Temperature effects on metabolism, ventilation, and oxygen extraction in a Neotropical bat

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Abstract. We examined the relationship between ambient temperature (Ta), body temperature (Tb), oxygen consumption ($\dot{V}_{O_2}$), carbon dioxide production ($\dot{V}_{CO_2}$), evaporative water loss ($\dot{m}H_2O$), respiratory frequency (f), tidal volume (VT), minute volume ($\dot{V}I$), and oxygen extraction (E_{O_2}) in the Neotropical bat *Noctilio albiventris* (mean mass 40 g). The factorial aerobic scope was 7.2 between Ta of 1–35 °C ($\dot{V}_{O_2}$ = 0.119 and 0.0165 ml/(g · min), respectively). The respiratory exchange ratio ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) did not change with Ta and $\dot{m}H_2O$ was constant between Ta of 10–35 °C. Thermal conductance was minimal at 30 °C and constant and low at Ta < 30 °C. Between 10 and 35 °C, *Noctilio* accommodated changing $\dot{V}_{O_2}$ with parallel and roughly equivalent changes in f, VT, and E_{O_2}. The change in $\dot{V}_{O_2}$ between 10 and 1 °C was accommodated mainly through changing f. Ventilation parameters in resting thermoneutral *Noctilio* are intermediate between allometric values for birds and mammals. Maximal E_{O_2} in *Noctilio* (35–40%) is higher than for other mammals but considerably less than maximal E_{O_2} in some birds.

In small mammals and birds, aerobic metabolism varies by a factor of 4–15 or more between minimal resting values and maximal rates of aerobic exercise or thermogenesis (Bartholomew, 1982; Dawson and Dawson, 1982). The associated changes in rates of oxygen consumption ($\dot{V}_{O_2}$) can be accommodated by adjusting lung ventilation (minute volume; $\dot{V}I$) and/or oxygen extraction (E_{O_2}). In turn, $\dot{V}I$ can be adjusted via changes in tidal volume (VT), respiration frequency (f), or a combination of the two. Which of these "options" animals employ is an interesting question, because the "choice" presumably reflects general design constraints, evolutionary adaptations to particular selective regimes, and the varying physiological and developmental states the animal experiences.

Ventilatory responses to changes in $\dot{V}_{O_2}$ elicited by different ambient temperatures (Ta) have been studied extensively in birds (Bech *et al.*, 1985; Brent *et al.*, 1984; Kaiser and Bucher, 1985; Chappell and Bucher, 1987; Chappell and Souza, 1988; reviews in

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Johansen and Bech, 1983, and in Bucher, 1985). These studies have revealed some consistent allometric relationships between body mass and parameters such as f, V_T, and $\dot{V}_I$ in resting birds under "standardized" thermal conditions. However, few patterns are apparent in the way birds accommodate changing $\dot{V}_{O_2}$, other than one of considerable intra- and interspecific flexibility and variation (Bucher, 1985).

The ventilatory responses of mammals to changing V_{O_2} at different Ta, and especially at low Ta, are poorly understood. Besides Stahl's (1967) work on ventilatory allometry in resting mammals, there have been few studies of the combined responses of $\dot{V}_{O_2}$, f, V_T, $\dot{V}_I$, and E_{O_2} to changing Ta (Casey et al., 1979; Withers et al., 1979; Chappell, 1985). The paucity of data for mammals makes comparisons tenuous, but resting mammals appear to have consistently higher f and $\dot{V}_I$, and lower E_{O_2} than resting birds of similar mass (Stahl, 1967; Bucher, 1985). This difference, together with the generally higher maximum $\dot{V}_{O_2}$ of birds, may be a consequence of the unique morphology of the avian lung (Piiper and Scheid, 1977).

In this paper we examine the thermoregulatory and respiratory physiology of *Noctilio albiventris*, an insectivorous Neotropical bat. These data are the first measurements of bat ventilatory characteristics obtained over a wide range of Ta and $\dot{V}_{O_2}$. Moreover, bats are of particular interest for comparative respiratory physiologists because they have a typically mammalian lung morphology, but during flight they attain maximal $\dot{V}_{O_2}$ similar to those of flying birds – much higher than maximal $\dot{V}_{O_2}$ of nonflying mammals of equivalent mass (Thomas, 1981). Here we address an important question: how do bat ventilatory characteristics compare with avian and mammalian ventilatory allometry? If ventilatory characteristics are constrained primarily by morphological or taxonomical considerations, then *Noctilio's* ventilation should conform to the generalized mammalian pattern (high f, high $\dot{V}_I$, and low E_{O_2}). On the other hand, if ventilatory characteristics are determined by performance demands (*i.e.*, high $\dot{V}_{O_2}$ during flight), then *Noctilio's* ventilation should more closely resemble the avian pattern (low f, low $\dot{V}_I$, and high E_{O_2}).

