

## SEXUAL DIMORPHISM AND SCALING OF ENERGETICS IN FLYING FOXES OF THE GENUS *PTEROPUS*

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The energetics of 5 species of the flying fox genus *Pteropus* were measured with respect to ambient temperature. These data and those from 2 species in the literature were examined in relation to body size and to their distribution on continents or small islands.  $\log_{10}$  body mass accounted for 94% of the variation in  $\log_{10}$  basal rate of metabolism of those 7 species. Females belonging to large species of *Pteropus* were smaller than conspecific males and consequently had lower (total) basal rates than males. No factor other than body mass in this analysis was correlated with basal rate in *Pteropus*. However, in the context of 21 species of pteropodids, continental *Pteropus* have basal rates that are 28% greater than small-island endemics. The effect of island size was not demonstrated in *Pteropus*, when examined alone, because the smallest species studied are small-island specialists, and the largest species live on continents, which means that effects of mass and island size are confounded, which leads to a high scaling power (1.06) for basal rate in this genus.  $\log_{10}$  thermal conductance in *Pteropus* increased with  $\log_{10}$  body mass, 5 species having low thermal conductances by mammalian standards. Body temperature was independent of body mass.

Key words: basal rate of metabolism, body mass, body temperature, island size, *Pteropus*, sexual dimorphism, thermal conductance

The extensive interest in the thermal biology of bats has been stimulated by their great ecological and taxonomic diversity. One source of this diversity is body mass; adult bats range from about 2 g (*Craseonycteris*) to 1,600 g (*Pteropus*), an 800-fold range. The genus *Pteropus* includes most of the largest species of bats, although some of the 60 species that belong to this genus are as small as 120 g. This diversity in mass is expected to have an appreciable effect on the energy expenditure in *Pteropus*, as it does in other bats (Bonaccorso and McNab 1997; McNab 1969) and mammals generally (McNab 1988). The impact of body size is complicated by sexual dimorphism in *Pteropus*, wherein males usually are larger than females.

Another source of diversity in *Pteropus*

is its distribution; some species are found on continents and large islands, whereas others are limited to small islands (Pierson and Rainey 1992). For example, *P. hypomelanus* lives on the small islands of Karkar and Bagabag, among others, within sight of the northern coast of New Guinea, but has strayed only twice to the mainland (Bonaccorso 1998). This species is a small-island specialist, as is *P. pumilus* in the Philippines, where it avoids the larger islands in this archipelago. *Pteropus* is found on islands throughout the Indian Ocean, including Pemba and Mafia Islands just off the coast of Tanzania, but it is not found on the African mainland, even though 11 other genera of pteropodids live there. *P. seychellensis* (on Mafia) and *P. voeltzkowi* (on Pemba) approach the African coast via the Indian Ocean, apparently as small-island

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specialists (Kingdon 1974). Kingdon (1989) suggested that *Pteropus* might depend on seawater as a source of salts, which would prevent them from inhabiting the central parts of the continent, but that does not explain why they do not live along coastal Africa. In coastal New Guinea, *P. conspicillatus* often flies offshore from a colony to drink seawater in the late afternoon before flying inland to feed (Bonaccorso 1998).

Only 2 species of *Pteropus* have had their energetics measured (Bartholomew et al. 1964), both from Australia: *P. scapulatus*, which weighs about 360 g, and *P. poliocephalus*, which weighs about 600 g. Basal rates of metabolism in these species are 105% and 96% of the values expected from an all-mammalian curve, respectively (McNab 1988); that is, they have rather typical mammalian basal rates, as do most other frugivorous bats (McNab 1969, 1989). We report data on the energy expenditure and thermoregulation of 5 additional species of *Pteropus* that range in mass from 194 g (*P. pumilus*) to 1,024 g (*P. vampyrus*). These data permit an examination of the factors that influence energy expenditure in this genus.

#### MATERIALS AND METHODS

*Animals.*—We present data on adults in 5 species of *Pteropus*, including *P. pumilus* (6 males, 4 females), *P. rodricensis* (6 males, 2 females), *P. hypomelanus* (6 males, 6 females), *P. giganteus* (4 males, 2 females), and *P. vampyrus* (5 males, 4 females). Those individuals were maintained in large, outdoor, circular flight enclosures at the Lube Foundation, Gainesville, Florida. All species at this facility were highly successful breeders, which suggested that they were in excellent physiological condition. These individuals consumed commercial fruit supplies supplemented with vitamins and were exposed to a warm-temperate environment. Cool nighttime temperatures in winter were avoided by permitting bats to cluster in a heated house at the center of each enclosure.

The *Pteropus* in this study have the following distributions: *P. pumilus* is native to small is-

lands in the Philippines, *P. rodricensis* is restricted to Rodrigues Island in the Indian Ocean, *P. hypomelanus* occurs mainly on small islands from Malaysia northeastward to the Philippines and eastward to New Guinea and the Solomons, *P. giganteus* is found in southern Asia, and *P. vampyrus* lives in southeastern Asia eastward to the Philippines and Indonesia (Corbet and Hill 1992).

