
The Energetics of Australasian Swifts, Frogmouths, and Nightjars

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Abstract

Body temperature and rate of oxygen consumption were measured as a function of environmental temperature in two swiftlets from New Guinea, Collocalia esculenta and Collocalia vanikorensis, two nightjars from New Guinea, Eurostopodus mystacalis and Caprimulgus macrurus, and two frogmouths, Podargus strigoides from Australia and P. papuensis from New Guinea. Compared to rates expected from mass, basal rates of metabolism in these birds progressively decrease with an increase in mass. The reduction in basal rate may reflect food habits in swiftlets and food habits, sedentary habits, and small pectoral muscle masses in nightjars and frogmouths. The combination of small mass and low rate of metabolism might account for the variable body temperatures found in swiftlets, but no evidence of torpor has been found in these swiftlets, frogmouths, or nightjars. At cool temperatures, C. esculenta often clustered in the field and in the laboratory, a behavior that led to a 30% reduction in energy expenditure. Thermal conductances, which tend to be low in all species with low basal rates, often fell markedly in the largest frogmouth when exposed to ambient temperatures below 16°C.

Introduction

Only a small fraction of the ecological and taxonomic diversity in birds has been studied with respect to energy expenditure, a disproportionate fraction being temperate passerines. For example, the summary of avian standard energetics compiled by Kendeigh, Dol'nik, and Gavrilov (1977) included 172 species, 113 of which were passerines, maximally three of which were limited in distribution to the tropics. The restricted nature of this sample prevents a thorough analysis of factors influencing avian energetics.

The greatest limitations in the data on avian energetics are that few tropical species and few species having food habits other than grain eating or meat eating have been studied. Consequently, an analysis of the impact of climate (Weathers 1979) and food habits (McNab 1988*b*, 1989*b*) on rate of metabolism has been difficult. Insectivorous birds particularly have been neglected. Few measurements have been made on the principal groups that feed on insects in flight, namely, swifts, nightjars, and swallows, in spite of their abundance and wide geographic distribution. Many tropical caprimulgi-forms, such as frogmouths, potoos, and some nightjars, have sedentary habits, which may also influence energy expenditure, especially through small pectoral masses (McNab 1994).

We here report measurements on the metabolism and body temperature of six species of insectivorous birds found in Australasia, two tropical swiftlets (*Collocalia*), two frogmouths (*Podargus*), and two tropical nightjars (*Caprimulgus* and *Eurostopodus*).

Material and Methods

Birds

Two swifts, the glossy (*Collocalia esculenta*) and uniform swiftlets (*Collocalia vanikorensis*), were studied in Madang Province, Papua New Guinea. A few glossy swiftlets were found in caves, but most were collected from a colony of 50–70 individuals roosting in a culvert in the Naru hills on the Madang-Lae road, approximately 45 km from the Christensen Research Institute. At dusk, four or five individuals were caught and brought to the laboratory, where measurements of oxygen consumption were begun 2–3 h after capture, when the swiftlets were postabsorptive. Most measurements occurred between 2000 and 0400 hours. The swiftlets were released the morning after capture. A total of ≤ 43 individuals were measured, the uncertainty occurring because we are unsure whether any individuals were captured more than once.

Uniform swiftlets nest in caves. Most of our specimens were collected in caves on a limestone plateau near the Gogol River along the Madang-Lae road, some 25 km from the laboratory. The experimental protocol in this species was the same as in the glossy swiftlet. We used ≤ 21 individuals but, again, are unsure whether any individuals were recaptured.

Two immature Papuan frogmouths (*Podargus papuensis*) were studied; one was caught on the grounds of the Christensen Research Institute, the second bought in the Madang central market. These frogmouths were maintained on a diet of grasshoppers, lizards, and canned dog food. All mea-

surements were made between 1000 and 1700 hours, more than 10 h after feeding.

Four tawny frogmouths (*Podargus strigoides*) were studied at the Wellington Zoo, New Zealand. Measurements were made between 0800 and 1630 hours, some 15 h after feeding. These birds belonged to a captive colony that has reproduced successfully. This species is widely distributed in Australia and Tasmania.

Three large-tailed nightjars (*Caprimulgus macrurus*) and one white-throated nightjar (*Eurostopodus mystacalis*) were collected along streambeds in the vicinity of Madang by Mr. Simon Seeto and his helpers. These birds maintained their mass in captivity when force-fed insects and meat.