Materials and methods

Animals.   Lesser bulldog bats, *Noctilio albiventris* (Chiroptera : Noctilionidae), were collected in Panama. This species (adult mass 35–45 g) inhabits lowland tropical forests, usually near open water. It feeds on flying insects and roosts colonially in hollow trees or abandoned buildings. Experimental animals ($N = 12$) were housed in a large flight cage maintained at $26 \pm 1\ ^\circ C$, 50–70% relative humidity, and a 12L : 12D photoperiod. Bats had *ad libitum* access to drinking water and were fed mealworms (*Tenebrio* larvae) and vitamin supplements. At the time of experiments they had been in captivity approximately one year. During this time they appeared healthy, maintained stable body mass, and flew readily.

Measurements.   Gas exchange measurements were performed in a lucite metabolism chamber (internal volume 395 ml) placed in an environmental cabinet which controlled Ta within 0.5 °C. We measured Ta in the metabolism chamber with a thermocouple in

the air outflow port. Bats were unrestrained; during experiments they perched in normal postures on a vertical wire-mesh platform. We obtained body temperatures (Tb) with a rectal thermocouple (inserted approximately 2 cm) within 30 sec after the completion of measurements at each Ta. All measurements were performed during the inactive (light) phase of the bats' circadian cycle.

We measured oxygen consumption, carbon dioxide production ($\dot{V}_{CO_2}$), and evaporative water loss ($\dot{m}H_2O$) using open-circuit respirometry at flow rates of 800–1200 ml/min (regulated $\pm 1\%$ with a Tylan mass flow controller). About 100 ml/min of excurrent air was diverted through a Weather-Measure (Viasala) HT-100 relative humidity (R.H.) sensor, dried and passed through an Anarad AR-50 CO_2 sensor, scrubbed of CO_2 with Ascarite and redried, and passed through an Applied Electrochemistry S-3A O_2 sensor. Sensors were connected to a computer sampling every 5 sec through a 12-bit analog-to-digital converter. With signal averaging during the intersample interval, the effective system resolutions were 0.1% R.H., 0.001% CO_2, and 0.001% O_2. $\dot{V}_{O_2}$ was calculated as:

$$\dot{V}_{O_2} = \dot{V} \cdot (F_{I_{O_2}} - F_{E_{O_2}})/(1 - F_{E_{O_2}}), \tag{1}$$

where $\dot{V}$ is flow rate (STPD), $F_{I_{O_2}}$ is fractional O_2 concentration in incurrent air and $F_{E_{O_2}}$ is fractional O_2 concentration in excurrent air. $\dot{V}_{CO_2}$ was calculated as:

$$\dot{V}_{CO_2} = \dot{V} \cdot (F_{E_{CO_2}} - F_{I_{CO_2}}), \tag{2}$$

where $F_{E_{CO_2}}$ is fractional CO_2 concentration in excurrent air and $F_{I_{CO_2}}$ is fractional CO_2 concentration in incurrent air. Rates of evaporative water loss (g H_2O/h) were computed by substituting water vapor concentrations for CO_2 concentrations in eq. (2). We computed thermal conductance by converting V_{O_2} and $\dot{m}H_2O$ into their heat equivalents, using values of 21 J/ml O_2 (see discussion of respiratory exchange ratios in Results) and 2404 J/g H_2O to yield metabolic heat production (MHP) and evaporative heat loss (EHL), respectively. Dry thermal conductance (C, W/°C) was calculated as:

$$C = (\text{MHP} - \text{EHL})/(\text{Tb} - \text{Ta}). \tag{3}$$

The metabolism chamber also functioned as a whole-body plethysmograph, allowing simultaneous measurements of gas exchange and ventilation (Bucher, 1985; Chappell and Bucher, 1987). Pressure changes caused by the warming and wetting of tidal air were measured with a pressure transducer (Omega PX 164-010) connected to a computer sampling every 0.02 sec (50 Hz). This sampling rate was sufficient to collect at least 8 data points/breath at the highest f measured. Each measurement encompassed 12.8 sec of continuous ventilation. The system was calibrated by injecting known air volumes into the chamber after each set of measurements. Deflection rates during calibration injections were similar to those during ventilation. Inspiratory VT was computed assuming lung temperature = Tb.

Values of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are corrected to STP; V_T and $\dot{V}_I$ ($= f \cdot V_T$) are presented as BTPS values (STPD values are available in the tables). E_{O_2} as % was computed from $\dot{V}_I$ (STPD) and $\dot{V}_{O_2}$ as $E_{O_2} = [V_{O_2}/(F_{E_{O_2}} \cdot \dot{V}_I)] \cdot 100$, after accounting for ambient CO_2 concentration. Ventilation parameters and rates of gas exchange were calculated for periods when $\dot{V}_{O_2}$ was low and stable for 5 min or longer.