*Experimental protocol.*—Rate of metabolism was measured in terms of oxygen consumption as a function of ambient temperature. All measurements were made in the dark on postabsorptive individuals during their inactive period between 0800 h and 1700 h. Bats were less active if kept in the dark while making measurements than if the chamber was lighted. Small *Pteropus* (*pumilus* and *rodricensis*) were placed in a chamber with a volume of 8.9 l and the intermediate *P. hypomelanus* in a chamber of 27.0 l. Those chambers were placed in a large (329-l), hollow-walled chamber, the temperature of which was regulated by pumping water into the walls from a controlled-temperature water bath. Larger *Pteropus* (*giganteus* and *vampyrus*) were placed directly into the large chamber. Room air was drawn through the chambers, scrubbed of CO<sub>2</sub> (by color-indicating soda lime) and water (by color-indicating silica gel), and sent to a flow meter and finally to an S-3AII Applied Electrochemistry oxygen analyzer (Applied Electrochemistry, Inc., Sunnyvale, California). The electrical output from the analyzer was sent to a strip-chart recorder. Flow rates in the chambers were maintained between 0.75 and 2.20, 2.60 and 4.30, and 3.40 and 9.60 l/min for chambers of 8.9, 27, and 329 l, respectively, which were sufficient to ensure an adequate mixture of gases, as was demonstrated by the independence of the calculated rate of metabolism from flow rate. That is, because rate of metabolism was calculated as a product of the flow rate and the  $\Delta O_2$  between incoming and outgoing gas, a reciprocal relation existed between those parameters as long as gas flow was sufficient for gas mixture in the chamber (B. K. McNab, in litt.). Air temperatures inside the chambers were measured with thermocouples attached to a Physitek BAT-12 thermocouple thermometer (Sensortek, Inc, Clifton, New Jersey).

Experimental periods lasted until a prolonged ( $\geq 2$  min) minimal rate of metabolism was attained repeatedly, which usually required 2 h for

small species and up to 4 h for large *Pteropus*. The periods collectively represented 920 h of measurements. Minimal rates of oxygen consumption were reported to reduce the impact of activity. All experiments in which an individual was continuously active were discarded, which in the case of *P. vampyrus* represented nearly half the experiments. Rates of oxygen consumption are presented as standard dry temperature and pressure. Within 10 s of the end of an experiment, we measured the rectal temperature of bats with the BAT-12 thermocouple thermometer.

For each species, the rate of oxygen consumption and body temperature were plotted as a function of ambient temperature. Those data were used to estimate basal (or standard) rate of metabolism (mean rate found in the zone of thermoneutrality when the animal was postabsorptive, thermoregulating, and inactive during the inactive period—McNab 1997), minimal thermal conductance (at temperatures below thermoneutrality—McNab 1980), and mean body temperature (at ambient temperatures over which body temperature was constant). Repeated measurements were made on most individuals at most ambient temperatures, which permitted us to determine whether any differences existed among individuals or between genders in response to temperature. Thermal conductance was calculated by  $C = \dot{V}_{O_2}/\Delta T$ , where  $\dot{V}_{O_2}$  was rate of metabolism and  $\Delta T$  was the temperature differential between the body and environment (McNab 1980). Minimal conductances were compared with an all-mammal standard (McNab and Morrison 1963).

Three complications with the data were encountered. First, the rate of metabolism in large *Pteropus* at temperatures below thermoneutrality is highly variable; all measurements below thermoneutrality cannot be meaningfully forced into one highly variable estimate of thermal conductance (McNab 1980). When measurements of metabolism below thermoneutrality are organized in large species by thermal conductance, conductance clearly decreases with a fall in ambient temperature. Reduction of conductance prevents use of a 2-phase regression to determine conductance and the lower limit of thermoneutrality, as advocated by Nickerson et al. (1989), unless a limited set of measurements just below thermoneutrality are used selectively, a decision that undercuts the implied “objectivi-

ty” of the 2-phase technique and ignores conductances at lower temperatures. Use of the 2-phase regression on these data is tantamount to returning to the older technique of using the slope of the regression below thermoneutrality as an estimate of conductance, which by definition is not correct unless the curve extrapolates to body temperature when metabolism is zero (McNab 1980).

When faced with that variability, we define 2 conductances below thermoneutrality, 1 that corresponds to the lower limit of thermoneutrality and the other that represents the lowest conductance compatible with effective thermoregulation. All other conductances below thermoneutrality fall between these extremes, as is demonstrated by plotting thermal conductance as a function of ambient temperature. In the smallest species, minimal thermal conductance usually defines the lower limit of thermoneutrality, which makes a comparison with large species difficult. No obvious solution to this dilemma exists: Should we compare minimal conductances, regardless of whether they define the lower limit of thermoneutrality, or should we compare conductances that define the lower limit of thermoneutrality, regardless of whether they are minimal? We prefer to compare minimal conductances, regardless of whether they correspond to the lower limit of thermoneutrality, under the belief that high conductances that define the lower limit are behavioral “choices,” not a measurement of the physical capacity to retard heat loss.

Second, the attempt to characterize a species in terms of energetics encounters a difficulty in sexually size-dimorphic pteropodids because of the impact of mass on basal rate and thermal conductance. If data from males and females are pooled, differences between sexes are masked, but if some species in an interspecific analysis are represented twice (once for males and once for females) and others are represented by a combined value for males and females, as would be the case if no difference were found between sexes or if data were derived from the literature, the species are represented unequally. We analyzed data on *Pteropus* by entering 1) the average of male and female masses, basal rates, and thermal conductances, what we refer to as the “species’ means,” and 2) male and female data separately, when available.