Experimental Techniques

Rates of metabolism were measured in terms of oxygen consumption as a function of chamber temperature. Room air was sucked into a chamber containing a bird, or in the case of glossy swiftlets, up to five individuals. Carbon dioxide and moisture were scrubbed from the airstream upon its exit from the chamber. The scrubbed air stream was sent to a flowmeter and either to a Beckman paramagnetic oxygen analyzer (model 755) or to an Applied Electrochemistry oxygen analyzer (S-3A), their electrical outputs being sent to stripchart recorders. Periods of measurement at a fixed ambient temperature usually lasted 1–2 h for swiftlets and nightjars and 2–3 h for frogmouths, depending on the animal's activity and the time required to get a repeated minimal energy expenditure. Swiftlets were placed in a 1.2-L chamber that was submerged in a water bath to maintain ambient temperature constant. *Caprimulgus* was placed either in a 4.0 or an 8.9-L chamber and the Papuan frogmouths and *Eurostopodus* were placed in a 29-L chamber within a temperature-controlled cabinet. Tawny frogmouths were placed in a 230-L chamber, the temperature of which was controlled by pumping thermoregulated water through the chamber's hollow walls.

Flow rates varied with animal and chamber size. Rates must be sufficiently high to ensure that air circulation will mix air in the chamber, which is the case if the calculated rate of metabolism at a given temperature is independent of flow rate. With swiftlets, flow rates varied from 110 to 250 cm³/min; with *Caprimulgus*, from 300 to 1,300 cm³/min in the 4.0-L chamber and from 230 to 1,930 cm³/min in the 8.9-L chamber; with *Eurostopodus*, from 1,360 to 1,425 cm³/min; with Papuan frogmouths, from 560 to 2,200 cm³/min; and with tawny frogmouths, from 5.4 to 7.8 L/min. In each species the

calculated rate of metabolism in thermoneutrality (when rate is independent of temperature) was independent of flow rate.

Cloacal temperature was measured at the end of each experiment. Estimates of thermal conductance were derived from measurements of oxygen consumption and body temperature at specific ambient temperatures (McNab 1980). Data are expressed as mean \pm SE (n , measurements) and summarized in table 1.

Results

Collocalia esculenta

The glossy swiftlet is small, its body mass averaging 6.8 g and ranging from 5.8 to 8.5 g. Thermoneutrality in this species extends from 31.5° to 34.0°C (fig. 1*a*). Basal rate of metabolism was 2.15 cm³O₂/g · h, which is 90% of the rate expected from inactive nonpasserines of this mass (Aschoff and Pohl 1970). At environmental temperatures below 30°C, rate of metabolism increased markedly. Rate of metabolism at low temperatures was variable, thermal conductance increasing directly with body temperature. A thermal conductance of 0.318 cm³O₂/g · h°C, or 98% of the value expected from mass (Lasiewski, Weathers, and Bernstein 1967), corresponds to the lower limit of thermoneutrality and to a mean body temperature of 38.2°C. At environmental temperatures below 30°C, body temperature, according to an analysis of covariance ($r^2 = 0.39$, $n = 31$), decreased both with ambient temperature ($P = 0.0070$) and body mass ($P = 0.0049$). In fact, the lowest body temperature (21.3°C) occurred at 12.9°C in an individual that weighed only 5.8 g (fig. 1*b*).

Groups of two to five glossy swiftlets often clustered together on a nest at night in the culvert from which they were collected. Therefore, we measured rate of metabolism in groups at various ambient temperatures. Below 26°C glossy swiftlets in experimental chambers always clumped together: rates of metabolism in clumped groups of five were lower by about 30% of the mean rate found in individual swiftlets at the same temperatures (fig. 1*a*). A similar reduction was found in clustering house martins (*Delichon urbica*) exposed to temperatures below thermoneutrality (Prinzinger and Siedle 1988). The body temperature of grouped swiftlets equaled or exceeded the temperatures of individuals at the same ambient temperature, which means that grouped swiftlets had a mean thermal conductance that is 63% of individuals, that is, 0.200 cm³O₂/g · h°C (fig. 1*a*). At 28°C grouped swiftlets dispersed: no difference in rate of metabolism occurred between solitary and dispersed swiftlets (fig. 1*a*).

