precise contributions of down-regulation, the Q_{10} effect, and possible intrinsic metabolic depression are difficult to discern (Snyder and Nestler, 1990), particularly if ΔT is substantial and thermal conductance decreases during torpor (as for *N. geoffroyi*). We graphically analyzed the relationship between $\dot{V}O_2$ and T_b for *N. geoffroyi* when euthermic and thermoneutral, and when torpid and non-thermoregulating, to estimate the Q_{10} for metabolic reduction during torpor (Fig. 4). It should be valid to calculate a Q_{10} from these data because $\dot{V}O_2$ of these bats is not elevated for thermogenesis (unlike $\dot{V}O_2$ of euthermic bats when non-basal and torpid bats when thermoregulating). Our analysis yields a Q_{10} of 3.94, which is higher than values of 2–3 (Withers, 1992) and Q_{10} for endotherms within torpor of 2.3–2.6 (Geiser, 1988). Thus, the high Q_{10} of 3.94 for *N. geoffroyi* suggests intrinsic metabolic depression. Metabolic acidosis during torpor may be one explanation (Malan, 1980, 1986, 1988).

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