A difference in basal rate between sexes or

among species can exist either because they have different masses or because the basal rate is influenced by factors other than scaling. To deal with those contingencies, mass-specific rates, body masses, and total rates of metabolism were compared between sexes and among species. Several standards could be used for *Pteropus*. For example, basal rate could be compared with a fitted equation for the genus *Pteropus*, an equation for pteropodids, or the general relationship for mammals. Difficulties exist with each standard; only 7 species of *Pteropus* have been measured, which is a small subset of the 60 species in this genus, although this sample nearly encompasses its complete size range. As will be seen, an inherent difficulty exists in using a *Pteropus* standard because factors that influence basal rate are correlated with each other. Use of the family Pteropodidae as a standard (McNab and Bonaccorso 2001) includes a much larger size range (which is important when examining the impact of body size) and a greater range of ecology and behavior. Basal rates of *Pteropus* also can be compared with the all-mammal standard (McNab 1988), which of course incorporates an even greater range in behavior and body size than is found in Pteropodidae and gives a broader perspective to the performance of *Pteropus*. These latter 2 standards were used preferentially to judge the level of basal rate in *Pteropus*.

Third, because each species was represented by several individuals, a question arises that is usually ignored in most studies of energetics: Is the best estimate of a physiological parameter obtained by pooling the multiple measurements made on all individuals, when the sample size would be  $n$ , the number of measurements, or by averaging the individual performances to get a mean of individual means, when the population size would be  $N$ , the number of individuals? The most unbiased estimate of basal rate is obtained by using the mean of the individual mean basal rates because the pooled estimate of all measurements would be influenced differentially by individuals that contributed more values to the mean pooled estimate. However, a problem also exists with the mean of individual means; individuals that are frequently measured have a more reliable estimate of their basal rates than those with only 1 measurement. In calculating a mean of individual means, these 2 kinds of estimates are weighted equally. For example, the

difference between the estimate of basal rate obtained by pooling all measurements and the estimate derived from the mean of individual means in *P. pumilus* was 5% (86% versus 81% expected from mass), a difference that decreases to 1% (88% versus 87%) if individuals with only 1 measurement are eliminated. This change occurs because 4 of the 5 individuals with the lowest mean basal rates were measured only once.

One solution is to estimate physiological parameters by testing whether a difference exists among the individuals measured; if no difference is found, data can be pooled, although that still does not deny the numerical impact of individuals that were measured more often. A better solution might be to make an equal number of measurements on several individuals; if 30 measurements were to be made in thermoneutrality, 6 measurements on each of 5 individuals would be much better than 2 measurements on each of 15 individuals or 1 measurement on each of 30 individuals (B. K. McNab, in litt.). That choice, however, is sometimes difficult to implement when working on animals captured in the field, especially when some species are not able to be maintained in captivity. In this study, mean pooled basal rates and thermal conductances are reported, but as a transition to a populational approach to the energetics of endotherms, the individual means and the mean of the individual means also are given. The conclusions of this study are not affected by that choice.

*Statistics.*—An analysis of covariance (ANCOVA) was used to compare the influence of various factors on the physiological performance of *Pteropus*. In the case of basal rate and minimal thermal conductance, we used ANCOVA to compare the correlation of  $\log_{10}$  basal rate of metabolism, or  $\log_{10}$  minimal conductance, with  $\log_{10}$  body mass in a series of “cells” defined by a set of noncontinuous character states, such as island size and food habits; each character state was a potential source of diversity that affected basal rate and thermal conductance. Total basal rates and total minimal thermal conductances were used in those analyses to prevent autocorrelation with body mass. The ANCOVA program used was SuperANOVA© (Abacus Concepts, Inc., Berkeley, California).

The estimated parameters were expressed as a  $\bar{X} \pm SE$  ( $n$  = measurements,  $N$  = individuals) for estimates obtained by pooling data from all individuals (“pooled mean”) and as a mean ( $n$

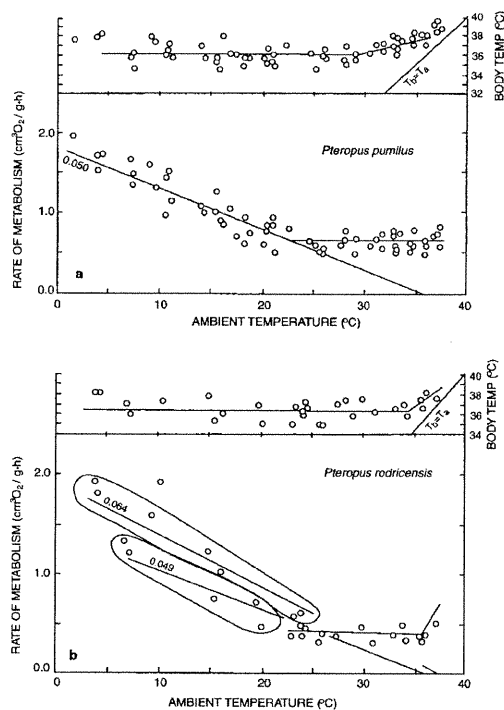


FIG. 1.—Standard body temperature and rate of metabolism as a function of ambient temperature in a) 10 *Pteropus pumilus* and b) 8 *P. rodricensis*. The curve below thermoneutrality, the slope of which equals thermal conductance (indicated by a number), extrapolates to the mean body temperature when rate of metabolism equals zero.