Collocalia vanikorensis

The uniform swiftlet at 11.6 g is nearly twice as large as the glossy swiftlet. Thermoneutrality in this species extends from 30° to 34°C (fig. 1c); basal rate was 1.85 cm³O₂/g · h. This rate is 90% of the value expected from mass. At environmental temperatures below 30°C, rate of metabolism increases, the mean thermal conductance that corresponds to the lower limit of thermoneutrality equaling 0.238 cm³O₂/g · h°C, or 95% of the value expected from mass. This conductance corresponds to a body temperature of 38.9°C. As in *C. esculenta*, lower conductances reflect in part a decrease in body temperature (fig. 1c). Body temperature in this species is quite variable and similar in level to that found in *C. esculenta* but independent of both ambient temperature ($P = 0.4734$) and body mass ($P = 0.6577$) (fig. 1b).

Rate of metabolism was not measured in groups of uniform swiftlets: although we collected this species in caves, we never encountered their nests and do not know whether they cluster.

Podargus papuensis

We were able to collect only a few data on this species. Its mean mass was 314.6 g. The lower limit of thermoneutrality (27°C) fell in the temperature range that we used (10°–33°C), so we can estimate both basal rate and thermal conductance. Basal rate in this species was 0.610 cm³O₂/g · h, which is 72% of the value expected from an inactive nonpasserine. The thermal conductance that defines the lower limit of thermoneutrality equaled 0.0524 cm³O₂/g · h°C, which is 109% of the value expected in birds. Body temperature was independent of ambient temperature between 10° and 30°C, the mean being 38.8° ± 0.15°C (14).

Podargus strigoides

The mean mass of the tawny frogmouth was 419.6 g. The zone of thermoneutrality extends from 30°C to at least 38°C (fig. 2). Basal rate was 0.384 cm³O₂/g · h, which is 49% of that predicted by the Aschoff-Pohl relationship. The thermal conductance that defines the lower limit of thermoneutrality equaled 0.0443 cm³O₂/g · h°C, which is 107% of the value expected in birds. At ambient temperatures below 16°C, the thermal conductance of tawny frogmouths usually decreased below that found at intermediate temperatures (fig. 2). The mean minimal conductance was 0.0280 cm³O₂/g · h°C, which is only 63% of the value that sets the lower limit of thermoneu-

TABLE 1
Basal energetics of swifts, frogmouths, and nighthawks

Species	Body Mass (g)	Basal Rate of Metabolism		Thermal Conductance		Source
		cm ³ O ₂ /g · h	% ^a	cm ³ O ₂ /g · h °C	% ^b	
Podidae:						
<i>Collocalia esculenta</i>	6.8 ± .8 (46)	2.15 ± .01 (9)	90	.318 ± .0002 (9)	98	This study
<i>Collocalia vanikorensis</i>	11.6 ± .1 (37)	1.85 ± .10 (15)	90	.238 ± .0040 (5)	95	This study
<i>Apus apus</i>	44.9	1.74	122	Kendeigh et al. 1977
Podargidae:						
<i>Podargus ocellatus</i>	145	.70	67	.051	72	Lasiewski et al. 1970
<i>Podargus papuensis</i>	314.6 ± 13.6 (17)	.610 ± .029 (7)	72	.0524 ± .0019 (4)	109	This study

<i>Podargus strigoides</i>	419.6 ± 13.8 (52)	.384 ± .007 (13)	49	.0443 ± .0007 (18)	107	This study
Caprimulgidae:0280 ± .006	67
<i>Phalaenoptilus nuttallii</i>	40	.80	54	.112	83	Batholomew et al. 1962
<i>Caprimulgus macrurus</i>	68.6 ± .7 (28)	.811 ± .0257 (11)	63	.0641 ± .0036 (8)	57	This study
<i>Chordeiles minor</i>	72	1.10	87	.103	103	Lasiewski and Dawson 1964
urostopodidae:						
<i>Eurostopodus guttatus</i>	88	.83	70	.093	103	Dawson and Fisher 1969
<i>Eurostopodus mystacalis</i>	162.0 ± 1.0 (20)	.531 ± .029 (9)	52	.0468 ± .0031 (6)	70	This study

Note. Data given as mean ± SE (no. of measurements).

