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The metabolism of New Guinean pteropodid bats

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Abstract Rate of metabolism and body temperature were measured in eight species of pteropodid bats that live in Papua New Guinea. These data and those from 13 other species available in the literature are examined to determine the factors with which the energetics of pteropodids are correlated. Lowland populations of species that weigh < 35 g generally have low basal rates and often become torpid, whereas their highland populations had standard or high basal rates and were precise thermoregulators, as were all adult pteropodids that weighed more than 60 g. In large pteropodids belonging to the genera *Dobsonia* and *Pteropus*, females are smaller and consequently have lower total basal rates than males. Compared to species found on continents and large islands, species limited in distribution to small islands have lower basal rates, both because of a smaller mass and a reduction of metabolism independent of body mass. These trends are most marked in females that belong to small-island species, adjustments that may facilitate reproduction and survival on small oceanic islands with a limited resource base. Minimal thermal conductances are usually low in species that roost exposed in trees, whereas large species that roost in caves have either standard or high conductances.

Key words Basal rate of metabolism · Minimal conductance · Oceanic islands · Pteropodidae · Torpor

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Abbreviation C thermal conductance · D metabolism coefficient for distribution · ΔT temperature differential between body and environment · R metabolism coefficient for roosting site · S slope of the metabolism-temperature curve below thermoneutrality · T_a ambient temperature · T_b body temperature · TR metabolism coefficient for temperature regulation · $\dot{V}_{O_2}$ rate of oxygen consumption

Introduction

The order Chiroptera is second among mammals only to Rodentia in the number of described species, the number reflecting the diversity of bats in body size, morphology, physiology, food habits, behavior, and climatic distribution. The variation in these characters, however, is often interdependent, which means that the realized diversity in character combinations among bats is less than might be expected from an assumption of character independence.

Character interaction is clearly seen in the factors influencing energy expenditure of bats. For example, nectarivorous, frugivorous, and vertebrate-eating bats, nearly all of which live in the tropics, tend to be effective thermoregulators and to have standard to high basal rates of metabolism by general mammalian standards, whereas insectivorous species, which live both in temperate and tropical environments, often enter torpor, and usually have low basal rates (McNab 1969, 1982). Exceptions exist: some small neotropical insectivorous bats have standard basal rates (Genoud and Bonaccorso 1986; Genoud et al. 1990) and basal rate appears to be associated with roost selection in mormoopid bats (Bonaccorso et al. 1992). Much of this information was derived from the neotropical families Mormoopidae, an insectivorous family, and Phyllostomidae and Noctilionidae, which include all New World nectarivorous, frugivorous, and vertebrate-eating species.

A complete understanding of chiropteran energetics requires data from more than a limited sample of neotropical microchiropterans. For instance, few data are available on the energetics and temperature regulation of megachiropterans (flying foxes), the suborder that includes all African and Australasian fruit- and nectar-bats, which belong to the family Pteropodidae. Only 10 of the some 170 species of pteropodids have had their rates of metabolism measured (McNab 1989), although data on the nectarivore *Melonycteris melanops* (Bonaccorso and McNab 1997) and on 5 additional species of *Pteropus* (McNab and Armstrong, 2001) have recently become available. These data suggest that intermediate to large flying foxes, all of which feed on fruits, or on fruits, blossoms, and leaves (Kunz and Ingalls 1994; Strahan 1995; Pierson et al. 1996, although see Dudley and Vermeij 1994), have basal rates similar to frugivorous phyllostomids and like them exhibit precise temperature regulation. The small megachiropteran nectarivores *Syconycteris* and *Macroglossus*, however, have low basal rates and imprecise temperature regulation (Bartholomew et al. 1964, 1970; McNab 1989; McNab and Bonaccorso 1995; Geiser et al. 1996; Bonaccorso and McNab 1997; Bartels et al. 1998). In contrast, small phyllostomid nectarivores reluctantly enter torpor (McNab 1969; Cruz-Neto and Abe 1997). Another difference between the pteropodids and phyllostomids is the much larger size of most pteropodids, which include species that weigh up to 1600 g, whereas the largest phyllostomid committed to frugivory only weighs 70 g.

Here we report measurements on rate of metabolism and body temperature (T_b) in eight species of megachiropterans mist-netted in Papua New Guinea, including one species each of *Paranyctimene* and *Rousettus*, two species of *Nyctimene*, and four species of *Dobsonia*. A preliminary summary of some of these data was published elsewhere (McNab and Bonaccorso 1995). Our data, coupled with those available from the literature on 13 additional species, permit a more complete analysis of the factors affecting the basal rate of metabolism, minimal thermal conductance, and T_b in pteropodids than has hitherto been available.

Materials and methods

Animals

We present data on the following species: *Paranyctimene raptor* (five adult males; three adult females, one of which was pregnant; one subadult male; one subadult female) is widespread in lowland New Guinea up to an altitude of 1200 m (for distributional and altitudinal records in all species, see Bonaccorso 1998); *Nyctimene albiventer* (five adult males) is found in New Guinea at altitudes between sea level and 1700 m; *Nyctimene cyclotis* (one adult female), a species found in New Guinea at altitudes between 800 m and 2600 m; *Rousettus amplexicaudatus* (two adult males; two subadult females), found from Southeast Asia, through New Guinea, to the Solomon Islands usually only up to an altitude of 400 m; *Dobsonia minor* (five adult males; four adult females; two subadult females), found in lowland New Guinea up to 600 m; *Dobsonia praedatrix* (two adult females), which is limited to the Bismarck Archipelago; *Dobsonia anderseni* (two adult females), found in the Bismarck Archipelago and the Admirality Islands; and *Dobsonia moluccensis* [= *Dobsonia magna* (Flannery 1995); three adult males; three adult females; one subadult female] occurs in New Guinea from sea level to an altitude of 2700 m.

Paranyctimene raptor, *N. albiventer*, *R. amplexicaudatus*, *D. minor*, and *D. moluccensis* were collected at altitudes < 100 m near Madang City, Madang Province, Papua New Guinea. *N. cyclotis* was captured near Herowana, 1400 m, Chimbu Province, Papua New Guinea. *D. praedatrix* and *D. anderseni* were collected at the Lowlands Agricultural Experimental Station, near Kerevat, 150 m, East New Britain Province, Papua New Guinea. Capture and measurements were made in Papua New Guinea during the months of May through August in 1991–1993 and 1996. In captivity all species were fed a variety of fruit and maintained body mass.

Experimental protocol

Measurements of rate of metabolism in terms of oxygen consumption were made as a function of ambient temperature (T_a) within a few days of capture, the only bats held for several weeks being the three largest species of *Dobsonia*. All measurements were made on post-absorptive individuals between 0800 hours and 1700 hours, i.e., during their inactive period; they were fed a variety of fruits ad libitum in the early evening after measurement. Small species were placed in jars of 0.50 l or 0.75 l that were closed with rubber stoppers; temperature was controlled by placing the chambers in a controlled temperature water bath. *D. praedatrix* and *D. anderseni* were placed in an 8.9-l chamber and *D. moluccensis* was placed in a 27.0-l chamber. These larger chambers were placed into a refrigerator modified for temperature control. Room air was pushed into small chambers and sucked through intermediate and large chambers, scrubbed of CO_2 (by color-coded soda lime) and water (by color-coded silica gel), sent to a flow meter (variously using Cole-Palmer and Brooks flowmeters), and to a S-3AII Applied Electrochemistry oxygen analyzer. The electrical output from the analyzer was sent to a stripchart recorder.

Flow rates in the chambers, which were maintained between 0.15–0.30, 0.35–0.70, 0.75–2.20, 2.60–4.30 l/min for chambers of 0.50, 0.75, 8.9, and 27 l, respectively, 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 is calculated (with appropriate corrections for temperature and pressure) as the product of flow rate and the differential in oxygen tension between the gas going into and coming out of the chamber, an adequate flow rate is one in which these two factors are reciprocally correlated with each other (B.K. McNab, personal observations), a condition that leads to the calculated rate of metabolism being independent of flow rate. Then, if flow rate is doubled, the oxygen differential is reduced to one-half and their product remains constant.