= measurements) for each individual, which were collectively used to calculate the mean of individual means. The results of statistical tests are given as the probability of a factor having an effect; factors were considered significant if  $P \leq 0.05$ .

## RESULTS

*Pteropus pumilus*.—This species, one of the smallest belonging to the genus ( $194.2 \pm 1.81$  g, 74, 10), maintained core body temperature equal to  $36.1 \pm 0.14^\circ\text{C}$  (40, 6) at ambient temperatures between  $0^\circ\text{C}$  and  $30^\circ\text{C}$  (Fig. 1a). Pooled basal rate of metabolism in this small-island species was  $0.651 \pm 0.0178$   $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (31, 10), which was 86% of the value expected from mammals

generally (McNab 1988). Mean individual basal rates in females were 63% (1), 74% (2), 76% (1), and 88% (2) and in males were 72% (1), 75% (1), 86% (7), 87% (6), 88% (5), and 98% (5) of the values expected from mass ( $\bar{X} = 81\%$ ). Mass-specific basal rate did not differ ( $P = 0.32$ ) among the 10 individuals, even though males were slightly larger ( $P < 0.001$ ) than females ( $202.5 \pm 2.68$  g, 25, 6, versus  $174.6 \pm 5.48$  g, 6, 4), the “species’ mean” mass being 188.6 g. Basal rate also did not differ by sex ( $P = 0.21$ ) when expressed relative to that expected from mass. However, total pooled basal rate in males was greater ( $P = 0.006$ ) than in females ( $133.7 \pm 4.07$   $\text{cm}^3\text{O}_2/\text{h}$ , 25, 6, versus  $106.2 \pm 8.31$   $\text{cm}^3\text{O}_2/\text{h}$ , 6, 4) because of the larger mass of males.

Minimal thermal conductance equaled  $0.050 \pm 0.0015$   $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (30, 6), which was 70% of the expected value (McNab and Morrison 1963) and defined the lower limit of thermoneutrality at  $23^\circ\text{C}$ . No difference ( $P = 0.61$ ) was found among the 6 individuals, the values being 65% (4), 66% (7), 69% (6), 71% (5), 76% (2), and 79% (4) of the values expected from mass ( $\bar{X} = 71\%$ ). This species has a thick, woolly fur coat.

*Pteropus rodricensis*.—The Rodrigues Island flying fox is another small *Pteropus*, weighing  $254.5 \pm 5.63$  g (44, 8). It had a mean body temperature of  $36.5 \pm 0.19^\circ\text{C}$  (23, 8) at ambient temperatures from  $3^\circ\text{C}$  to  $34^\circ\text{C}$  (Fig. 1b). Pooled basal rate of metabolism equaled  $0.530 \pm 0.0188$   $\text{cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (15, 7), which was 75% of the value expected from mammals. Mass-specific basal rate did not differ ( $P = 0.092$ ) among 7 individuals. Individual basal rates in males were 61% (2), 71% (5), 75% (2), 78% (1), 88% (1), and 88% (3) and in a female was 73% (1) of the values expected from mass ( $\bar{X} = 76\%$ ). The sexes did not differ in mass ( $P = 0.83$ ). Although data on females were limited, available information indicated no difference ( $P = 0.83$ ) in total pooled basal rate (males,  $129.4 \pm 6.08$   $\text{cm}^3\text{O}_2/\text{h}$ , 14, 6, versus females  $124.3$   $\text{cm}^3\text{O}_2/\text{h}$ , 1, 1).

Estimates of thermal conductance were

variable, depending in part on body temperature. Thus, the minimal thermal conductance was  $0.049 \pm 0.0030 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (5, 4), which was 79% of the value expected from mass and corresponded to a mean body temperature of  $36.1^\circ\text{C}$ . No difference ( $P = 0.53$ ) was found in minimal thermal conductance among the 4 individuals, values being 66% (2), 80% (1), 85% (1), and 86% (1) ( $\bar{X} = 79\%$ ). That conductance defined the lower limit of thermoneutrality. Sometimes rates of metabolism at ambient temperatures below  $24^\circ\text{C}$  were higher without including noticeable activity; they corresponded to a mean conductance of  $0.064 \pm 0.0027 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (6, 3), or 101% of the expected value, and to a higher body temperature,  $37.4^\circ\text{C}$ . That curve intersected thermoneutrality near the midpoint (Fig. 1b). The Rodrigues Island flying fox has a woolly fur coat, although not as dense as *P. pumilus*.

*Pteropus hypomelanus*.—This intermediate-size species exhibited sexual dimorphism in body size ( $P < 0.001$ ): Males weighed  $571.5 \pm 4.24 \text{ g}$  (62, 6) and females weighed  $470.1 \pm 2.50 \text{ g}$  (79, 6). Mean body temperature at ambient temperatures between  $1^\circ\text{C}$  and  $18^\circ\text{C}$  was  $35.7 \pm 0.10^\circ\text{C}$  (44, 10), which was lower ( $P < 0.001$ ) than at ambient temperatures between  $18^\circ\text{C}$  and  $30^\circ\text{C}$  ( $36.3 \pm 0.10^\circ\text{C}$ , 41, 10). Body temperature increased further at ambient temperatures  $>30^\circ\text{C}$  (Fig. 2a).