% Basal rate = (measured basal rate)/(4.0 g⁻²⁷).

Thermal conductance = (measured conductance)/(.85 g⁻⁵⁰).

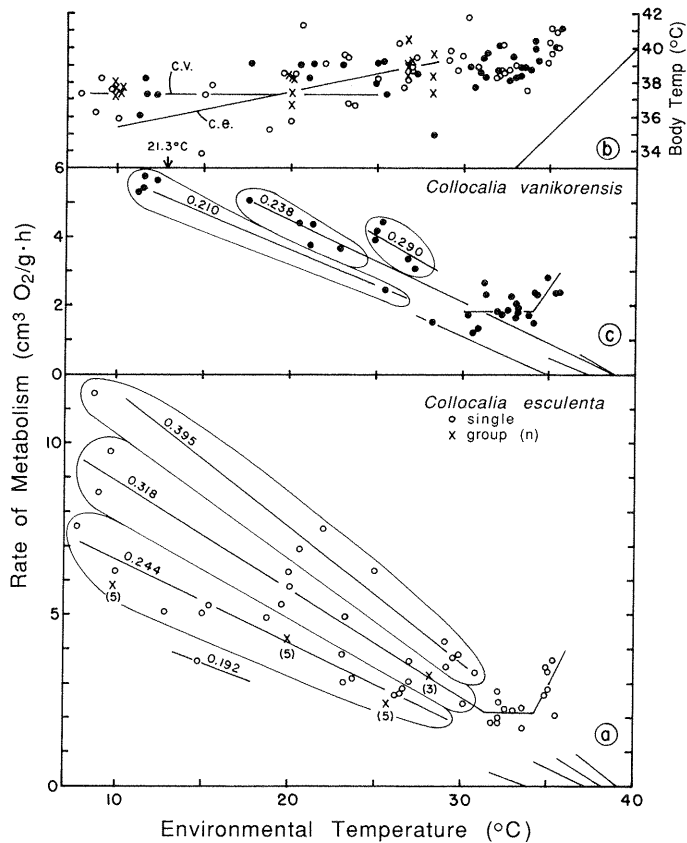


Fig. 1. a, Rate of metabolism as a function of environmental temperature in *Collocalia esculenta*. b, Body temperature in relation to environmental temperature in *C. esculenta* (open circles) and *Collocalia vanikorensis* (solid circles). c, Rate of metabolism as a function of environmental temperature in *C. vanikorensis*. Measurements associated with a particular conductance are enclosed within the surrounding ellipse.

trality and 67% of the value expected from mass. Body temperature in this species at ambient temperatures down at least to 6°C is regulated at $38.6^{\circ} \pm 0.07^{\circ}\text{C}$ (49).

Caprimulgus macrurus

The long-tailed nightjar had a mass of 68.6 g and a basal rate equal to $0.811 \text{ cm}^3\text{O}_2/\text{g} \cdot \text{h}$, which is 63% of the value expected from mass. The minimal thermal conductance that defines the lower limit of thermoneutrality equaled $0.0641 \text{ cm}^3\text{O}_2/\text{g} \cdot \text{h} \cdot ^{\circ}\text{C}$ (fig. 3a), which is 57% of the expected value and