Air temperatures inside the chambers were measured with a Series 390 Atkins Digital Thermocouple Thermometer. Experimental periods usually continued until a minimal rate of metabolism that lasted for ≥2 min was repeatedly attained, which usually required 1–2 h for small species and up to 4 h in *D. moluccensis*. The data reported here were derived from 590 h of measurements. Minimal rates of oxygen consumption are reported to avoid the influence of activity. All experiments in which an individual was continuously active, evidence of which was movement in the chamber or a continuously variable oxygen tension in the gas exiting the chamber, were discarded. Within 10 s of the end of each experiment, we measured the rectal T_b of bats with the Atkins Digital Thermometer. Most individuals were measured once at each T_a, except in cases where only one or two individuals were available; then repeated measurements were made at most temperatures, but never on the same individual at the same temperature on the same day.

For each species the rate of oxygen consumption and T_b are plotted as a function of T_a, each measure of oxygen consumption corresponding to a measurement of T_b. These data are used to estimate the basal (or standard) rate of metabolism and minimal thermal conductance at temperatures below thermoneutrality. The basal rate is the mean rate found in the zone of thermoneutrality when an adult endotherm is post-absorptive, thermoregulating, and inactive during the inactive period (see McNab 1997). Thermal conductances (C) were calculated by $C = \dot{V}_{O_2}/\Delta T$, where ΔT (temperature differential between body and environment) = T_b–T_a, for each measurement of metabolism and T_b below thermoneutrality, as proposed by McNab (1980), which is mathematically equivalent to drawing a line, the slope of which is conductance, through each point and the T_b at zero rate of metabolism, as is required by the above equation. Many endotherms change thermal conductance at temperatures below thermoneutrality (McNab 1980), a complication that can be accommodated by grouping conductances in narrow ranges of T_a (McNab 1980). The reduction in conductance with a fall in T_a, however, makes the application of a two-phase regression (Nickerson et al. 1989) impossible because then the slope of the curve fitted below thermoneutrality (*S*) is not thermal conductance because the curve extrapolates to $T_b > T_a$ when $\dot{V}_{O_2} = 0.0$; i.e., $\dot{V}_{O_2} \neq S\Delta T$ (McNab 1980). The estimated pooled parameters are expressed as a mean ± SE [*n* (measurements), *N* (individuals)].

Statistics

Sample size is often a concern when dealing with animals captured in the field. All biologists understand that a number of individuals is required to estimate the diversity found within a population or species. In this study, individuals were mist-netted in mainland New Guinea and New Britain over a period of 14 months scattered over 4 years. The numbers of individuals captured for the eight species included here were 1, 2, 2, 4, 7, 8, 10, and 11, which reflected our ability to capture these species under the environmental conditions encountered. These data were held back for several years in the hope that sample sizes would increase with time and our field experience, as they did. But when dealing with rare, cryptic, evasive, or endangered species, we are of the opinion that some information on these species is infinitely better than no information, especially in context of a comparative study when most species have large – or at least adequate – sample sizes. An analysis of individual variation in basal rate within the species studied here demonstrates that an individual mean obtained from an adult is within 6% of the mean obtained from a sample of individuals, as long as the number of measurements in the individual ≥8. The mean pooled basal rates are within 2% of the mean of individual estimates. Mean basal rates are compared to an all-mammal curve derived from 321 species (McNab 1988) and at small masses with the boundary curve (McNab 1983), which generally separates endotherms that thermoregulate with precision from those that have a propensity to enter torpor; this is a higher standard than the all-mammal curve at masses < 50 g.

The basal rate of metabolism, minimal thermal conductance, and regulated T_b are examined by an analysis of covariance to determine the factors with which they are correlated. Such an analysis compares the correlation of the $\log_{10}$ basal rate of metabolism or $\log_{10}$ minimal conductance, the dependent variables, with $\log_{10}$ body mass in a series of “cells” defined by a set of noncontinuous character states (the data for which are summarized in Table 1), including here entrance or not into torpor, distribution on large or small islands, food habits, shelter type, altitudinal limits to distribution, and colonial habits. Total basal rates and minimal thermal conductances are used in these analyses. T_b and body mass are not logged when examined in an analysis of covariance because T_b is not a power function of body mass.

The attempt to characterize a species in terms of energetics encounters several difficulties in pteropodids. One is found in species that show sexual dimorphism in body mass because of the correlation of basal rate and minimal conductance with mass. As an approximation, we have used the average mass, basal rate, and minimal conductance to represent the sexually dimorphic species *D. moluccensis*. [A similar problem was faced in *Pteropus* (McNab and Armstrong 2001), where the results of an analysis were unchanged by entering the data as species averages or by sex]. Another difficulty occurs in the nectarivores *Syconycteris australis* and *Macroglossus minimus* in which highland and lowland populations were entered into the analysis separately because their thermal physiologies were as different as is often found between species (Bonaccorso and McNab 1997). To combine these data would obscure the physiological diversity within these species, although we are aware that keeping the populations separate is equivalent to double-weighing these species in the ANCOVA.

All statistical tests are considered significant if $P \leq 0.05$.

Results

Paranyctimene raptor

This small [23.6 ± 0.24 g ($n = 34$, $N = 7$)] pteropodid showed a modest capacity for temperature regulation (Fig. 1a): at T_as > 27 °C, T_b increased, whereas at lower T_as mean T_b was 33.8 ± 0.37 °C ($n = 19$, $N = 7$) with much variance, even after obvious cases of torpor were excluded. Indeed, adults and subadults, exposed to temperatures between 15 °C and 20 °C, often had T_b fall to 24–25 °C. Associated with a variable T_b was a highly variable rate of metabolism (Fig. 1a). At T_as between 29 °C and 35 °C, the pooled standard rate of adults averaged 1.04 ± 0.039 cm^3 O_2/g·h ($n = 17$, $N = 5$), which is 75% of the basal rate expected from mass by the all-mammal standard described by McNab (1988) and 56% of the value expected from the boundary curve that usually separates effective from poor thermoregulation in small endotherms (McNab 1983). Basal rate in this species differed with respect to sex among five non-pregnant adults ($F = 6.93$, $P = 0.019$): males had mean (*n*) basal rates that were 57(4)%, 71(3)%, and 77(4)% of the values expected in mammals (mean = 67%), whereas females had basal rates that were 82(3)% and 86(3)% of the values expected in mammals (mean = 84%). The mean basal rate derived from the five adults averages 75%. Subadults [mass = 19.9 ± 0.36 g ($n = 14$, $N = 2$)] in thermoneutrality had a higher rate of metabolism [1.27 ± 0.108 cm^3 O_2/g·h ($n = 5$, $N = 2$)], which is 87% of the value expected for adult mammals having the mass of subadult *Paranyctimene raptor*).

As T_a fell below 27 °C, rate of metabolism either increased (in association with maintenance of a regulated T_b) or decreased (reflecting a fall in T_b). Minimal thermal conductance was 0.146 ± 0.0046 cm^3 O_2/g·h °C ($n = 9$, $N = 4$), which corresponds to a T_b equal to 33.4 °C, which may partially explain why thermal conductance is only 64% of the value expected from mass by the relation reported by McNab and Morrison (1963). Minimal thermal conductances did not differ ($F = 1.35$, $P = 0.36$) among the four individuals. Lower estimates of thermal conductance reflected lower T_bs, whereas a pregnant female had a higher conductance [0.191 ± 0.0103 cm^3 O_2/g·h °C ($n = 3$)] and T_b (35.8 °C; Fig. 1a). Bartholomew et al. (1970) reported a few data on this species, also finding that it was a poor thermoregulator.

Table 1 The comparative energetics of pteropodid bats. Estimates modified from the literature are enclosed in parentheses. *TR* (temperature regulation) column: *n* poor temperature regulator, *i* intermediate temperature regulator, *y* good temperature regulator. *Islands* (limited in distribution to small islands) column: *y* yes, *n* no. *Roost* column: *t* tree canopy, *c* caves. *Altitude* at the site of collection: *h* high (> 600 m); *l* low (< 600 m). *Colonial* column: *n* solitary, *y* colonial