Ventilation was measured at Ta of 1, 10, 15, 20, 25, 30, and 35 °C. We allowed bats at least 45 min of acclimation before beginning measurements except at 1 °C, where acclimation was limited to 20 min to minimize cold stress (we did not use lower Ta in order to avoid the risk of frostbite injury). Individuals experienced two or three different Ta per experimental run and were rested at least one day between experiments.

Statistics. Six bats were run at each Ta between 10 and 35 °C; because of logistical problems we used another six for measurements at 1 °C (the latter individuals performed similarly to the initial six at intermediate Ta; unpublished data). We made 4–12 measurements of ventilation and gas exchange for each individual at each Ta. All data were used for comparisons not directly involving Ta. For comparisons between Ta, we computed single mean values for each individual in order to avoid biasing results in favor of bats with many data points. ANOVA's or *t*-tests were used to compare means; regressions were fitted by the method of least squares. E_{O_2} data (expressed as %) were arcsine transformed prior to analysis. Results differing at $P < 0.05$ are considered significantly different; data are presented as mean $\pm$ 95% confidence intervals.

Results

The bats adapted well to the experimental conditions. After initial exploration of the metabolism chamber, all individuals sat quietly during experiments except for occasional brief bouts of grooming. The mean body mass of the 12 bats was 39.9 ± 1.5 g.

Body temperature. Mean body temperature was significantly affected by Ta ($P = 0.024$; $N = 42$, ANOVA), but the lowest mean Tb (34.5 ± 1.4 °C) occurred at the intermediate Ta of 20 °C and mean Tb at 1 and 35 °C (36.7 ± 0.6 and 37.0 ± 0.6 °C, respectively) did not differ significantly (fig. 1A). The minimum observed Tb was 32.2 °C (at Ta = 20 °C) and the maximum was 38.4 °C (at Ta = 35 °C). There was considerable variation both within and between individuals, particularly at intermediate Ta.

Gas exchange and conductance. Minimum $\dot{V}_{O_2}$ (basal metabolic rate; BMR) was 0.0165 ± 0.0030 ml/(g·min) at Ta = 35 °C. $\dot{V}_{O_2}$ did not differ significantly between Ta of 30 and 35 °C. At lower temperatures $\dot{V}_{O_2}$ was inversely related to Ta (fig. 1B), and at 1 °C it was 0.119 ± 0.007 ml/(g·min), or 7.2 × larger than at 35 °C. This relationship is accurately described by the linear regression $\dot{V}_{O_2} = 0.1192 - 0.00342 \cdot Ta$ ($r^2 = 0.91$; $N = 36$, $P < 0.001$). The lower critical temperature (T_{lc}) for *Noctilio* is about 30 °C.
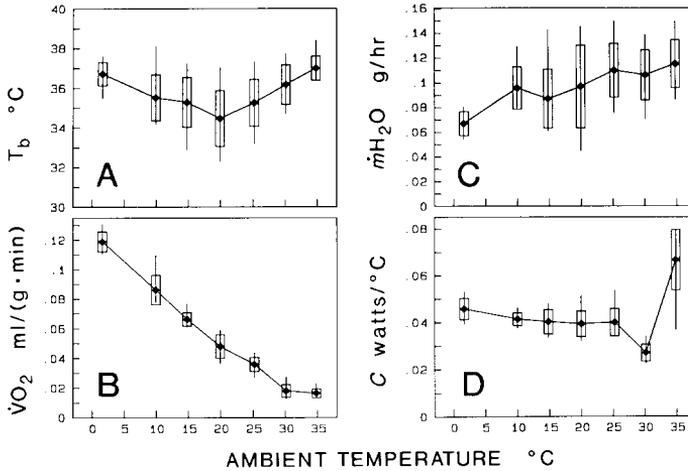
Fig. 1. Thermoregulatory parameters of *Noctilio albiventris* at different ambient temperatures. Vertical lines indicate range; boxes enclose 95% confidence intervals; $N = 6$ for all Ta. A. Body temperature (Tb). B. Oxygen consumption ($\dot{V}_{O_2}$). C. Evaporative water loss ($\dot{m}H_2O$). D. Dry thermal conductance (C).

$\dot{V}_{CO_2}$ closely paralleled $\dot{V}_{O_2}$. The respiratory exchange ratio ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) did not change significantly with changing Ta, averaging 0.73 ± 0.02. That value is consistent with fat catabolism in postabsorptive animals. Accordingly, the heat equivalence of $\dot{V}_{O_2}$ was about 21 joules/ml O_2. Rates of evaporative water loss showed considerable individual variation. Between 1 and 35 °C $\dot{m}H_2O$ was positively correlated with Ta ($r^2 = 0.24$; $N = 42$, $P = 0.001$). However, between 10 and 30 °C $\dot{m}H_2O$ was independent of Ta, averaging about 0.104 ± 0.010 g/h (fig. 1C).

