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THE ECOLOGICAL ENERGETICS OF BIRDS IN NEW GUINEA

Brian K. McNab

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THE ECOLOGICAL ENERGETICS OF BIRDS IN NEW GUINEA

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Painting of the Naru River, Madang Province, Papua New Guinea by Brian K. McNab © 2013

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ABSTRACT

The energetics of 79 species of birds living in greater New Guinea, data for 44 of which are presented here for the first time, is examined to determine the extent to which it reflects the behavior of species and the conditions they encounter in the environment. Body mass alone accounts for 86.6% of the variation in the basal rate of metabolism of these species, whereas the combination of body mass, foraging substrate, flightless condition, activity, and life on islands or continents collectively account for 95.2% of its variation. When the passerine/non-passerine dichotomy is added to the analysis, the six factors account for 96.7% of the variation in basal rate. Basal rate also correlates with other factors, including maximal altitude of distribution, torpor, and food habits when individually combined with body mass, but they lose significance when other factors are brought into the analysis. Altitudinal limits to distribution can be included in the analysis only if activity is dropped because of the correlation between these factors. Torpor correlates with an aerial feeding strategy. Food habits correlated with activity level and the passerine/non-passerine dichotomy. The attempt to account for the variation in the energetics of birds by a phylogenetic analysis is inappropriate because the fundamental basis of energetics is physiological with strong behavioral and ecological overtones. Body mass accounts for 90.4% of the variation in thermal conductance. The regulated level of body temperature varies from ca. 39 to 41°C at masses > 100 g, below which it decreases to 37 and 39°C at 10 g, with a few small species having body temperatures as low as 35°C. New Guinea is an important source for the terrestrial avifauna of South Pacific islands. The characteristics of its birds therefore are appropriate standards by which to judge the adjustments occurring in, and required of, birds endemic to these islands.

Key words: activity, altitude, basal rate of metabolism, birds, body temperature, flightless, food habits, habitat, islands, New Guinea, passerine/non-passerine, physiology, thermal conductance, torpor.

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INTRODUCTION

Two aspects of the ecology of birds that are pivotal to their survival are their relationship to the physical conditions in the environments in which they live and their exploitation of resources that vary in diversity, abundance, composition, and availability. No successful species can expend material and energy resources at rates that exceed their long-term availability. Therefore, many species must adjust their responses to the resources consumed and the environmental conditions encountered, often taking extreme measures (McNab 2012). Here these responses are examined for their potential quantitative impacts on the energy expenditure of birds native to greater New Guinea.

Energy expenditure funds the life history of species, including body maintenance, activity, and reproduction. The minimal cost of maintenance in birds is relatively easy to measure and has interspecific equivalency, but its real value is that it reflects their behavior and response to conditions in the environment. However, most measurements of energy expenditure have been of temperate species, which give a biased view of avian performance because of the great seasonal variations in the ambient temperatures encountered and foods consumed. In fact, the greatest cost of avian maintenance in temperate and polar environments coincides with the smallest resource supplies, i.e., during winter, the commonest response to which is seasonal migration. For example, of approximately 175 passerines that breed in eastern North America, 100 breed in Canada, only 29 of which winter in Canada and then mainly along its southern border near the Great Lakes. Only eight species winter as far north as Hudson's Bay. As a result, bird diversity in temperate and polar environments is much greater in summer than would be the

case if the species were restricted to life in these environments.

The few studies of the energetics of species in the wet tropics reflect the near absence of biologists resident in the tropics that work on the physiological ecology of birds (and other vertebrates). Most of the available data have been gathered piece-meal by temperate-based biologists foraging in the tropics for limited periods of time. Consequently, knowledge of the energetics of tropical birds is limited. The great taxonomic, behavioral, and ecological diversity of birds in the tropics might be expected to be associated with an extensive diversity in energetics. Furthermore, tropical terrestrial environments are diverse, including paramos, punas, cloud forests, lowland rain forests, dry forests, and savannas, collectively providing another reason to anticipate physiological diversity in tropical birds.

Most previous physiological studies of tropical species have been on a few narrowly defined groups (Hawaiian honeyeaters [MacMillan 1974, 1981]; sunbirds and flowerpeckers [Prinzinger et al. 1989; Seavy 2006]; swifts, frogmouths, and nightjars [McNab & Bonaccorso 1995]; pigeons [McNab 2000]; toucans [McNab 2001]; birds-of-paradise [McNab 2003, 2005]; and bubuls [Seavy & McNab 2007]). Wiersma et al. (2007) reported the only study of the energetics of a diverse set of tropical birds. They presented estimates of the rates of metabolism in 62 species from lowland, Gamboa, Panamá, 52 of which were passerines, concluding that tropical species are characterized by a 'slow pace of life,' as reflected in low rates of metabolism.

A SHORT PRIMER ON AVIAN ENERGETICS

Some organisms have such high rates of energy expenditure that they often encounter difficulties

in balancing their energy expenditures with available energy resources (McNab 2012). High expenditures in many species only occur during periods of activity, whereas others have high expenditures over extended periods. The clearest example of a commitment to high expenditures is found in species that are endothermic. Endothermy is the condition in which a species maintains a constant body temperature over an appreciable range in ambient temperatures principally by the generation of heat derived from the metabolism of ingested food. Endotherms are often referred to as 'warm-blooded,' but that term refers only to the level of body temperature, not to the source of the heat. Endothermy is most clearly seen in two vertebrate classes, Aves and Mammalia. The high cost of endothermy must be compromised under some environmental conditions to ensure a balanced energy budget. As noted, migration is a way of avoiding high expenditures, as is entrance into daily torpor by some small birds and mammals. Seasonal torpor for extended periods, hibernation and aestivation, occurs in some mammals, a behavior not known in birds with the possible exception of hibernation in the Common Poorwill (*Phalaenoptilus nuttallii*) (Jaeger 1948, 1949).

The energy expenditure of organisms is difficult to measure directly. It is usually estimated by oxygen consumption. Oxygen consumption can be converted into energy units: $\text{mLO}_2/50 \approx \text{kJ}$. Consequently, the rate of metabolism can be expressed in units of mLO_2/h or as kJ/h . Measured rates of oxygen consumption are often presented in mass-specific units, $\text{mLO}_2/\text{g h}$, as is done here out of convention, but the ecologically meaningful units are total rates (McNab 1999), which are what is used in the analyses in this monograph.

The energetics of endothermy is best illustrated by a graph of body temperature and the rate of metabolism as a function of ambient temperature (Fig. 1). Rates vary with ambient temperature, except for a range of temperatures in which they are constant in spite of variations in the temperature differential between the body and environment, ΔT (Fig. 1). The constancy in rate occurs because changes in posture, insulation, and

peripheral circulation compensate for changes in the temperature differential. The temperature range of constant rates is called the zone of thermoneutrality within which the rate is basal (BMR), as long as the animal is post-absorptive, inactive during the period of inactivity, and maintaining its normal body temperature. Basal rate of metabolism is the lowest rate compatible with maintaining a normal body temperature in endotherms and therefore is an estimate of the lowest cost of body maintenance.

A potential difficulty with the measurements provided by Wiersma et al. (2007) is that they were made at one ambient temperature, 30°C , which probably was within thermoneutrality in most species, although this is not certain. (If one ambient temperature were chosen, 25.0 to 27.5°C would have been better, except possibly for the smallest species, but see *Sericornis* [Fig. 8].) The best means of estimating basal rate of metabolism is to measure the rate over a range of ambient temperatures to be sure that it is within the zone. That was the approach used here.

A simplified description of the energy expenditure of endotherms is:

$$M = C \times (T_b - T_a) = C \times (\Delta T) \quad (1)$$

where M is the rate of metabolism (mLO_2/h), a measure of heat production; C is thermal conductance ($\text{mLO}_2/\text{h}^\circ\text{C}$), a measure of heat loss; T_b is body temperature ($^\circ\text{C}$); T_a is ambient temperature ($^\circ\text{C}$); and ΔT is the temperature differential between the body and environment ($^\circ\text{C}$) (Scholander et al. 1950).

This relationship does not include radiant and convective exchange with the environment nor evaporative water loss. The increase in rate at temperatures below thermoneutrality occurs because ΔT is sufficiently large that an increase in heat production is required to balance the increased heat loss. Thermal conductance in Figure 1 is the slope of the curve of rate of metabolism below thermoneutrality, *if* the metabolism-temperature curve extrapolates, when the rate is zero, to the mean body temperature of the measurements used to constitute the curve. The inverse of thermal conductance is insulation.

FACTORS AFFECTING THE ENERGETICS OF ENDOTHERMS

The endothermy of birds and mammals is similar. They differ marginally in that birds generally have higher basal rates and body temperatures. Some investigators have suggested that the high basal rates of birds reflect their high body temperatures (e.g., Gillooly et al. 2001), an interpretation that is compatible with the physiology of ectotherms. The reverse explanation is more likely in the case of endotherms, i.e., the high body temperatures of birds reflect their high basal rates. A clue that may account for the higher basal rates of birds is suggested by the observation that flightless birds

have BMRs and body temperatures similar to those of mammals (McNab 1996, 2009; McNab & Ellis 2006). This suggests that the high basal rates in most birds reflect their commitment to flight. Bats, however, do not have higher basal rates than other mammals. Their lower rates may reflect a lower cost of flight than in birds (Winter & Helversen 1998), as well as the propensity of insectivorous bats to enter torpor, a behavior associated with low basal rates (McNab 2008), whereas bats with other food habits have higher basal rates (McNab 2003c), although still not at the level of most birds.

Body size, as measured by body mass, is the single most important factor influencing the

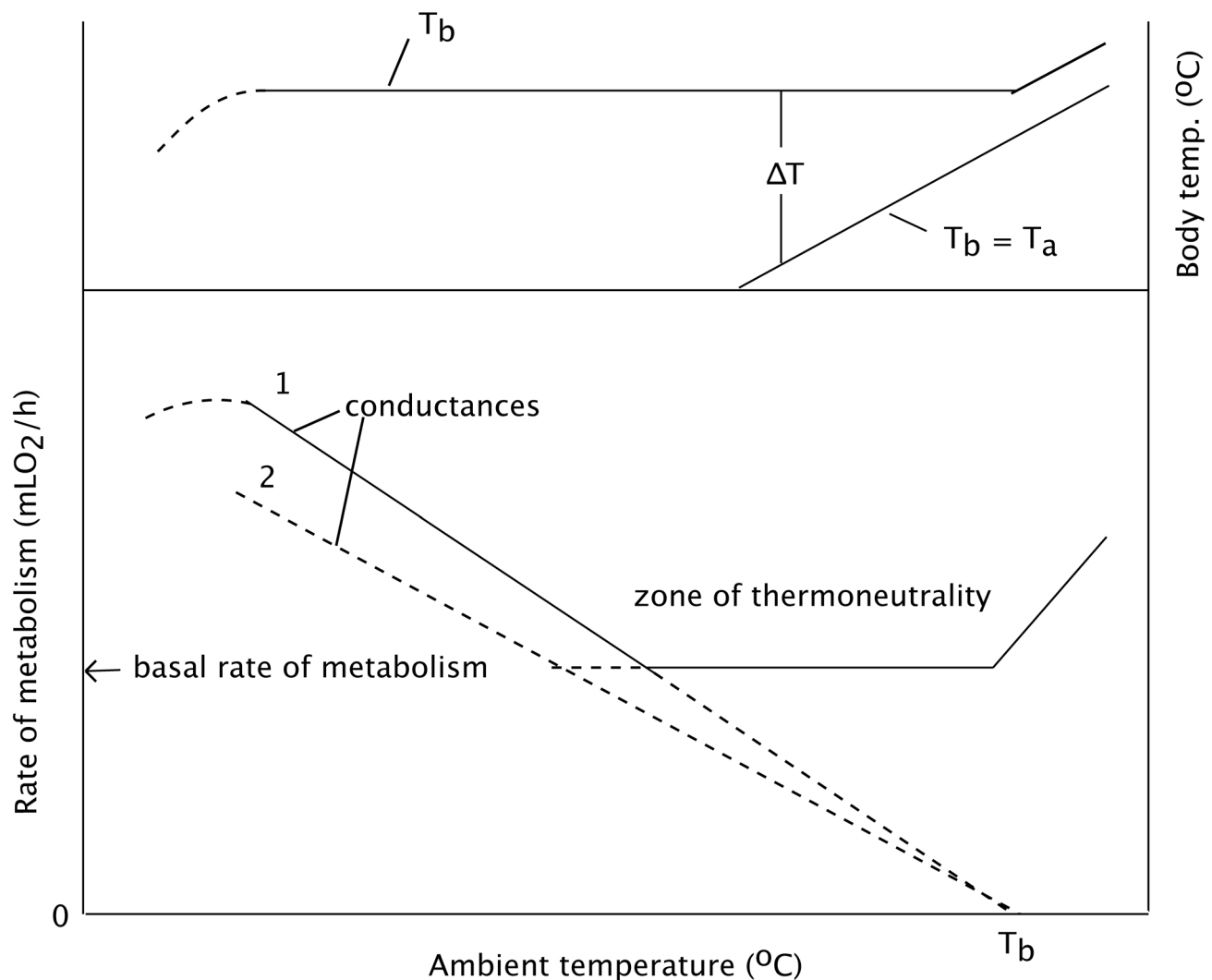


Figure 1. An idealized relationship of the body temperature and rate of metabolism of an endotherm with ambient temperature.

rate of energy expenditure of mammals and birds. This conclusion was first quantitatively stated for mammals by Max Kleiber (1932) followed by Benedict (1936), Brody (1945), and many others. Brody called this relationship the “mouse-to-elephant curve.” It is a power function:

$$\text{BMR} = a \times m^b \quad (2),$$

where BMR is the basal rate of metabolism, a is a coefficient that dictates the level of the relationship, m is body mass, and b is the power of the relationship, which is < 1.00 . A similar function is found in birds (Lasiewski and Dawson 1967; Aschoff and Pohl 1970; Reynolds and Lee 1996; McNab 2009), which might be called the “the hummingbird-to-ostrich curve”. The principal value of these scaling relationships, besides accounting for much of the variation in basal rate, is that they are standards against which to compare the measured basal rates of species. Equation (2) is most commonly analyzed in logarithmic form: $\log_{10} \text{BMR} = (b \times \log_{10} m) + \log_{10} a$.

The analysis of energetics would be easy if mass accounted for all of its variation, but one of the most interesting and informative observations is that all birds do not have the same BMR at the same mass. What is responsible for this non-uniformity? The answer has been the subject of controversy. Two competing views are that the variation around the metabolism-mass curve, i.e., the residual variation, 1) reflects the historical relationships of species (Reynold & Lee 1996; Rezende et al. 2002; Wiersma et al. 2007), or 2) it correlates with the behavior of species and their response to the environmental conditions that they face (McNab 2003c, 2008, 2009, 2012). The difficulty with this dichotomy is that some investigators tend to force the acceptance of one of these explanations to the exclusion of the other, when in fact both factors are determinative because they ask different questions. Part of the problem is that the characteristics of species are often tightly associated with phylogeny and therefore the ability to distinguish among their individual influences has been difficult. Phylogenetic analyses indicate where particular character states occur and where they historically change, but they do not address the *numerical*

variation in a quantitative character and therefore for the source of that variation. Fundamentally, the analytical problem is that the attempt to account for the variation in basal rate is a physiological, not an evolutionary, question, which therefore requires a quantitative answer.

Several studies have specified factors other than body mass that affect basal rate in birds. In a sample of 13 species of birds-of-paradise (Paradisaeidae), 99.0% of the variation in basal rate was accounted for by a combination of mass, food habits, and an altitudinal distribution (McNab 2003b, 2005a). An analysis of the basal rates of 11 species of rails (Rallidae), five of which were flightless, indicated that the combination of mass, flight condition, and food habits accounted for 96.2% of the variation in their basal rates (McNab & Ellis 2006). Nine factors that influence the basal rates of 533 species of birds included mass, food habits, climate, habitat, a flightless condition, use of torpor, an altitudinal distribution, a continental/island distribution, and the passerine/nonpasserine dichotomy. Collectively they accounted for 97.7% of the variation in avian basal rates (McNab 2009). Other demonstrations of the influence of factors on the basal rate of birds include Tieleman et al. (2004), Williams and Tieleman (2005), White et al. (2007), and Williams et al. (2010). Therefore, any thorough quantitative analysis of the basal rates of birds requires the inclusion of factors other than body mass.

THE GOALS OF THIS MONOGRAPH

This monograph will describe the energetics of birds in the rainforests and cloud forests of greater New Guinea, which includes the Bismarck Archipelago and many small, offshore islands. Detailed analysis of the data from 33 species that belong to 14 families have been previously published. Data on an additional 44 species from 19 families are reported in this monograph. Also included is a frogmouth, *Podargus ocellatus*, (Lasiewski et al. 1970), studied at Madang, Papua New Guinea, and a meliphagid, *Lichmera indistincta*, studied in Australia (Vitali et al. 1999) and marginally found in southern New Guinea.

Consequently, data on the energetics of 79 species, including 33 non-passerines and 46 passerines that belong to 26 families and nine orders are analyzed in this monograph.

The principal defects with this accumulation of data and with the resulting general analysis are that the species in this study represent only about 11% of the terrestrial bird fauna in New Guinea, no data are available from the many orders of aquatic species with the exception of a rail, which however is a terrestrial species, and few lowland passerines were studied. Preliminary estimates of the basal rate of 37 of the 44 species included in this monograph were reported in the general analysis of avian basal rates (McNab 2009), where they were indicated as McNab (pers. obs.). Those data should be replaced by the more definitive estimates presented in this monograph. Although both estimates are usually similar, any appreciable differences result from additional measurements. Seven additional species were caught and measured, including *Cateroscelis nigrorufa*, *Clytomyias insignis*, *Colluricincla megarhyncha*, *Eulacestoma nigropectus*, *Machaerirhynchus nigripectus*, *Monarchus axillaris*, and *Poecilodryas albonotata*. These data in retrospect are so limited and gave such inconsistent results that they are not reported here, although preliminarily included in the 2009 table. These data are abandoned.

This monograph has several goals: 1) to present original data on the basal rate of metabolism, thermal conductance, and body temperature of 44 species; 2) to explore the energy intensity and diversity of the 79 species in the avifauna to determine the relationship of their energetics to their ecology, behavior, and phylogeny; 3) to determine whether patterns exist in the energetics of component species; and 4) to examine energetics in the context of the biogeography (e.g., Steadman 2006) and evolution of birds (Filardi & Smith 2005) on islands in the tropical South Pacific.

METHODS

SPECIES COLLECTION

The data were obtained in Papua New Guinea during 12 expeditions over 19 years,

which collectively totaled more than 21 months of residence, during which over 2300 measurements were made, some in cooperation with Frank Bonaccorso. The collection of birds usually occurred in the field, but 32 of the 77 species measured in this study were obtained from captivity, including 13 pigeons from the personal collection of Simon Seeto in Madang and 12 birds-of-paradise from the aviary at The Rainforest Habitat in Lae, whence also came three species of owls and Loria's Satinbird (*Cnemophilus loriae*). This species, along with the congeneric Crested Satinbird (*C. macgregorii*), was until recently considered to be a bird-of-paradise (Cracraft & Feinstein 2000; Barker et al. 2004), but they are now placed in their own family, the Cnemophilidae (Irestadt & Ohlson 2008). Other captive species measured included a chick cassowary, which probably was a Dwarf Cassowary (*Casuarius bennetti*), and Blyths' Hornbill (*Rhyticeros plicatus*) from Madang; New Guinea Flightless Rail (*Megacrex inepta* [= *Amaurornis ineptus*]) from the Fly River; and Noisy Pitta (*Pitta versicolor*) from Mt. Bruce Wildlife Centre, Wellington, New Zealand. Two species that were studied at The Rainforest Habitat, Loria's Satinbird and the Papuan Boobook (*Ninox theomacha*), were also captured in the field at Ambua Lodge, which permitted a comparison of energy expenditure of captive and free-living individuals of the same species.

Field locations of capture included Mahonia na Dari biological station, West New Britain; Madang, Madang Province; Lae, Morobe Province; and Port Moresby, National Capital District, all of which are at, or near, sea level. Two high-altitude sites were repeatedly visited, three times at Ambua Lodge (2100 m altitude in Southern Highlands Province) and twice at Kumul Lodge (2860 m altitude in Enga Province).

Free-living species were captured in the wild by mist-nets in the late afternoon to ensure their survival, measured at night, and released early the next morning. The only exceptions were species of an intermediate size that ate fruit in captivity and therefore could be kept for 2-3 days while maintaining their body mass. Of course, this

was not a problem for species held in captivity. Nocturnal species (members of Caprimulgiformes and Strigiformes) were captured in the evening, measured during the next day, and released late that afternoon.

TECHNIQUES OF MEASUREMENT AND ANALYSIS

Individuals were placed into an appropriately sized chamber that had an opening to the outside atmosphere. Room air was drawn through the chamber, then CO₂ and water were filtered out of the air stream exiting the chamber, its flow rate measured, and sent to an oxygen analyzer. The equipment used early was a Beckman paramagnetic oxygen analyzer with Sho-Rate flowmeters, although most measurements used an AEI S-3A-II oxygen analyzer with TSI mass flowmeters, model 4140. All flow volumes were corrected to standard conditions for temperature and barometric pressure (O°C and 760 mm Hg). The AEI analyzer had two channels, which permitted two birds to be measured at the same time, each in its own system. The output of the analyzer was sent to a two channel SERVOGOR 124 stripchart recorder. Two to four measurements were made on diurnal birds in an evening starting at ca. 19:00, often continuing until 01:00 the next morning and occasionally later, each measurement in an evening being at a different ambient temperature and lasting about two hours. Body mass and body temperature were measured at the end of each experiment.

A persistent problem working with kingfishers, given their hole-dwelling behavior, was that they often tried to dig out of the chamber. When this occurred, the experiments continued until the animal rested or that it was obvious that no acceptable data were going to be obtained and the run was terminated often after four hours.

Data for the 79 species are summarized in Appendix 1. They include food habits, maximal limits to an altitudinal distribution, occurrence of torpor, feeding substrate, habitats used, presence on islands or continents, activity level, use of torpor, and phylogenetic affiliation. Data from this study include measurements of body mass, basal rate of metabolism, and body temperature, as well as estimates of minimal thermal conductance. The

data are presented in the text as a mean \pm standard error (number of measurements). In the case of basal rate of metabolism and thermal conductance, the mean is also expressed as a percentage of the value expected from mass in general avian standards. The standard for BMR is a general avian curve (McNab 2009):

$$\text{BMR (mLO}_2\text{/h)} = 7.25 \times m^{0.652} \quad (3)$$

and that for thermal conductance (Lasiewski et al. 1967) is:

$$C (\text{mLO}_2\text{/h}^\circ\text{C}) = 0.85 \times g^{0.492} \quad (4).$$

A difficulty with the estimates of conductance in this study is that only cool ambient temperatures were available, which often were not sufficient to obtain a marked increase in metabolism. Therefore, the lowest conductances may not represent the minimum. Yet, the majority of the estimates, as shall be seen, are below the values expected from equation (4).

A scaling relationship between BMR and mass was first determined. Then factors other than mass were brought with mass into an ANCOVA to determine the extent to which they individually and collectively accounted for the variation in BMR of the entire set of New Guinea avian data.