Species	Body mass (g)	Basal rate of metabolism (cm^3 O$_2$/h)	Minimal thermal conductance (cm^3 O$_2$/h °C)	Body temperature (°C)	TR	Islands	Food habits	Roost	Altitude	Colonial	Source
Syconycteris australis	15.3	26.5	3.37	36.5	y	n	Nectar	t	h	n	Bonaccorso and McNab 1997
Syconycteris australis	16.5	17.2	2.97	35.3	n	n	Nectar	t	l	n	Bonaccorso and McNab 1997
Macroglossus minimus	15.3	22.6	3.37	37.1	y	n	Nectar	t	h	n	Bonaccorso and McNab 1997
Macroglossus minimus	16.4	14.4	3.44	35.3	n	n	Nectar	t	l	n	Bonaccorso and McNab 1997
Paranyctimene raptor	23.6	24.5	3.45	33.8	i	n	Fruit	t	l	n	This study
Nyctimene albiventer	30.9	27.3	2.87	35.9	i	n	Fruit	t	l	n	This study
Cynopterus brachyotis	37.4	47.5	6.96	36.5	y	n	Fruit	t	l	y	McNab 1989
Nyctimene cyclotis	40.4	64.6	3.47	36.0	y	n	Fruit	t	h	n	This study
Eonycteris spelaea	51.6	48.0	7.89	34.0	y	n	Nectar	c	l	y	McNab 1989
Melonycteris melanops	53.3	43.3	6.93	34.9	y	y	Nectar	t	l	n	Bonaccorso and McNab 1997
Dobsonia minor	73.7	74.4	8.84	36.5	y	n	Fruit	t	l	n	This study
Rousettus amplexicaudatus	91.5	104.3	9.70	36.5	y	n	Fruit	c	l	y	This study
Rousettus aegyptiacus	146.0	122.6	(14.60)	34.8	y	n	Fruit	c	l	y	Noll 1979
Dobsonia praedatrix	179.5	142.5	13.69	37.1	y	y	Fruit	c	l	y	This study
Pteropus pumilus	194.2	126.4	9.71	36.1	y	y	Fruit	t	l	y	McNab and Armstrong 2001
Dobsonia anderseni	241.4	174.0	20.76	36.4	y	y	Fruit	c	l	y	This study
Pteropus rodricensis	254.5	134.9	12.47	36.5	y	y	Fruit	t	l	y	McNab and Armstrong 2001
Pteropus scapulatus	362.0	242.5	19.55	(37.0)	y	n	Nectar	t	l	y	Bartholomew et al. 1964
Dobsonia moluccensis	404.3[a]	367.9[a]	36.19[a]	36.8	y	n	Fruit	c	l	y	This study
Pteropus hypomelanus	520.8[a]	290.1[a]	13.54[a]	35.7	y	y	Fruit	t	l	y	McNab and Armstrong 2001
Pteropus giganteus	562.2[a]	290.7[a]	9.00	36.7	y	n	Fruit	t	l	y	McNab and Armstrong 2001
Pteropus poliocephalus	598.0	316.9	(14.35)	(36.5)	y	n	Fruit	t	l	y	Bartholomew et al. 1964
Pteropus vampyrus	1024.3[a]	804.1[a]	33.80	36.9	y	n	Fruit	t	l	y	McNab and Armstrong 2001

[a] Interpolated values between males and females

Nyctimene albiventer

This species, which is somewhat larger [30.9 ± 0.37 g ($n = 34$, $N = 5$)] than *P. raptor*, showed a variable T_b that was higher [35.9 ± 0.18 °C ($n = 22$, $N = 5$)] and more precisely regulated (as measured by the smaller standard error of the mean) than was found in *Paranyctimene*.

The pooled basal rate of metabolism in *N. albiventer* was 0.854 ± 0.0204 cm^3 O$_2$/g·h ($n = 12$, $N = 5$), which is 66% of the value expected from the all-mammal curve and 56% of the value expected from the boundary curve. Basal rate did not differ ($F = 3.45$, $P = 0.07$) among the five males: they were 57(2), 66(2), 67(3), 70(3), and 72(2)% of the mammal curve, the mean of which is 66%.

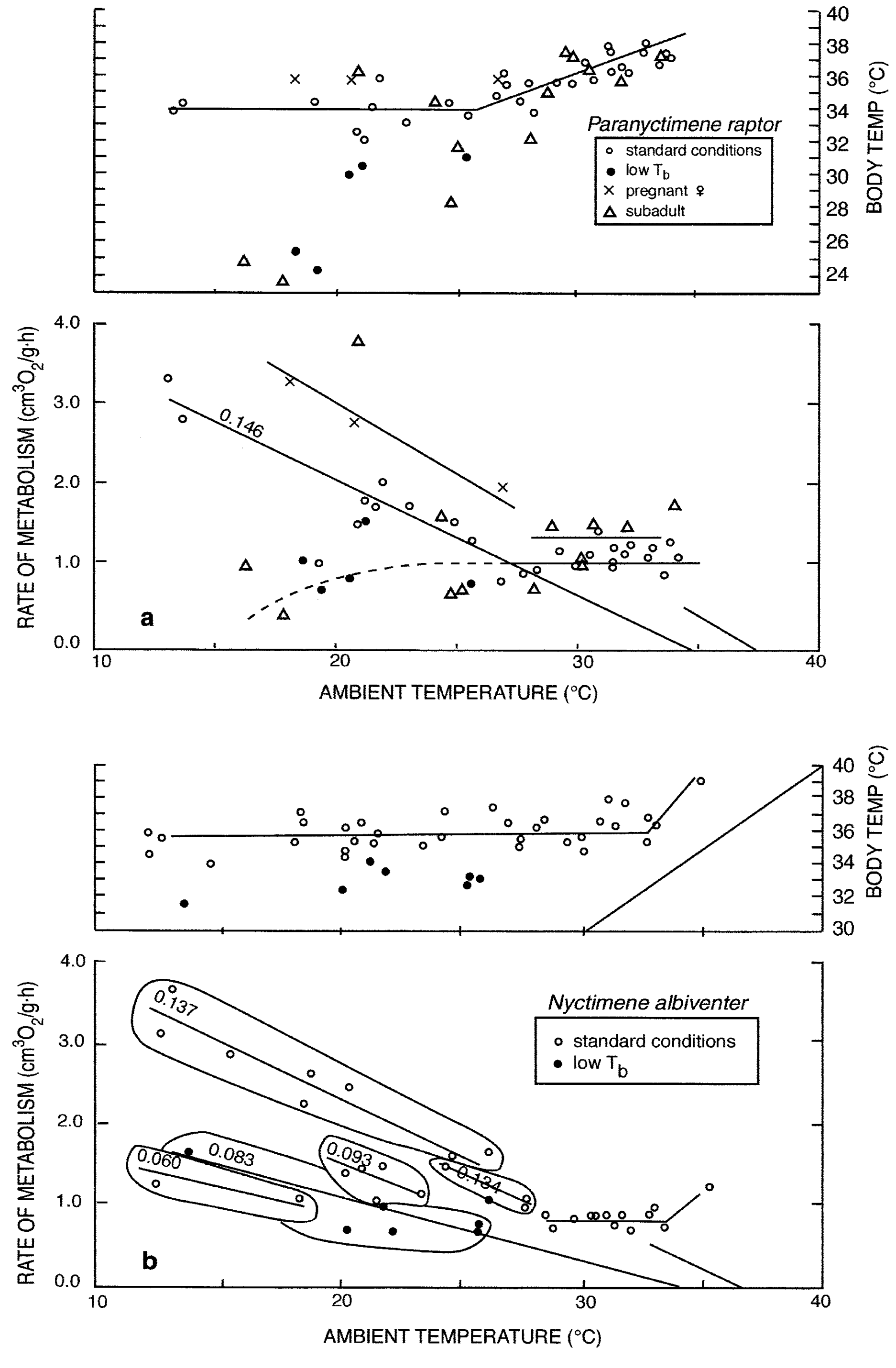


Fig. 1 Body temperature and rate of metabolism as a function of ambient temperature (T_a) in: **a** nine *Paranyctimene raptor*, and **b** five *Nyctimene albiventer*. Standard conditions occur when adult animals were post-absorptive during the period of inactivity, and when the animals were thermoregulating, non-reproductive, and without activity (McNab 1997). *Numbers* in the figure indicate estimates of thermal conductance as derived from the group of *implied* or *encircled points*

Rate of metabolism at T_as < 28 °C, the approximate lower limit of thermoneutrality, was highly variable, little of which was due to a variable T_b (Fig. 1b). The lower limit of thermoneutrality was described by a thermal conductance that was 0.134 ± 0.0023 cm^3 O$_2$/g·h °C ($n=3$, $N=3$), which is 74% of the value expected from mass. At $T_a < 16$ °C thermal conductance was similar, namely 0.137 ± 0.0054 cm^3 O$_2$/g·h °C ($n=8$, $N=6$), the principal difference between these curves being that the first had a higher T_b (36.5 °C) than the second (35.6 °C). These conductances were not minimal (Fig. 1b): at temperatures between 20 °C and 24 °C, thermal conductance was often 0.093 ± 0.0042 cm^3 O$_2$/g·h °C ($n=5$, $N=5$), which is 52% of the expected value, without a decrease in T_b (mean = 35.7 °C). This value is used as the minimal conductance because of its frequency in spite of a lower conductance [0.060 cm^3 O$_2$/g·h °C ($n=2$, $N=2$)] being occasionally found at temperatures < 20 °C also without a decrease in T_b (mean = 35.4 °C). A thermal conductance equal to

0.083 ± 0.0077 cm^3 O_2/g·h °C ($n=6$, $N=4$) at T_as between 14 °C and 26 °C (Fig. 1b) was associated with a low T_b (mean = 33.5 °C). These variable responses to cool environmental temperatures were often found in the same individual, which prevented any attempt to determine whether individuals had different thermal conductances.