Dry thermal conductance (C) was constant at Ta of 25 °C and colder (0.0410 ± 0.0020 w/ °C), but was significantly lower at Ta = 30 °C (0.0308 ± 0.0047 w/ °C; $P < 0.001$, $N = 36$, t-test). At Ta = 35 °C, C was 0.0667 ± 0.0125 w/ °C, significantly higher than at any other Ta ($P < 0.01$, $N = 42$, ANOVA) and about twice the minimal value (fig. 1D). Evaporative heat loss (EHL) accounted for $2.7 \pm 0.4\%$ of MHP at Ta = 1 °C, increasing significantly ($P < 0.001$, $N = 42$, ANOVA) to $35.6 \pm 2.6\%$ of MHP at Ta = 35 °C.

Ventilation. Values of ventilation parameters measured for *Noctilio* at the lower critical temperature are compared to allometric estimates for a 40 g mammal (Stahl, 1967) and a 40 g nonpasserine bird (Bucher, 1985; Bucher and Bartholomew, 1986) in table 1.

The 7.2-fold change in $\dot{V}_{O_2}$ between Ta of 1 and 35 °C was accommodated by changes in all ventilation parameters (table 2, figs. 2,3). Two patterns of change were apparent. The first occurred between 10 and 35 °C. Within this Ta range, $\dot{V}_{O_2}$ was positively and significantly correlated to f, VT, $\dot{V}$I, and E_{O_2}; when used as predictors in least-squares regression these parameters explained 53, 48, 82, and 49% of the variation in $\dot{V}_{O_2}$, respectively ($N = 276$, $P < 0.001$ in all cases). Ventilation parameters changed with

TABLE 1

Metabolism and ventilation of *Noctilio albiventris* at different ambient temperatures. Data presented as mean ± 95% confidence interval; $N = 6$ at all T_a. Bottom two rows are results of ANOVA across temperatures (df = 6,35 in all cases).

T_a (°C)	T_b (°C)	$\dot{V}_{O_2}$ (ml/min)	f (br/min)	V_I (BTPS) (ml)	V_T (STPD) (ml)	$\dot{V}_I$ (BTPS) (ml/min)	$\dot{V}_I$ (STPD) (ml/min)	E_{O_2} (%)
1	36.7 ± 0.6	4.88 ± 0.46	272.5 ± 36.3	0.389 ± 0.045	0.315 ± 0.036	104.5 ± 7.9	84.6 ± 6.2	28.5 ± 3.3
10	35.5 ± 1.2	3.32 ± 0.33	157.7 ± 17.3	0.369 ± 0.031	0.298 ± 0.025	57.6 ± 4.7	46.6 ± 3.7	34.9 ± 2.9
15	35.3 ± 1.2	2.59 ± 0.9	141.6 ± 20.8	0.350 ± 0.060	0.284 ± 0.051	48.7 ± 6.4	39.6 ± 5.5	32.8 ± 4.2
20	34.5 ± 1.5	1.88 ± 0.29	127.2 ± 21.7	0.327 ± 0.035	0.267 ± 0.030	41.5 ± 6.6	33.8 ± 5.3	27.4 ± 1.4
25	35.3 ± 1.2	1.39 ± 0.16	110.5 ± 13.7	0.299 ± 0.031	0.243 ± 0.027	32.9 ± 2.3	26.7 ± 1.9	25.8 ± 2.0
30	36.2 ± 1.0	0.701 ± 0.153	94.7 ± 23.8	0.225 ± 0.024	0.181 ± 0.020	21.0 ± 4.9	16.9 ± 3.9	21.2 ± 4.2
35	37.0 ± 0.6	0.637 ± 0.098	91.6 ± 27.0	0.251 ± 0.045	0.200 ± 0.036	21.9 ± 4.0	17.5 ± 3.1	18.3 ± 2.1
F	2.807	131.8	27.11	9.11	8.90	108.1	110.2	14.83*
P	0.025	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

* F from arcsine-transformed data.

TABLE 2

Comparison of ventilation parameters of *Noctilio albiventris* to predicted values for birds (Bucher, 1985; Bucher and Bartholomew, 1986) and mammals (Stahl, 1967). *Noctilio* and bird data are for ambient temperatures at which f and $\dot{V}_{O_2}$ are minimal. Data for mammals are for resting individuals in thermoneutral conditions. $\dot{V}_I$ were computed as f · V_T (not from allometric equations). The avian $\dot{V}_{O_2}$ and ventilation values are for nonpasserines.