RESULTS

Casuariiformes

Casuariidae

Dwarf Cassowary (*Casuaris bennetti*)

One cassowary chick, which apparently belonged to this species, was measured in Madang. The chick had a mean body temperature of $40.0 \pm 0.26^\circ\text{C}$ (4). Its zone of thermoneutrality extended at least from 22 to 31°C (Fig. 2a). This individual had a mean basal rate equal to $0.466 \pm 0.081 \text{ mLO}_2\text{/g}\cdot\text{h}$ (3), which is 99% of the value expected from a mass equal to $2612 \pm 39.3 \text{ g}$ (5). The Emu (*Dromaius novaehollandiae*), another Casuarii, has a basal rate that is 88% of the value expected from body mass (Maloney & Dawson 1994). The difference may be associated with diet (frugivory vs. omnivory), environment (rainforest versus plains and woodlands), or possibly the cost of growth and development. Because the data are

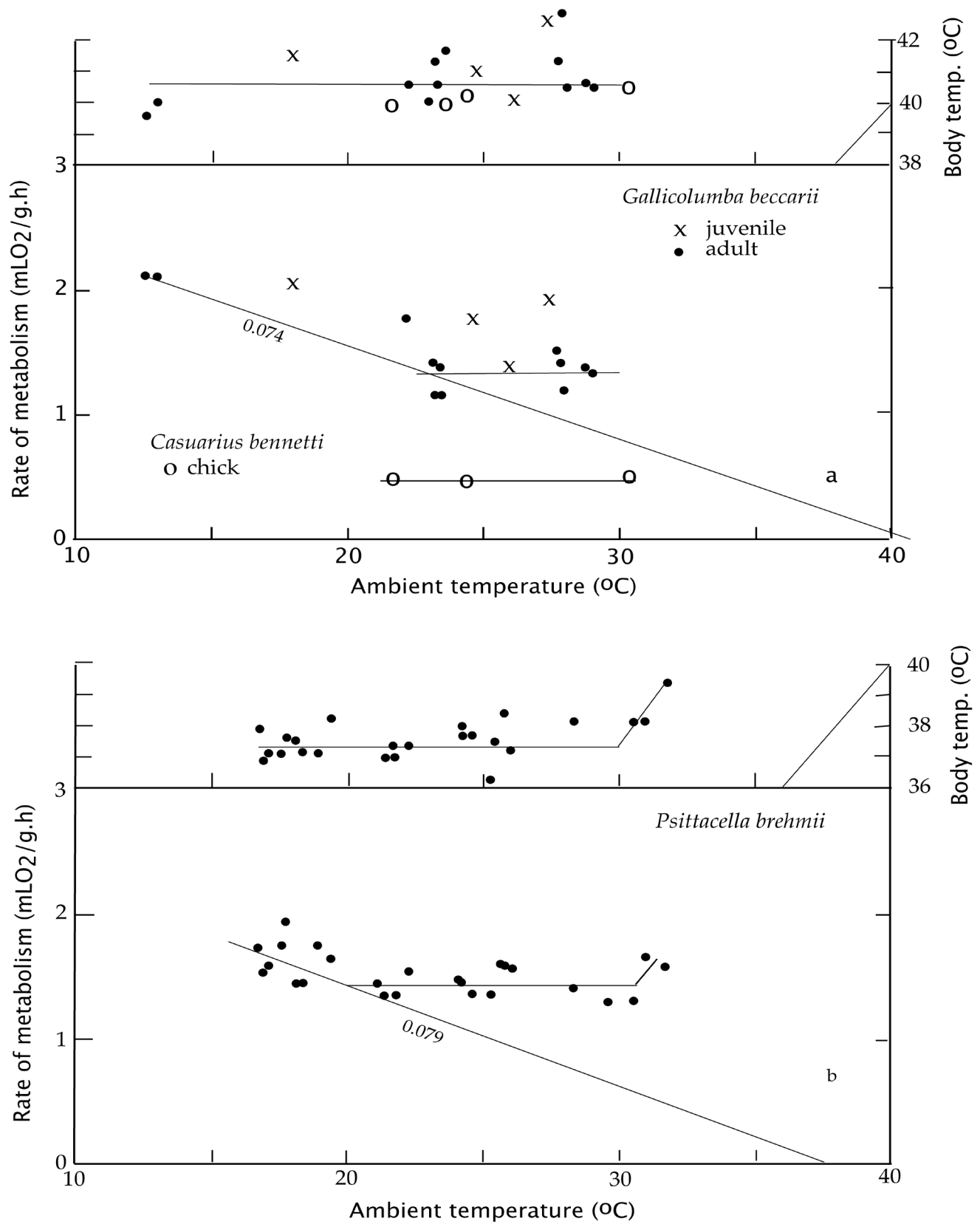


Figure 2. Rate of metabolism and body temperature as a function of ambient temperature in a) three Bronze Ground-doves (*Gallicolumba beccarii*) and one Dwarf Cassowary chick (*Casuarius bennetti*) and b) four Brehm's Tiger-parrots (*Psittacella brehmii*).

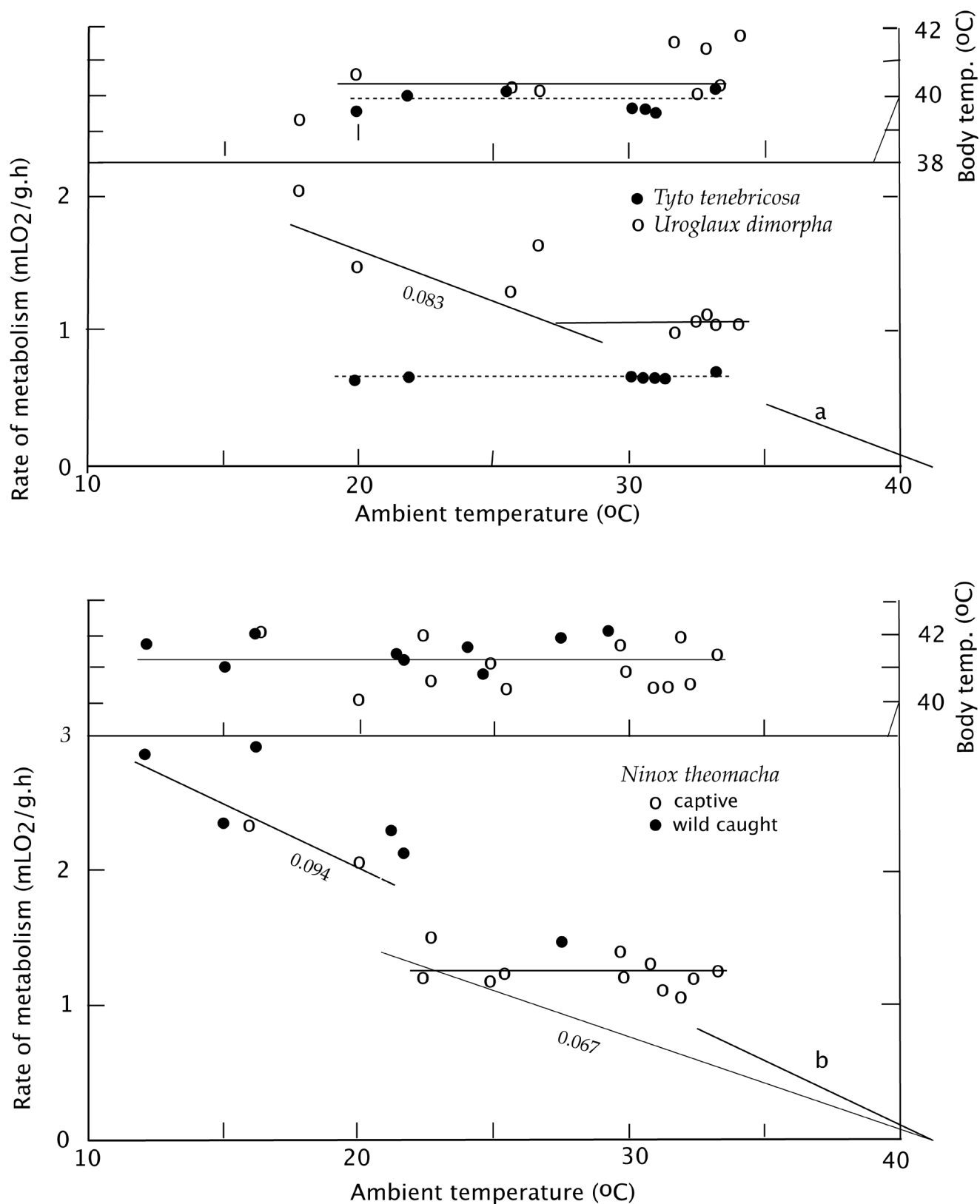


Figure 3. Body temperature and rate of metabolism as a function of ambient temperature in a) two Sooty Owls (*Tyto tenebricosa*) and one Papuan Hawk-owl (*Uroglauux dimorpha*) and b) three Papuan Boobooks (*Ninox theomacha*).

from a chick, they are not included in the general analysis.

Columbiformes

Columbidae

Bronze Ground-dove (*Gallicolumba beccarii*)

Three individuals, two adults and a juvenile, were captured at Ambua Lodge. Body mass of the adults was 68.8 ± 3.93 g (12). The zone of thermoneutrality in the adults extended from at least 23 to 29°C (Fig. 2a) within which the BMR equaled 1.32 ± 0.041 mL O₂/g·h (9), which is equivalent to 79% of the value expected from mass. Body temperature equaled 40.7 ± 0.16 °C (14) at ambient temperatures from 12 to 29°C. Adult thermal conductance equaled 0.074 ± 0.0025 mL O₂/g·h°C (6), 75% of the value expected from mass.

Four measurements are available from the juvenile, but they are dispersed (Fig. 2a), which may have reflected activity. One thermoneutral value equals the basal rate of the adults. This individual had a smaller mass than the adults (50.5 ± 0.29 g [4]).

Psittaciformes

Psittacidae

Brehm's Tiger-parrot (*Psittacella brehmii*)

Four individuals, three females and one male, were captured and measured at Kumul Lodge. Body mass equaled 99.8 ± 1.63 g (26). The zone of thermoneutrality extended from 20 to 31°C (Fig. 2b), within which BMR equaled 1.42 ± 0.028 mL O₂/g·h (15), 97%. Mean body temperature, at ambient temperatures between 16 and 29°C, equaled 37.4 ± 0.12 °C (21). Thermal conductance at ambient temperatures < 20°C, equaled 0.079 ± 0.0017 mL O₂/g·h°C (7), 90%.

Strigiformes

Tytonidae

Sooty Owl (*Tyto tenebricosa*)

Two Sooty Owls were borrowed from The Rainforest Habitat. The mean mass of these owls was 710.0 ± 16.33 g (10). The zone of thermoneutrality extended at least from 20 to 33°C

(Fig. 3a). The mean BMR equaled 0.67 ± 0.009 mL O₂/g·h (7), 91%. Mean body temperature was 40.4 ± 0.17 °C (10). No estimate of conductance was available.

Strigidae

Papuan Hawk-owl (*Uroglaux dimorpha*)

One hawk-owl was obtained from The Rainforest Habitat. It weighed 245.3 ± 4.32 g (9). Thermoneutrality included temperatures from 27 to 35°C. BMR equaled 1.07 ± 0.021 mL O₂/g·h (5), 100% (Fig. 3a). Mean body temperature was 40.3 ± 0.20 °C (6). Minimal conductance equaled 0.083 ± 0.0071 mL O₂/g·h°C (3), 160%. This value is high (Fig. 25), but it is only based on three measurements.

Papuan Boobook (*Ninox theomacha*)

Two captive Boobooks from The Rainforest Habitat and one caught in the field at Ambua Lodge were measured. The captives had a zone of thermoneutrality that extended from 22 to 33°C, within which the BMR equaled 1.24 ± 0.033 mL O₂/g·h, (11), 98% (Fig. 3b). The mean mass of the three individuals was 151.4 ± 2.01 g (21) and their mean body temperature was 41.2 ± 0.15 °C (22). Most of the measurements on the field-caught individual were high, conforming to a high estimate of conductance derived from the two captives, although the one thermoneutral measurement was similar to those of the captives. A thermal conductance equal to 0.094 ± 0.0027 mL O₂/g·h°C (4), an estimate derived from all three birds (Fig. 3b). The minimal conductance appears to be 0.067 ± 0.0055 mL O₂/g·h°C (2), 101%.

Coraciiformes

Alcedinidae

Variable Dwarf Kingfisher (*Ceyx lepidus*)

Five individuals were captured near Madang and another on New Britain. The mean body mass was 14.9 ± 0.97 g (15). The zone of thermoneutrality extended from 27 to 35°C (Fig. 4a) within which BMR equaled 2.19 ± 0.057 mL O₂/g·h (8), 77%. One of the two measurements on the individual from New Britain agreed with the measurements in individuals from New Guinea proper, whereas the other probably reflected activity. Mean body

temperature equaled $38.4 \pm 0.37^\circ\text{C}$ (10). Minimal thermal conductance was $0.215 \pm 0.0010 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (3), 98%.

Azure Kingfisher (*Alcedo azurea*)

This species of kingfisher, caught near Madang, was represented by 23 individuals. Its mean mass was $31.5 \pm 0.48 \text{ g}$ (30). The zone of thermoneutrality extended from 19 to 34°C (Fig. 4b) and BMR equaled $1.36 \pm 0.033 \text{ mL O}_2/\text{g h}$ (14), 62%. Body temperature was highly variable, associated with an excitable response to handling, the mean equaling $38.0 \pm 0.29^\circ\text{C}$ (16). An estimate of the minimal thermal conductance equaled $0.069 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (2), 47%, which was compatible with the lower limit of thermoneutrality. A higher conductance equals $0.148 \pm 0.0051 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (5), 101%.

Sacred Kingfisher (*Todiramphus sanctus*)

The Sacred Kingfisher is a non-breeding migrant from Australia. Sixteen, captured near Madang, had a mean mass of $41.5 \pm 1.12 \text{ g}$ (20). The zone of thermoneutrality extended from 25 to 35°C (Fig. 5a). BMR was 1.34 ± 0.048 (10), 67%. Body temperature equaled $39.0 \pm 0.17^\circ\text{C}$ (15). Minimal conductance was $0.103 \pm 0.0006 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (3), 81%.

Common Paradise-kingfisher (*Tanysiptera galatea*)

One Common Paradise-kingfisher, captured near Madang, was measured. The zone of thermoneutrality was between 15 and 33°C (Fig. 5b). This species had a mass of $50.7 \pm 0.61 \text{ g}$ (19) and a BMR equal to $1.01 \pm 0.015 \text{ mL O}_2/\text{g h}$ (12), 55%. Mean body temperature at ambient temperatures between 27 and 33°C equaled $37.7 \pm 0.27^\circ\text{C}$ (7), although body temperature fell at ambient temperatures $< 28^\circ\text{C}$, reaching ca. 33.0°C at ambient temperatures $< 20^\circ\text{C}$. Only two estimates of thermal conductance are available, the mean of which is $0.076 \text{ mL O}_2/\text{g h}^\circ\text{C}$, 66%.

Buff-breasted Paradise-kingfisher (*Tanysiptera sylvia*)

Two individuals were caught near Mahonia na Dari biological station, near Kimbe, West New Britain. (The New Britain population is sometimes considered to be a separate species, *T. nigriceps*.) They weighed $63.1 \pm 1.90 \text{ g}$ (10). A fragment of the

zone of thermoneutrality extended from 26 to ca. 30°C (Fig. 5b). BMR equaled $1.23 \pm 0.003 \text{ mL O}_2/\text{g h}$ (3), 73%. Body temperature was $37.7 \pm 0.11^\circ\text{C}$ (10). One estimate of conductance, $0.105 \text{ mL O}_2/\text{g h}^\circ\text{C}$, 101%, may reflect activity.

Hook-billed Kingfisher (*Melidora macrorrhina*)

One individual was caught near Madang. It weighed $84.9 \pm 1.25 \text{ g}$ (6). The zone of thermoneutrality included temperatures between 24 and 34°C (Fig. 5a). BMR was $0.88 \pm 0.040 \text{ mL O}_2/\text{g h}$ (6), 57%. Mean body temperature was $39.1 \pm 0.17^\circ\text{C}$ (4).

Rufous-bellied Kookaburra (*Dacelo gaudichaud*)

Two adults and a juvenile were captured near Madang, all from the same nest in a termitarium. One adult weighed $152.0 \pm 2.20 \text{ g}$ (20), which may have been a female, and the other, which may have been a male, weighed $124.9 \pm 0.97 \text{ g}$ (35). The zone of thermoneutrality in both adults extended from 25 to 36°C (Fig. 6a). The larger individual had a BMR equal to $0.64 \pm 0.034 \text{ mL O}_2/\text{g h}$ (9), whereas it equaled $0.84 \pm 0.143 \text{ mL O}_2/\text{g h}$ (13) in the smaller individual, these values being 51 and 62% of the values expected from mass, respectively. The weighted collective for the two individuals are 146.2 g and $0.76 \text{ mL O}_2/\text{g h}$, which is 59%. The collective body temperature equaled $39.4 \pm 0.12^\circ\text{C}$ (55). Thermal conductance of the smaller adult was $0.056 \pm 0.071 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (11) and $0.047 \pm 0.001 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (11) for the larger adult. The collective thermal conductance equals $0.052 \text{ mL O}_2/\text{g h}^\circ\text{C}$, 75%.

The juvenile weighed $104.8 \pm 1.24 \text{ g}$ (6), had a thermoneutral zone similar to that of the adults, and a BMR equal to $0.67 \pm 0.029 \text{ mL O}_2/\text{g h}$ (4), which is identical to that of the larger adult, but because of its smaller mass, equals 49%. Mean body temperature in this individual was $38.4 \pm 0.22^\circ\text{C}$ (6).

Passeriformes

Pittidae

Noisy Pitta (*Pitta versicolor*)

This species is principally a winter visitor to New Guinea from Australia. Two individuals were measured at Mt. Bruce Conservation Centre, New

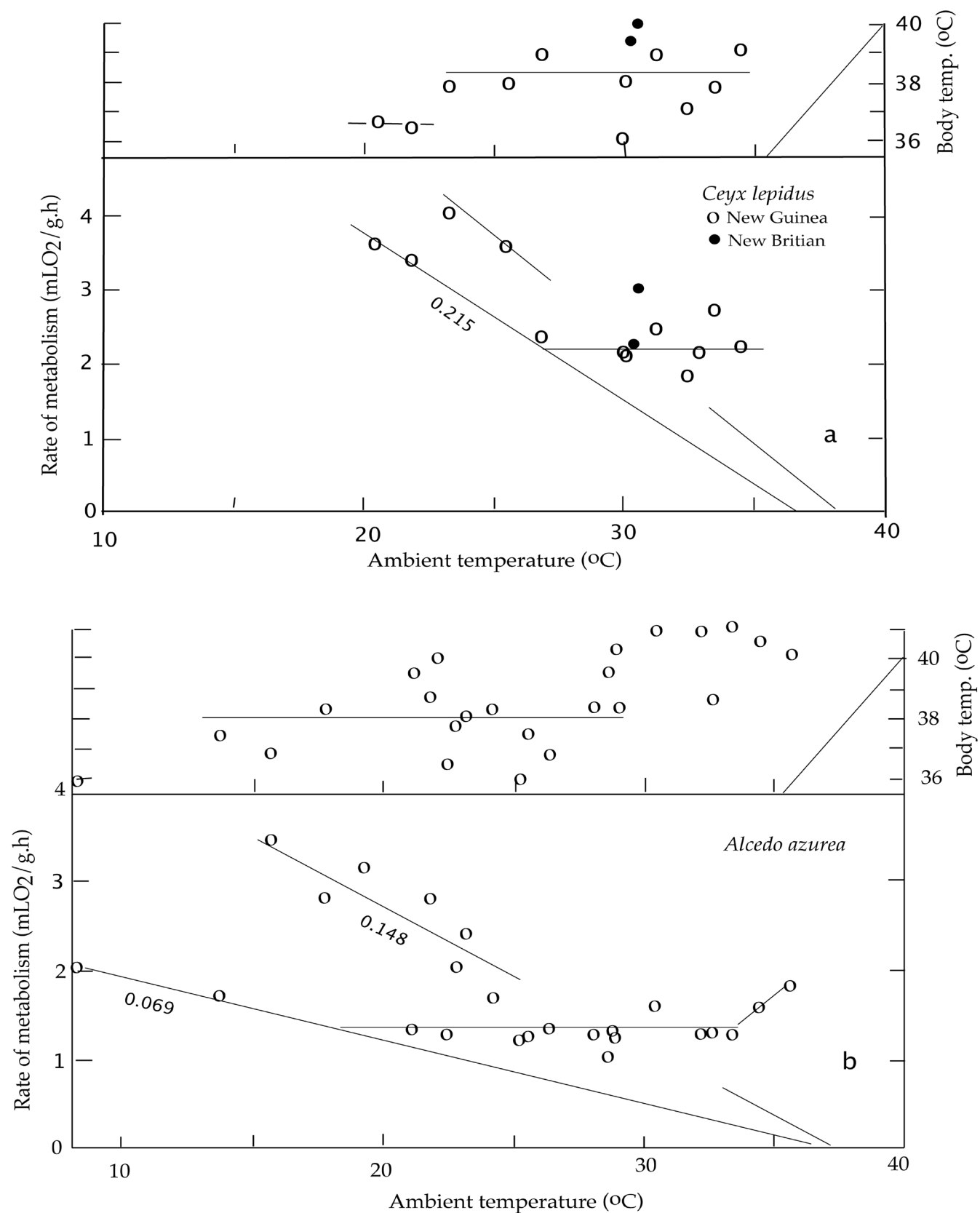


Figure 4. Body temperature and rate of metabolism as a function of ambient temperature in a) five Variable Dwarf Kingfishers (*Ceyx lepidus*) and b) 23 Azure Kingfishers (*Alcedo azurea*).

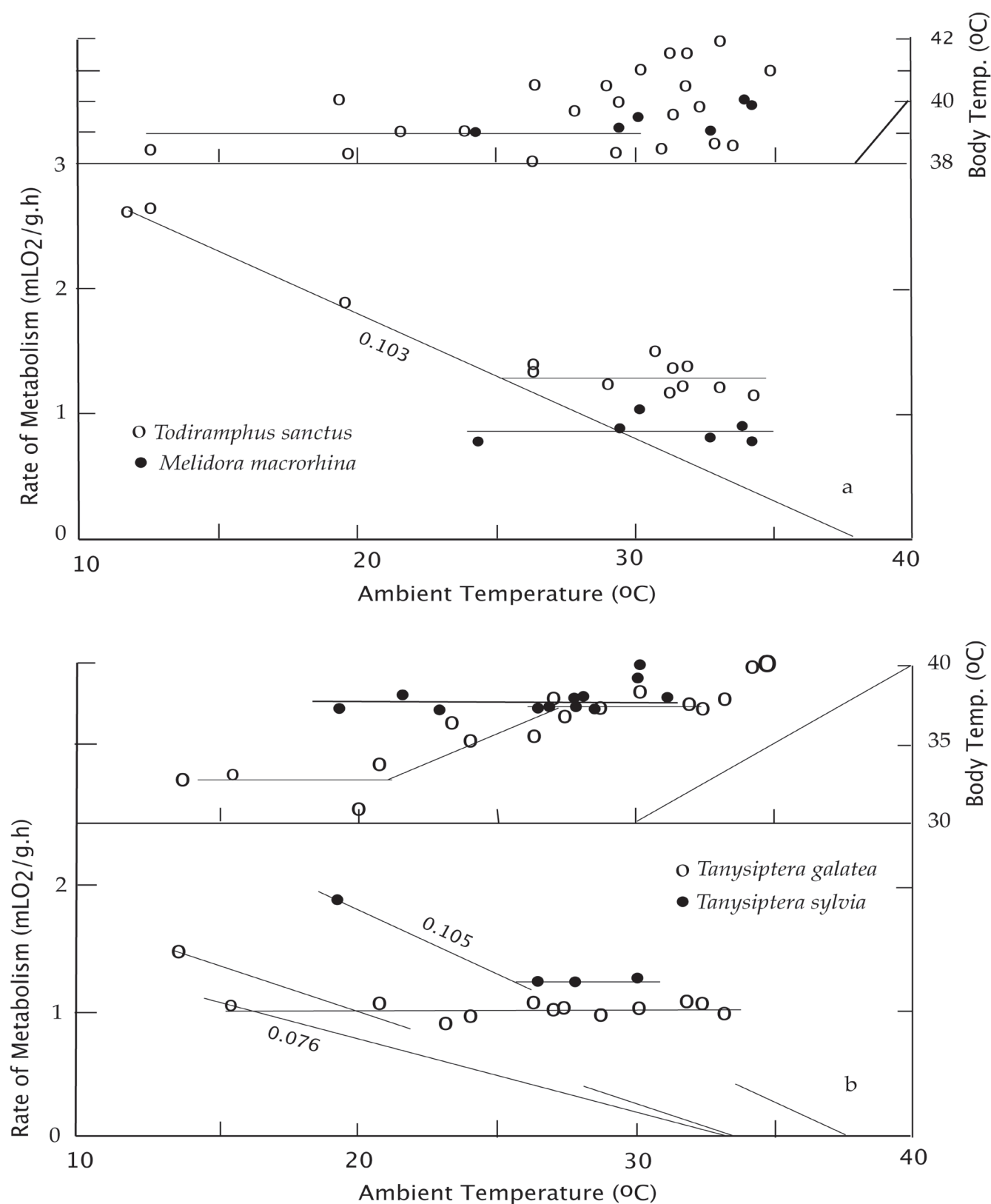


Figure 5. Body temperature and rate of metabolism as a function of ambient temperature in a) 16 Sacred Kingfishers (*Todiramphus sanctus*) and one Hook-billed Kingfisher (*Melidora macrorrhina*) and b) one Common Paradise-kingfisher (*Tanysiptera galatea*) and two Buff-breasted Paradise-kingfishers (*Tanysiptera sylvia*).