Nyctimene cyclotis

The one female weighed 40.4 ± 0.33 g ($n=24$). As with *N. albiventer*, this species regulated temperature more precisely than the smaller *Paranyctimene raptor*: at $T_a < 27$ °C, T_b was 36.0 ± 0.18 °C ($n=13$). Thermoneutrality in this individual extended to temperatures as low as 17 °C (Fig. 2a) within which basal rate was 1.60 ± 0.046 cm^3 O_2/g·h ($n=18$), which is 134% of the rate expected from mass and 123% of the value expected from the boundary curve. Thermal conductance in this individual was highly variable (Fig. 2a): sometimes it conformed to a conductance equal to 0.157 ± 0.0089 cm^3 O_2/g·h °C ($n=3$), which is what is expected from mass, although it intersects thermoneutrality near the midpoint. A conductance equal to 0.086 ± 0.0051 cm^3 O_2/g·h °C ($n=5$), or only 55% of the expected value, defines the lower limit of thermoneutrality and may be minimal.

Rousettus amplexicaudatus

This *Rousettus* is appreciably smaller [91.5 ± 0.47 g ($n=28$, $N=2$)] than the congener that has been previously studied (*R. aegyptiacus*, 146 g; Noll 1979). Adults of this species were precise thermoregulators (Fig. 2b), the mean T_b being 36.5 ± 0.13 °C ($n=16$, $N=2$). They had a basal rate equal to 1.14 ± 0.036 cm^3 O_2/g·h ($n=10$, $N=2$), which is 121% of the value expected from mass and 151% of the value expected from the boundary curve. No difference in basal rate was found ($F=0.31$, $P=0.74$) between the two adults; their mean basal rates were 121(1)% and 121(9)% of the expected rates. Thermal conductance in one adult was 0.164 ± 0.0055 cm^3 O_2/g·h °C ($n=13$), which is 157% of the expected mammalian value, but it is not minimal because it intersects thermoneutrality near the midpoint (Fig. 2b); thermal conductance at the lower limit is approximately 0.106 cm^3 O_2/g·h °C, which is 101% of the expected value. Like adult *R. amplexicaudatus*, Noll (1979) found that adult *R. aegyptiacus* were excellent thermoregulators with a slightly high basal rate (102%) and a high thermal conductance (134%).

Subadults, with a smaller mass [58.3 ± 0.71 g ($n=10$, $N=2$)], had a thermoneutral rate equal to 1.19 ± 0.087 cm^3 O_2/g·h ($n=4$, $N=2$), which is 111% of the basal rate expected from their mass and 116% of the value expected from the boundary curve. In spite of this somewhat high basal rate, the subadults were poor thermoregulators upon capture, and their capacity for temperature regulation decreased during 2 days in captivity, even though their mass remained constant.

Dobsonia minor

In association with the smallest mass in *Dobsonia* [73.7 ± 1.18 g ($n=62$, $N=9$)], this species had a variable T_b (Fig. 3a). T_b in adults, like in some phyllostomids (McNab 1969), was lowest and most variable at intermediate environmental temperatures ($F=13.75$, $P=0.0007$): at T_as between 22 °C and 27 °C T_b was 35.2 ± 0.48 °C ($n=8$, $N=4$), whereas at higher (27–30 °C) and lower (8–22 °C) T_as, T_b was 36.5 ± 0.18 ($n=28$, $N=9$). The pooled basal rate of metabolism was 1.01 ± 0.025 cm^3 O_2/g·h ($n=31$, $N=9$), which is 101% of the value expected from mass and 116% of the boundary value. No difference in basal rate was found ($F=0.59$, $P=0.77$) among nine adults, and specifically no difference was found ($F=0.48$, $P=0.49$) between the sexes. Females had mean basal rates that were 85(1), 89(2), 98(2), 99(5), and 105(2)% of the values expected from mass, whereas males had basal rates that were 98(2), 100(8), 104(3), and 109(6)% of the values expected from mass; the mean of all individual means is 99%. Minimal conductance (with a mean T_b of 36.1 °C) was 0.120 ± 0.0027 cm^3 O_2/g·h °C ($n=28$, $N=6$), or 103% of the expected value; this conductance defined a lower limit of thermoneutrality equal to 28 °C. Minimal conductances did not differ ($F=1.40$, $P=0.26$) among the six individuals. Bartholomew et al. (1970) also showed that this species had a T_b that varies from 34 °C to 37 °C at cool T_as.

Subadults had a low thermoneutral rate of metabolism [0.659 ± 0.0700 cm^3 O_2/g·h ($n=4$, $N=2$)], or 58% of the value expected from mass [47.9 ± 1.52 g ($n=9$, $N=2$)] and 57% of the boundary value. They had a low thermal conductance [0.094 ± 0.0104 cm^3 O_2/g·h °C ($n=4$, $N=2$), or 63% of the expected value], and a low, variable T_b [33.6 ± 0.43 °C ($n=6$, $N=2$); Fig. 3a].

Dobsonia praedatrix

This intermediate-sized *Dobsonia* [179.5 ± 2.29 g ($n=23$, $N=2$)] had a slightly higher T_b than *D. minor* (Fig. 3b): 37.1 ± 0.19 °C ($n=14$, $N=2$) at T_as between 10 °C and 30.5 °C. Its basal rate equaled 0.794 ± 0.0309 cm^3 O_2/g·h ($n=11$, $N=2$), which is 102% of the value expected from body mass. Basal rate in the two females did not differ ($F=3.12$, $P=0.11$); they had basal rates that were 94(3)% and 105(8)% of the expected rates, the mean of which is 100%. Minimal thermal conductance in this species equaled 0.076 ± 0.0033 cm^3 O_2/g·h °C ($n=9$, $N=2$), which is 101% of the expected value and corresponds to a lower limit of thermoneutrality equal to 27 °C. Minimal conductance did not differ ($F=0.90$, $P=0.37$) between the two individuals.

Dobsonia anderseni

Another intermediate-sized *Dobsonia* [241.4 ± 1.90 g ($n = 26$, $N = 2$)] is *D. anderseni*, which McNab and Bonaccorso (1995) referred to as *D. pannietensis* (but see Flannery 1995). This species regulated T_b at 36.4 ± 0.22 °C ($n = 15$, $N = 2$) at T_as between 12 °C and 30 °C (Fig. 4a). The basal rate in this species equaled 0.721 ± 0.0309 cm^3 O$_2$/g·h ($n = 17$, $N = 2$), which is 101% of the value expected from mass. Basal rate did not differ