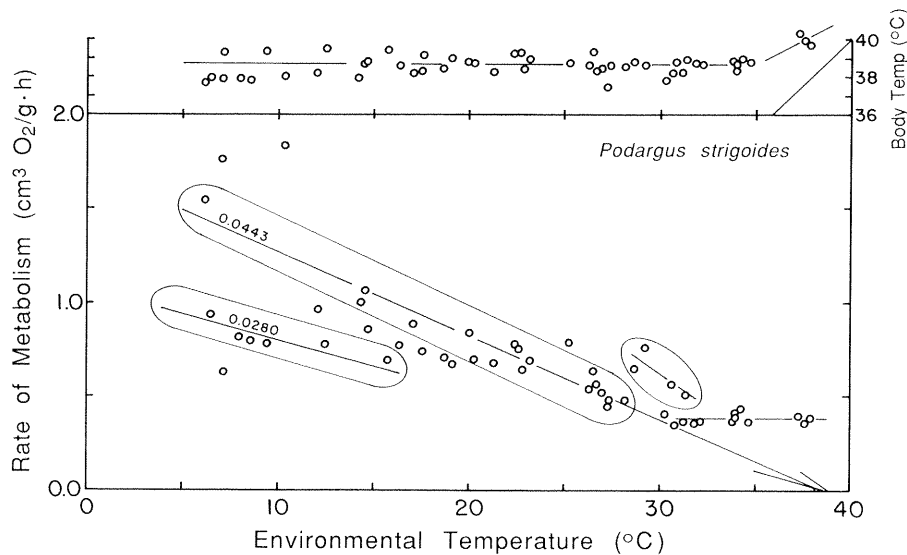


Fig. 2. Rate of metabolism and body temperature in relation to environmental temperature in four *Podargus strigoides*.

corresponds to a body temperature equal to 38.1°C . All measurements in this species were made during the daytime. At cool temperatures this caprimulgid often is characterized by high thermal conductances, usually in association with high body temperatures and confinement in a small chamber (i.e., 4.0 liters). Body temperature in this species is correlated with ambient temperature ($r^2 = 0.59$, $P < 0.0001$).

Eurostopodus mystacalis

The mass of the white-throated nightjar was 162.0 g, or 2.4 times that of *C. macrurus*. Its basal rate was $0.531 \text{ cm}^3\text{O}_2/\text{g} \cdot \text{h}$, measured principally during the day, nighttime measurements overlapping with those made during the day (fig. 3b). This rate is only 52% of the basal rate expected from mass. Even though basal rate did not reflect the time of measurement, body temperature was greater during the night ($40.1^{\circ} \pm 0.16^{\circ}\text{C}$ [15]) than during the day ($39.1^{\circ} \pm 0.47^{\circ}\text{C}$ [6]), as was thermal conductance ($0.0511 \pm 0.0026 \text{ cm}^3\text{O}_2/\text{g} \cdot \text{h}^{\circ}\text{C}$ [5] and $0.0468 \pm 0.0031 \text{ cm}^3\text{O}_2/\text{g} \cdot \text{h}^{\circ}\text{C}$ [6], respectively). The daytime conductance is 70% of the value expected from mass and corresponds to a body temperature of 39.1°C . Combined body temperatures in *E. mystacalis* varied with ambient temperature down at least to 10°C ($r^2 = 0.45$, $P = 0.032$).

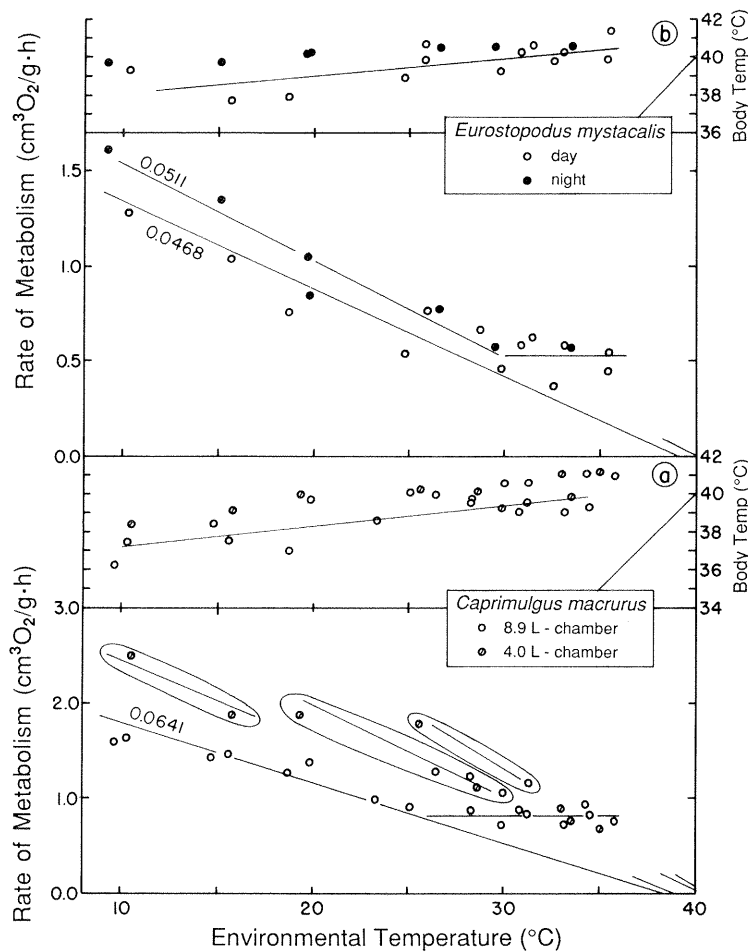


Fig. 3. a, Rate of metabolism and body temperature in relation to environmental temperature in three *Caprimulgus macrurus*. Note that confinement in a small chamber usually led to high rates of metabolism and high body temperature, always at environmental temperatures below 29°C. b, Rate of metabolism and body temperature in relation to environmental temperature in one *Eurostopodus mystacalis*.