Mass-specific basal rate of metabolism depended on sex: Males had a rate equal to  $0.627 \pm 0.0216 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (15, 6), or 112% of the value expected in mammals. Females, despite their smaller mass, had a lower mass-specific basal rate equal to  $0.487 \pm 0.0167 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (30, 6), which corresponded to 83% of the value expected in mammals. Basal rate did not differ ( $P = 0.174$ ) among 6 females, but it did ( $P < 0.002$ ) among 6 males, mainly because of a correlation of basal rate with body mass ( $P < 0.002$ ). Basal rates in individual females were 61% (2), 74% (2), 77% (2), 84% (20), 94% (2), and 96% (2) of the ex-

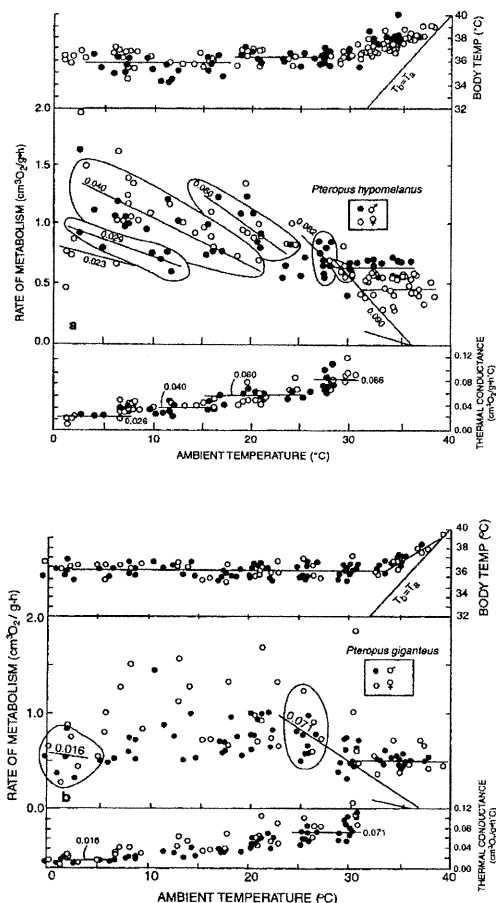


FIG. 2.—Standard body temperature, rate of metabolism, and thermal conductance as a function of ambient temperature and gender in a) 12 *Pteropus hypomelanus* and b) 6 *P. giganteus*. The thermal conductances described in the lowest curve for each species also are indicated in the middle curve by a number and the slope of the curve below thermoneutrality (see text).

pected values ( $\bar{X} = 81\%$ ); individual males had basal rates that were 91% (3), 110% (4), 119% (1), 120% (3), 121% (1), and 144% (3) of the expected values ( $\bar{X} = 118\%$ ). The pooled basal rate of females, expressed relative to the value expected from mass for mammals, was lower ( $P < 0.001$ ) than the basal rate in males ( $82.8 \pm 4.8\%/112.0 \pm 3.9\% = 0.71$ ). As a result of those correlations, males had much greater

( $P < 0.001$ ) total pooled basal rate than females ( $355.7 \pm 11.29 \text{ cm}^3\text{O}_2/\text{h}$ , 15, 6, versus  $233.0 \pm 13.83 \text{ cm}^3\text{O}_2/\text{h}$ , 30, 6). The “species’ mean” for mass was 520.8 g and for basal rate was  $0.557 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$ , which was 97% of the expected basal rate (notice how the high basal rate in males obscures the low basal rate found in females when the basal rate is expressed as the species’ mean).

The most distinctive aspect of the energetics of this species is that at ambient temperatures below about  $30^\circ\text{C}$ , rate of metabolism increased with great variability in a nonlinear manner (Fig. 2a). First of all, a lower limit of thermoneutrality of  $30^\circ\text{C}$  is exceedingly high for a mammal weighing 500 g—a lower limit of  $30^\circ\text{C}$  is defined by minimal thermal conductance in endotherms as small as 6–8-g shrews (McNab 1991); the lower limit here clearly is not defined by the minimal conductance. Second, the great variability in rate of metabolism below thermoneutrality was not correlated with either a systematic failure to regulate core body temperature or obvious activity, but because the variation in rate of metabolism was greater than that found in thermal conductance, some of the variation in rate of metabolism was associated with variation in body temperature. Much of the remaining variability was correlated with a reduction in ambient temperature, as indicated by the progressive decrease in the slope of the metabolism–temperature curves and calculated conductances (Fig. 2a).

In males the conductance that defined the lower limit of thermoneutrality was  $0.082 \pm 0.0055 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (9, 6), which was 196% of the expected value; it corresponded to a core temperature equal to  $36.3^\circ\text{C}$ . The lowest conductance in males was  $0.029 \pm 0.0012 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (6, 2), which was 69% of the conductance expected from mass and 35% of the conductance that defines the lower limit of thermoneutrality. It corresponded to a core temperature of  $34.7^\circ\text{C}$ —a slightly low body temperature.

In females the conductance that defined the lower limit of thermoneutrality was  $0.090 \pm 0.0023 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (5, 2), which was 195% of the value expected from mass and corresponded to a core temperature of  $36.3^\circ\text{C}$ . The lowest conductance in females, which was measured at ambient temperatures between  $1^\circ\text{C}$  and  $2^\circ\text{C}$ , was  $0.023 \pm 0.0010 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (4, 2), which was only 50% of the conductance expected from mass and 28% of the value that defined the lower limit of thermoneutrality; that value corresponded to a body temperature equal to  $36.3^\circ\text{C}$ . The “species’ mean” for the thermal conductance that defined the lower limit of thermoneutrality was  $0.086 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ , and the minimal conductance was  $0.026 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ .