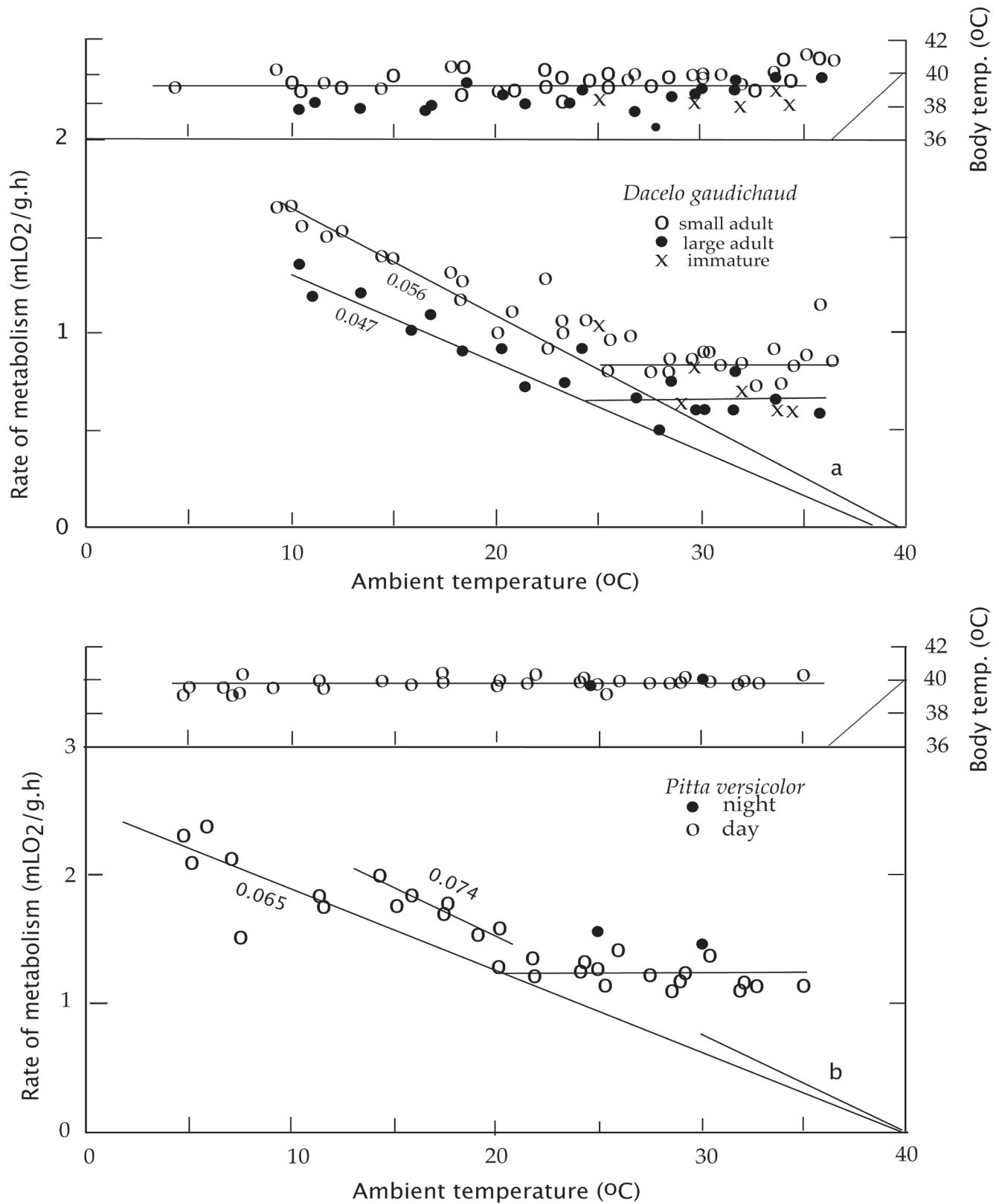


Figure 6. Body temperature and rate of metabolism as a function of ambient temperature in a) three Rufous-bellied Kookaburras (*Dacelo gaudichaud*) and b) two Noisy Pittas (*Pitta versicolor*).

Zealand. They could be measured only during the day, except for two nighttime measurements (Fig. 6b). The zone of thermoneutrality extended from 20 to 35°C within which the BMR equaled 1.21 ± 0.025 mL O_2 /g·h (17), a value that is 78% of the value expected from a mass equal to 83.1 ± 0.62 g (45). The two measurements made at night were slightly higher than those made during the day (Fig. 6b). The mean body temperature was $39.9 \pm 0.06^\circ\text{C}$ (31). Two estimates of thermal conductance equaled 0.074 ± 0.0019 (7) and 0.065 ± 0.0015 mL O_2 /g·h°C (6), 72%, the latter defining the lower limit of thermoneutrality (Fig. 6b).

Muscicapidae

Island Thrush (*Turdus poliocephalus*)

A highland species in New Guinea, five were captured, one at 2500m, i.e., 400 m above Ambua Lodge, and the other four at Kumul Lodge (2860m). Mean body mass equaled 66.1 ± 1.40 g (26). The zone of thermoneutrality ranged from 15 to 30°C (Fig. 7a). The BMR was 2.08 ± 0.037 mL O_2 /g·h (21), 123%. Mean body temperature at ambient temperatures $> 20^\circ\text{C}$ equaled $39.7 \pm 0.29^\circ\text{C}$ (13), but it decreased to 37°C at lower ambient temperatures (Fig. 7a). Minimal thermal conductance was 0.082 ± 0.0019 mL O_2 /g·h°C (5), 81%.

Eupetidae

Blue-capped Ifrita (*Ifrita kowaldi*)

Four individuals were captured at Kumul Lodge. Their mean mass was 28.9 ± 0.40 g (10). Thermoneutrality extended from 17 to 27°C (Fig. 7b) within which BMR equaled 2.12 ± 0.066 mL O_2 /g·h (6), 94%. Minimal thermal conductance was about 0.100 ± 0.0058 mL O_2 /g·h°C (4), 61%. Measurements of body temperature are highly variable (Fig. 7b): the pooled value was $36.8 \pm 0.66^\circ\text{C}$ (10), which is independent of ambient temperature (Fig. 7b). However, body temperature fell into two groups, higher values, $38.4 \pm 0.38^\circ\text{C}$ (6) and lower values, $34.6 \pm 0.47^\circ\text{C}$ (4). These groups occur throughout thermoneutrality, the basis of which is unclear, but their variation is not reflected in basal rate.

Acanthizidae

Buff-faced Scrub-wren (*Sericornis perspicillatus*)

Eleven Buff-faced Scrub-wrens were meas-

ured at Ambua Lodge. The zone of thermoneutrality extended from 19 to 31°C and possibly down to 12°C (Fig. 8a). The mean BMR equaled 3.45 ± 0.095 mL O_2 /g·h (23), which is 100% of the value expected from a mass of 8.5 ± 0.16 g (39). Body temperature equaled $37.8 \pm 0.20^\circ\text{C}$ (20) at ambient temperatures $> 22.5^\circ\text{C}$ and $36.6 \pm 0.17^\circ\text{C}$ (20) at lower temperatures. A thermal conductance equal to 0.244 ± 0.0099 mL O_2 /g·h°C (5), 85%, does not correspond to the lower limit of thermoneutrality. If the lower limit of thermoneutrality is approximately 14°C, it corresponds to a conductance equal to 0.155 ± 0.0070 mL O_2 /g·h°C (3). However, this value is only 39% of expectations.

Papuan Scrub-wren (*Sericornis papuensis*)

This scrub-wren was represented by five individuals caught at Kumul Lodge. Their mean mass was 9.8 ± 0.15 g (17). Thermoneutrality extended from 15 to 28°C (Fig. 8b). Basal rate equaled 3.02 ± 0.070 mL O_2 /g·h (9), 92%. Mean body temperature was $35.3 \pm 0.21^\circ\text{C}$ (16), but varied from 32.4 to 37.9°C. This scrub-wren had a minimal thermal conductance of 0.165 ± 0.0117 mL O_2 /g·h°C (4).

Large Scrub-wren (*Sericornis nouhuysi*)

Sixteen Large Scrub-wrens were captured. They were found at both lodges. Their mean body mass equaled 16.1 ± 0.28 g (65) and the zone of thermoneutrality extended from 10 to 30°C (Fig. 9a). The rate of metabolism within the zone was highly variable, some of which reflects a variation in body temperature (Fig. 9b). Eleven of the 14 lowest body temperatures were associated with rates < 3.00 mL O_2 /g·h, although three were associated with higher rates (Fig. 9a, b). Furthermore, at rates < 3.00 mL O_2 /g·h, only 11 of 26 runs had body temperatures $< 35.5^\circ\text{C}$. If "regulated" body temperature falls between 35.5 and 38°C, under the assumption that lower temperatures represent hypothermia and higher values indicated activity, the mean body temperature equaled $37.4 \pm 0.15^\circ\text{C}$ (28). Then, if the best estimate of BMR excludes rates associated with body temperatures outside of this range, it equals 2.90 ± 0.056 mL O_2 /g·h (30), 105%. Two measurements may represent an

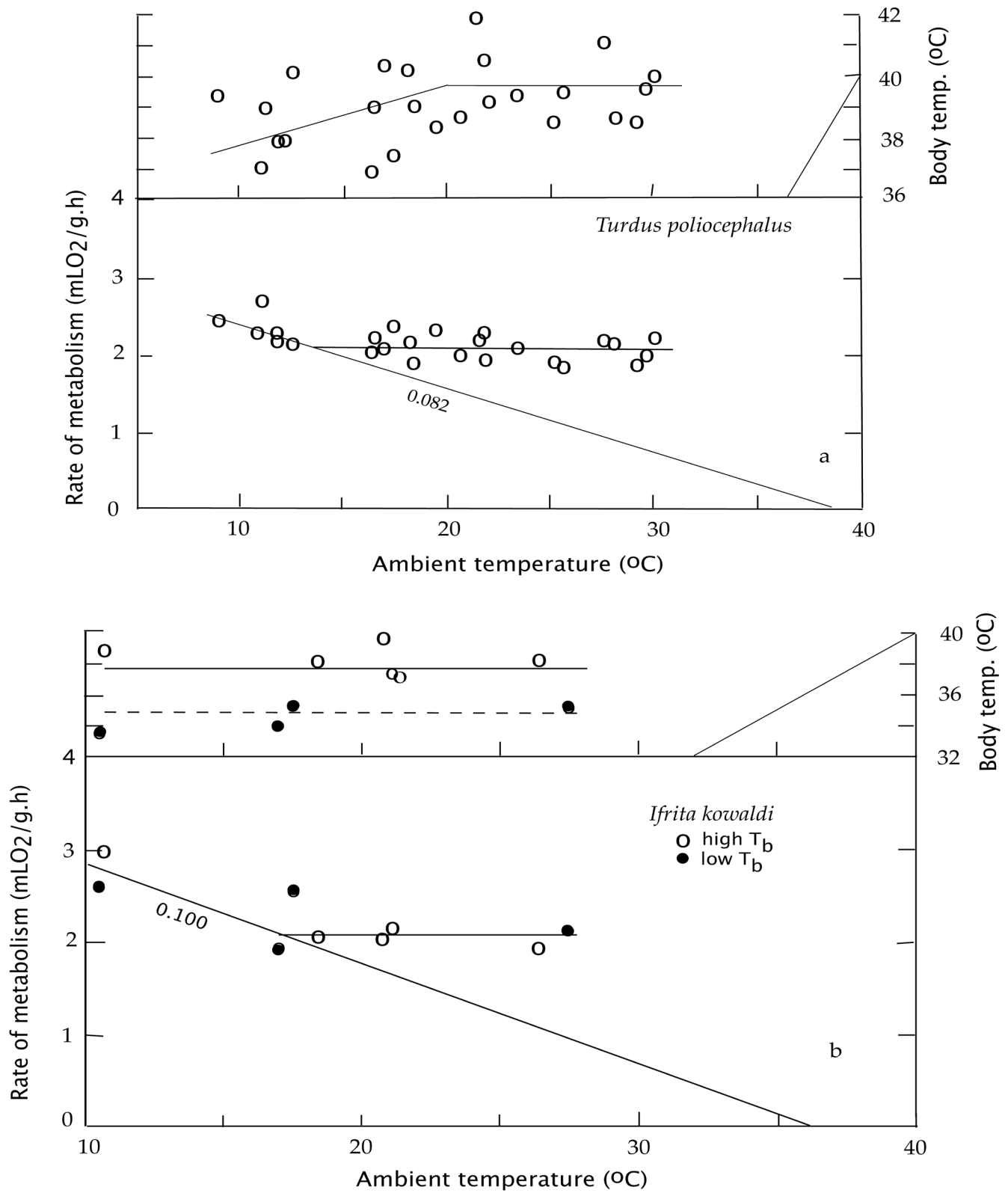


Figure 7. Body temperature and rate of metabolism as a function of ambient temperature in a) five Island Thrushes (*Turdus poliocephalus*) and b) four Blue-capped Ifritas (*Ifrita kowaldi*).

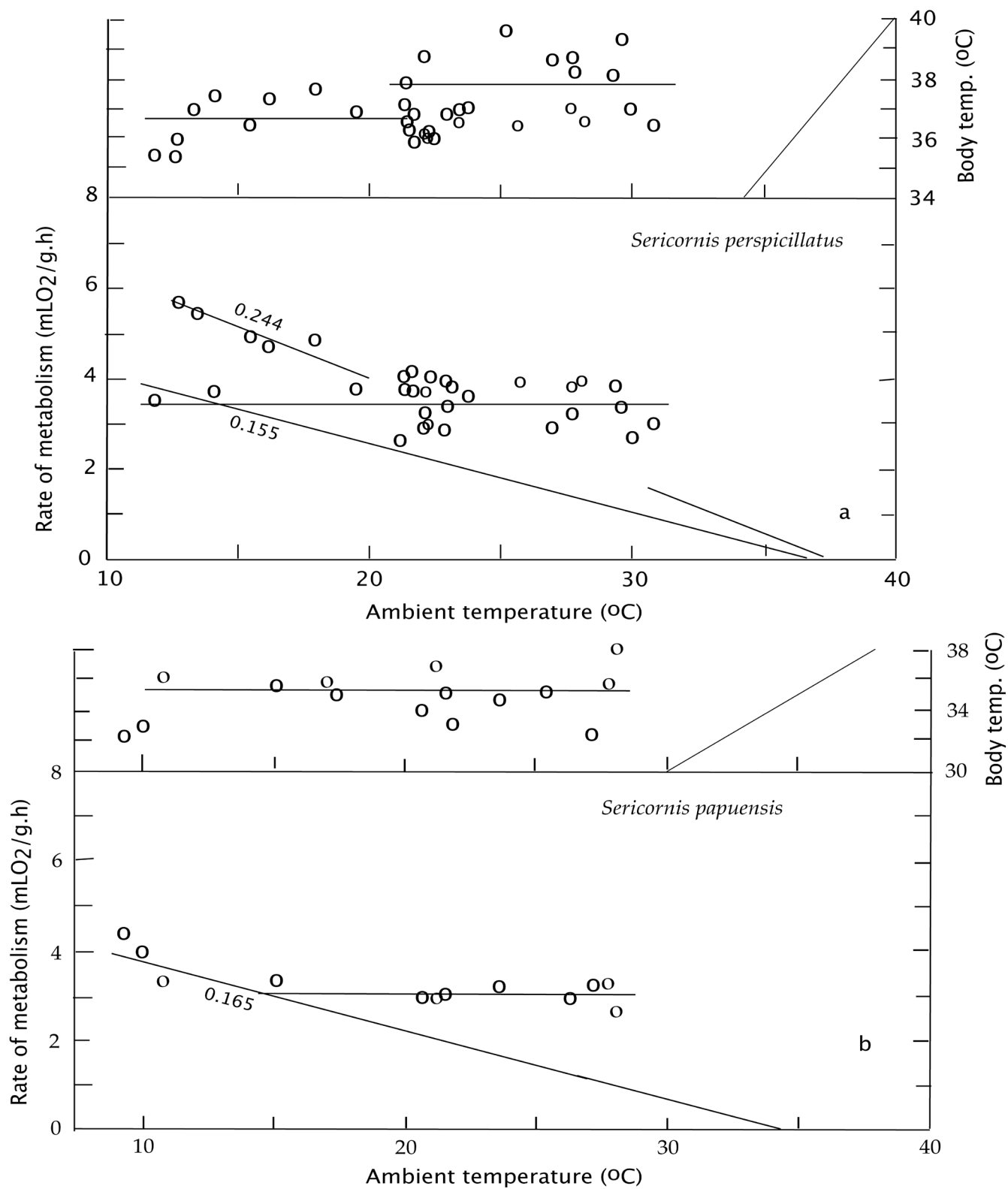


Figure 8. Body temperature and rate of metabolism as a function of ambient temperature in a) 11 Buff-faced Scrub-wrens (*Sericornis perspicillatus*) and b) five Papuan Scrub-wrens (*Sericornis papuensis*).

estimate of minimal thermal conductance, $0.115 \text{ mL O}_2/\text{g h}^\circ\text{C}$, 57%.

Mountain Mouse-warbler (*Crateroscelis robusta*)

This species, represented by eight individuals, was captured at both lodges. It had a mean body mass equal to $17.3 \pm 0.18 \text{ g}$ (27). The zone of thermoneutrality extended from 11 to 28°C (Fig. 10a) within which BMR equaled $2.73 \pm 0.034 \text{ mL O}_2/\text{g h}$ (21), 102%. Mean body temperature was $37.0 \pm 0.21^\circ\text{C}$ (20) at ambient temperatures between 21 and 30°C , whereas at lower ambient temperatures, body temperature equaled $35.6 \pm 0.26^\circ\text{C}$ (16) (Fig. 10a). Minimal thermal conductance is $0.117 \pm 0.0060 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (2), 58%.

Rhipiduridae

Friendly Fantail (*Rhipidura albolimbata*)

This fantail, represented by 12 individuals, was caught at both lodges. Its mean mass was $10.3 \pm 0.18 \text{ g}$ (44) and the zone of thermoneutrality extended from 19 to 30°C (Fig. 10b). Within this range, rate of metabolism is difficult to interpret. It is highly variable, as is body temperature, a pattern similar to that seen in *Sericornis nouhuysi*, except that low rates of metabolism in the fantail were not consistently correlated with low body temperatures. Under the assumption that body temperatures between 35 and 38°C are normothermic, the mean equaled $36.2 \pm 0.18^\circ\text{C}$ (22) and the rate of metabolism was $5.23 \pm 0.074 \text{ mL O}_2/\text{g h}$ (19), 163%! However, when mean body temperature equaled $32.8 \pm 0.28^\circ\text{C}$ (8), standard rate of metabolism in thermoneutrality was $3.15 \pm 0.132 \text{ mL O}_2/\text{h}$ (9), which is 98% of the BMR expected from mass. This value probably is not the basal rate because of the low body temperatures (Fig. 10b). The higher mass-independent estimate of basal rate is similar to that found in the Black Fantail, which can further justify using the higher estimate in this species. Estimates of thermal conductance, as expected, depend on body temperature, $0.230 \pm 0.0148 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (5) with a lower temperature (32.5°C) and $0.321 \pm 0.0058 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (7) with a higher temperature (35.5°C). These values are 89 and 124% of expectations, respectively.

Black Fantail (*Rhipidura atra*)

The Black Fantail is represented by six individuals that were captured at Ambua. They had a mean mass of $11.0 \pm 0.26 \text{ g}$ (24). The zone of thermoneutrality extended from 13 to 29°C (Fig. 11a) and BMR equaled $4.20 \pm 0.139 \text{ mL O}_2/\text{g h}$ (13), 133%, without the complications seen in the Friendly Fantail. Mean body temperature was $38.3 \pm 0.16^\circ\text{C}$ (12) at ambient temperatures between 11 and 23°C , whereas body temperature increased at higher ambient temperatures (Fig. 11a). Minimal thermal conductance equaled $0.181 \pm 0.013 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (3), 72%.

Petroicidae

Canary Flycatcher (*Microeca papuana*)

The flycatcher was captured at both lodges. Four individuals weighed $12.9 \pm 0.28 \text{ g}$ (14). The zone of thermoneutrality ranged at least from 17 to 28°C (Fig. 11b) within which the BMR equaled $2.89 \pm 0.102 \text{ mL O}_2/\text{g h}$ (6), 97%. Body temperature was $34.5 \pm 0.58^\circ\text{C}$ (12). An estimate of thermal conductance is $0.195 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (1), 84%.

White-winged Robin (*Peneothello sigillatus*)

This species was found at both lodges. The 11 individuals weighed $21.1 \pm 0.51 \text{ g}$ (40). The zone of thermoneutrality extended from 10 to 30°C (Fig. 12a); BMR was $2.68 \pm 0.040 \text{ mL O}_2/\text{g h}$ (36), 107%. Body temperature equaled $38.9 \pm 0.19^\circ\text{C}$ (17) at ambient temperatures $> 21^\circ\text{C}$ and $37.1 \pm 0.17^\circ\text{C}$ (19) at lower ambient temperatures (Fig. 12a). Minimal thermal conductance was 0.103 ± 0.0075 (2), 60%.

Blue-gray Robin (*Peneothello cyanus*)

The Blue-gray Robin was found only at Ambua Lodge. The 21 individuals weighed $23.8 \pm 0.28 \text{ g}$ (65). The zone of thermoneutrality occurred between 11 and 30°C (Fig. 12b). Its BMR equaled $2.63 \pm 0.051 \text{ mL O}_2/\text{g h}$ (44), 109%. Body temperature was $37.8 \pm 0.21^\circ\text{C}$ (23) at ambient temperatures $< 23^\circ\text{C}$. At higher ambient temperatures, body temperature increased. Minimal conductance may be as low as $0.089 \pm 0.0033 \text{ mL O}_2/\text{g h}^\circ\text{C}$ (3), 52%.

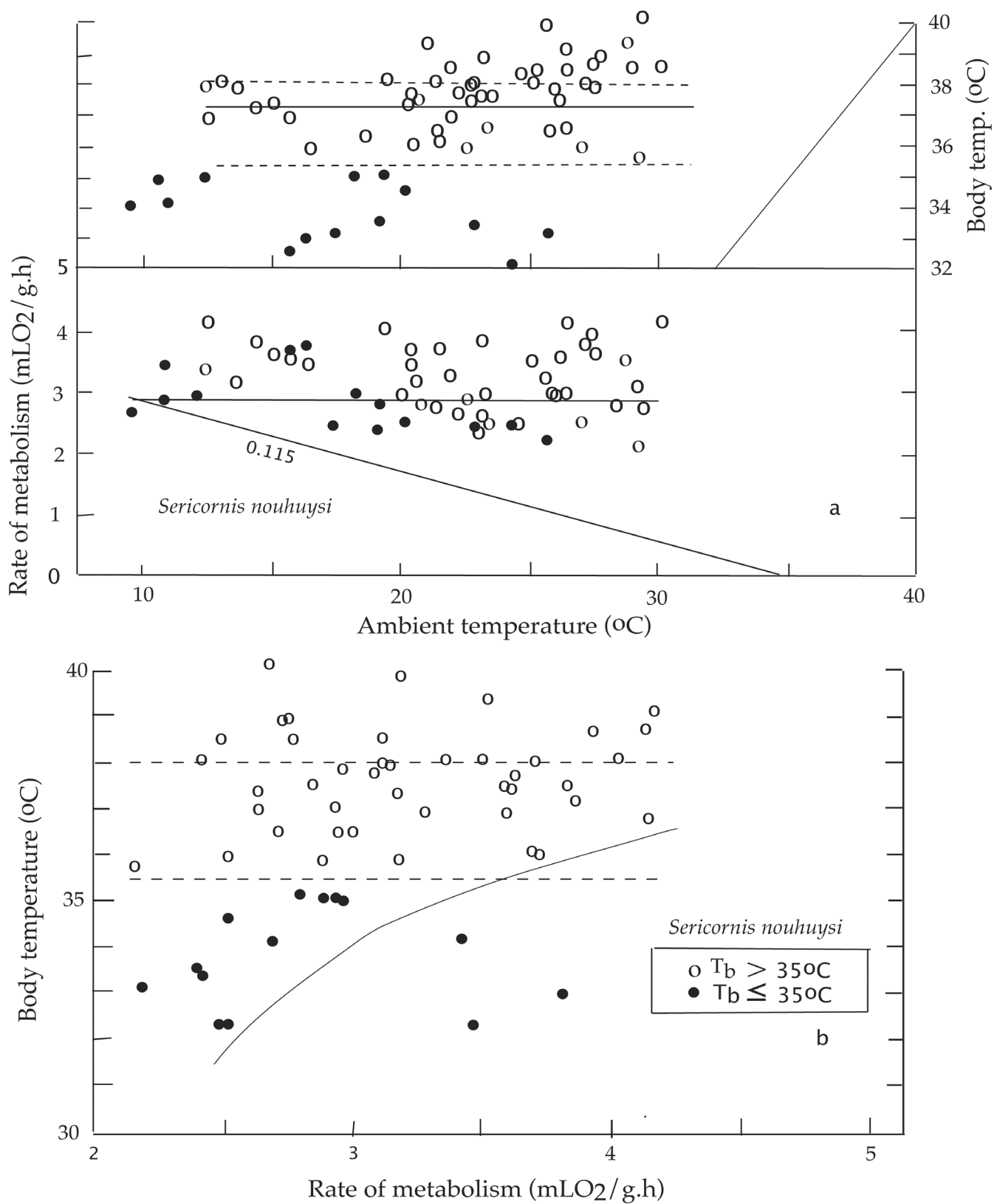


Figure 9. a) Body temperature and rate of metabolism as a function of ambient temperature and b) body temperature as a function of rate of metabolism in 16 Large Scrub-wrens (*Sericornis nouhuysi*).