Discussion

Body Temperature

Although many groups of small mammals enter torpor, few birds do. Among birds that enter torpor are some that feed on insects in flight. These include the European and North American swifts *Apus* (Koskomies 1950) and *Aëronautes* (Bartholomew, Howell, and Cade 1957), swallows *Tachycineta*

(Lasiewski and Thompson 1966) and *Delichon* (Prinzinger and Siedle 1988), and goatsuckers *Phalaenoptilus* (Marshall 1955; Bartholomew et al. 1957; Howell and Bartholomew 1959; Bartholomew, Hudson, and Howell 1962; Brigham 1992), *Chordeiles* (Lasiewski and Dawson 1964), and *Caprimulgus* (Peiponen 1965). One goatsucker, the North American poorwill (*Phalaenoptilus nuttallii*), is the only bird known to enter seasonal torpor (Jaeger 1948, 1949), although some temperate swallows and swifts have been claimed to show this behavior (see McAtee 1947).

In this study, body temperature was highly variable in both swiftlets, especially in the smaller *Collocalia esculenta*, at ambient temperatures below 30°C (fig. 1*b*). As would be expected from their much larger masses, nightjars and frogmouths have more precisely regulated body temperatures, even though, compared to a mass standard, they have lower basal rates than swiftlets. Although one glossy swiftlet had core temperature fall as low as 21.3°C, no clear evidence of torpor (i.e., spontaneously reversible hypothermia) was seen in any of the six species studied here. Dawson and Fisher (1969), however, have reported torpor in a temperate (Australian) *Eurostopodus*.

Rate of Metabolism

Swiftlets, frogmouths, and nightjars have basal rates that are lower than expected from a standard curve for birds other than passerines, the decrease from the standard increasing with mass. Swiftlets (*Collocalia*, Apodidae), however, have slightly higher basal rates than emballonurid and mormoopid bats and markedly higher basal rates than molossid and vespertilionid bats (fig. 4), these bats being a relevant standard because they too feed on insects in flight. Low basal rates in insectivorous bats have been interpreted to reflect a temporal variability in the abundance of flying insects (McNab 1969, 1989*a*), fasting and dehydration endurance (Genoud, Bonaccorso, and Arnds 1990), or warm cave temperatures (Bonaccorso et al. 1992).

The cost of temperature regulation is greatest at low environmental temperatures, which in tropical environments like New Guinea are principally encountered at high elevations. One way to reduce energy expenditures at low temperatures is to enter torpor. In contrast to swiftlets, many insectivorous bats readily enter torpor. In fact, the propensity to enter torpor appears to increase with the reduction of metabolism from the so-called boundary curve, that is, the curve of basal rate on mass that separates endotherms that enter torpor from those that do not (McNab 1983, 1992). For example, torpor is most frequent in the Vespertilionidae, much less so in the Molossidae (Herreid 1963; Leitner 1966), marginally present in (only captive?) Emballonuridae and Mormoopidae, and infrequent in the Apodidae (Kos-