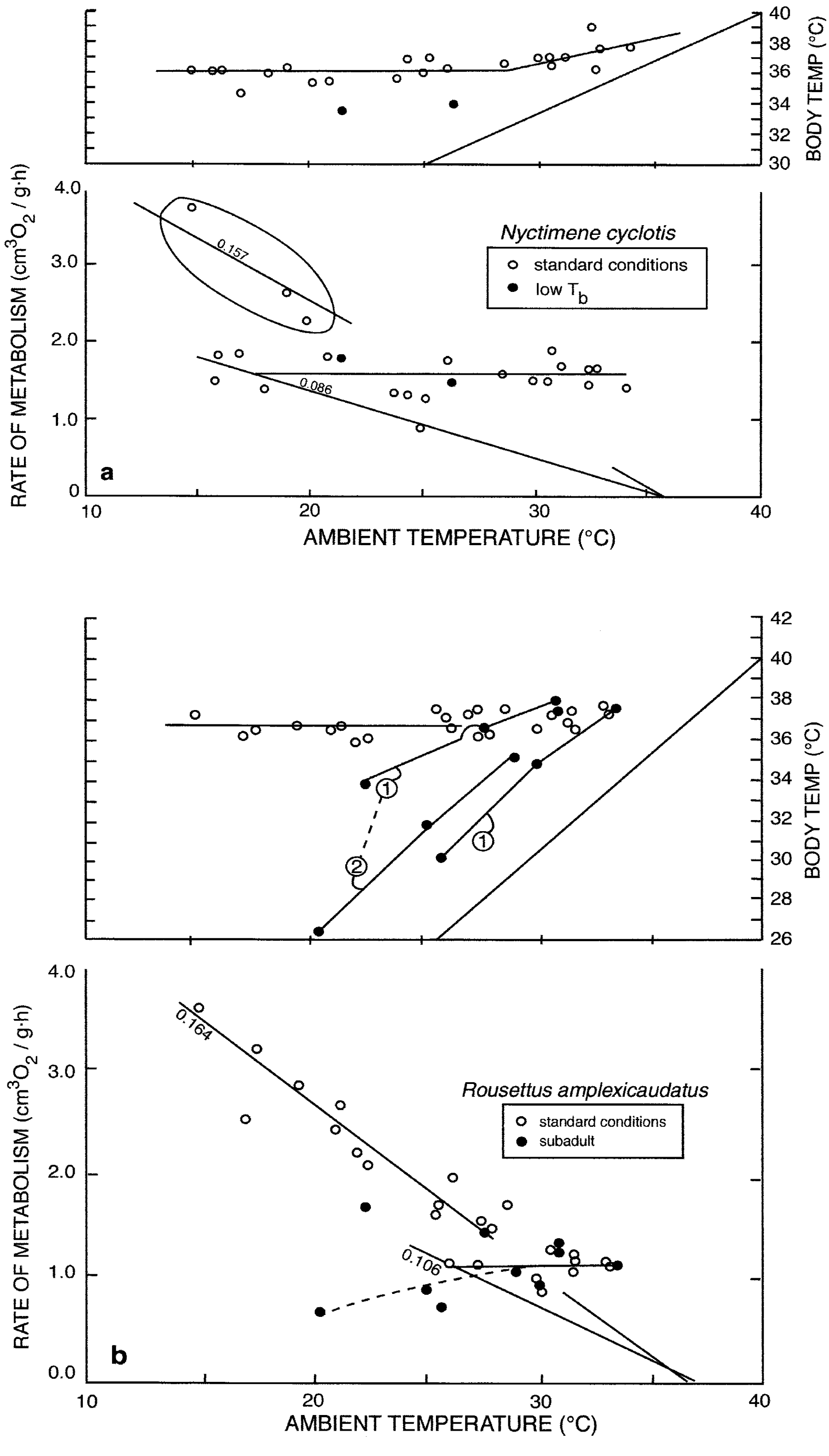
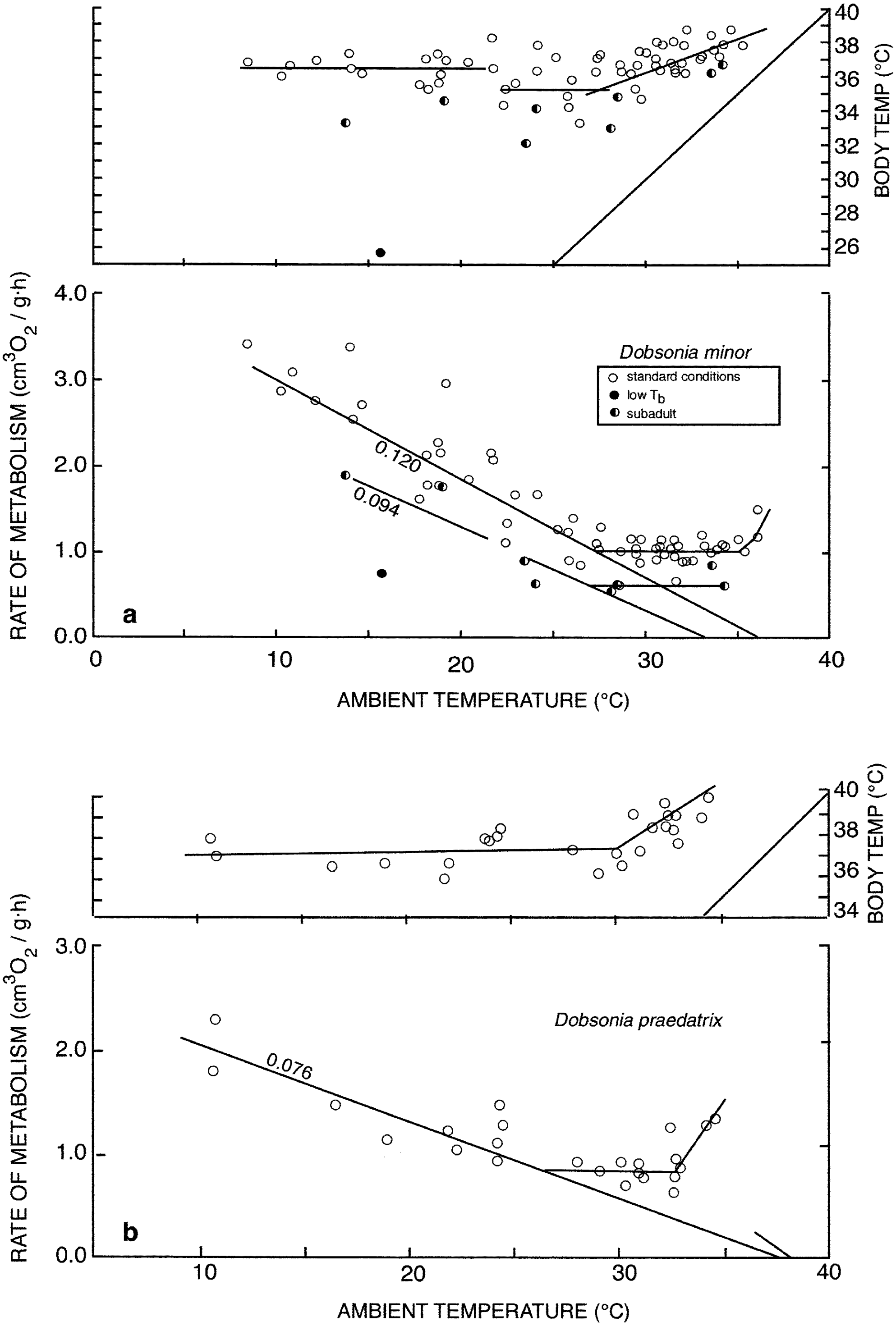


Fig. 2 Body temperature (T_b) and rate of metabolism as a function of T_a in: **a** one *Nyctimene cyclotis*, and **b** two adult and two subadult *Rousettus amplexicaudatus*. The *numbered curves* for T_b in *Rousettus* represent T_b as a function of T_a on the 1st and 2nd day after capture. Other *symbols* as in Fig. 1

Fig. 3 T$_b$ and rate of metabolism as a function of T_a in: **a** 11 *Dobsonia minor*, and **b** two *Dobsonia praedatrix*. Other *symbols* as in Fig. 1