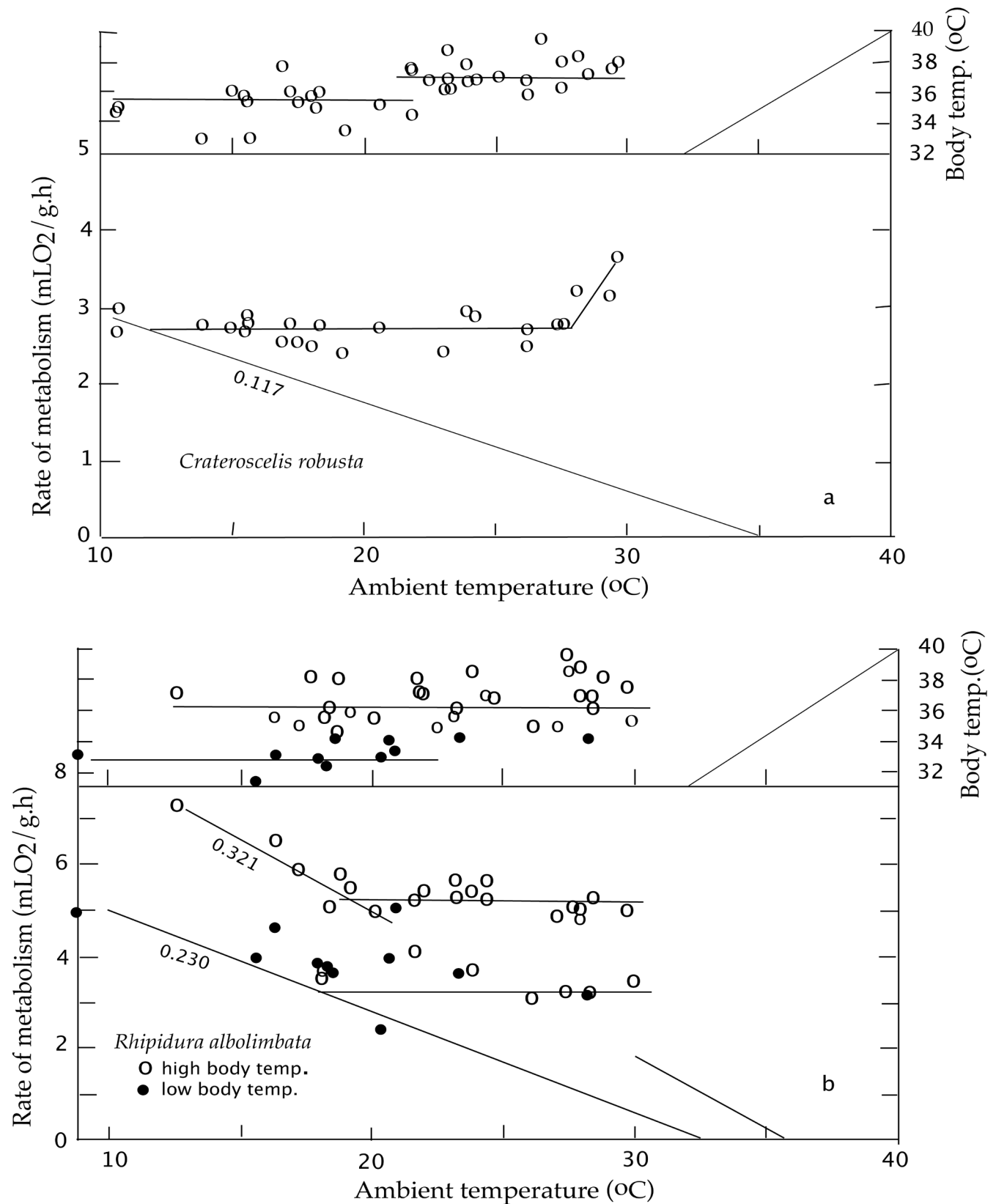


Figure 10. Body temperature and rate of metabolism as a function of ambient temperature in a) eight Mountain Mouse-warblers (*Crateroscelis robusta*) and b) 12 Friendly Fantails (*Rhipidura albolimbata*). .

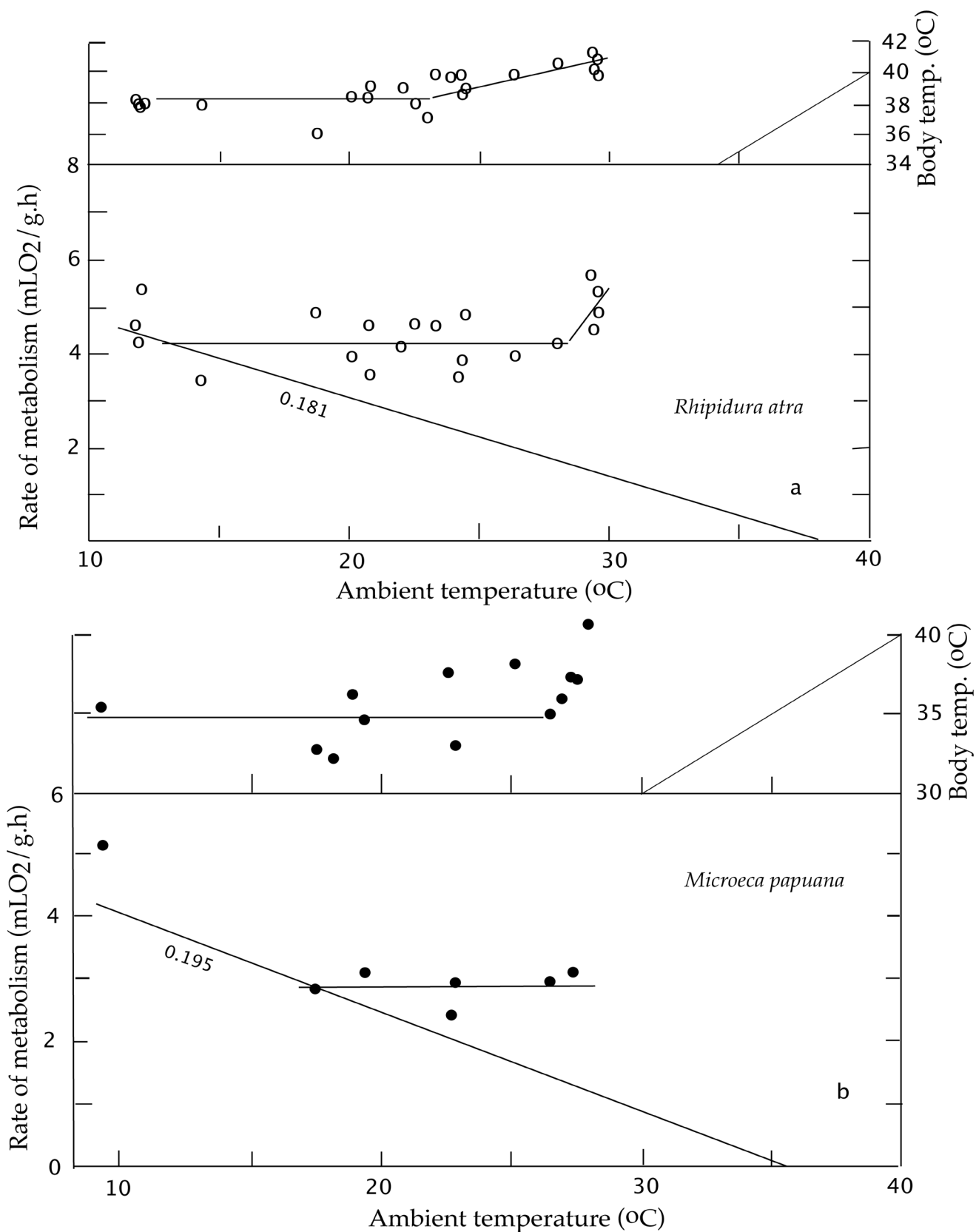


Figure 11. Body temperature and rate of metabolism as a function of ambient temperature in a) six Black Fantails (*Rhipidura atra*) and b) four Canary Flycatchers (*Microeca papuana*).

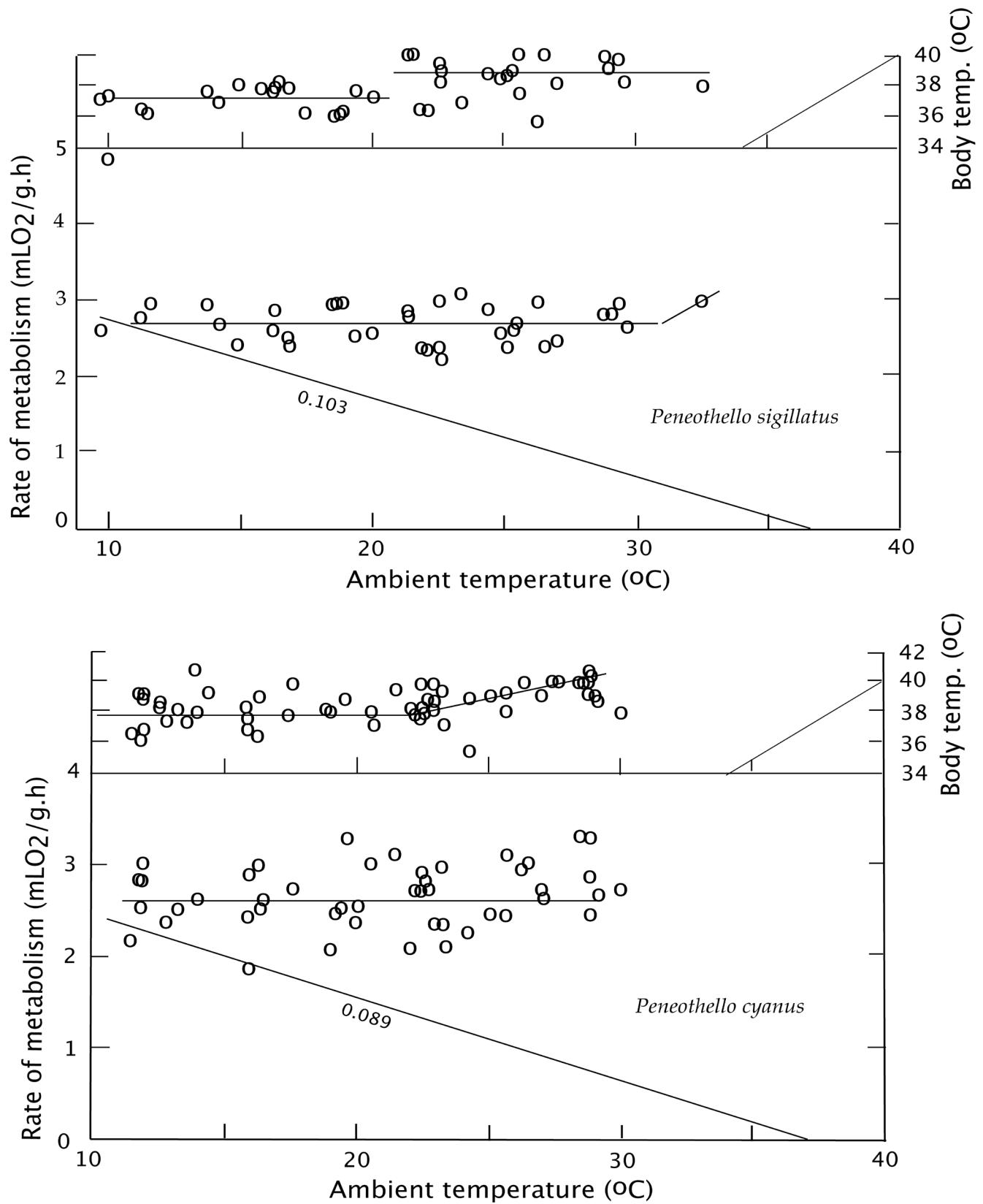


Figure 12. Body temperature and rate of metabolism as a function of ambient temperature in a) 11 White-winged Robins (*Peneothello sigillatus*) and b) 21 Blue-gray Robins (*Peneothello cyanus*).

Pachycephalidae

Regent Whistler (*Pachycephala schlegelii*)

This whistler was captured at both lodges. The six individuals weighed 22.0 ± 0.39 g (22). The zone of thermoneutrality occurred from 14 to 30°C (Fig. 13a). Three of the rates measured in the zone were low without any association with low body temperatures; they were not included in the estimate of basal rate under the assumption that they might be erroneous estimates. BMR equaled 2.37 ± 0.043 mL O_2 /g h (11), 94%. This species had a mean body temperature of $37.6 \pm 0.28^\circ\text{C}$ (13), although some measurements fell to 35°C (Fig. 13a). Minimal thermal conductance was ca. 0.102 ± 0.0079 mL O_2 /g h°C (3), 62%.

Hill Golden Whistler (*Pachycephala soror*)

Eight individuals from Ambua Lodge had a mean mass of 23.4 ± 0.23 g (39). The zone of thermoneutrality extended from ca. 13 to 32°C (Fig. 13b). BMR equaled 2.78 ± 0.067 mL O_2 /g h (24), 115%. Body temperature was $38.5 \pm 0.19^\circ\text{C}$ (28) at ambient temperatures < 26°C. A conductance equals 0.163 ± 0.0017 mL O_2 /g h°C (3), 95%, but it appears that the minimal thermal conductance possibly equaled 0.097 ± 0.0055 mL O_2 /g h°C (3), 57%.

Rufous-naped Whistler (*Pachycephala rufinucha*)

The whistler was captured at both lodges. The 11 individuals weighed 40.0 ± 0.04 g (30). Its zone of thermoneutrality extended at least from 12 to 30°C (Fig. 14a). Within that range BMR equaled 2.01 ± 0.041 mL O_2 /g h (30), 100%. Mean body temperature equaled $38.5 \pm 0.13^\circ\text{C}$ (21) at ambient temperatures between 12 and 30°C, but often fell to 34 to 35°C at ambient temperatures < 22°C (Fig. 14a). Minimal thermal conductance may be as low as 0.081 ± 0.0086 mL O_2 /g h°C (3), 61%.

Black Pitohui (*Pitohui nigrescens*)

One Black Pitohui was captured at Ambua Lodge. Its mean mass was 70.5 ± 0.96 g (8). The zone of thermoneutrality was found between 13 and 30°C (Fig. 14a) in which BMR equaled 2.12 ± 0.079 mL O_2 /g h (5), 129%. Mean body temperature equaled $38.3 \pm 0.39^\circ\text{C}$ (6). Minimal conductance may be as low as 0.082 mL O_2 /g h°C (1), 84%.

Meliphagidae

Rufous-backed Honeyeater (*Ptiloprora guisei*)

Ten individuals of this species were captured at Ambua Lodge. Body mass equaled 20.2 ± 0.61 g (36). Its zone of thermoneutrality extended from 15 to 30°C (Fig. 14b). The BMR was 2.52 ± 0.038 mL O_2 /g h (18), 100%. Body temperature averaged $36.4 \pm 0.18^\circ\text{C}$ (16) at ambient temperatures < 25°C. An estimate of minimal thermal conductance is 0.129 ± 0.0057 mL O_2 /g h°C (5), 62%.

Gray-streaked Honeyeater (*Ptiloprora perstriata*)

This high-altitude honeyeater was caught only at Kumul Lodge, where 12 individuals were measured. This species weighed 24.7 ± 0.47 g (46). The zone of thermoneutrality extends from 10 to 30°C (Fig. 15a). Its BMR equaled 2.49 ± 0.042 mL O_2 /g h (25), 105%. Body temperature was $36.5 \pm 0.17^\circ\text{C}$ (27), excluding values > 38°C, assuming that rates of metabolism > 2.80 mL O_2 /g h represented activity. Minimal thermal conductance equaled 0.100 ± 0.0055 mL O_2 /g h°C (2), 61%.

Sooty Honeyeater (*Melidectes fuscus*)

This high-altitude species, one of which was caught at Kumul Lodge, weighed 27.4 ± 0.17 g (10). The zone of thermoneutrality extended from 21 to at least 29°C (Fig. 15a). This species had a BMR equal to 2.02 ± 0.070 mL O_2 /g h (7), 88%. Body temperature, which was highly variable, decreased to 34°C at ambient temperatures < 25°C, whereas at warmer temperatures, body temperature increased to $38.1 \pm 0.54^\circ\text{C}$ (5) (Fig. 15b). Minimal thermal conductance may be 0.150 mL O_2 /g h°C (1), 95%.

Common Smoky Honeyeater (*Melipotes fumigatus*)

This species was found at Ambua Lodge, where 11 individuals were captured. Its mean mass was 57.4 ± 0.92 g (47). Body temperature equaled $38.6 \pm 0.19^\circ\text{C}$ (32). Thermoneutrality exists from ca. 11 to 30°C (Fig. 15b). The BMR was 2.18 ± 0.045 mL O_2 /g h (41), 124%. Minimal thermal conductance may equal 0.070 ± 0.0033 mL O_2 /g h°C (4), 64%.

Yellow-browed Honeyeater (*Melidectes rufocrissalis*)

Thirteen individuals of this honeyeater were caught at Ambua Lodge. Their mean mass was 63.9

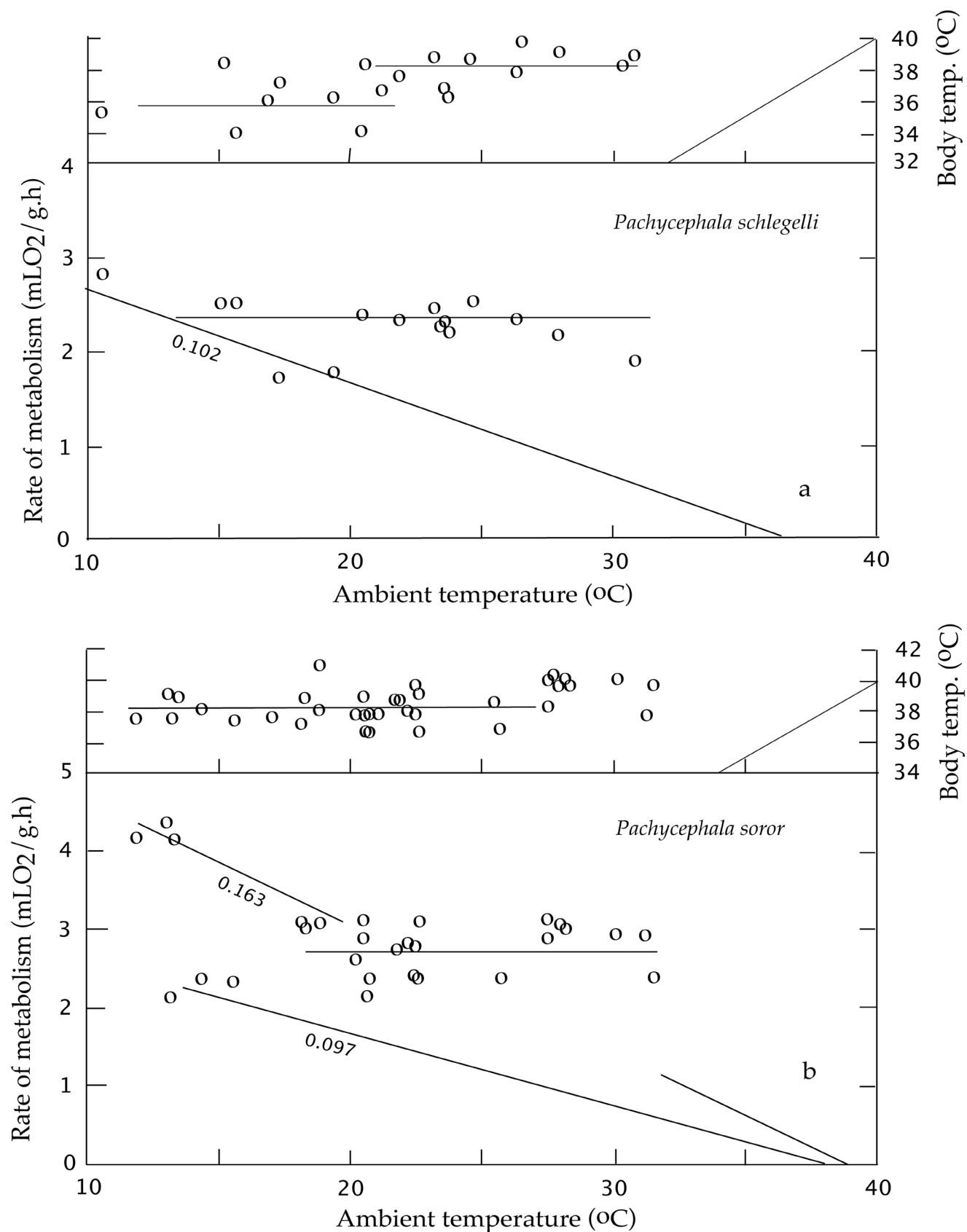


Figure 13. Body temperature and rate of metabolism as a function of ambient temperature in a) six Regent Whistlers (*Pachycephala schlegelii*) and b) eight Hill Golden Whistlers (*Pachycephala soror*).

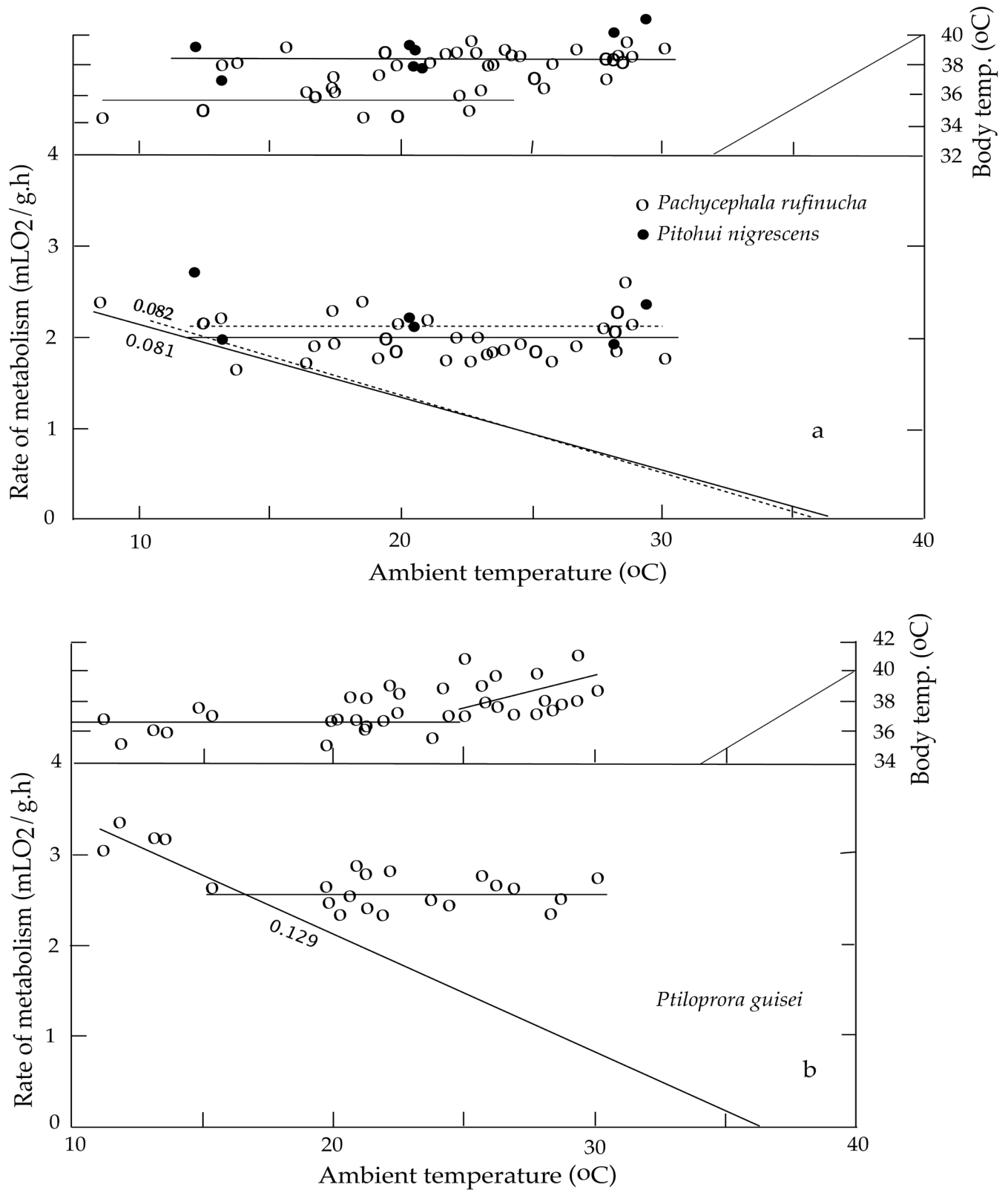


Figure 14. Body temperature and rate of metabolism as a function of ambient temperature in a) 11 Rufous-naped Whistlers (*Pachycephala rufinucha*) and one Black Pitohui (*Pitohui nigrescens*) and b) 10 Rufous-backed Honeyeaters (*Ptiloprora guisei*).