	Noctilio albiventris	40 g mammal	40 g bird	*Noctilio mammal*	*Noctilio bird*
$\dot{V}_{O_2}$ (ml/min)	0.637	1.005	1.113	0.63	0.75
f (br/min)	91.5	123.5	28.8	0.74	3.18
V_T (ml STPD)	0.200	0.270	0.888	0.74	0.23
$\dot{V}_I$ (ml STPD)	17.5	28.9	25.6	0.61	0.68
E_{O_2}	18.3	16.6	20.8	1.10	0.88

constant ratios as $\dot{V}_{O_2}$ changed (fig. 3). The bats responded differently at 1 °C: E_{O_2} declined slightly (but not significantly) from its value at 10 °C (fig. 2D), and a large increase was observed in f (and hence V_I; figs. 2A,C,3). A multiple regression with f, V_T, and E_{O_2} as predictors explained 96% of the variance in $\dot{V}_{O_2}$ over the entire temperature range:

$$\dot{V}_{O_2} \text{ (ml/min)} = 0.0143 \cdot f + 6.76 \cdot V_T + 0.0668 \cdot E_{O_2} - 3.78 \quad (N = 331, P < 0.001)$$

The six bats used for 10–35 °C measurements showed substantial individual variation in the manner in which they adjusted f, V_T, and E_{O_2} to accommodate changing $\dot{V}_{O_2}$
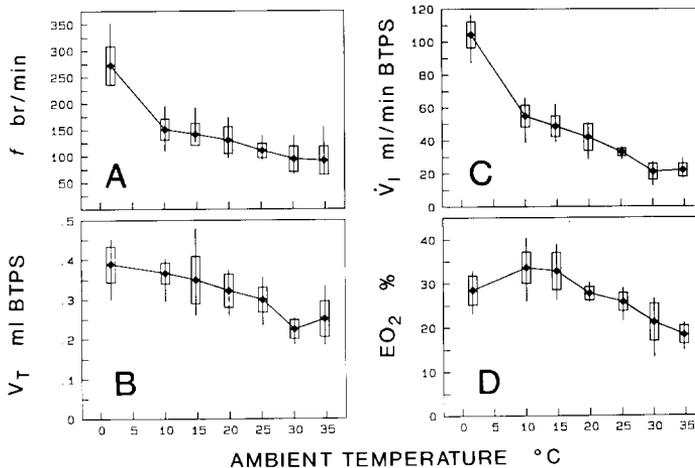

Fig. 2. Ventilation parameters of *Noctilio albiventris* at different ambient temperatures. Symbols as in fig. 1; $N = 6$ at all Ta. A. Respiration frequency (f). B. Tidal volume (V_T). C. Minute volume ($\dot{V}_I$). D. Oxygen extraction (E_{O_2}).
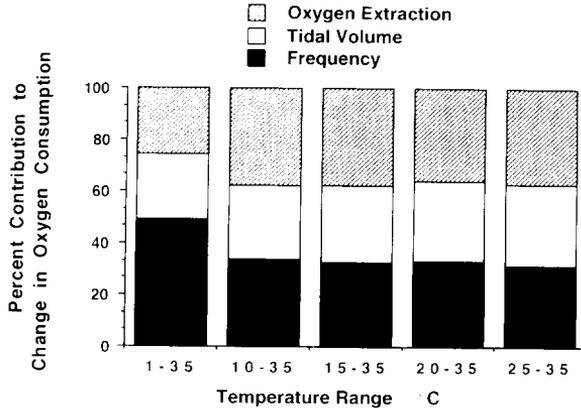
Fig. 3. Relative contribution of f, V_T, and E_{O_2} to the factorial change in oxygen consumption across different ambient temperature ranges.
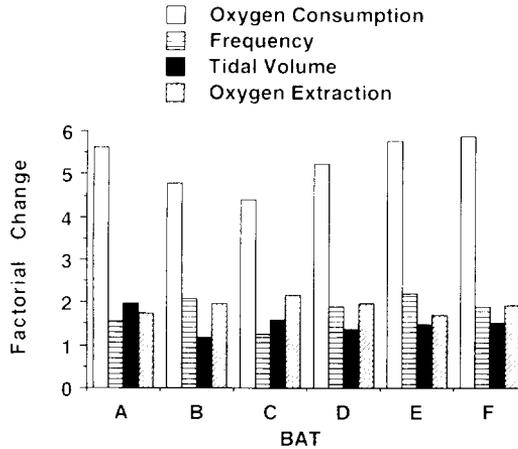

Fig. 4. Individual differences in ventilatory accommodation of the change in oxygen consumption between ambient temperatures of 10 and 35 °C. Bars indicate the factorial change in each variable across this range of Ta.