*Pteropus giganteus*.—In this intermediate-size species, males weighed  $739.2 \pm 15.22 \text{ g}$  (69, 4) and females  $385.1 \pm 3.80 \text{ g}$  (41, 2). Core body temperature was  $36.7 \pm 0.07^\circ\text{C}$  (85, 6) at ambient temperatures from  $0^\circ\text{C}$  to  $32^\circ\text{C}$  (Fig. 2b). Pooled basal rate of metabolism in males equaled  $0.508 \pm 0.0131 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (15, 4), which was 98% of the value expected from mass; in females it equaled  $0.525 \pm 0.0460 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (9, 2), which was 84% of the expected value. Basal rate varied among individuals, both in 4 males ( $P = 0.013$ ) and in 2 females ( $P < 0.001$ ). In females ( $P < 0.001$ ) but not males ( $P = 0.61$ ), basal rate was correlated with body mass. Individual female basal rates were 69% (6) and 113% (3) of the expected values ( $\bar{X} = 91\%$ ), whereas individual males had basal rates that were 83% (3), 98% (6), 102% (3), and 103% (3) of the expected values ( $\bar{X} = 97\%$ ). The basal rate in females, expressed relative to the value in mammals expected from mass, is not different ( $P = 0.74$ ) from males ( $91.0 \pm 12.4\%/96.5 \pm 8.8\% = 0.94$ ) because the discrepant basal rates of the 2 females encompassed the basal rates of the 4 males. As a result of a larger mass ( $P < 0.001$ ), males had a higher ( $P < 0.001$ ) total pooled basal rate ( $361.1 \pm 15.15 \text{ cm}^3\text{O}_2/\text{h}$ , 15, 4) than females ( $200.1 \pm 19.55 \text{ cm}^3\text{O}_2/\text{h}$ , 15, 4) than females ( $200.1 \pm 19.55 \text{ cm}^3\text{O}_2/\text{h}$ , 15, 4).

h, 9, 2). The "species' mean" for basal rate is  $0.517 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$ , which was 92% of the value expected from the mean mass of 562.2 g.

As in *P. hypomelanus*, this species shows great variation in rate of metabolism at all temperatures below thermoneutrality despite a constant core body temperature (Fig. 2b). The variation was most marked in females but was also seen in males. Notice that in males the minimal rate of metabolism was about equal at temperatures from  $38^\circ\text{C}$  down to  $0^\circ\text{C}$ , so that by discarding the higher values at temperatures between  $27^\circ\text{C}$  and  $7^\circ\text{C}$ , the lower limit of thermoneutrality would be about  $0^\circ\text{C}$ . No one estimate of thermal conductance will accurately describe the response of this species to temperature; conductance decreases with ambient temperature (Fig. 2b). The conductance that corresponded to the lower limit of thermoneutrality in males and females was  $0.071 \pm 0.0043 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (12, 6), which was 175% of the value expected from the mean mass. At ambient temperatures between  $0^\circ\text{C}$  and  $4^\circ\text{C}$ , mean thermal conductance of males and females was  $0.016 \pm 0.0019 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (11, 5), or 39% of the value expected from the mean mass (562.2 g) and 23% of the conductance that defined the lower limit of thermoneutrality. The low thermal conductance at low ambient temperatures was not associated with a low core body temperature.

*Pteropus vampyrus*.—This species is one of the 2–3 largest bats. Males weighed  $1,153.3 \pm 16.60 \text{ g}$  (35, 4), and females weighed  $895.2 \pm 19.78 \text{ g}$  (27, 3). This species was extremely gregarious; grooming, harem defense, and wing fanning occurred throughout much of the daytime in the flight cages. Even in the experimental chamber, when bats were isolated, kept in the dark, and sheltered from noise, activity often occurred; results of 28 of the 62 experiments had to be discarded because of persistent activity. Body temperature at ambient temperatures  $<34^\circ\text{C}$  equaled  $36.9 \pm 0.15^\circ\text{C}$  (36, 7); core temperatures  $>38^\circ\text{C}$

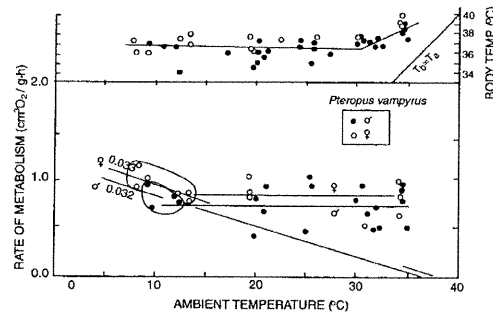


FIG. 3.—Standard body temperature, rate of metabolism, and thermal conductance (indicated by numbers) as a function of ambient temperature and gender in 9 *Pteropus vampyrus*.

generally represented activity. When measurements with activity were discarded, a standard but highly variable relationship was found between rate of metabolism and ambient temperature (Fig. 3). Thermoneutrality extended at least from  $35^\circ\text{C}$  down nearly to  $13^\circ\text{C}$  in females and to about  $11^\circ\text{C}$  in males (Fig. 3), but if the discarded measurements were included, the lower limit to thermoneutrality was near  $30^\circ\text{C}$ , and the relationship between rate of metabolism and ambient temperature was similar to *P. hypomelanus* and *P. giganteus*.