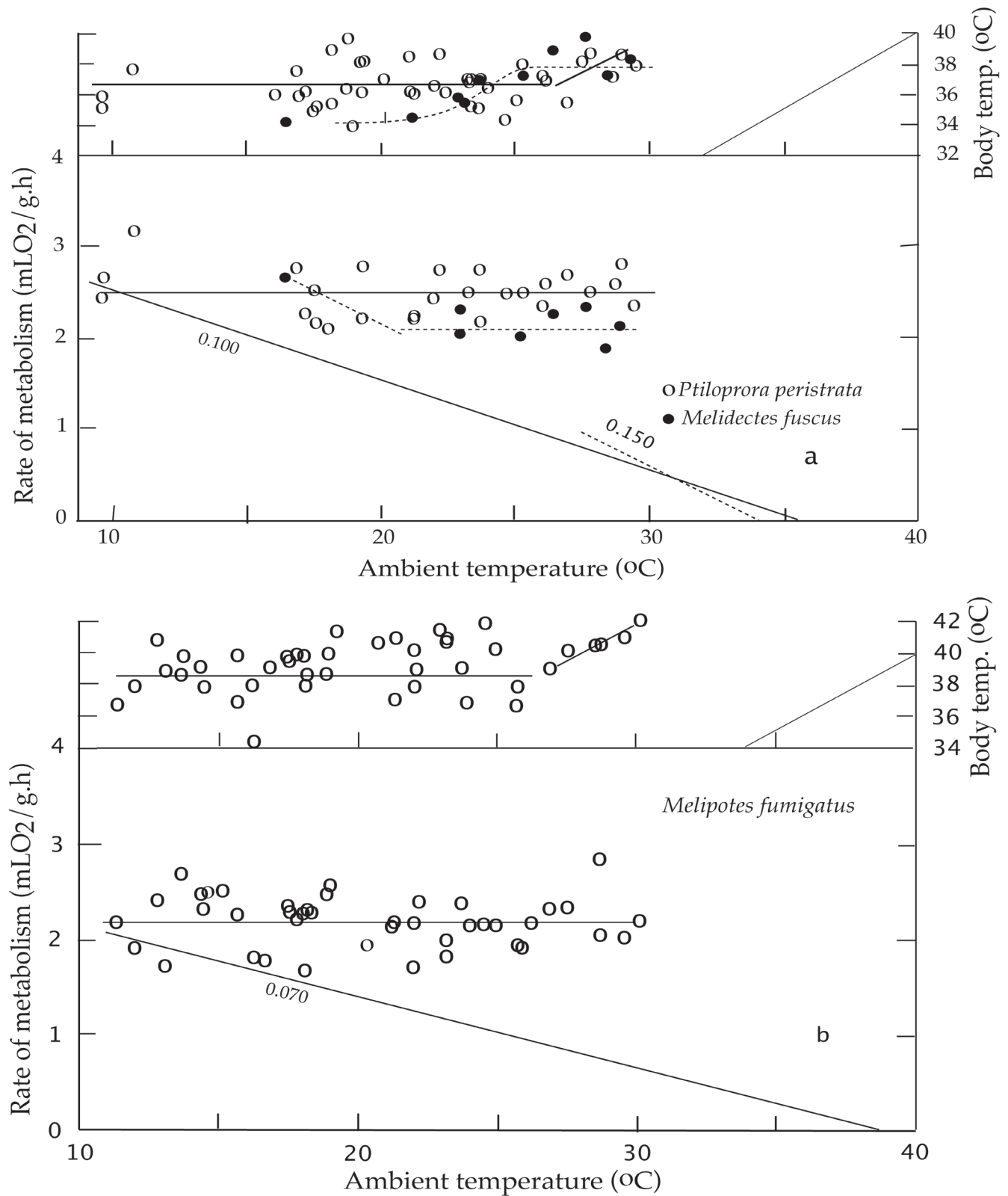


Figure 15. Body temperature and rate of metabolism as a function of ambient temperature in a) 12 Grey-streaked Honeyeaters (*Ptiloprora perstriata*) and one Sooty Honeyeater (*Melipotes fuscus*) and b) 11 Common Smoky Honeyeaters (*Melipotes fumigatus*).

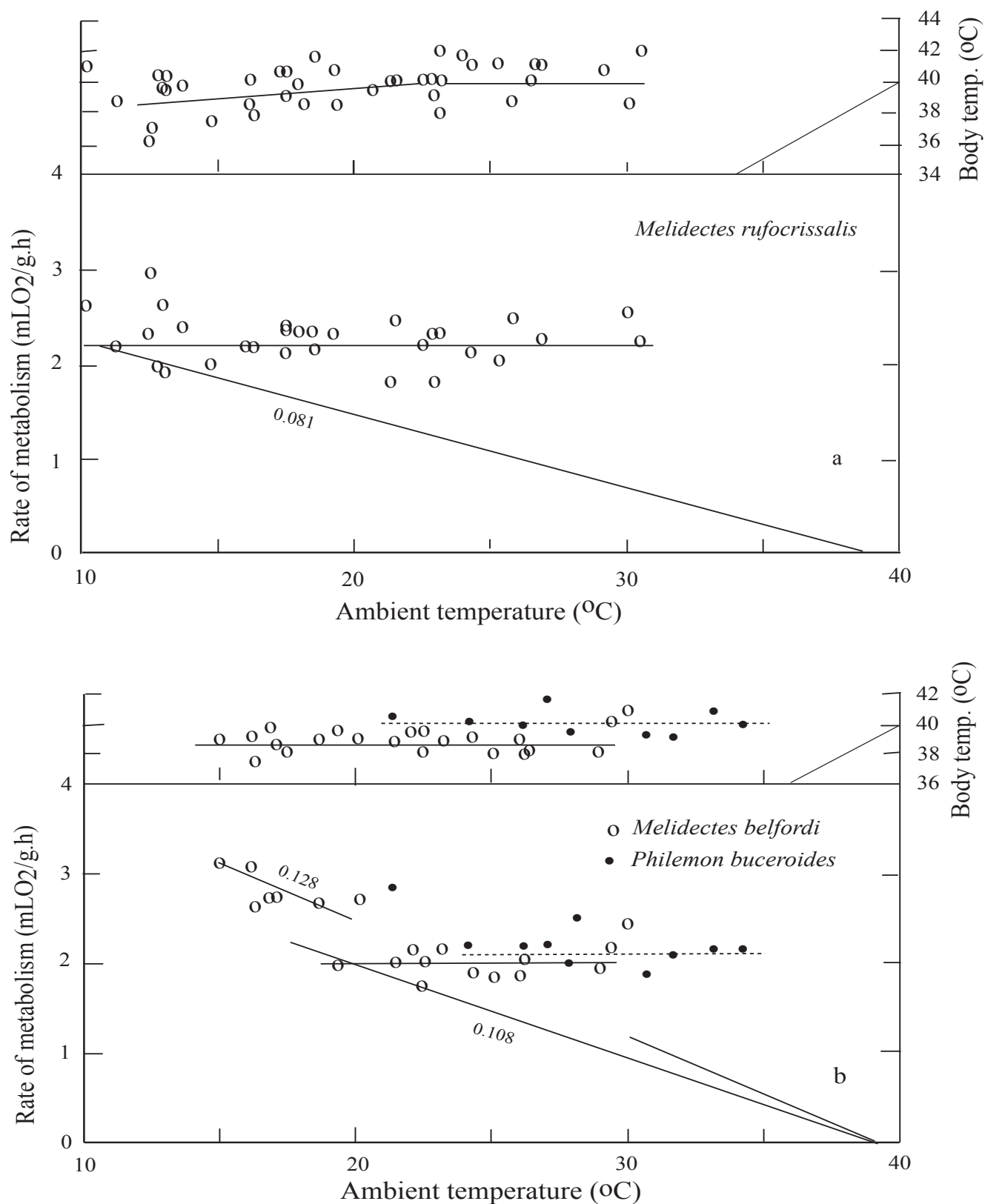


Figure 16. Body temperature and rate of metabolism as a function of ambient temperature in a) 13 Yellow-browed Honeyeaters (*Melidectes rufocrissalis*) and b) three Belford's Honeyeaters (*Melidectes belfordi*) and two Helmeted Friarbirds (*Philemon buceroides*).

± 1.59 g (43). Zone of thermoneutrality extended from 11 to 30°C (Fig. 16a), within which the BMR equaled 2.20 ± 0.035 mL O_2 /g h (26), 133%. Mean body temperature at ambient temperatures < 27°C was 40.0 ± 0.18 °C (27). An estimate of minimal thermal conductance is 0.081 ± 0.0050 mL O_2 /g h°C (5), 79%.

Belford's Honeyeater (*Melidectes belfordi*)

Captured only at Kumul Lodge, three individuals of this honeyeater weighed 66.6 ± 0.59 g (22). The zone of thermoneutrality ranged from 19 to 29°C (Fig. 16b). Its BMR equaled 2.00 ± 0.036 mL O_2 /g h (12), 119%. Body temperature equaled 38.8 ± 0.13 °C (19). A tentative estimate of minimal thermal conductance is 0.108 ± 0.0100 mL O_2 /g h°C (2), 109%, although a higher estimate equals 0.128 ± 0.0043 mL O_2 /h°C (7), 128%.

Helmeted Friarbird (*Philemon buceroides*)

Two friarbirds were captured near Madang. Mean mass was 140.5 ± 3.33 g (10). The zone of thermoneutrality extended at least from 24 to 35°C (Fig. 16b). The BMR equaled 2.09 ± 0.041 mL O_2 /g h (8), 161%, an exceedingly high rate. Body temperature in this species was 40.1 ± 0.24 °C (9). Given its large mass, no reasonable estimate of thermal conductance is available.

Melanochartidae

Slaty-chinned Longbill (*Toxorhamphus poliopterus*)

The six individuals, two males and four females, were captured at Ambua Lodge. They weighed 12.2 ± 0.55 g (18). The zone of thermoneutrality extended from 16 to 30°C (Fig. 17a) within which BMR was 2.51 ± 0.082 mL O_2 /g h (10), 86%. Mean body temperature equaled 36.9 ± 0.24 °C. (16). An estimate of thermal conductance equals 0.128 ± 0.00 mL O_2 /g h°C (2), 55%.

Fan-tailed Berrypecker (*Melanocharis versteri*)

This berrypecker was captured at both lodges. Ten individuals (3 males and 7 females) weighed 14.3 ± 0.44 g (33). The zone of thermoneutrality ranged from 10 to 28°C (Fig. 17b). Their BMR equaled 3.29 ± 0.090 mL O_2 /g h (23), 115%. Body temperature was 35.4 ± 0.17 °C (8) at ambient

temperatures between 10 and 21°C. At higher temperatures, body temperature was exceedingly variable (Fig. 17b), some of which reached 40°C, undoubtedly associated with activity, a pattern marginally seen in rate of metabolism. Minimal thermal conductance equaled 0.135 ± 0.0075 mL O_2 /g h°C (2), 60%.

Paramyithidae

Tit Berrypecker (*Oreocharis arfaki*)

One Tit Berrypicker was captured at Ambua Lodge. It weighed 22.3 ± 0.63 g (4). In a limited fraction (23 to 30°C) of the zone of thermoneutrality (Fig. 18a), the BMR was 2.58 ± 0.120 mL/g h (4), 105%. Body temperature was 40.1 ± 0.33 °C (4).

Crested Berrypecker (*Paramythia montium*)

Two individuals, captured at Kumul Lodge, weighed 40.3 ± 0.22 g (11). The zone of thermoneutrality extended at least from 15 to 30°C (18a). The BMR equaled 1.85 ± 0.067 mL O_2 /g h (10), 92%. Body temperature was 36.0 ± 0.21 °C (9). An estimate of minimal thermal conductance is 0.085 mL O_2 /g h°C (2), 66%.

Estrildidae

Blue-faced Parrot-finch (*Erythrura trichroa*)

Two individuals caught at Ambua Lodge weighed 15.1 ± 0.30 g (10). The zone of thermoneutrality extended at least from 20 to 29°C (Fig. 18b). The BMR equaled 3.96 ± 0.092 mL O_2 /g h (6), 140%. Body temperature was 37.5 ± 0.33 °C (10). Minimal thermal conductance was 0.232 ± 0.0102 mL O_2 /g h°C (4), 108%.

Mountain Firetail (*Oreostruthus fuliginosus*)

This species is represented by four individuals that were captured at Kumul Lodge. Their mean mass was 16.2 ± 0.12 g (14). Thermoneutrality was 20 to 32°C (Fig. 18b). The BMR was 2.04 ± 0.115 mL O_2 /g h (7), 74%. Body temperature was 35.8 ± 0.16 °C (10). Minimal thermal conductance equaled 0.135 ± 0.0048 mL O_2 /g h°C (7), 66%.

Artamidae

New Guinea Wood-swallow (*Artamus maximus*)

Nine wood-swallows, measured at Ambua Lodge, weighed 61.2 ± 0.87 g (42). Thermoneutrality

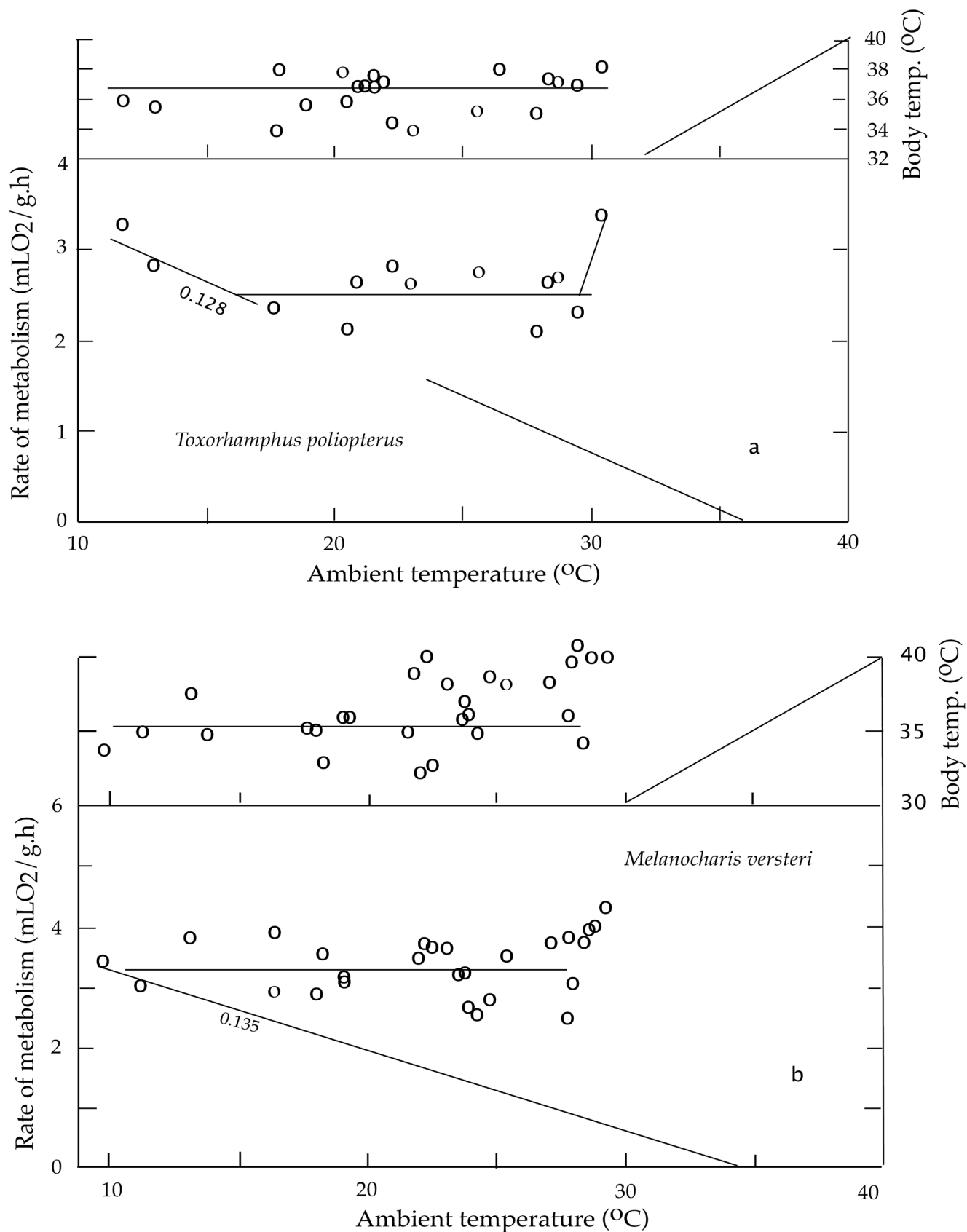


Figure 17. Body temperature and rate of metabolism as a function of ambient temperature in a) six Slatychinned Longbills (*Toxorhamphus poliopterus*) and b) 10 Fan-tailed Berrypeckers (*Melanocharis versteri*).

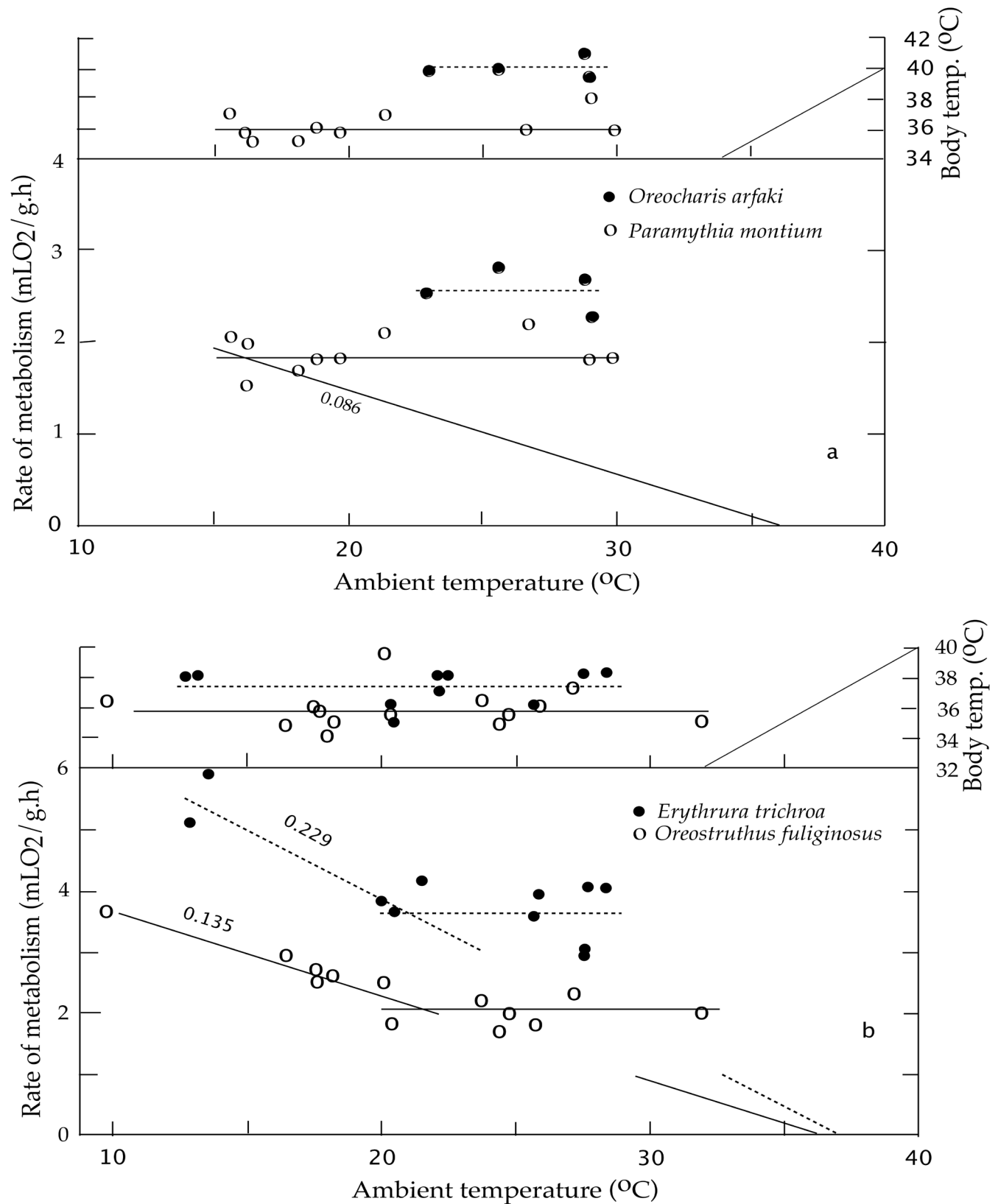


Figure 18. Body temperature and rate of metabolism as a function of ambient temperature in a) one Tit Berrypecker (*Oreocharis arfaki*) and two Crested Berrypeckers (*Paramythia montium*) and b) two Blue-faced Parrot-finches (*Erythrura trichroa*) and four Mountain Firetails (*Oreostruthus fuliginosus*).

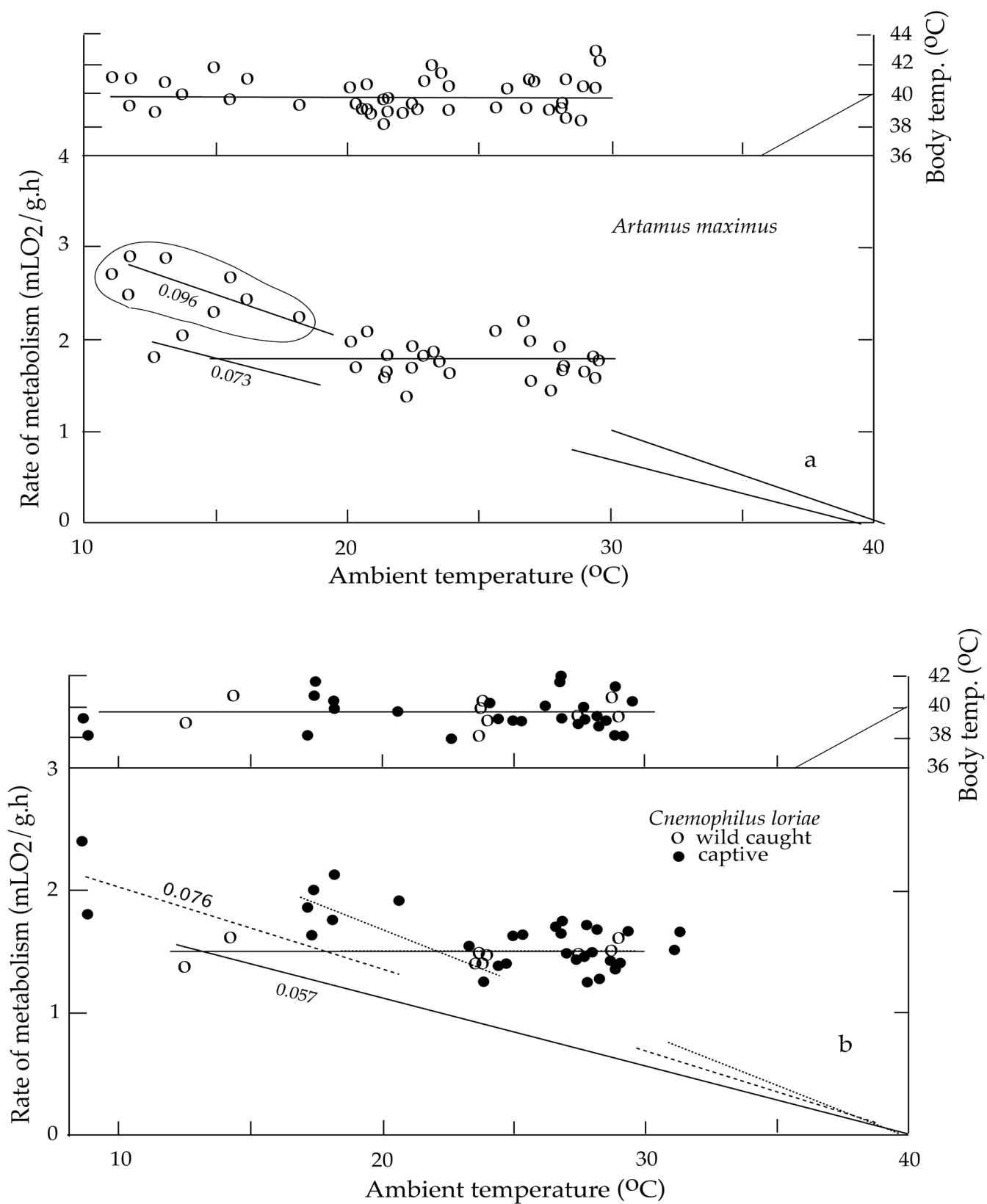


Figure 19. Body temperature and rate of metabolism as a function of ambient temperature in a) nine New Guinea Wood-swallows (*Artamus maximus*) and b) three, one wild caught and two captive, Loria's Satin-birds (*Cnemophilus loriae*).

extended from 15 to at least 30°C (Fig. 19a). The BMR equaled 1.80 ± 0.039 mL O_2 /g·h (27), 107%. Body temperature was $39.9 \pm 0.15^\circ\text{C}$ (39), excluding temperatures $\geq 41.5^\circ\text{C}$, due to apparent activity (Fig. 19a). A thermal conductance equaled 0.096 ± 0.0045 mL O_2 /g·h°C (8), 91%, but a better estimate of minimal conductance may be 0.073 ± 0.0040 mL O_2 /g·h°C (2), 70%.