(fig. 4). More variation was apparent in ventilation than in extraction. Between Ta of 10 and 35 °C, the coefficients of variation of the factorial change in $\dot{V}_{O_2}$ and E_{O_2} were similar and relatively low (10.9 and 8.36%, respectively). By comparison, coefficients of variation of the factorial changes of V_T (18.2%), f (19.3%) and $\dot{V}_I$ (17.9%) were more than twice as large as for E_{O_2}.

Discussion

Metabolism, thermoregulation and water loss. The basal metabolic rate of *Noctilio albiventris* is 66% of the allometrically predicted value for a 40 g eutherian (Bartholomew, 1982). This is consistent with previous reports of low BMR in *Noctilio* and other insectivorous Neotropical bats (McNab, 1969). *Noctilio's* mass and low BMR place it below the theoretical "boundary curve for endothermy" (McNab, 1982), so it is predicted to show daily torpor. However, *Noctilio* maintained stable body temperature throughout our measurements, even at Ta considerably colder than any likely to occur in the species' warm tropical habitat. There was considerable individual variation of Tb, but mean values did not decline with declining Ta and we saw no indication of torpor at any Ta. These data, together with observations of moderately active individuals with $\dot{V}_{O_2}$ substantially higher than resting $\dot{V}_{O_2}$ at 1 °C, indicate that *Noctilio's* maximal aerobic scope for thermogenesis is probably greater than the measured scope of 7.2. That value is probably less than half the aerobic scope for flight (Thomas, 1984), but it is large compared to the thermogenic scope of 4–6 typical of most small eutherians (Bartholomew, 1982) and small birds (Dawson and Marsh, 1989). In this respect *Noctilio* resembles small dasyurid marsupials, which also have large thermogenic scopes and low BMR (Dawson and Dawson, 1982).

At Ta below T_{lc} *Noctilio* has a thermal conductance about 21% higher than predicted for a 40 g eutherian (Aschoff, 1981), so thermoregulation is energetically expensive. At 20 °C (a Ta the bats probably experience routinely in the wild and just 10 °C below T_{lc}) metabolic rate is 2.5–3 times BMR. In nature, these high thermoregulatory costs are probably mitigated by the species' propensity to huddle in large groups when roosting (personal observations; unpublished data).

Captive *Noctilio* suffer from dehydration-related pathologies unless housed in a humid environment (personal observations). However, between 10 and 30 °C their average rates of evaporative water loss (about 105 mg H_2O/h) do not differ significantly from the predicted value for a resting 40 g mammal and the lowest means for individuals (60–80 mg H_2O/h) are similar to those of xeric-adapted heteromyid rodents (Hinds and MacMillen, 1985). Low temperature dependence of $\dot{m}H_2O$ is presumably a result of high ventilation rates at low Ta (where the potential for evaporation is small) compensating for low ventilation rates at high Ta (where the potential for evaporation is large).

Ventilatory responses to changing Ta and $\dot{V}_{O_2}$. In theory, the respiratory system can adjust f, VT, E_{O_2}, or any combination of these parameters to meet changing oxygen demand. Most birds accommodate changing $\dot{V}_{O_2}$ at Ta below T_{lc} largely through modulation of $\dot{V}_I$. E_{O_2} is usually fairly constant (Bucher, 1985; Bech et al., 1985; Kaiser and Bucher, 1985; Chappell and Bucher, 1987; Chappell and Souza, 1988), although in some species it increases with increasing $\dot{V}_{O_2}$ (e.g., the European coot *Fulica atra*; Brent et al., 1984). Roughly similar responses (near-constant E_{O_2}, changing $\dot{V}_I$) occur in the few mammals for which adequate data are available (Casey et al., 1979; Withers et al., 1979; Chappell, 1985). In both birds and mammals there is little consistency in the mechanisms used

to change $\dot{V}_I$; different species adjust f and V_T to different degrees and the overall pattern is one of considerable plasticity and flexibility.

Noctilio albiventris is unusual in that it accommodates changing thermogenic $\dot{V}_{O_2}$ through simultaneous changes in f, V_T, and E_{O_2}. Between Ta of 10 to 35 °C (encompassing a 5.2-fold range of $\dot{V}_{O_2}$), all three parameters are adjusted in parallel by roughly similar proportions (figs. 2,3). The importance of large (2-fold) changes in E_{O_2} contrasts strongly with the responses of other mammals and most birds. For example, deer mice (*Peromyscus maniculatus*; 18–22 g) support an aerobic scope of 5–6 primarily by adjusting f with little change in E_{O_2} (Chappell, 1985), and small arctic mammals actually decrease E_{O_2} from thermoneutral values as thermogenic $\dot{V}_{O_2}$ increases (Withers *et al.*, 1979).