Males had a mean pooled basal rate of  $0.743 \pm 0.0403 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (21, 4), which was 163% of the value expected from mass. Females had a pooled basal rate of  $0.827 \pm 0.0413 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$  (10, 3), which was 169% of the value expected from mass. In this species, variability (measured in terms of *SE*) of rate of metabolism in thermoneutrality was twice that of most other pteropodids, even after discarding almost half the measurements. Some of the higher measurements remaining may still have reflected (undetected) activity. Nevertheless, all rates measured in thermoneutrality were greater than those expected in mammals from body mass, so we concluded that this continental species indeed had a high basal rate. Basal rate did not differ among 4 males ( $P = 0.10$ ) or 3 females ( $P = 0.64$ ). Individual basal rates in females equaled

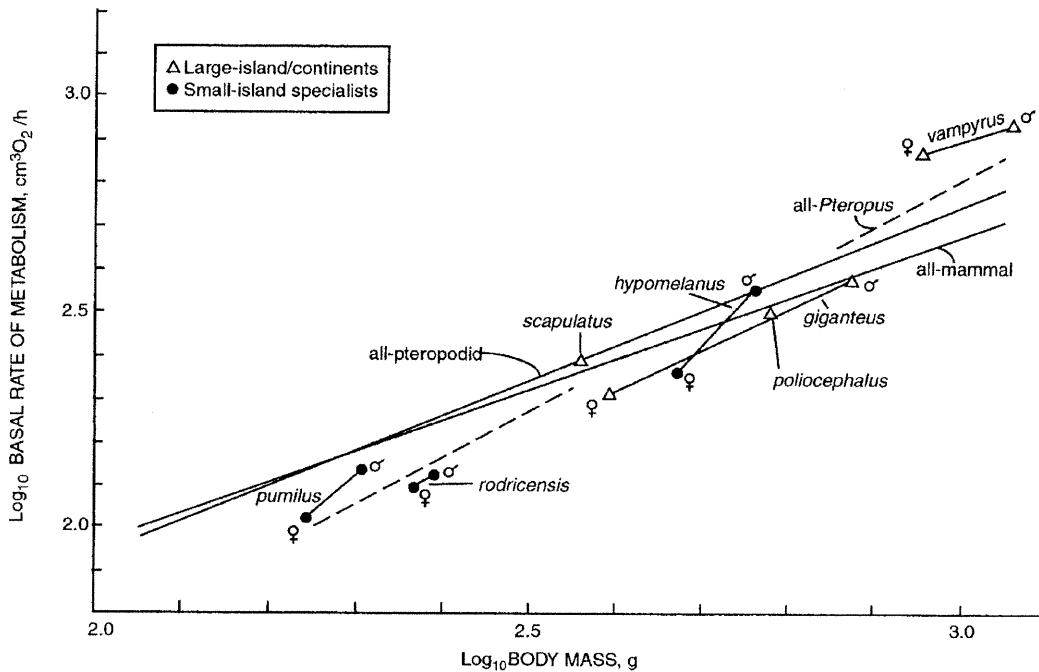


FIG. 4.— $\log_{10}$  total basal rate of metabolism as a function of  $\log_{10}$  body mass in *Pteropus*. The curves for all mammals (McNab 1988), all pteropodid bats (McNab and Bonaccorso 2001), and all *Pteropus* (see text) are indicated. Where available, data on sexes in a species are linked.

149% (4), 181% (3), and 182% (3) ( $\bar{X}$  = 171%) and in males were 128% (6), 169% (5), 177% (5), and 183% (5) ( $\bar{X}$  = 164%). No difference ( $P = 0.73$ ) was found in basal rates, corrected for body size, between males and females. Although males were larger than females, their total pooled basal rates ( $851.2 \pm 37.81 \text{ cm}^3\text{O}_2/\text{h}$ , 21, 4) were not different ( $P = 0.095$ ) from those of females ( $736.4 \pm 54.79 \text{ cm}^3\text{O}_2/\text{h}$ , 10, 3). A "species" mean" for basal rate was  $0.785 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}$ , which is 168% of the value expected from a mean mass of 1,024.3 g.

This species only occasionally tolerated temperatures  $<15^\circ\text{C}$  without becoming active. In fact, if an experiment started at temperatures  $<8^\circ\text{C}$ , no resting values were obtained, and activity was diminished only by raising chamber temperature to  $>20^\circ\text{C}$ . Minimal thermal conductance in males equaled  $0.032 \pm 0.0017$  (4, 2), which corresponded to a body temperature of  $36.1^\circ\text{C}$  and was 109% of the value expected from

mass, but in females it equaled  $0.033 \pm 0.0008 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$  (6, 3), which corresponds to a body temperature of  $37.7^\circ\text{C}$  and was 99% of the conductance expected from mass. The mean minimal thermal conductance in this species was  $0.033 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ , or 103% of the value expected from the species' mean mass (1,024.3 g).