Cnemophilidae

Loria's Satinbird (*Cnemophilus loriae*)

One female Loria's Satinbird was captured at Ambua Lodge. It weighed 75.2 ± 0.36 g (9). Its zone of thermoneutrality extended from 12 to 29°C (Fig. 19b), within which the BMR equaled 1.49 ± 0.029 mL O_2 /g·h (9), 92%. Body temperature equaled $39.7 \pm 0.30^\circ\text{C}$ (9). The minimal thermal conductance of the Ambua individual equaled 0.057 ± 0.0040 mL O_2 /g·h°C (2), 62%.

Two captive individuals of this species from The Rainforest Habitat had a mass equal to 78.1 g and a BMR of 1.52 ± 0.058 mL O_2 /g·h (24), 96% (McNab 2005a), essentially identical to that reported from Ambua Lodge (Fig. 19b). The agreement of the measurements on this species from two captive individuals and the one free-living individual gives some security with regard to using captive individuals. Captives, however, are often the only opportunity to obtain information of species that are rare, evasive, or endangered. The minimal conductance in the captive individuals was 0.076 mL O_2 /g·h°C (2), 82%.

The weighted collective body mass equals 77.3 g and basal rate equals 1.51 mL O_2 /g·h, which is 95% of the value expected from mass. The weighted collective thermal conductance equals 0.067 mL O_2 /g·h°C, 71%. The collective body temperature is 38.9°C .

Crested Satinbird (*Cnemophilus macgregorii*)

Three female Crested Satinbirds were captured one at Ambua and two at Kumul. Mean body mass was 87.1 ± 0.75 g (27). Thermoneutrality ranged from 15 to at least 30°C (Fig. 20a). The BMR was 1.53 ± 0.039 mL O_2 /g·h (24), 100%. Body temperature equaled $39.2 \pm 0.26^\circ\text{C}$ (27). Minimal conductance is 0.060 ± 0.0048 mL O_2 /g·h°C (4), 68%.

Ptilonorhynchidae

Archibold's Bowerbird (*Archiboldia papuensis*)

One female was captured at Kumul Lodge. It weighed 171.3 ± 3.95 g (11). Thermoneutrality ranged from ca. 17 to 34°C (Fig. 20b). The BMR equaled 1.37 ± 0.040 mL O_2 /g·h (8), 116%. Body temperature was $38.6 \pm 0.11^\circ\text{C}$ (10). Minimal conductance was approximately 0.066 ± 0.0015 mL O_2 /g·h°C (2), 106%.

ANALYSES

The goal of this analysis is to identify the factors that account for the variation in energy expenditure in the data assembled for the 79 species of birds from New Guinea. The extent to which the accounting can be maximized will indicate the degree to which we understand the factors that influence energy expenditure and the consequences of its variation. As the taxonomic and behavioral diversity in the assembly of species increases, a greater number of factors presumably may be required to account for their diversity in energy expenditure.

BASAL RATE OF METABOLISM

The factors potentially influencing BMR in New Guinea birds include body mass, generic affiliation, family affiliation, the passerine/non-passerine dichotomy, food habits, torpor, foraging substrate, habitat, altitudinal limits to distribution, activity, an island or continental distribution, and the presence or absence of a flightless condition. Each of these factors will be individually examined and then in combination.

Factor Analysis

Body Mass: Body mass is always the factor that has the greatest impact on basal rate, as long as an appreciable range in mass is present, which in this sample varies by a factor of 340:1 (Fig. 21). Body mass alone accounts for 86.6% of the variation in the basal rate of the 79 species ($P < 0.0001$):

$$\text{BMR (mL}O_2\text{/h)} = 8.81 \times m^{0.581 \pm 0.026} \quad (5)$$

The great impact of body mass on BMR requires it to be included in all subsequent analyses, but it does not account for 13.4% of the variation in BMR, which reflects a limited range in body mass and a large diversity of species.

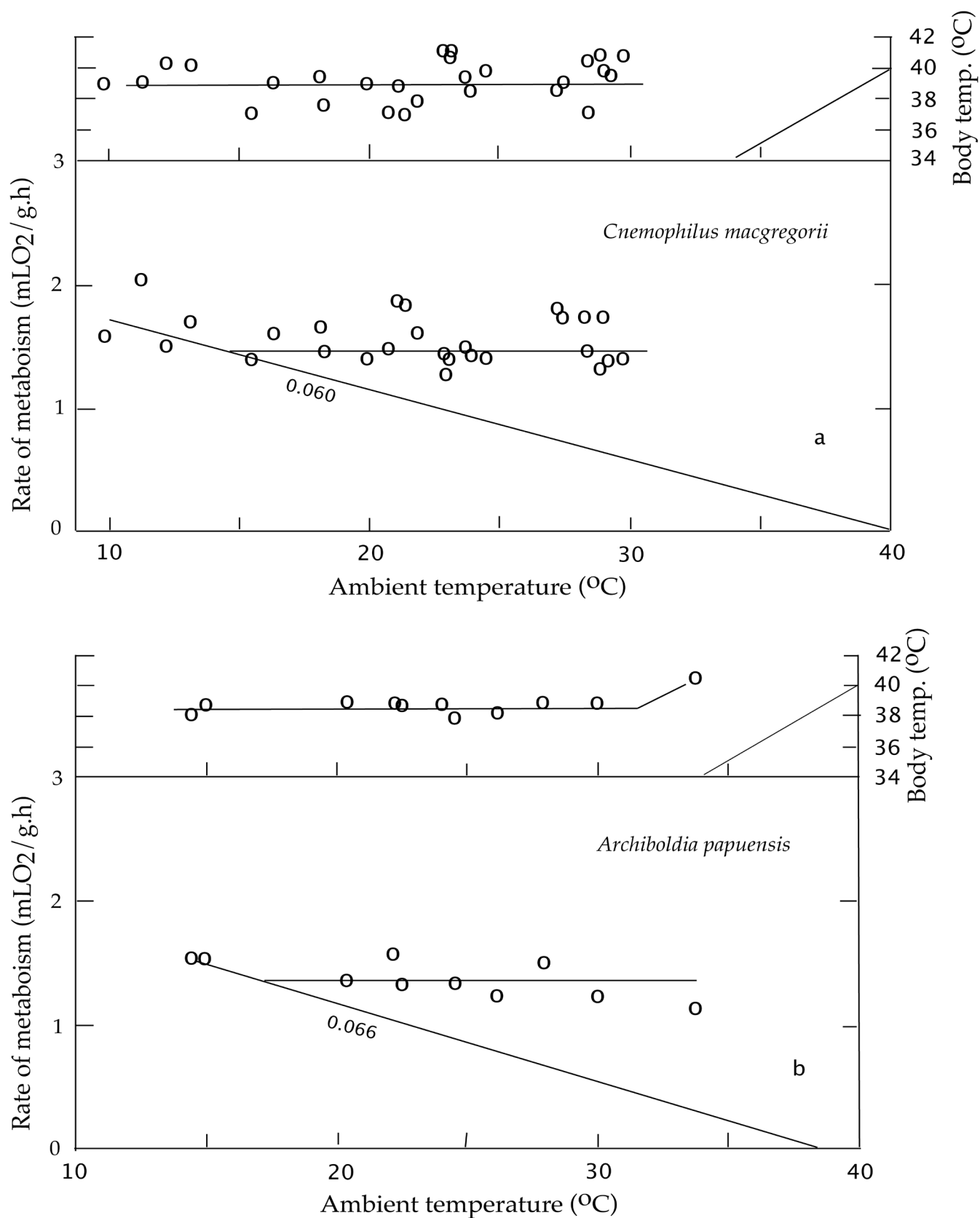


Figure 20. Body temperature and rate of metabolism as a function of ambient temperature in a) three Crested Satinbirds (*Cnemophilus macgregorii*) and b) one Archibold's Bowerbird (*Archiboldia papuensis*).

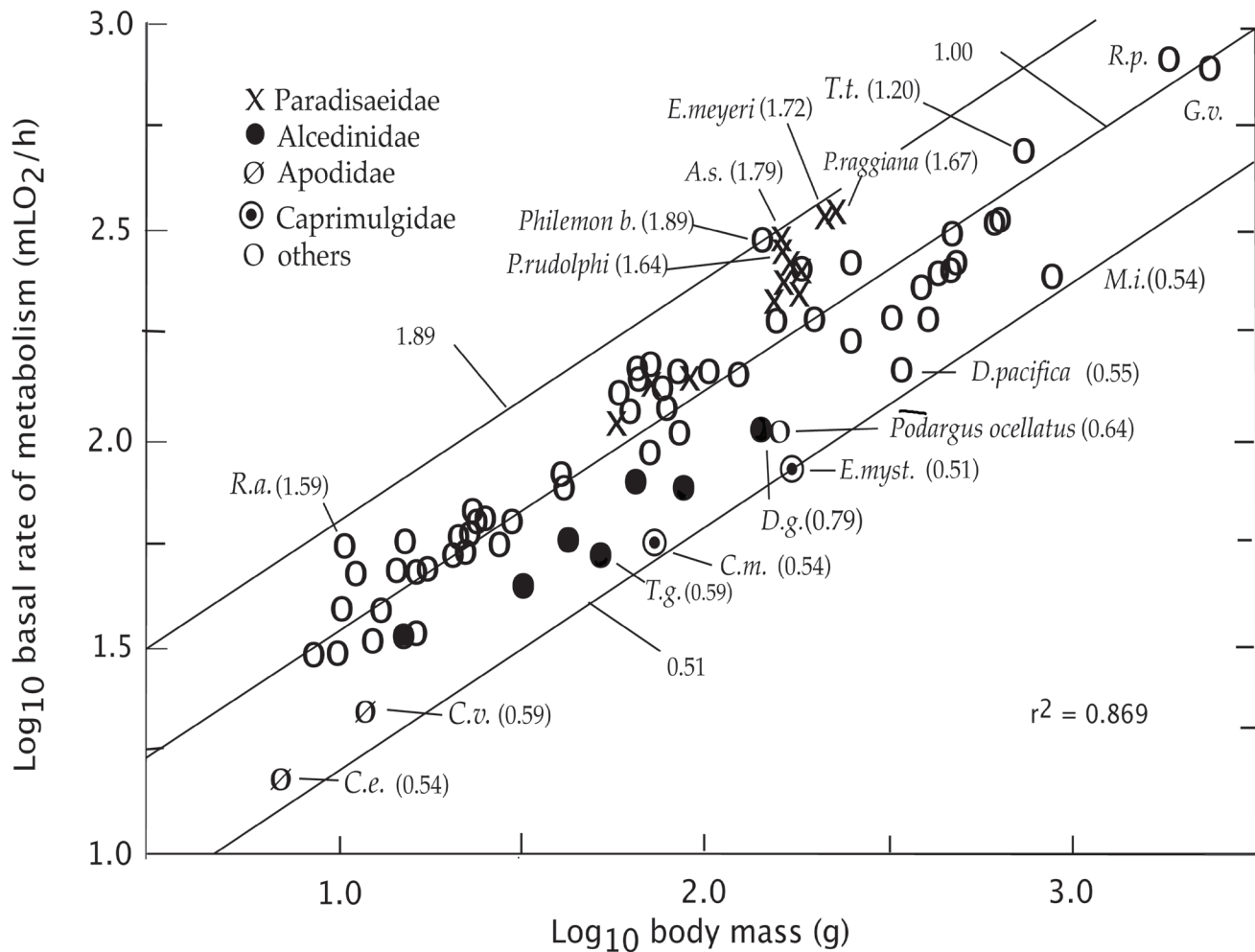


Figure 21. \log_{10} basal rate of metabolism as a function of \log_{10} body mass in 79 species of birds resident in New Guinea. The mean fitted curve is derived from equation (5). Indicated species are the New Guinea Flightless Rail (*M. i.*), two island fruit-pigeons (*D. pistrinaria* and *D. pacifica*), White-throated Nightjar (*E. m.*), Large-tailed Nightjar (*C. m.*), Uniform Swiftlet (*C. v.*), Glossy Swiftlet (*C. e.*), Common Paradise Kingfisher (*T. s.*), Hook-billed Kingfisher (*M. m.*), Rufous-bellied Kookaburra (*D. g.*), Helmet Friarbird (*P. b.*), Friendly Fantail (*R. a.*), and birds-of-paradise (x). These species are characterized by a fraction that represents the mean measured basal rate divided by the rate estimated from equation (5), which is the reference equal to 1.00. The maximal mass-independent rate equals 1.89, a value set by the Helmeted Friarbird, and the lowest rate equals 0.51, set by the White-throated Nightjar.

Notice that as various factors are included in the analysis, the power b varies because these factors are not independent of mass, as shall be seen in the general analysis. Furthermore, a reciprocal relationship exists between a and b in the same set of data; i.e., as the level (a) of the equation increases, its power (b) decreases to assure that the equation goes through the data. This pattern undercuts the view that the power b is a universal

constant (for an extended analysis of the variation in b see Glazier [2008]).

Some 15 species are the most distant from the fitted curve. The residual variation is patterned (Fig. 21). Some birds-of-paradise, the Friendly Fantail (*R. albolimbata*), and the Helmeted Friarbird (*P. buceroides*), many of which are frugivorous, have higher basal rates than expected from mass. In contrast, species with low basal rates include those

that feed on flying insects (*Collocalia esculenta* and *C. vanikorensis*, *Caprimulgus macrurus*, *E. mysticalis*), island-dwelling fruit-pigeons (*D. pacifica*, *D. spilorrhoea*, *D. pistrinaria*), and the flightless rail (*M. inepta*). Can the addition of these and other factors to the analysis substantially increase r^2 ?

Generic Affiliation: An approach to examine the impact of phylogeny on the energetics might be demonstrated by a correlation of BMR with generic affiliation. A problem with examining its potential influence is that the 79 species belong to 53 genera, which indicates that few genera have repetitive estimates of BMR. For example, 39 genera have only one species, 12 with two species, three with three species, and one (*Ducula*) with seven species. This distribution of species by genus has little chance to demonstrate any significant correlation of BMR with generic affiliation. This analysis would be similar to the analysis of species.

\log_{10} BMR is significantly correlated with generic affiliation ($P < 0.0001$), when it is paired with \log_{10} mass ($P < 0.0001$) ($r^2 = 0.997$). However, the 18 genera that have significantly higher basal rates are all passerines and the 15 that have significantly lower basal rates are all non-passerines, the remaining passerines and non-passerines being not significantly different from the mean. Therefore, this analysis essentially collapses into the passerine/non-passerine dichotomy.

Family Affiliation: The potential influence of phylogeny can be also examined with the addition of family affiliation. When family affiliation is paired with \log_{10} mass, \log_{10} BMR correlates both with mass ($P < 0.0001$) and family affiliation ($P < 0.0001$). This pairing accounts for 97.9% of the variation in basal rate, i.e., accounting for much more of the variation in basal rate than mass alone. Family affiliation is as effective as it is because it breaks the data into 26 groups, one for each family, the more the categories, the higher the r^2 . However, all 26 families do not have distinctive basal rates, so r^2 is exaggerated.

The families were variously grouped in the attempt to get the largest number of categories with statistically significant basal rates. They

ultimately coalesced into four groups. The group with the highest basal rates included fantails, the island thrush, birds-of-paradise, honeyeaters, the bowerbird, whistlers, and the wood-swallow. A large diverse group has intermediate basal rates. A group with low basal rates includes pigeons, kingfishers, swifts, and frogmouths. The group with the lowest basal rates consists of nightjars and the flightless rail. This pattern was summarized:

$$\text{BMR (mLO}_2\text{/h)} = 5.51 \times (E) \times m^{0.651 \pm 0.013} \quad (6),$$

where E , a non-dimensional coefficient, equals 2.70 for the species with the highest basal rates, 2.20 in the intermediate group, 1.48 in the low group, and 1.00 in the group with the lowest basal rates, the groups defined above; $r^2 = 0.972$. This analysis does not explain why a family has its particular mean basal rate or why these particular categories form: they surely are not based on phyletic relationships, and any suggestion that it is is inherently superficial.

Some patterns exist in the family groupings. The group with the highest basal rates is principally found at higher altitudes; the group with low basal rates lives at low altitudes, some of which feed on flying insects and enter torpor; and the group with the lowest basal rates feed on flying insects, enter torpor, or is flightless.

A concern with a familial level of basal rate is found in kingfishers. The seven New Guinea species had basal rates between 55 and 77% of the values expected from mass (Appendix 1). The consistently lower rates reported here for kingfishers are a concern with regard to measurement techniques. To test whether these rates are unacceptably low, measurements were made on two captive Laughing Kookaburras (*Dacelo novaeguineae* = *D. gigas*), the formal species name being erroneous in that this species is confined to Australia. These measurements were compared with measurements made on four wild-caught individuals by Buttemer et al. (2003). Their measurements were 63% of the value expected from mass, whereas measurements on the captives were 58% of the expected value. This small difference may reflect a difference between captive and wild birds, but it reassures that the measurements on New Guinea kingfishers are

reasonable. The BMR measured in the congeneric Rufous-bellied Kookaburra (*D. gaudichaud*) was 59% of the value expected from mass, which gives further confidence to the measurements made in New Guinea. The data summarized in Appendix 1 indicates that mass-independent basal rates of kingfishers tend to decrease with mass (Appendix 1).

One characteristic found in the smallest kingfishers was a highly variable body temperature. This variability appears to reflect a combination of low basal rates and small body masses, further justification for their low measured rates. Species that weigh > 60 g had less variable body temperatures.

Passerine/Non-passerine Dichotomy: A controversy has swirled around the existence or not of a difference in energy expenditure between passerines and non-passerines (McNab 2012). All analyses that used ANCOVA demonstrated that passerines collectively have higher basal rates than non-passerines (Lasiewski & Dawson 1967, Aschoff & Pohl 1970, Kendeigh et al. 1977, McNab 2009, 2012), whereas the use of phylogenetic methods has denied this difference (Reynolds & Lee 1996, Rezende et al. 2002). Using ANCOVA again, \log_{10} BMR of New Guinea birds clearly correlated with \log_{10} mass ($P < 0.0001$) and the passerine/non-passerine dichotomy ($P < 0.0001$); $r^2 = 0.947$:

$$\text{BMR (mLO}_2\text{/h)} = 5.33 \times (P) \times m^{0.686 \pm 0.011} \quad (7),$$

where the dimensionless coefficient P equals 0.57 for non-passerines and 1.00 for passerines. That is, passerines in this sample have a mean basal rate that is 75% greater than non-passerines of the same mass with little overlap (Fig. 22)!

The difference in basal rate between passerines and non-passerines is difficult to deny, although the use of phylogenetic analyses has tried. Phylogenetic analyses have had at least three difficulties. A minor one is that they have used the phylogeny of Sibley and Ahlquist (1990), which is no longer accepted. A major difficulty is the unwillingness to recognize that taxonomic affiliation also codes for many of the ecological and behavior characteristics of species.

The third difficulty is that body mass cannot account for all of the quantitative variation in basal rate and the invocation of 'phylogeny' describes

the evolutionary pathway of character inheritance, but it makes no contribution to resolving the *numerical* variation in basal rate not accounted for by mass. The attempt to account for all of the variation in basal rates is a physiological goal and not appropriate for a phylogenetic analysis.

The separation of the effects of phylogeny from those of behavior and ecology on BMR is complicated. The analysis must be done in a manner that avoids the influence of body mass because all three factors are tied together by mass. These analyses require that the rates of metabolism must be mass-independent, which are obtained by dividing the measured basal rates by the values expected for a species' mass from an appropriate mass standard, such as equations (3) or (5). This adjustment frees the rate from the direct influence of mass. Mass-independent rates cannot be obtained by dividing the rate by body mass because that overcorrects the influence of mass. Rate of metabolism is proportional to m^b , where $b < 1.0$. Dividing rate by mass is dividing by $m^{1.0}$ and therefore mass-specific rate is proportional to $m^{b-1.0}$, here $m^{-0.419}$.

The consequences of using mass-independent rates are seen in Figure 23. The frequency distribution of basal rates peaks in non-passerines at about 65% of the value expected from equation (3), with a range of 41–100%. The peak rate in passerines is about 105%, with a range of 78–163%. The difference in the peak frequencies of mass-independent basal rates between passerines and other birds is ca. $1.05/0.65 = 1.62:1$, a difference similar to that estimated by equation (7), 1.75:1.

Some avian orders, at least Anseriformes, Procellariiformes, and Charadriiformes, have mean basal rates that do not differ from that of Passeriformes (McNab 2009), so the difference in basal rates between passerines and the collective of non-passerines is not phylogenetic. Species belonging to these three orders are highly active, i.e., by migration or a pelagic existence. This pattern emphasizes that the fundamental difference between most passerines and non-passerines may be a difference between an active and an inactive lifestyle. Such a difference occurs even within the Anseriformes, i.e., between Northern Hemisphere and New Zealand ducks, a difference between an

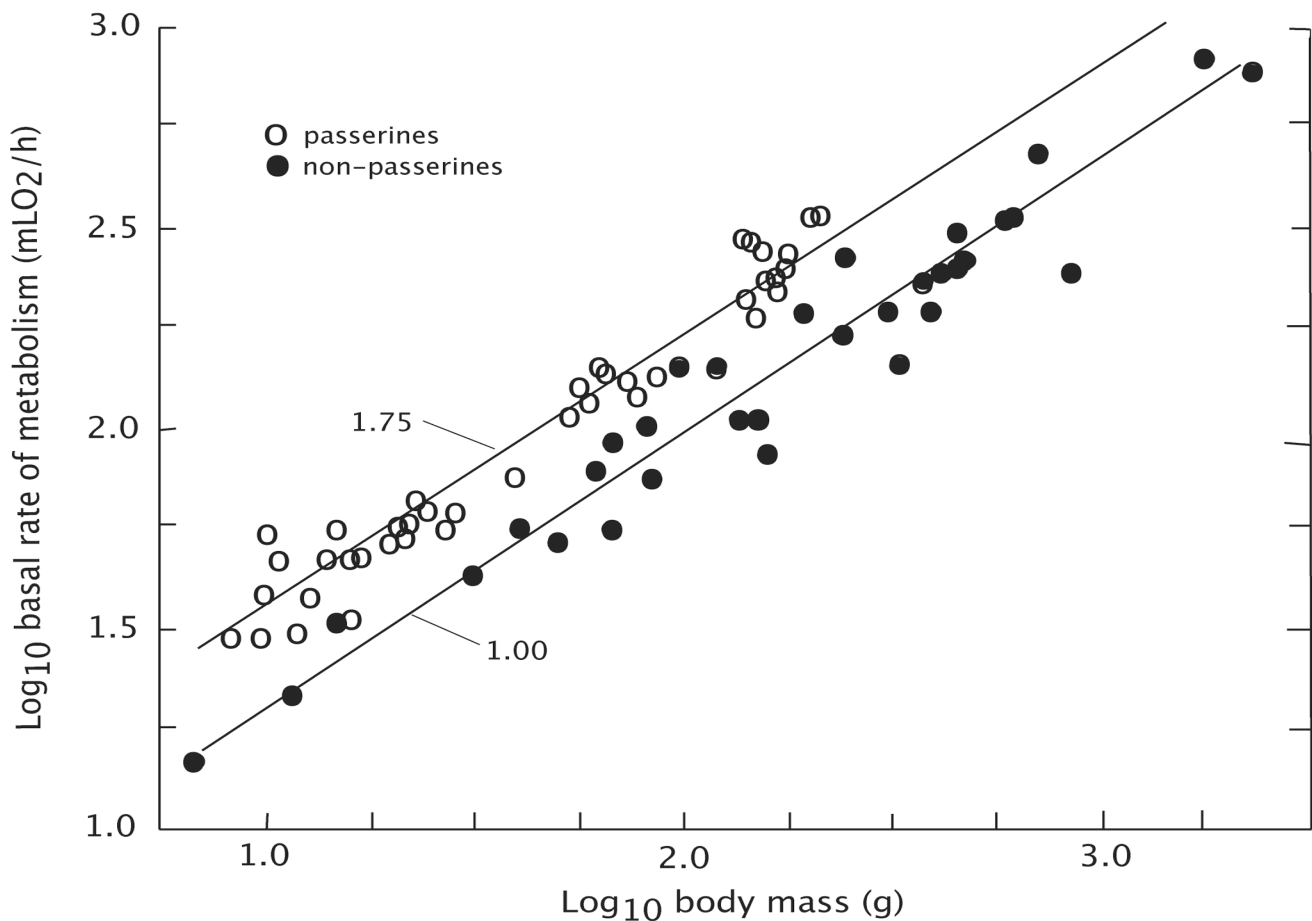


Figure 22. Log_{10} basal rate of metabolism as a function of log_{10} body mass in 79 species, as in Figure 21, with passerine and non-passerine affiliations indicated.

active and a sedentary lifestyle (McNab 2003a). Furthermore, the high level of passerine basal rates may reflect a sample biased for temperate, migratory passerines. Therefore, the dichotomy found in basal rate may reflect the differential occurrence of behavioral states in passerines and other birds, but with the data presently available, the dichotomy does exist (Fig. 22).