A different pattern, resembling the typical mammalian response, occurs when *Noctilio* are exposed to low Ta. Mean E_{O_2} reaches a maximum of about 35% at 10 °C, remaining stable or declining slightly at 1 °C. The additional $\dot{V}_{O_2}$ at Ta below 10 °C is accommodated largely by increased f, which is almost twice as high at 1 °C as at 10 °C (figs. 2,3).

High lability and variance are important aspects of ventilation in most birds and mammals (Bucher, 1985). Typically, f, V_T, and E_{O_2} vary by factors of 2–3, even in resting animals held in constant conditions (*e.g.*, Casey *et al.*, 1979; Chappell, 1985; Chappell and Bucher, 1987; Bucher and Chappell, 1989). By comparison, the variability of ventilation parameters in *Noctilio* is relatively low. Coefficients of variation at Ta < T_{lc} averaged 14–17% for f, V_T, and $\dot{V}_I$, and 11.3% for E_{O_2} (table 2). Variation was somewhat greater at Ta of 30 and 35 °C.

Few data exist on ventilatory responses to Ta in other bats. Ventilation adjustments to accommodate the $\dot{V}_{O_2}$ shift between rest and flight have been reported for *Pteropus gouldii* (870 g; Thomas, 1981) and *Phyllostomus hastatus* (110 g; Thomas *et al.*, 1984). To support the 10 to 11-fold greater $\dot{V}_{O_2}$ during flight, both species relay on increased V_T and f; E_{O_2} is stable or declines slightly from resting (but probably not thermoneutral) values. Flight E_{O_2} (10% in *Pteropus* and 20% in *Phyllostomus*) is considerably lower than the E_{O_2} of *Noctilio* exposed to low Ta, possibly because the 1 : 1 synchronization between breathing and wingbeat during flight produce a relative hyperventilation (Thomas *et al.*, 1984). Our data suggest that E_{O_2} stabilizes (and perhaps begins to decline) as $\dot{V}_{O_2}$ attains high values in inactive as well as in flying bats.

Comparisons of ventilation in bats, other mammals, and birds.   Gas exchange in the mammalian alveolar lung with tidal flow is, in theory, less efficient (*i.e.*, E_{O_2} should be lower) than in the avian parabronchial lung with unidirectional flow and cross-current exchange (Piiper and Scheid, 1977). Accordingly, comparisons of ventilation between birds and mammals should reveal functional differences related to the different morphologies of avian and mammalian lungs. Robust comparisons are hampered by the high variability of ventilation parameters, the paucity of mammalian data, and the difficulty of identifying standardized physiological reference conditions for these temperature-sensitive variables (Bucher, 1985). Nevertheless, it seems clear from allometric

studies that resting mammals tend to have considerably higher f and lower V_T and E_{O_2} than resting birds of similar mass (Stahl, 1967; Bucher, 1985; Bucher and Bartholomew, 1986), which is consistent with predictions based on differences in lung morphology. However, these results might also be explained as an artifact of selection for different levels of aerobic performance: at a given body mass, maximal rates of oxygen consumption are usually much greater in birds because of the high power requirements of flight.

Studies of bats can provide useful insights into this question, since bats possess ventilatory characteristics of both birds and mammals. In terms of lung morphology bats are typical mammals, although lung volume is unusually large (Maina *et al.*, 1982). However, in terms of aerobic capacity and scope bats closely resemble birds. Results from available data suggest that bat ventilatory characteristics are quite variable and are not tightly constrained by either morphology or selection for high $\dot{V}_{O_2}$. Ventilation in resting *Pteropus* and *Phyllostomus* generally follows the mammalian pattern (Thomas, 1981; Thomas *et al.*, 1984). In contrast, ventilation in resting *Noctilio* at thermoneutral Ta is intermediate between the mammalian and avian allometry (table 1). *Noctilio*'s f and V_T are close to the mammalian allometry, its $\dot{V}_I$ is low compared to allometric values for both birds and mammals, and its E_{O_2} is intermediate. At lower Ta where $\dot{V}_{O_2}$ is substantially above BMR, *Noctilio*'s E_{O_2} rises to 30–35%, a value equal to or greater than the E_{O_2} of most birds in similar conditions (Bucher, 1985) and considerably greater than E_{O_2} typical for other mammals. Contrary to theoretical predictions, flying bats do not have greater air convection requirements and lower E_{O_2} than flying birds, despite roughly equivalent and very high $\dot{V}_{O_2}$ in both groups (Thomas *et al.*, 1984).

In conclusion, bats are able to achieve ventilatory efficiencies similar to those of most birds, despite having a typically mammalian lung morphology. The theoretically greater efficiency of the avian lung may be evident in some situations, however. For example, birds can function at higher altitudes than mammals (Bouverot, 1985). Also, the highest E_O, we observed in resting bats (about 40–45%), though greater than for most other mammals, are much less than the maximal E_{O_2} of 60–70% reported for several species of birds (Brent *et al.*, 1984; Stahel and Nicol, 1988; Bucher and Chappell, 1989).