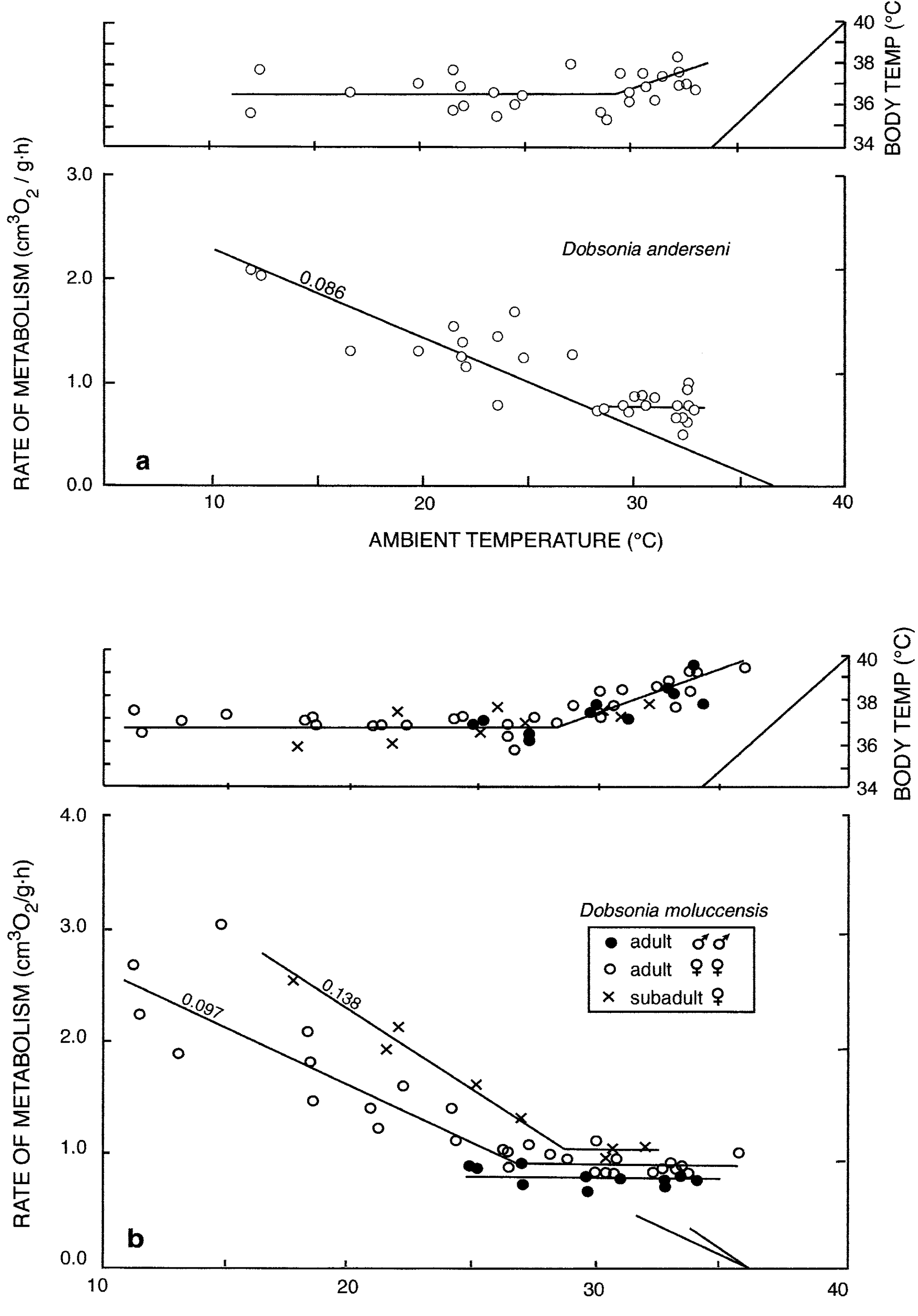


($F = 0.60$, $P = 0.45$) between the two females; they had basal rates that were 93(9)% and 105(8)% of the expected value, the mean of which is 99%. Minimal thermal conductance was 0.086 ± 0.0045 cm^3 O_2/g·h °C ($n = 11$, $N = 2$), or 134% of the expected value; it corresponds to a lower limit of thermoneutrality equal to 28 °C and did not differ ($F = 0.34$, $P = 0.55$) between the two individuals.

Dobsonia moluccensis

This is the largest species of *Dobsonia*. Several size-age-sex categories were captured: a subadult female weighed 208.0 ± 3.12 g ($n = 9$), three adult females weighed 344.7 ± 4.02 g ($n = 29$), and three adult males weighed 463.8 ± 9.87 g ($n = 11$). As a result of this range in body mass, log$_{10}$ total basal rate was correlated with

Fig. 4 T$_b$ and rate of metabolism as a function of T_a in: **a** two *Dobsonia anderseni*, and **b** seven *Dobsonia moluccensis*. Other *symbols* as in Fig. 1



$\log_{10}$ body mass ($F = 114.53$, $P < 0.0001$). Pooled basal rates in these groups were very high compared to the values expected from mass [1.08 ± 0.018 cm^3 O$_2$/g·h ($n = 3$, $N = 1$), or 145% of the expected value in the subadult female; 0.969 ± 0.0240 cm^3 O$_2$/g·h ($n = 16$, $N = 3$), or 150% for the adult females; and 0.850 ± 0.0200 cm^3 O$_2$/g·h ($n = 11$, $N = 3$), or 143% in the adult males]. These rates were not influenced by activity. Basal rate did not differ among individuals belonging to a category, including three adult females ($F = 0.06$, $P = 0.94$), which had mean basal rates that were 149(12)%, 155(3)%, and 158(1)% of the expected rates, the mean of which is 154%, and three adult males ($F = 1.99$, $P = 0.20$), which had basal rates that were 141(5)%, 142(5)%, and 160(1)% of the expected values, the mean of which is 148%. T_b in this species equaled

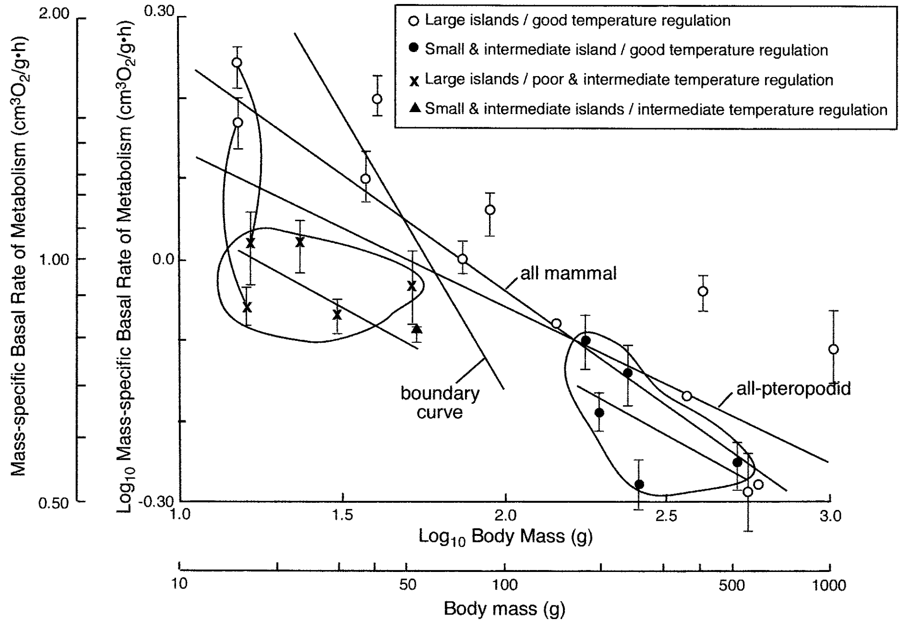


Fig. 5 $\log_{10}$ mass-specific basal rate of metabolism as a function of $\log_{10}$ body mass in pteropodid bats. Also indicated are a fitted curve for pteropodid bats, the boundary curve for endothermy (McNab 1983), and the all-mammal curve (McNab 1988). The 95% confidence intervals for each value is given when available. Populations belonging to the same species are linked. Species that live on large islands or continents and have poor temperature regulation are *encircled* along with a fitted equation (derived from Eq. 2), as are species with good temperature regulation that are limited in distribution to small or intermediate islands

36.8 ± 0.09 °C ($n = 27$, $N = 7$) at T_as between 10 °C and 28.5 °C (Fig. 4b); no differences occurred between the sexes or between the adults and the subadult.

As noted in Materials and methods, the difference in basal rate and body mass between males and females in this species complicates the goal of assigning values to this species. The mean basal rate can be attained in two ways: the pooled basal rates for male and female may be averaged, and then the basal rate is 0.910 cm^3 O$_2$/g·h, which is 148% of the rate expected from a mass of 404.3 g; or the individual performances may be averaged and then the basal rate is 151% of the expected value, which for 404.3 g would be 0.930 cm^3 O$_2$/g·h. The former is used because some of the individual estimates were derived from few measurements. However the data are analyzed, they indicate that this species has a very high basal rate; no evidence suggests that it was due to activity.

Minimal thermal conductance in this species also varied with body mass: in adult females it averaged 0.097 ± 0.0030 cm^3 O$_2$/g·h °C ($n = 14$, $N = 3$), or 180% of the expected value (mean T_b was 36.8 °C); it did not differ ($F = 0.09$, $P = 0.91$) among the three individuals. In the subadult female minimal conductance equaled 0.138 ± 0.0015 cm^3 O$_2$/g·h °C ($n = 5$), or 199% (mean T_b was 36.6 °C). Rate of metabolism was not measured at temperatures below thermoneutrality in adult males so their minimal conductance could not be estimated. This species obviously has a high thermal conductance. The thermal conductance of the adult females is used to represent this species, corrected to the species' mean mass.

Discussion

The data presented above and those accumulated from the literature are analyzed to determine the factors that influence basal rate of metabolism, minimal thermal conductance, and T_b in 21 species of pteropodids. The data used in these analyses are summarized in Table 1.