#### DISCUSSION

*Basal rate of metabolism.*— $\log_{10}$  body mass accounts for 93.7% ( $P < 0.001$ ) of the variation in  $\log_{10}$  basal rate in *Pteropus* (Fig. 4):  $\dot{V}_{\text{O}_2} = 0.42 \text{ m}^{1.06}$ . The question remains whether any factor other than body mass has an impact on basal rate. When ANCOVA is limited to the 7 species of *Pteropus* that have been studied, basal rate is not correlated with any other factor. Specifically,  $\log_{10}$  basal rate did not correlate with the pattern of distribution ( $P = 0.85$ ) when combined with  $\log_{10}$  mass ( $P = 0.005$ ) or when examined alone ( $P =$

0.106). Thus, large-island species had basal rates that were only 4% greater than those found in small-island species when the measured basal rates are compared with those expected from the fitted curve. This conclusion, however, is flawed because 2 of the 3 small-island species also are the smallest species of *Pteropus* studied, a correlation that does not permit the effect of island size on basal rate to be isolated from that of body mass and leads to an unusually high fitted power (1.06) of mass for basal rate in this genus (Fig. 4). The positive correlation in *Pteropus* of body size with island size is widespread (McNab 1994). The species of *Pteropus* studied have insufficient diversity in food habits (all fruit eaters, except *P. scapulatus*, which feeds on nectar, pollen, and fruit juice—Richards 1983) for this factor to account for the residual variation in  $\log_{10}$  basal rate ( $P = 0.48$ ).

By using “species’ means” in sexually dimorphic species, differences between basal rates of males and females are obscured. Basal rates in the large continental species *P. giganteus* and *P. vampyrus* are scaled intraspecifically parallel to interspecific scaling, but in the small- and intermediate-size, small-island species *P. pumilus* and *P. hypomelanus*, the basal rate of the small females is depressed (Fig. 4), which leads to an even higher scaling power in the 5 species when sexes are separated:  $\dot{V}_{O_2} = 0.31 m^{1.11}$  ( $r^2 = 0.95$ ). An intraspecific scaling power that is equivalent to the interspecific power or higher is counter to the observation that intraspecific scaling power is usually lower than interspecific the power (Heusner 1991), but most intraspecific scaling described in mammals to date has involved a change in mass associated with growth, whereas here the intraspecific scaling is in sexually dimorphic adults. Nevertheless, no separation of basal rate into male and female values within the 5 species of *Pteropus* for which we have data permitted basal rate to be correlated with island size ( $P = 0.92$ ). Again, the smallest species live

on small islands and the largest species on continents.

When data derived from 21 species of pteropodids, including the 7 *Pteropus*, are used as the basis of ANCOVA,  $\log_{10}$  basal rate of metabolism is correlated with  $\log_{10}$  body mass ( $P < 0.001$ ), entrance or not into torpor ( $P < 0.002$ ), and distribution on large or small islands ( $P = 0.009$ ;  $r^2 = 0.980$ —McNab and Bonaccorso 2001). In this family, species that live on large islands or continents have basal rates that are 28% greater than those limited in distribution to small islands (cf. McNab 1994). This difference would be even greater if *P. hypomelanus* had been represented by females rather than by the “species’ mean,” which (as noted) obscures the low basal rate in females of this species.

These analyses indicate that species belonging to the genus *Pteropus* have low basal rates if they are specialists for life on small islands. The reduction is most marked in *P. pumilus* and *P. rodricensis* because of a small mass and a residence on small islands. In the rather large small-island specialist *P. hypomelanus*, a depression in basal rate produced by other than a decrease in mass is found only in females. Continental *Pteropus* have standard or high basal rates. These data are interpreted to mean that small-island specialists encounter a resource base limited by island area (McNab 1994), which has its most acute impact on females (i.e., those with high resource requirements in association with the cost of reproduction). The logic behind this argument is that, although we have only measured standard rates of energy expenditure, field rates of energy expenditure are correlated strongly with basal rates in mammals independent of body mass (Ricklefs et al. 1996), which means that species with low basal rates are expected to have low field expenditures, of and requirements for, energy.

Factors that influence basal rate of metabolism in pteropodids generally, and in *Pteropus* specifically, are many and have

complex interactions, so that a clear, unambiguous statement of causality is difficult to attain. Analyses such as these require large sets of data compiled from a diverse array of species, of varying degrees of relationship, and having a wide range in body mass. By adding data from other species and genera belonging to the family Pteropodidae, we obtained a better standard against which to evaluate performance of the species of *Pteropus*.

*Thermal conductance and body temperature.*— $\log_{10}$  minimal total thermal conductance in *Pteropus* is independent of  $\log_{10}$  body mass ( $P = 0.14$ ), although caution is required because of the high variability of conductance at cool to cold ambient temperatures. This high variability undoubtedly is due to behavior; indeed, if all the measurements on *P. vampyrus* were included in Fig. 3, data would appear similar to the pattern seen in Figs. 2a and 2b, which implies that some (or most?) of the variation in rate of metabolism at temperatures below thermoneutrality in *P. hypomelanus* and *P. giganteus* resulted from activity, even though it was not as apparent in these species as in *P. vampyrus*. These observations emphasize the value of minimal thermal conductance over that which behaviorally defines the lower limit of thermoneutrality. Absence of significance in the correlation of minimal conductance with mass is due principally to the unusually low conductance of *P. giganteus*, which is only 38% of the value expected from mammals. If the conductance for *P. giganteus* is deleted, then  $\log_{10}$  minimal total conductance was correlated marginally with  $\log_{10}$  body mass ( $r^2 = 0.66$ ,  $P = 0.049$ ). All 3 small-island endemics have low minimal conductances by general mammalian standards.

The mean interspecific body temperature in *Pteropus* was 36.6°C; species means varied between 35.7°C and 36.9°C and were independent of all known factors, including body mass ( $P = 0.36$ ).

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