References

Aschoff, J. (1981). Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* 69A: 611–619.

Bartholomew, G. A. (1982). Energy metabolism. In: Animal Physiology: Principles and adaptations, edited by M. S. Gordon. Macmillan, New York, pp. 57–110.

Bech, C., W. Rautenberg and B. May (1985). Ventilatory oxygen extraction during cold exposure in the pigeon (*Columba livia*). *J. Exp. Biol.* 116: 499–502.

Bouverot, P. (1985). Adaptation to altitude-hypoxia in vertebrates. New York, Springer, 176 pp.

Brent, R., P.F. Pedersen, C. Bech and K. Johansen (1984). Lung ventilation and temperature regulation in the European coot (*Fulica atra*). *Physiol. Zool.* 57: 19–25.

Bucher, T.L. (1985). Ventilation and oxygen consumption in *Amazona viridigenalis*: a reappraisal of 'resting' respiratory parameters in birds. *J. Comp. Physiol. B* 155: 269–276.

Bucher, T.L. and G.A. Bartholomew (1986). The early ontogeny of ventilation and homeothermy in an altricial bird, *Agapornis roseicollis* (Psittaciformes). *Respir. Physiol.* 65: 197–212.

Casey, T.M., P.C. Withers and K.K. Casey (1979). Metabolic and respiratory responses of Arctic mammals to ambient temperature during the summer. *Comp. Biochem. Physiol.* 64A: 331–341.

Chappell, M.A. (1985). Effects of ambient temperature and altitude on ventilation and gas exchange in deer mice (*Peromyscus maniculatus*). *J. Comp. Physiol. B* 155: 751–758.

Chappell, M.A. and T.L. Bucher (1987). Effects of temperature and altitude on ventilation and gas exchange in chukars (*Alectoris chukar*). *J. Comp. Physiol. B* 157: 129–136.

Chappell, M.A. and S.L. Souza (1988). Thermoregulation, gas exchange, and ventilation in Adélie penguins (*Pygoscelis adeliae*). *J. Comp. Physiol. B* 157: 783–790.

Dawson, T.J. and W.R. Dawson (1982). Metabolic scope and conductance in response to cold of some dasyurid marsupials and Australian rodents. *Comp. Biochem. Physiol.* 71A: 59–64.

Dawson, W.R. and R.L. Marsh (1989). Metabolic acclimatization to cold and season in birds. In: Physiology of cold adaptation in birds, edited by C. Bech and R.E. Reinertsen. New York and London: Plenum Press, pp. 83–94.

Hinds, D.S. and R.E. MacMillen (1985). Scaling of energy metabolism and evaporative water loss in heteromyid rodents. *Physiol. Zool.* 58: 282–298.

Johansen, K. and C. Bech (1983). Heat conservation during cold exposure in birds (vasomotor and respiratory implications). *Polar Res.* 1: 259–268.

Kaiser, T. and T.L. Bucher (1985). The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation and water loss in relation to ambient temperature in the Prairie Falcon, *Falco mexicanus*. *Physiol. Zool.* 58: 748–758.

Maina, J.N., A.S. King and D.Z. King (1982). A morphometric analysis of the lung of a species of bat. *Respir. Physiol.* 50: 1–11.

McNab, B.K. (1969). The economics of temperature regulation in Neotropical bats. *Comp. Biochem. Physiol.* 31: 227–268.

McNab, B.K. (1982). Energetics, body size, and the limits to endothermy. *J. Zool.* 197.

Piiper, J. and P. Scheid (1977). Comparative physiology of respiration: functional analysis of gas exchange organs in vertebrates. *Int. Rev. Physiol.* 14: 219–253.

Stahel, C.D. and Stuart C. Nicol, 1988. Ventilation and oxygen extraction in the little penguin (*Eudyptula minor*), at different temperatures in air and water. *Respir. Physiol.* 71: 387–398.

Stahl, W.R. (1967). Scaling of respiratory variables in mammals. *J. Appl. Physiol.* 22: 453–460.

Thomas, S.P. (1981). Ventilation and oxygen extraction in the bat *Pteropus gouldii* during rest and steady flight. *J. Exp. Biol.* 94: 231–250.

Thomas, S.P., M.R. Lust and H.J. Van Riper (1984). Ventilation and oxygen extraction in the bat *Phyllostomus hastatus* during rest and steady flight. *Physiol. Zool.* 57: 237–250.

Withers, P.C., T.M. Casey and K.K. Casey (1979). Allometry of respiratory and haematological parameters of Arctic mammals. *Comp. Biochem. Physiol.* 64A: 343–350.