Basal rate of metabolism

The principal factor setting pteropodid basal rate of metabolism is body mass ($F = 504.35$, $P \leq 0.0001$; $r^2 = 0.960$), the fitted equation for which is:

$$\dot{V}_{O_2}(cm^3 O_2/h) = 2.14 g^{0.806} \tag{1}$$

Appreciable scatter occurs around the mean curve, which is most evident when the basal rate is expressed in mass-specific units (Fig.5). Eleven pteropodids had basal rates that are similar (90–110%) to those expected from the all-mammal curve (McNab 1988); four had high (>110%) basal rates, including *N. cyclotis* (40 g), *R.amplexicaudatus* (92 g), *D. moluccensis* (404 g), and *Pteropus vampyrus* (1024 g); and eight had low (<90%) basal rates, including lowland populations of *Macroglossus* (16 g) and *Syconycteris* (17 g), and *Paranyctimene* (24 g), *N. albiventer* (31 g), *Eonycteris* (52 g), *Melonycteris* (53 g), *Pteropus pumilus* (194 g), and *Pteropus rodricensis* (255 g). That is, pteropodids with low basal rates are small to intermediate in size, whereas those with high basal rates are intermediate to large, with the exception of the highland *N. cyclotis* (40 g).

Basal rate of metabolism in mammals is often correlated with factors other than body mass (McNab 1992). When entrance or not into torpor, distribution on small or large islands/continents, food habits, the type of diurnal roosts used, altitudinal limits to distribution, and whether the species is colonial or solitary are simultaneously included in an analysis of covariance, $\log_{10}$ basal rate in pteropodids is correlated only with

$\log_{10}$ body mass ($F = 568.53$, $P \leq 0.0001$), entrance or not into torpor ($F = 13.43$, $P = 0.0016$), and distribution on large or small islands ($F = 8.42$, $P = 0.0092$); $r^2 = 0.980$. Then:

$$\dot{V}_{O_2} = 2.29(TR \cdot D)g^{0.767} \tag{2}$$

where TR and D are dimensionless coefficients that measure the impact of temperature regulation and distribution, respectively. Species that had an intermediate or poor capacity for thermoregulation had basal rates that were 67% of those that regulate T_b precisely and those found on large islands and continents had basal rates 28% greater than those that were restricted to intermediate and small islands. These dimensionless coefficient factors are summarized in Table 2. Therefore, species that have good temperature regulation and that live on continents have the coefficient equal to 2.29 (1.00 × 1.28) = 2.93, whereas species with poor-to-intermediate temperature regulation and that live on continents have the coefficient equal to 2.29 (0.67 × 1.28) = 1.96. In contrast, small-island species that have good temperature regulation have the coefficient equal to 2.29 (1.00 × 1.00) = 2.29 (see Fig. 5).

Most (4/6) small (< 35 g) pteropodids had basal rates that fall below those expected from mammals generally (Fig. 5), which is why the power of the fitted metabolism-mass function was greater when mass is the only factor used in the analysis (i.e., 0.767 vs 0.806). The low basal rates are most obvious in the small specialist nectarivores that belong to the genera *Megaloglossus* (Kulzer and Storf 1980, which was not included in the analysis because of the fragmentary knowledge of its energy expenditure); lowland populations of *Syconycteris* and *Macroglossus* (McNab and Bonaccorso 1995; Geiser et al. 1996; Bonaccorso and McNab 1997; Bartels et al. 1998); and the nyctimenine frugivores *Paranyctimene* and *Nyctimene* (Bartholomew et al. 1970; McNab and Bonaccorso 1995; this study). These bats have a tendency to enter torpor, as might be expected from having a basal rate well below those described by the boundary curve (Fig. 5). Highland populations of *Syconycteris* and *Macroglossus*, however, had a high basal rate and good temperature regulation (Bonaccorso and McNab 1997).

Most pteropodids that weigh between 35 g and 60 g had intermediate basal rates and thermoregulatory capacities. For example, *Cynopterus* had a basal rate above the all-mammal curve, but below the boundary curve and it occasionally permitted T_b to fall below 31 °C at intermediate T_as (McNab 1989). *Eonycteris* and *Melonycteris* had lower basal rates relative to the standard than *Cynopterus* and were more prone to have T_b fall when exposed to cool T_as (McNab 1989; Bonaccorso and McNab 1997). No other adult pteropodids studied regularly permitted T_b to fall below 34 °C: all had basal rates above the boundary curve (Fig. 5). In the two smallest species that weighed more than 60 g as adults (*D. minor* and *R. amplexicaudatus*), subadults that weighed < 60 g often had T_bs that fell below 34 °C, a response that occurred the day after capture, which suggests that it was not simply reflective of a poor nutritional condition in captivity. This analysis suggests that three thermoregulatory categories exist: when (small) species that regularly enter torpor are separated from those (intermediate-sized) species that occasionally have low T_bs, the conclusions remain the same: $\log_{10}$ basal rate is correlated with $\log_{10}$ mass ($F = 544.61$, $P < 0.0001$), entrance or not into torpor ($F = 6.76$, $P = 0.0065$), and distribution on large or small islands ($F = 8.11$, $P = 0.011$); $r^2 = 0.981$.

Table 2 Coefficient factors that measure the impact of temperature regulation and distribution on the basal rate of metabolism

Temperature regulation (TR)		Distribution (D)	
Good	1.00	Continents/large islands	1.28
Poor to intermediate	0.67	Intermediate/small islands	1.00

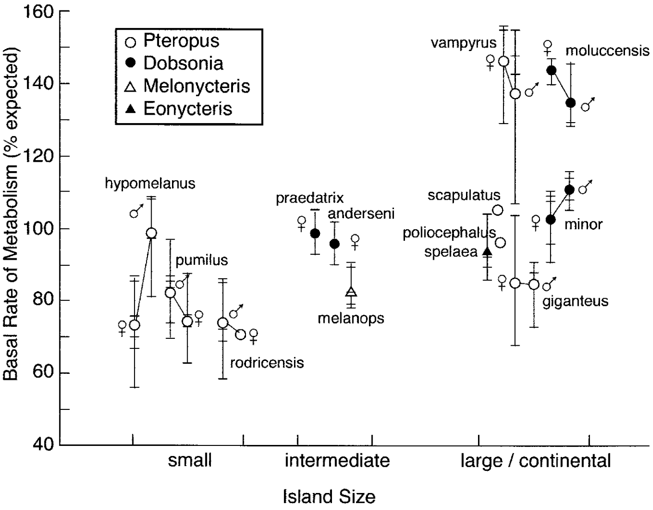


Fig. 6 Basal rate of metabolism in pteropodid bats other than those that enter torpor, expressed relative to the rate expected from the all-pteropodid curve, as a function of island size. Where available, the data for a species are divided into those for males and females, the value for each individual is indicated by a *horizontal bar*, and the mean of the individuals is indicated by the *generic symbol*

The correlation of pteropodid basal rate with island size was found when islands are divided into two categories, large or intermediate and small. Individual variation within a species or sex is less than 20% in 9 of 16 cases and less than 30% in 13 of 16 cases when the rates are expressed relative to the value expected from the all-pteropodid curve. The correlation with island size remains ($F = 6.12$, $P = 0.024$) even if the high-rate *Pteropus vampyrus* is excluded under the (unlikely) assumption that its high rate was simply due to activity. Furthermore, this correlation remains if island size is divided into three classes, small, intermediate, and large (Fig. 6): then $\log_{10}$ basal rate was correlated with $\log_{10}$ body mass ($F = 519.56$, $P \leq 0.0001$), temperature regulation ($F = 6.28$, $P = 0.0091$), and distribution ($F = 4.25$, $P = 0.0318$); $r^2 = 0.991$. The correlation of basal rate with island size is seen in the genus *Dobsonia*, where the intermediate-island endemics *praedatrix* and *anderseni* have lower basal rates than the large-island *moluccensis* of similar mass, and in *Pteropus*, where the small-island endemics *pumilus* and *rodricensis* have lower basal rates than the continental species *scapulatus*, *poliocephalus*, and *vampyrus* (McNab and Armstrong 2001). The intermediate-sized island endemic *Melonycteris melanops* has a lower basal rate than the large-island endemic *Eonycteris spelaea*. A similar correlation of basal rate with island size has been seen in fruit-eating pigeons belonging to the genus *Ducula* (McNab 1994, 2000). What appears to be important is not whether a species is found on small islands, but whether the species is *limited* in distribution to small islands, i.e., is isolated on small islands. Nevertheless, some of the residual variation in basal rate remains after temperature regulation and island size are considered: e.g., continental *D. minor* and *Pteropus giganteus* have rather low basal rates.