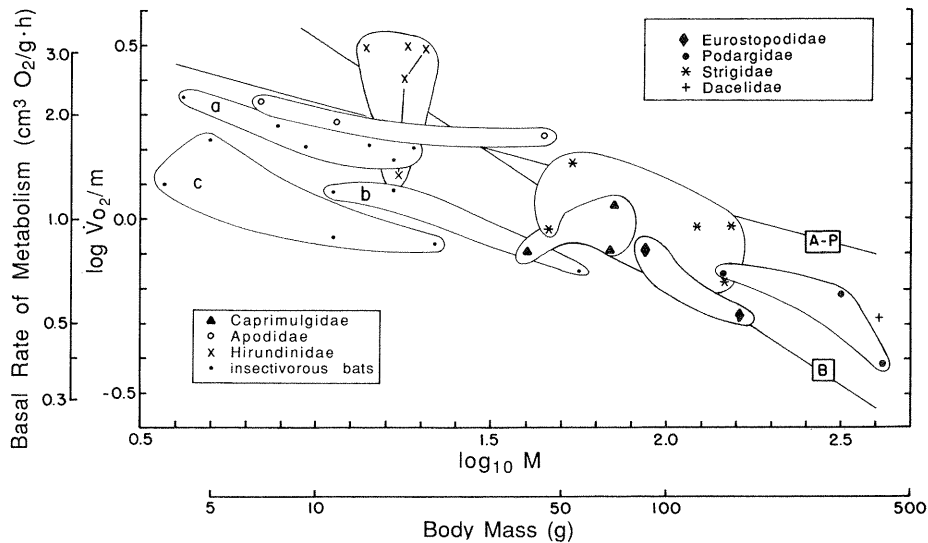


Fig. 4. \log_{10} basal rate of metabolism in insectivorous birds and bats as a function of \log_{10} body mass. Data are from this study and the literature on swifts (Kendeigh et al. 1977), caprimulgids (Bartholomew et al. 1962; Lasiewski and Dawson 1964), eurostopodids (Dawson and Fisher 1969), frogmouths (Lasiewski, Dawson, and Bartholomew 1970), owls (Ligon 1969; Coulombe 1970), and swallows (Kendeigh et al. 1977; Hails 1979). A standard curve for nonpasserines (A-P) is derived from Aschoff and Pohl (1970) and for the boundary curve (B) from McNab (1983). Data on various insectivorous bats were obtained from the literature, including (a) emballonurids and mormoopids (Genoud and Bonaccorso 1986; McNab 1989a; Bonaccorso et al. 1992), (b) molossids (McNab 1989a), and (c) vespertilionids (McNab 1989a). Measurements made on the same species are connected.

komies 1950). Swallows (Hirundinidae) have still higher basal rates and apparently enter torpor only occasionally (Lasiewski and Thompson 1966). From this view the absence of torpor in *Collocalia* is surprising because they have basal rates that are only 51%–63% of the values expected by mass from the boundary curve (fig. 4), although use of torpor in these species, as in many hibernators, may require specific physiological or environmental cues that were not provided. Clearly, feeding on insects in flight alone cannot explain the variation in basal rate and the occurrence of torpor found in insectivorous bats and birds.

The complex interaction found among basal rate, body mass, and entrance into torpor is seen in swallows. The few swallows studied generally have

basal rates greater than expected from the boundary curve (fig. 4), which suggests that these species are unlikely to enter torpor. But measurements on the house martin (*Delichon urbica*) are highly varied: basal rates range from 150% (Kendeigh et al. 1977) and 110% (Hails 1979) to 57% (Prinzinger and Siedle 1988) of the values expected from the boundary curve. Such variation among different studies on one species is rare and undoubtedly reflects different conditions either in the procedures or in the birds; most independent estimates of basal rate in a species agree within 5%–10%, unless evidence of climate adaptation is present (B. K. McNab, personal observation). Especially noteworthy are that torpor in this martin occurred only in the study that reported a basal rate below the boundary curve and that the depth of torpor in the field was directly related to mass loss associated with low ambient temperatures and rainy weather (Prinzinger and Siedle 1988). Thus, torpor may be found only if it is looked for and if triggered by an appropriate stimulus. Much more work is needed on appropriate species before we understand the interactions among these factors.

If swiftlets do not depend on torpor, how can they tolerate the low ambient temperatures that some species encounter at high elevations? For example, *C. esculenta* is commonly encountered at elevations as high as 3,600 m and locally to 4,500 m on the Carstenz Massif in Irian Jaya (Coates 1985). The propensity of this species to form clusters reduces energy expenditure by 30% without sacrificing temperature regulation, which may contribute to its tolerance of high elevations. Theoretically, glossy swiftlets could also select roosts at high altitudes that trap heat. In contrast, *Collocalia vanikorensis* is usually limited to elevations less than 500 m, although occasionally it is found to 1,400 m (Beehler, Pratt, and Zimmerman 1986).