Science is distinctive among intellectual endeavors in that *data ultimately rule*. Theories are very valuable in that they often guide intellectual inquiries, but their conclusions must be compatible with quality data. The available data on energy expenditure are not sufficiently flawed to explain away the difference observed between the basal rates of passerines and non-passerines. To deny the observed difference bizarrely ignores the obvious

(Figs. 22–23).

Food Habits: Food habits in this study are grouped into 14 categories (Appendix 1). When they are paired with log_{10} mass, log_{10} basal rate correlates with log_{10} mass ($P < 0.0001$) and food habits ($P = 0.039$), but the BMRs associated with many food habits are not significantly different from the BMRs correlated with other food habits. Consequently, r^2 ($= 0.90$) is artificially high. To simplify the analysis, the categories were variously combined. When two categories, fruit/seeds vs all other foods, are combined with mass, log_{10} BMR correlated with log_{10} mass ($P < 0.0001$) and with food habits ($P = 0.028$); $r^2 = 0.874$. This correlation is not reassuring because r^2 increased only by 0.008 compared with that produced by mass alone.

Another categorical division was made:

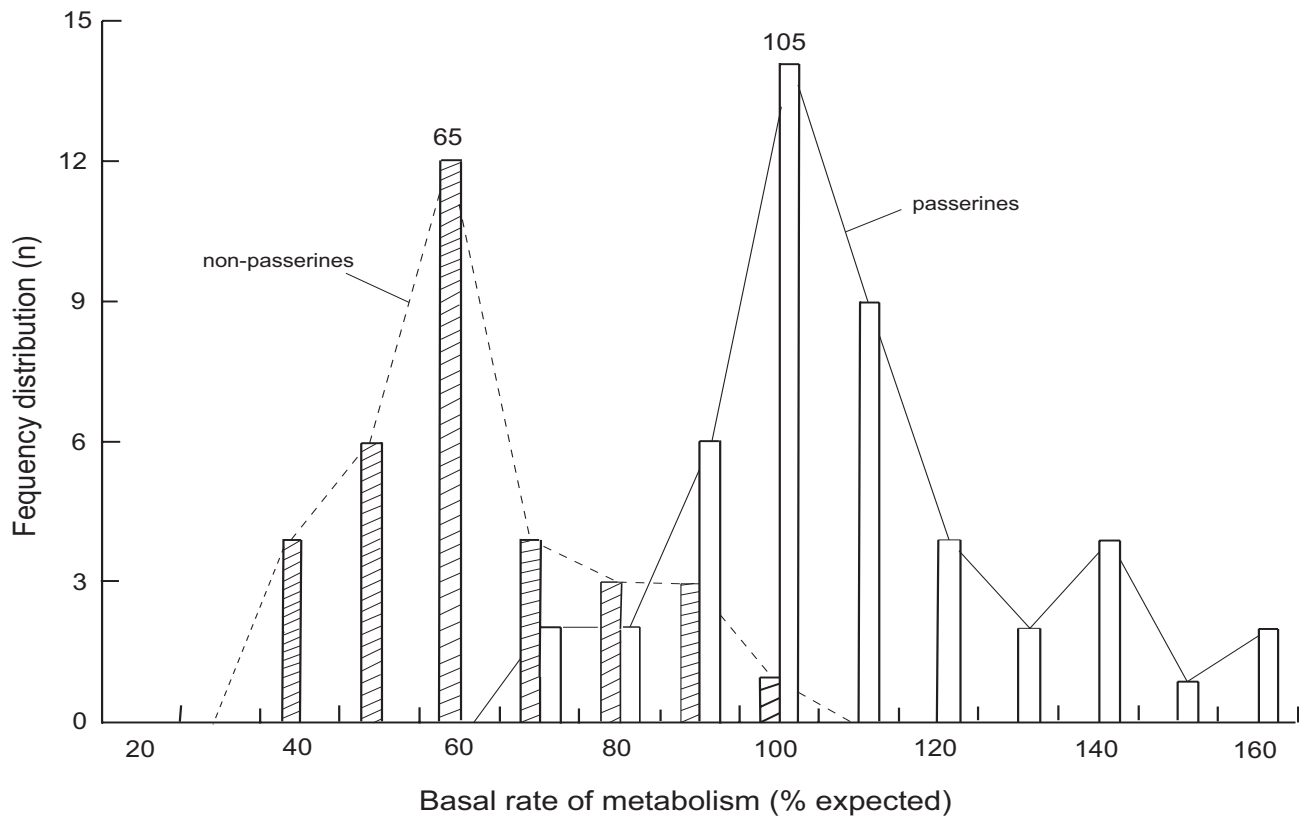


Figure 23. Frequency distribution of the basal rate of metabolism expressed as a percentage of the rate expected from body mass in equation (3) for passerines and non-passerines.

animal vs. plant diets. However, such a division is a problem because two common diets are fruit/insects and nectar/insects. When these two mixed diets were arbitrarily considered to be plant diets, \log_{10} BMR correlated with \log_{10} mass ($P < 0.0001$) and diet ($P = 0.0040$)! This combination accounts for 88.0% of the variation in \log_{10} basal rate, a modest increase of r^2 (1.4%). The results can be summarized:

$$\text{BMR (mLO}_2\text{/h)} = 9.68 \times (F) \times m^{0.557 \pm 0.026} \quad (8),$$

where F is a dimensionless coefficient for food habits equaling 0.81 for an animal diet and 1.00 for a plant diet: herbivores have basal rates that average 23% greater than those with an animal diet.

The potential difficulty with this analysis is the arbitrary allocation of species with a mixed diet to the herbivory category. To give some perspective to that decision, the mixed diets were now assigned to the animal diet category. As a result, \log_{10} basal

rate correlated with \log_{10} mass ($P < 0.0001$), but not with food habits ($P = 0.28$)! That is, eating plants is associated with a higher basal rate irrespective of whether they are mixed with insects or not, which contrasts with the pattern seen in birds-of-paradise (McNab 2003b, 2005a) and emphasizes the complexity of character state determination in a diverse avifauna.

The impact of food habits might be exaggerated by combining passerines and non-passerines because their variety is much greater in non-passerines. If only passerines are analyzed, no difference is found ($P = 0.73$) when the foods were combined with body mass and divided into fruit, insects, nectar, and seeds, although frugivorous species have slightly higher basal rates. Part of the inability to demonstrate a difference may be small numbers of species with some food habits, two seed-eaters and seven nectarivorous species. Nevertheless, the diversity of food habits in non-

passerines is responsible for the correlation of basal rate in the collective avifauna.

Torpor: One factor that influences the basal rate of metabolism is the use of torpor. Mammals and birds that enter torpor have lower mass-independent basal rates even when species are normothermic (McNab 2008, 2009). Torpor was demonstrated to occur in four species of the 79, two nightjars and two swifts (McNab & Bonaccorso 1995). Some question exists whether the variable body temperature in the Large Scrub-wren is torpor, or simply sloppy temperature regulation (Fig. 9), whatever that may mean. At no body temperature did the scrub-wren appear lethargic, principally because the rate of metabolism did not appreciably decrease with body temperature (Fig. 9b). Torpor is a regulated state, not representative of incompetent temperature regulation. Here, the use of torpor does not include the scrub-wren. Then, \log_{10} basal rate correlates with \log_{10} mass ($P < 0.0001$) and torpor ($P < 0.0001$), $r^2 = 0.898$.

$$BMR \text{ (mLO}_2\text{/h)} = 7.13 \times (T) \times m^{0.572 \pm 0.023} \text{ (9)},$$

where coefficient T equals 1.00 in species that enter torpor and 1.79 for those that do not.

Foraging Substrate: Feeding substrates are divided into four categories: areal, ground, trees, and widespread. Then when substrate is combined with \log_{10} mass, \log_{10} BMR correlates with substrate, $r^2 = 0.903$. Each substrate, however, is not correlated with different basal rates. Two substrate combinations are significant: areal/ground paired with trees/widespread, and aerial paired with the other three substrates, ($P < 0.0001$) and ($P = 0.0005$), respectively. The first led to coefficients equal to 1.00 for aerial/ground and 1.39 trees/widespread, whereas the second gave coefficients equal to 1.00 aerial and 1.51 for the combination of the other substrates. Because aerial substrate was common to both groups and because the second analysis gave a clearer difference between the two states, it is used in this analysis:

$$BMR \text{ (mLO}_2\text{/h)} = 7.90 \times (S) \times m^{0.557} \text{ (10)},$$

where $r^2 = 0.891$. This conclusion reflects the low BMRs found in species that feed on a temporally unreliable food supply (insects).

Habitat: A related factor that potentially influences BMRs are habitat types. In this study, the species fall into three general habitat categories: forest, open areas (including grasslands and savannas), and at the interface between these two environments. When these habitats are combined with \log_{10} body mass, habitat is not a significant correlate of BMR ($P = 0.41$): none of the three habitats are distinguishable, as is the case when forest-dwelling species are combined with those that live at the interface ($P = 0.21$). The habitat factor is similar to the foraging substrate factor with aerial foraging, which gives substrate statistical significance. As a result of the absence of any correlation of BMR with habitat residence, it is not included in any of the later analyses.

Altitude: Maximal altitudinal limits to distribution were broken into four ranges: 0–1000 m, 1000–2000 m, 2000–3000 m, and > 3000 m, i.e., categories 1, 2, 3, and 4, respectively. The allocation of a species to a particular category is a bit arbitrary because some species, for example, might be found from sea level to 2100 m. Such an altitudinal distribution was called category 2, because its distribution is only marginally in category 3. Furthermore, some species may have different altitudinal limits based on the presence or absence of other species. The maximal limit to an altitudinal distribution may not be due to altitude *per se*, but reflecting climate, food availability, or some other correlate of altitude.

\log_{10} BMR correlates with \log_{10} body mass ($P < 0.0001$) and altitude ($P = 0.0073$); $r^2 = 0.886$. But again, all of the categories are not associated with distinctive basal rates. Two groupings of the categories give a better picture of the correlation of \log_{10} BMR with altitude. When category 1 is paired with the sum of the other three categories, \log_{10} BMR correlates with \log_{10} mass ($P < 0.0001$) and altitude ($P = 0.0020$); $r^2 = 0.882$. However, if the lowest two altitudinal categories are combined and posed against the upper two, then \log_{10} BMR also correlates with \log_{10} mass ($P < 0.0001$) and altitude ($P = 0.0047$); $r^2 = 0.879$. Obviously, little difference is present between these two analyses. The common element associated with low basal

rates is an altitudinal limit < 1000 m, which may, or may not, apply to altitudes as high as 2000 m. The first analysis is used because of a greater difference in basal rate and slightly higher probability:

$$\text{BMR (mLO}_2\text{/h)} = 7.39 \times (A) \times m^{0.607 \pm 0.026} \quad (11)$$

where dimensionless coefficient A for < 1000 m equals 0.77 and 1.00 for higher altitudes. Higher altitude species average basal rates are 1.30 (i.e., $1/0.77$) times those species found at altitudes < 1000 m.

The correlation of basal rate with altitude is seen when the entire fauna is examined, but no correlation of the mass-independent basal rates in passerines occurs with altitude ($P=0.89$) (Fig. 24). Because most of the non-passerines studied are limited to altitudes < 2000 m, their low basal rates appears to account for the correlation of basal rate with altitude that occurs in the entire sample. Yet, an appreciable variation in basal rate occurs in birds at all altitudes.

The variation in basal rate with respect to altitude has some patterns. Species that feed on insects with extended flight (e.g., *Collocalia*, *Podargus*, and Caprimulgidae) have low mass-independent basal rates at all altitudes (Fig. 24). Birds-of-paradise, all of which feed on fruit and/or insects, have high basal rates at all altitudes. Owls collectively have similar, slightly low, basal rates, which may indicate the pattern to be seen in other predatory species, reflecting an abundance of vertebrate food that is independent of altitude. The basal rate of nectarivorous *Melidectes* decreases with altitude, possibly reflecting a reduced availability of nectar at high altitudes (McNab, in prep.). The differential correlations of basal rate with altitude undoubtedly reflect to some extent the distribution of resources in relation to altitude.

These observations raise the question of the subtly of the impact of altitude. Another approach would be to examine the variation of basal rate with respect to altitude within genera. In this study 15 genera are represented by two or more species (*Ducula*, *Ptilinopus*, *Collocalia*, *Tanysiptera*, *Sericornis*, *Rhipidura*, *Peneothello*, *Pachycephala*, *Melidectes*, *Ptiloprora*, *Cnemophilus*, *Cicinnurus*, *Parotia*, *Manucodia*, and *Paradisaea*). Eight of

these genera have species with either no appreciable difference in mass-independent basal rate ($\leq 4\%$) or no difference in altitudinal distribution (Table 1).

Three genera show a reduction in basal rate with altitude, namely *Sericornis*, *Pachycephala*, and *Melidectes*. The first two genera are insectivorous and, as noted, *Melidectes*, is nectarivorous. Why the two insectivorous genera have basal rates that decrease with altitude is unclear, especially since this correlation is not present in insectivorous birds-of-paradise, e.g., *Epimachus*. Four genera have a positive correlation of mass-independent basal rate with altitude, including *Rhipidura* and *Ptiloprora*, both of which had highland species with mass-independent basal rates at least 8% greater than lowland species (Fig. 24). These two genera are principally insectivorous. *Ducula zoeae* has a higher altitudinal distribution and a mass-independent basal rate that is 12% greater than lowland *Ducula rufigaster* on New Guinea, and 15–24% greater than lowland *Ducula* on intermediate islands, all species being frugivorous. Intermediate-altitude *Tanysiptera sylvia* has a 17% higher basal rate than lowland *T. galatea*. The clearest examples of an apparent increase in basal rate in response to altitude are found in non-passerine genera.

Most intra-generic correlations exist between mass-independent basal rate and a limit to an altitudinal distribution. One of the difficulties with this analysis is that 11 of 15 congeneric comparisons are between species that both have maximal distributions > 1000 m. Because the significant difference in mass-independent basal rate in the entire sample appears to occur at ca. 1000 m, a better comparison would be between congeneric species whose limits are above and below 1000 m, which may explain why an appreciable positive correlation occurred in *Ducula* and *Tanysiptera*. Unfortunately, no data are available from lowland and highland populations of passerines with a wide altitudinal distribution. The basal rates in species captured at Ambua (2100m) and Kumul (2860m) lodges were the same, as might be expected.

Activity: A correlation between basal rate and the level of activity in these birds might exist, a suggestion that may account for some of the

difference in basal rate found between passerines and non-passerines. However, the analysis of activity is greatly complicated by defining levels of activity, and here the attempt is to define the level of activity associated with a species' lifestyle. Activity levels used here were derived from the 16-volume Handbook of Birds of the World (del Hoyo et al. 1992–2011). Four states were used, migratory, nomadic, resident, and sedentary. One difficulty is that the passerines that were designated as sedentary are probably not sedentary in the

same sense as are some non-passerines, such as the flightless rail. These passerines are here are considered to be resident. When this modification is made, \log_{10} basal rate correlates with \log_{10} mass ($P < 0.0001$) and activity ($P < 0.0001$), but each activity level is not distinct. They can be grouped in several ways. If migratory species are compared to the collective of other species, \log_{10} basal rate correlates with \log_{10} mass ($P < 0.0001$) and activity ($P = 0.023$); $r^2 = 0.875$. Then, migratory species have basal rates that average only 70% of

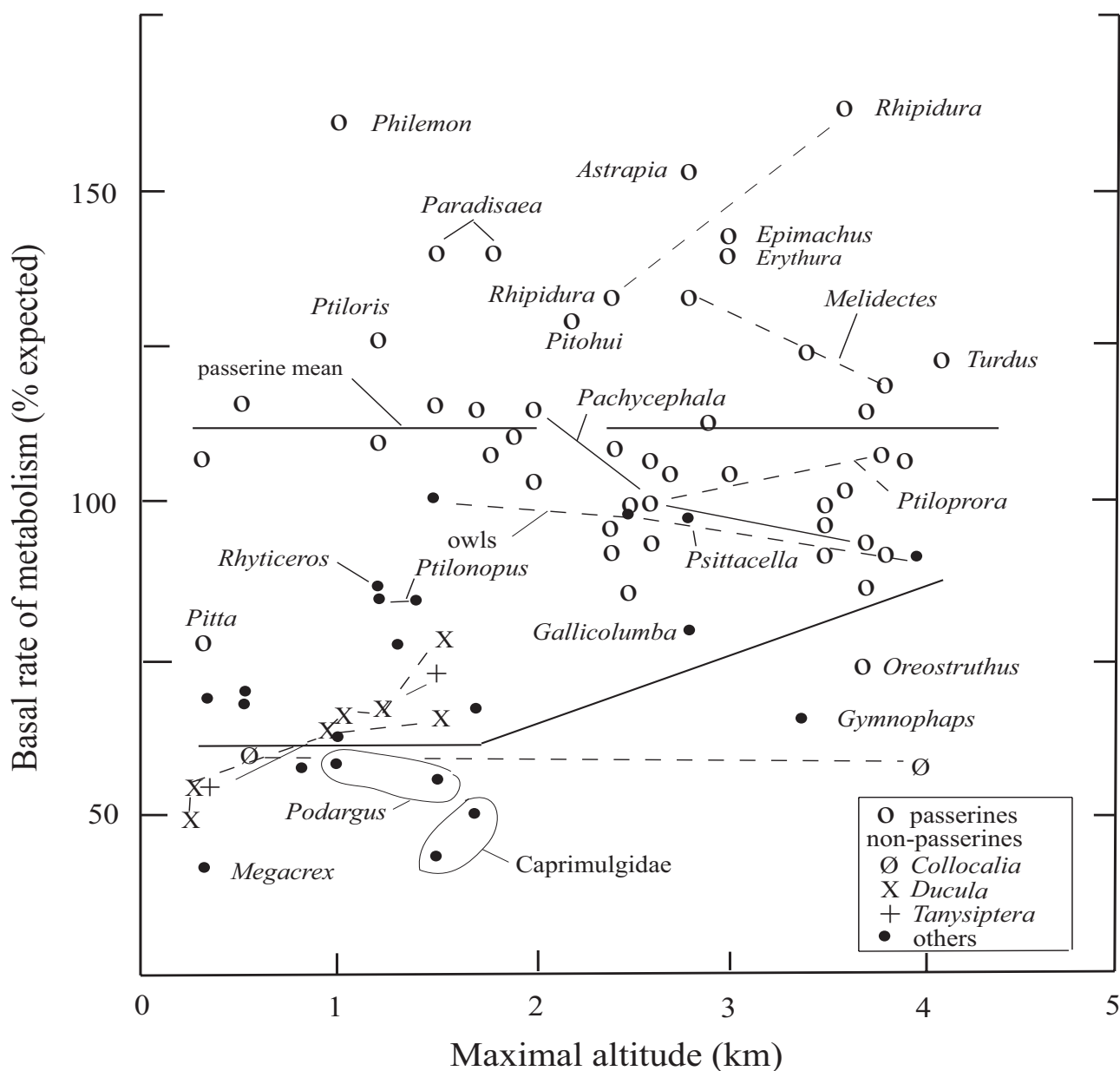


Figure 24. Mass-independent basal rate of metabolism in passerines and non-passerines as a function of latitude.

other species. If the active states are grouped in another way, resident species vs species with other habits, \log_{10} basal rate correlates with \log_{10} mass ($P < 0.0001$) and activity ($P = 0.0011$); $r^2 = 0.926$:

$$\text{BMR (mLO}_2\text{/h)} = 6.38 \times (M) \times m^{0.634 \pm 0.021} \quad (12),$$

where M equals 1.00 in resident species and 0.62 in other species. The greater r^2 suggests that the second division of species by activity is most effective.

Because the original designation classified many high-altitude passerines as sedentary, it is appropriate to combine these species with the 10 sedentary non-passerines and contrast them with species that have migratory or nomadic habits. Activity was again significant ($P = 0.0011$), but r^2 equaled 0.883, well below that represented by equation (12), and therefore not used.

Islands: Birds in the South Pacific are found on landmasses of various sizes, some on very large islands, such as New Guinea, some on islands of an intermediate size, namely the Solomons and the Bismarcks, and others endemic to very small islands, such as the Hermits, Misima, and Crown Island. Furthermore, New Guinea was part of the Australian/New Guinea (Sahul) continent in the Pleistocene, which indicates a biological history very different from that of small, isolated, oceanic islands, many of which are volcanic cones.

The consequences for energetics of some birds on islands are illustrated by the frugivorous imperial-pigeons (*Ducula*) (Fig. 25). These species are classified by the largest landmass on which they are resident. Therefore species that reside on New Guinea are considered to be continental/large-island species, even though they may spill over to nearby small islands (e.g., *D. pinon*). Intermediate-island species in this area are found principally on New Britain, New Ireland, and the Solomons. Unfortunately, *D. pistrinaria* was previously misclassified as a small-island species (McNab 2000, 2012b), in spite of being found on the islands of the Bismarck Archipelago and the Solomons. It should have been classified as an intermediate-island species. *Ducula spilorrhoa*, a species that is often placed into *D. bicolor*, has a more complicated distribution. It is marginally found on New Guinea along two major rivers, the Fly and Sepik, but

it is mainly found on intermediate islands in the Bismarcks and Solomons, as well as on many small islands. As a result, *D. spilorrhoa* has been kept with some ambiguity as an intermediate-island species in Figure 25a.

\log_{10} mass-independent BMR in these fruit pigeons correlates with \log_{10} mass ($P < 0.0001$) and an island existence, represented by two groups, New Guinea vs the combination of intermediate- and small-island species ($P = 0.016$); $r^2 = 0.876$ (McNab 2000). New Guinea species have mean basal rates that are 1.44 times those of island species. However, when small- and intermediate-island species are separated, no difference is found in the BMRs of large- and intermediate-island species ($P = 0.094$) or between intermediate- and small-island species ($P = 0.13$) (Fig. 25a). If large- and intermediate-island species are combined and contrasted with small-island species, then \log_{10} BMR correlated with both \log_{10} mass ($P < 0.0001$) and the island category ($P = 0.021$); $r^2 = 0.875$. This combination avoids the concern with the classification of *D. spilorrhoa* by island size. The coefficient I equals 1.69 for the combination of the large- and intermediate-island species and 1.00 for the small-island endemic *D. pacifica*. The latter configuration is preferred because it shows a greater difference in the coefficients:

$$\text{BMR (mLO}_2\text{/h)} = 6.55 \times (I) \times m^{0.592 \pm 0.026} \quad (13).$$

The impact of island size is most clearly seen in the decrease of the mass-independent BMRs in *Ducula pacifica* (McNab 2000; Fig. 25a). This species is endemic to the smallest islands and has a mass-independent BMR that is only 59% of those *Ducula* that live on intermediate and large islands. A similarly low mass-independent basal rate would be expected in another small-island endemic, *D. oceanica*, which unfortunately has not been measured. *Ducula pacifica* and *D. oceanica* have been referred to as supertramps (Diamond 1974, Steadman 2006). Furthermore, the mass-independent basal rates of *Ducula* decrease with their relative pectoral muscle masses (Fig. 25b) (N.A. Wright [pers. comm.]). This suggests a sedentary existence in species endemic to the smallest islands. Intermediate-island species are

Table 1. Altitudinal limits and BMR in congeneric species.