Another factor that influences the energy expenditure of pteropodids is sexual size dimorphism, which is most marked in *D. moluccensis* (this study) and *Pteropus* (McNab and Armstrong 2001). In large-island/continental species, such as *D. moluccensis*, *Pteropus giganteus*, and *Pteropus vampyrus*, adult females had a mass that is 74%, 52%, and 78%, respectively, of adult males. Because these females have relative basal rates that are equal to those of males [$(150 \pm 3.9\%)/(143 \pm 3.2\%) = 1.05$; $(91 \pm 12.4\%)/(97 \pm 8.8\%) = 0.94$; $(170 \pm 13.1\%)/(164 \pm 11.3\%) = 1.04$, respectively], they have lower (total) basal rates than males.

Small-island endemic pteropodids tend to be smaller bodied than large-island/continental species (McNab 1994), which further depresses (total) rate of metabolism beyond that attained with the reduction that is independent of body mass. In the small-bodied, small-island endemic *Pteropus pumilus*, females are somewhat smaller (86%) than males ($F = 20.95$; $P < 0.0001$), although they do not have total basal rates that differ from those in males ($F = 1.88$; $P = 0.21$). However, in the rather large-bodied, small-island endemic *Pteropus hypomelanus*, females combine a small ($F = 162.4$, $P \leq 0.0001$) body mass (82% of males) with a lower ($F = 7.27$, $P = 0.031$) relative basal rate [$(81 \pm 5.6\%)/(107 \pm 7.9\%) = 0.76$]. Consequently, females belonging to this small-island species have a basal rate that is 66% $\{\sim[(0.82)^{0.767} \times 0.76]\cdot 100 = 65\%\}$ that of males ($F = 77.67$, $P \leq 0.0001$). That is, the reduction in female basal rate, compared to that of males may increase with body size in species that are endemic to small islands. We conclude that pteropodids limited in distribution to small islands have a reduced energy expenditure as a result of (1) a reduction in mass, (2) a reduction in female mass, and (3) a reduction in basal rate independent of body mass. A reduction in basal rate of small-island specialists implies a reduction in resource requirements, most notably in females, which pay the high cost of reproduction. These adjustments probably facilitate long-term survival on small islands (McNab 1994), where the resource base is area limited and where long-term survival on South Pacific islands requires a large population size (Lande 1995) in the face of the stochastic events, such as El Niño, La Niña, and cyclonic storms. Indeed, Craig et al. (1994) and Pierson et al. (1996) showed that the populations of *Pteropus somoensis* and *Pteropus tonganus* in

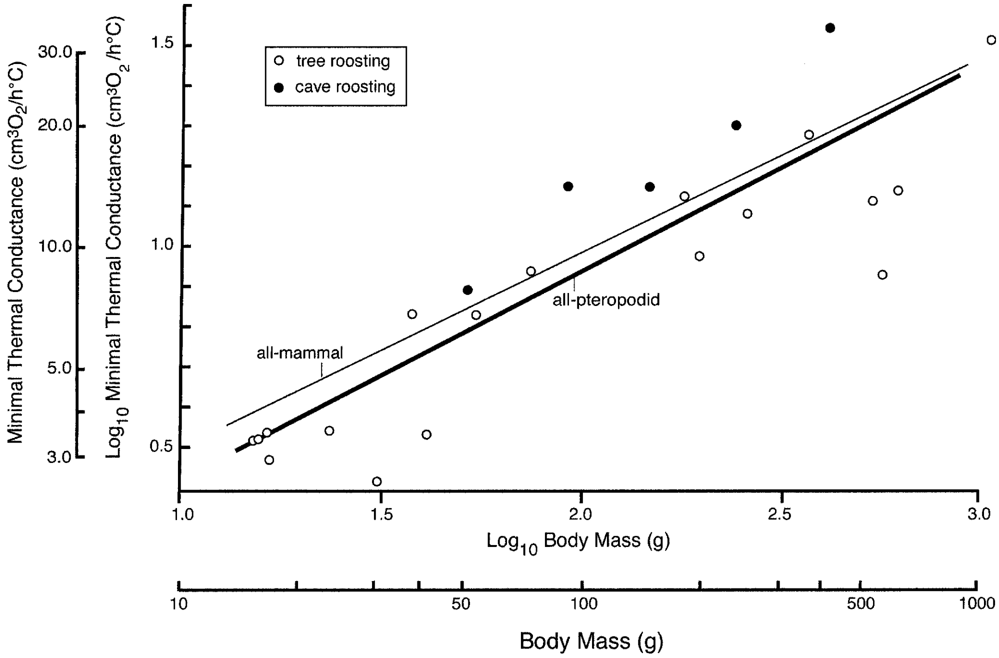


Fig. 7 –Log$_{10}$ total minimal thermal conductance as a function of log$_{10}$ body mass in pteropodid bats. The all-mammal curve for thermal conductance (McNab and Morrison 1963) and the fitted curves are indicated

Samoa greatly declined as a result of severe cyclonic storms.

Basal rate was not correlated with food habits ($F=2.06$, $P=0.17$) when paired with the three significant factors or when paired only with $\log_{10}$ mass ($F=0.60$, $P=0.44$). This is not surprising, given the narrow range of food habits in pteropodids. Altitude limits to distribution, colonality, and roosting site also were not significant. Altitude would not substitute for entrance or not into torpor, as might be expected, because the observation that lowland pteropodids are poor thermoregulators applies only to species that weigh less than 35 g (Fig. 5), all larger pteropodids being good thermoregulators, irrespective of their altitudinal limits to distribution.

Another factor potentially associated with energy expenditure is phylogeny, at least as long as an operative factor correlated with phylogeny can be identified (e.g., McNab 1986). For example, the genera *Dobsonia* and *Pteropus* appear physiologically distinct: *Dobsonia* has intermediate to high basal rates, even when isolated on intermediate-size islands, whereas *Pteropus* has species with high, intermediate, and low basal rates, the latter occurring in species isolated on small oceanic islands. Whether the absence of low basal rates in *Dobsonia* is functionally related to differences between these genera in morphology (e.g., associated with wing-membrane attachments) and ecological habits, or whether it reflects the absence of a *Dobsonia* small-island specialist, is unclear. The shared characteristics of small nectarivorous pteropodids, including a small mass, cephalic specializations for nectarivory, low basal rate, and entrance into torpor, does not reflect a common ancestry because Kirsch et al. (1995) have shown that nectarivory has evolved independently at least five times among pteropodids: these similarities reflect convergence (Bonaccorso and McNab 1997).

Minimal thermal conductance

Minimal thermal conductance is principally correlated with body mass ($F=100.61$; $P \leq 0.0001$): $C=0.50g^{0.634}$; $r^2=0.827$ (Fig. 7). At masses less than 50 g pteropodids tend to have lower conductances than those expected from the relationship described by McNab and Morrison (1963). At larger masses minimal thermal conductance is highly variable. Much of the residual variation in conductance is accounted by roost site: $\log_{10}$ conductance in pteropodids is significantly correlated with $\log_{10}$ mass ($F=108.76$, $P \leq 0.0001$) and roost site ($F=12.66$, $P=0.0020$); $r^2=0.875$. Then, $C\cdot(\mathrm{cm^3 O_2/h\ °C})=0.82(R)g^{0.481}$, where R is the dimensionless coefficient describing the effect of roost. Cave-sheltering pteropodids have minimal conductances that are 1.64-times those of species that roost in trees. Thus, the two species of *Rousettus* have high minimal conductances, as do *Eonycteris*, *D. anderseni*, and *D. moluccensis*, all of which tend to be gregarious and cave-dwelling, behaviors that potentially subject these species to high temperatures and require high thermal conductances to facilitate heat dissipation. The two smaller species of *Dobsonia*, *D. minor* and *D. praedatrix*, have standard conductances; both primarily roost in foliage and open caves (Bonaccorso 1998). Species belonging to the genus *Pteropus* generally have low minimal thermal conductances, especially in small-island species (*Pteropus pumilus* and *Pteropus rodricensis*)–produced by a thick, dense fur coat–or in large species that radically reduce conductance by peripheral vasoconstriction.

Body temperature

T_b in pteropodids is correlated with basal rate ($F=6.08$, $P=0.022$); i.e., a low T_b is weakly associated with a low basal rate; $r^2=0.225$. T_b is independent of $\log_{10}$ body mass ($F=4.10$, $P=0.056$).

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