Frogmouths (Podargidae) capture their prey on the ground (Serventy 1936). Their low basal rates may reflect their food habits and/or the sedentary behavior of a sit-and-wait predator with its potentially small pectoral muscle mass (McNab 1994). Another intermediate-sized, sedentary avian predator, the laughing kookaburra (*Dacelo novaeguineae*), has a basal rate similar to that found in the tawny frogmouth (B. K. McNab, personal observation), as do insectivorous owls (Ligon 1969; Coulombe 1970) (fig. 4), which also are sedentary predators.

Most nightjars (Caprimulgidae) feed on insects in flight. In association with this habit, nightjars have basal rates below the Aschoff-Pohl curve, but usually greater than the boundary curve (fig. 4). The one caprimulgid with a basal rate appreciably below the boundary curve is the poorwill, which as stated is the only bird known to enter seasonal torpor. The poorwill, unlike nighthawks, waits for prey to fly by, then sallies forth to capture them and returns to wait again (Csada and Brigham 1992), a behavior that may be

associated with its low basal rate. At a mass of ca. 70 g the long-tailed nightjar from New Guinea has a lower basal rate (Lasiewski and Dawson 1964) than the common nighthawk (*Chordeiles minor*) of temperate North America, which may be evidence of a climate adjustment of basal rate in caprimulgids and/or reflective of more sedentary habits in *Caprimulgus macrurus*. In fact, *Chordeiles acutipennis*, a close relative of the common nighthawk, has larger pectoral muscle masses (21.5% total mass) than the less active pau-raque (*Nyctidromus albicollis*; 17.2% total mass [Hartman 1961]).

The generally large eared-nightjars (Eurostopodidae, see Sibley and Ahlquist 1990) also have low basal rates compared to the Aschoff-Pohl curve, but on the boundary curve (fig. 4). Beehler et al. (1986, p. 135) observed that New Guinean "nightjars forage by sitting motionless on an exposed perch . . . and [fly] swiftly upward to catch passing insects." The low basal rates in this family, therefore, may also reflect sedentary habits. This analysis suggests that the intermediate to low basal rates in swiftlets, frogmouths, and nightjars may reflect several factors, including body mass, body composition, food habits, and behavior.

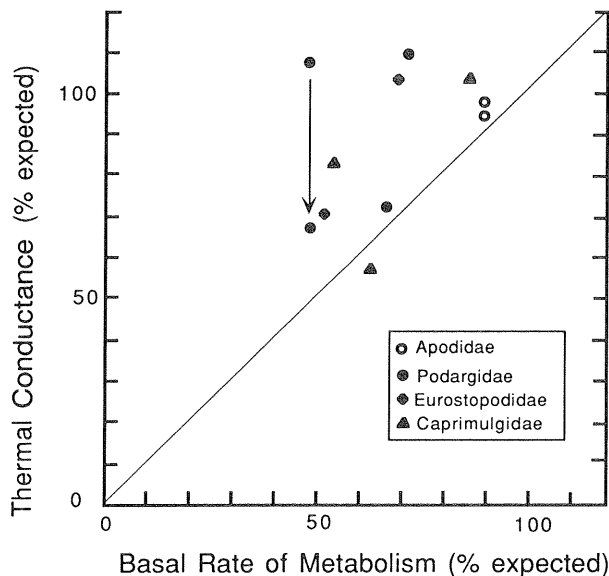


Fig. 5. Thermal conductance in swifts, nightjars, and frogmouths as a function of basal rate of metabolism, each factor represented as a percentage of the value expected from body mass (see text and table 1). The two values for *Podargus strigoides* are connected by an arrow. The diagonal line represents an equivalent reduction in conductance and basal rate.

Frogmouths and nightjars compensate for low basal rates with low conductances (fig. 5), which permits effective thermoregulation with low rates of heat production. *Podargus strigoides*, presumably reflecting its large mass, shows a marked capacity to reduce conductance at low ambient temperatures, thereby bringing its thermal conductance into agreement with the reduction in basal rate (fig. 5). A similar reduction in conductance has been described in some mammals (McNab 1988a) and in the trumpeter *Psophia crepitans* (McNab 1989b) and seen in the kookaburra and the toucan *Ramphastos toco* (B. K. McNab, personal observation). These reductions are most marked in tropical endotherms that have low basal rates of metabolism, sedentary habits, and a body mass between 0.4 and 14.0 kg.

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