Species	Basal Rates ¹	Altitudinal Limit ²	Conclusion ³
<i>Ptilinopus superbus</i>	84	2	
<i>perlatus</i>	84	1	O
<i>Ducula pacifica</i>	49	1	
<i>rufigaster</i>	66	1	
<i>pistrinaria</i>	54	1	
<i>rubricera</i>	66	1	
<i>spilorrhoea</i>	63	1	
<i>pinon</i>	69	1	
<i>zoeae</i>	78	2	+
<i>Collocalia esculenta</i>	58	4	
<i>vanikorensis</i>	60	1	O
<i>Tanysiptera galatea</i>	55	1	
<i>sylvia</i>	72	2	+
<i>Sericornis perspicillatus</i>	100	3	
<i>papuensis</i>	92	4	
<i>nouhuysi</i>	105	3	-
<i>Rhipidura albolimbata</i>	163	4	
<i>atria</i>	133	3	+
<i>Peneothello sigillatus</i>	107	4	
<i>cyanus</i>	109	3	O
<i>Pachycephala schlegelii</i>	94	4	
<i>soror</i>	115	2	
<i>rufinucha</i>	100	3	-
<i>Ptilopropa guisei</i>	100	3	
<i>perstriata</i>	108	4	+
<i>Melidectes fuscus</i>	87	4	
<i>rufocrissalis</i>	133	3	
<i>belfordi</i>	119	4	-
<i>Cnemophilus loriae</i>	96	3	
<i>macgregorii</i>	100	4	O
<i>Cincinnurus regius</i>	107	1	
<i>magnificus</i>	110	1	O
<i>Parotia lawesii</i>	111	2	
<i>wahnesi</i>	115	2	O
<i>Manucodia keraudrenii</i>	104	2	
<i>chalybata</i>	116	2	O
<i>Paradisaea rudolphi</i>	140	2	
<i>raggiana</i>	140	2	O

¹ rates % mass-independent from the all-bird curve (McNab 2009).² upper altitudinal limits: 1, 1000 m; 2, 2000 m; 3, 3000 m; 4, 3000 m +³ conclusions: O, no correlation of BMR with altitudinal limit, -, negative correlation of BMR with altitudinal limit; +, positive BMR with altitudinal limits

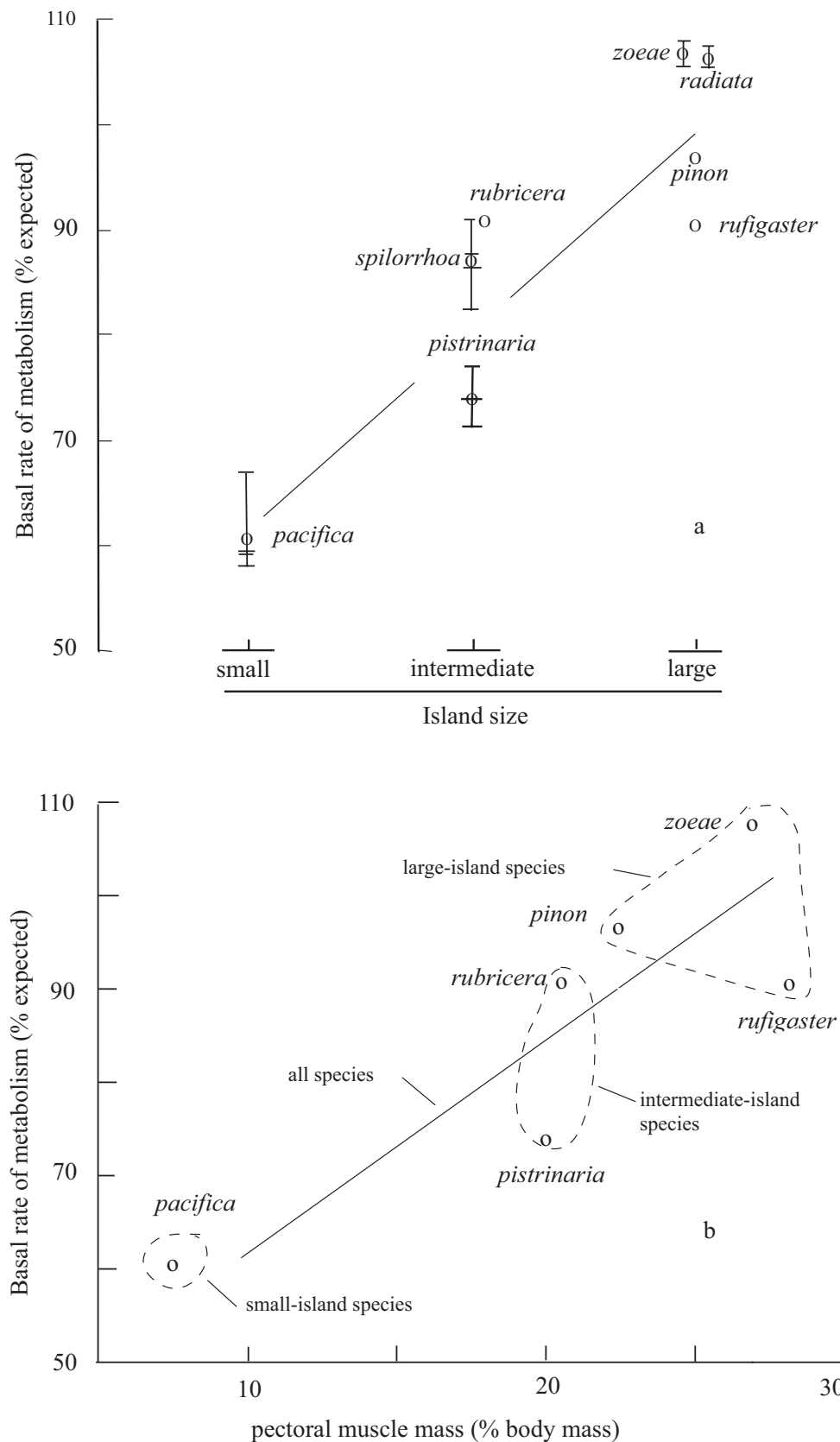


Figure 25. a) Basal rate of metabolism in imperial fruit-pigeons of the genus *Ducula*, expressed as a percentage of the value expected from mass on islands of various sizes and b) relative basal rate of metabolism as a function of the pectoral muscle masses expressed as a percentage of total body mass.

intermediate in basal rate and pectoral muscle mass (Fig. 25b).

The widespread distribution of small-island endemics implies that they must occasionally move from one island to another, in spite of a reduction in activity, pectoral muscle mass, and BMR, possibly aided by cyclonic events. These species must have accidentally landed on larger islands, but presumably could not establish viable populations in the presence of species endemic to those islands (Mayr & Diamond 2001). An apparent contradiction therefore appears to exist between the distribution of these species and their small muscle masses, a pattern that needs detailed study of populations island by island.

Flightless: A flightless condition in birds has been shown to correlate with a low mass-independent basal rate of metabolism (McNab 1994; McNab & Ellis 2006; McNab 2009, 2012). When a flightless condition is examined in the 79 species in New Guinea, \log_{10} BMR correlates with \log_{10} mass ($P < 0.0001$) and a flightless condition ($P = 0.041$); $r^2 = 0.873$. The dimensionless coefficient for flight, V , equals 1.00 for flightless species and 1.92 for volant species. Then,

$$BMR \text{ (mLO}_2\text{/h)} = 6.12 \times (V) \times m^{0.592 \pm 0.026} \quad (14).$$

However, only one flightless species, *Megacrex inepta*, is included in this study, but it nevertheless has an impact on the analysis.

GENERAL ANALYSIS

The pattern seen is that \log_{10} BMR correlates with at least nine factors. What is most remarkable is that most factors in conjunction with \log_{10} mass, with the exception of the taxonomic characters, have similar capacities to account for the variation in basal rate. For example, mass alone accounted for 86.6% of the variation, whereas mass and flightless for 87.3%, mass and islands for 87.6%, mass and food habits for 88.0%, mass and altitude for 88.2%, mass and substrate for 89.1%, mass and torpor for 89.4%, and mass and activity for 92.6%. Other than activity, these factors maximally increase r^2 by 2.8%.

Is the capacity to account for the variation in basal rate improved by considering more than two

factors at the same time? One approach is to combine all of the statistically significant the factors found in equations (5), (8), (9), (10), (11), (12), (13), and (14). The phylogenetic factors will be examined later. Then \log_{10} BMR simultaneously correlated with \log_{10} mass ($P < 0.0001$), substrate ($P = 0.044$), activity ($P < 0.0001$), an island/continental distribution ($P = 0.0007$), and flightless condition ($P = 0.020$), but not with torpor ($P = 0.12$), maximal altitude ($P = 0.30$), or food habits ($P = 0.79$).

When torpor, altitude, and food habits were dropped, \log_{10} BMR correlated with \log_{10} mass ($P < 0.0001$), substrate ($P < 0.0001$), activity ($P < 0.0001$), island/continental distribution ($P = 0.0002$), and flightless condition ($P = 0.011$). This analysis accounts for 95.2% of the variation in basal rate, an appreciable improvement beyond that provided by mass alone (86.6%) or mass combined with any one non-taxonomic factor. This analysis is summarized:

$$BMR \text{ (mLO}_2\text{/h)} = 3.03 \times (V \times I \times M \times S) \times m^{0.640 \pm 0.018} \quad (15),$$

where the dimensionless coefficients V equals 0.59 in flightless species and 1.00 in volant species; I equals 1.00 in species endemic on small islands and 1.74 in those that live on intermediate and large landmasses; M equals 1.00 in resident species and 0.66 in other species; and S equals 1.00 in aerial feeders and 1.38 in those that are not.

Torpor was dropped because all four species are aerial feeders and therefore indistinguishable from substrate divided into aerial feeders and other species. Altitude was dropped because most residents were found at high altitudes. And food habits were dropped because of their association with substrate and activity. A flightless condition usually cannot be combined with an island existence because most flightless species are found only on oceanic islands; i.e., both conditions code for the same information. However, the one flightless species in this study is found on mainland New Guinea, which is a piece of a continent without a eutherian predator. (Most flightless birds cannot survive in the presence of eutherian carnivores [McNab & Ellis 2006], but apparently they can live with marsupial carnivores, as is the case with *Megacrex inepta* on New Guinea and *Gallinula mortierii* on Tasmania.)

The effectiveness of equation (15) to account for the variation in basal rate is seen by comparing Figures 21 and 26, realizing that the x-axis of the figures has shifted from \log_{10} mass to the \log_{10} rate calculated from equation (15). Now the number of species most deviant from this fitted curve was reduced to ca. 10.

Given this analysis, is there a place for the addition of taxonomic factors to the analysis without undoing the effect of the factors included in equation (15)? The addition of genus affiliation leads to dropping activity ($P=0.14$) and with flight and foraging substrate losing degrees of freedom, while retaining mass ($P<0.0001$), genus ($P<0.0001$), and islands ($P=0.0010$). As noted, no clear way of consolidating genus into a limited

number of statistically significant categories is possible because the majority of genera have only one species.

When familial affiliation is added to the analysis, \log_{10} BMR correlated with \log_{10} mass ($P<0.0001$), family affiliation ($P<0.0001$), and an island/continental distribution ($P=0.0002$), but not with activity ($P=0.78$), flight (no degrees of freedom), or substrate ($P=0.58$). This result occurs because the designation of the family to which a particular species belongs indicates the likely occurrence of a flightless condition, torpor, and level of activity. All combinations of family affiliation result in the loss of various factors present in equation (15).

This pattern is responsible for the ability of

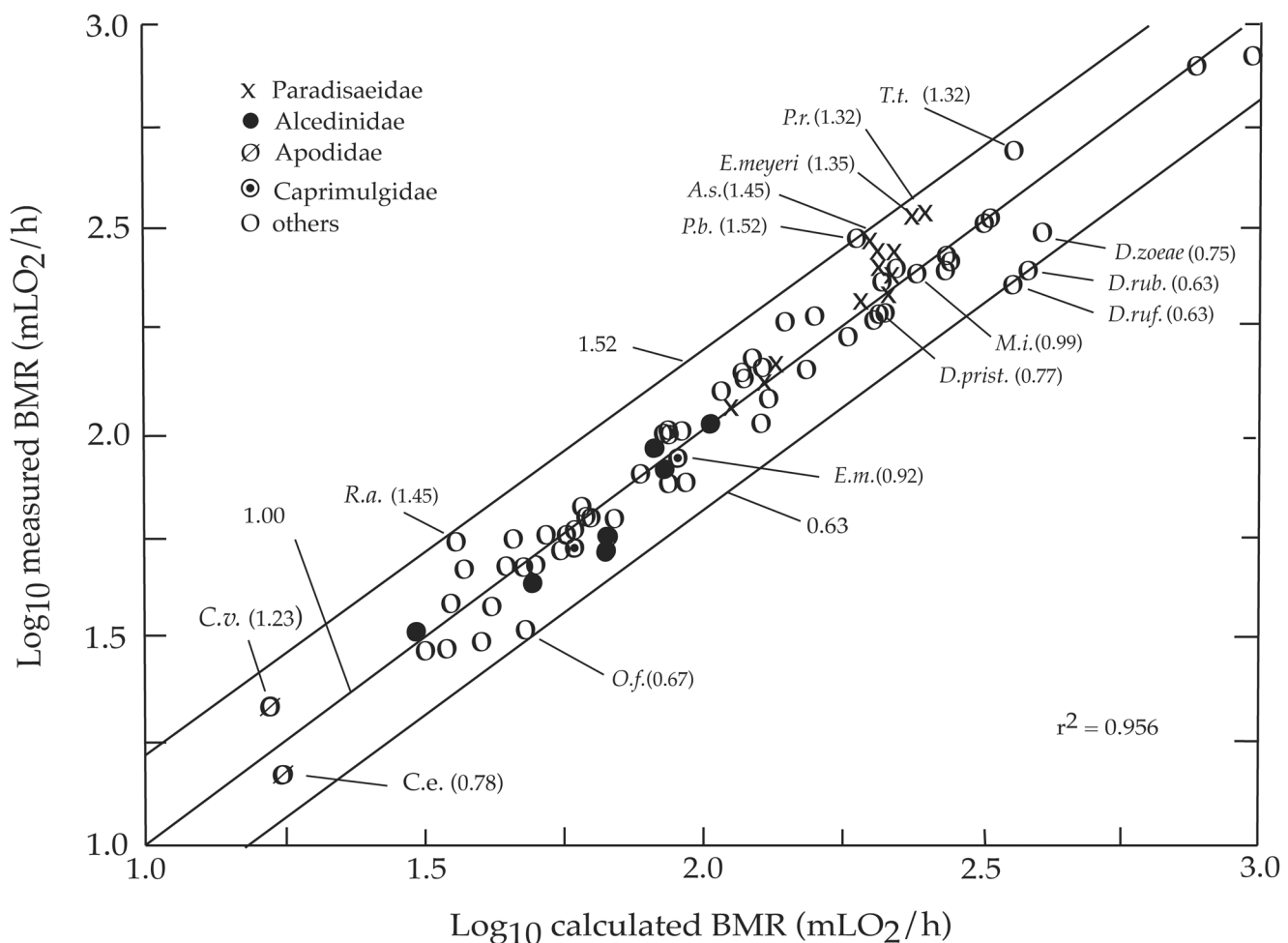


Figure 26. \log_{10} measured basal rate of metabolism in 79 species of birds from New Guinea as a function of \log_{10} calculated basal rate from equation (15). Species and ratios indicated as in Figure 21.

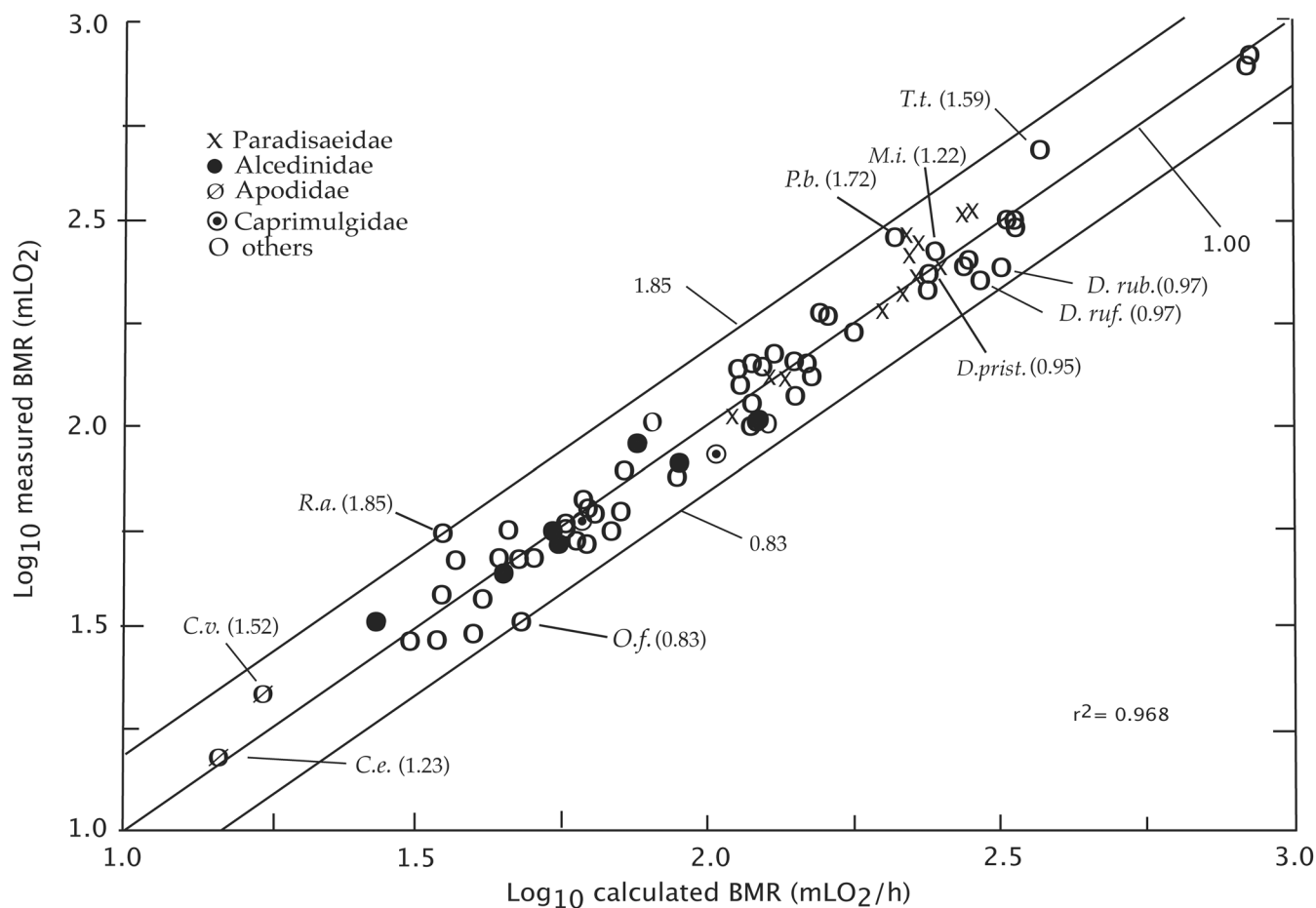


Figure 27. \log_{10} measured basal rate of metabolism in 79 species of birds from New Guinea as a function of \log_{10} calculated basal rate from equation (16). Species and ratios indicated as found in Figure 21.

family affiliation, when combined with mass, to account for much of the variation in basal rate (i.e., $r^2 = 0.972$) because the three dropped factors are through their correlation with family affiliation, surreptitiously incorporated into the analysis. The attempt to account for the level of energy expenditure through family affiliation is circular: swifts have low basal rates because they are found in the Apodidae, which does not explain why that family has ‘those’ rates. There is no reason to continue the use of family affiliation, principally because its use diminishes our ability to delineate the factors that really influence the level of energy expenditure: in the quest for this knowledge, family affiliation is an intellectual ‘black hole,’ explaining everything and nothing at the same time.

The passerine/non-passerine dichotomy was shown to enhance the ability to account for the variation in basal rate when added to seven

ecological and behavioral factors in 533 species of birds (McNab 2009), but it did so, unlike the impact of family affiliation, without the loss of those factors. Would that happen here? When the dichotomy is added to equation (15), \log_{10} BMR correlates with \log_{10} mass ($P < 0.0001$), the passerine/non-passerine dichotomy ($P < 0.0001$), flight ($P = 0.0012$), activity ($P = 0.0012$), substrate ($P = 0.0011$), and an island distribution ($P = 0.0004$); $r^2 = 0.967$ (Fig. 27), i.e., with no factors dropped. This relationship is summarized as

$$\text{BMR (mLO}_2\text{/h)} = 3.01 \times (V \times I \times M \times S \times P) \times m^{0.681 \pm 0.016} \quad (16),$$

where the dimensionless coefficients V equals 0.57 in flightless species and 1.00 in volant species, I equals 1.00 in small-island species and 1.56 in large- and intermediate-island species, M equals 1.00 in resident species and 0.82 in other species, S

is 1.00 in aerial feeders and 1.24 in those that have other feeding substrates, and P equals 0.70 in non-passerines and 1.00 in passerines.

Equation (16) is marginally more effective accounting for the variation in BMR than equation (15) ($r^2 = 96.7$ vs 95.2% , respectively). Of the 15 species that were most deviant from the fitted mass curve (Fig. 21), the analysis represented by equation (16) reduced this number to five, two fruit pigeons and the Mountain Firetail are low and the Friendly Fantail and Helmeted Friarbird are high (Fig. 27). The addition of the dichotomy without dropping any of the factors is radically different from the impact produced by the addition of family affiliation because the contribution of the dichotomy goes beyond the influence of the factors in equation (15).

Evidence of the impact of factor interactions is the tendency for food habits to be dropped from these analyses. Food habits are a significant factor influencing basal rate when they are paired with \log_{10} body mass (equation [8]), but never when combined with the passerine/non-passerine dichotomy or with activity because food habits correlate with this dichotomy ($P=0.0016$) and with activity ($P=0.0009$). In the absence of the dichotomy and activity, \log_{10} BMR is a significant correlate ($P=0.0030$) of food habits in the presence of altitude ($P=0.018$) and an island existence ($P=0.030$).

Three equations, 5, 15, and 16, describe the variation of BMR in the 79 species (Appendix 2). The poorest is equation (5), the body mass relationship, especially when the assembled species includes those with highly diverging behaviors and environments. Of course, this is to be expected because body mass is the only factor included in this equation. This equation overestimates species that have low basal rates, including the flightless rail, kingfishers, birds that enter torpor, or live on islands, whereas it underestimates owls, the parrot, the hornbill, and passerines. For example, the flightless rail has a basal rate predicted by this equation equal to 185% of the measured value, Brehm's Tiger-parrot's estimated basal rate is 90% of the measured value, and the bowerbird has a

predicted rate only equal to 75% of the measured value.

Equation (15) is the mass curve with the addition of a flightless condition, an island distribution, activity level, and foraging substrate. These additions, then, should solve some of the problems associated with the mass curve. As expected, it improves predictions of the basal rate of all categories of birds compared to that predicted by equation (5) (Appendix 2). Equation (15) predicts a basal rate that is 96% of the measured rate in the flightless rail, 106% in the tiger-parrot, and 91% in the bowerbird.

In spite of slightly higher r^2 found with equation (16), only 7 of 51 species have better predictions than obtained from equation (15) (Appendix 2). Equation (16) predicts a basal rate equal to 79% of the rate measured in the flightless rail, 69% in the tiger-parrot, and 82% in the bowerbird, all estimates poorer than derived from equation (15), but much better than obtained from equation (5).

What is really clear is that none of these equations were able to predict the high basal rates of passerines. The best was equation (15) in which estimated rates of high-altitude species averaged 85% of the measured rates, whereas in equation (16) they had an average of 73% (Appendix 2). Equation (15) also predicts that low-altitude passerines have basal rates equal to those of highland species at 86%. Were some appropriate factors not included in the analysis in both equations that might explain this failure? If so, what could they be?

One that immediately comes to mind is altitude. Equation (11) demonstrated that species found at altitudes over 1000 m had basal rates that averaged 1.29 times those restricted to lower altitudes. This factor would 'correct' the mean estimate in equation (15) from 85 to 110% of the measured rates (Appendix 2). Therefore, altitude possibly should be included in the analysis.

Most of high-altitude species also have a resident status. These factors are correlated ($P=0.0009$), so they cannot be included in the same analysis. If activity is dropped from the analysis in equation (15), altitude is retained ($P=0.014$):

$$\text{BMR (mLO}_2\text{/h)} = 3.76 \times (V \times I \times S \times A) \times m^{0.609 \pm 0.0230} \quad (17).$$

The coefficient for altitude in this equation equals 1.19 for species that live > 1000 m. This equation potentially has a better capacity to estimate the basal rates of high-altitude passerines, which is the case, with the mean predicted value being $0.98 \pm 0.039\%$ of the measured value (Appendix 2). If the coefficient 1.19 is used to “correct”, the estimate obtained by equation (15) now becomes 1.10 (Appendix 2). The poorest estimate (59%) was for *Philomen*, a lowland species that has a very high basal rate for unknown reasons. Thus, to suggest that altitude is an important contributor to high basal rates in this fauna is reasonable. But, what equation (17) actually does is to increase the estimates of BMR for nearly all birds (Appendix 2), thereby improving its estimates for high-altitude passerines, but exaggerating its estimates for other birds. A larger and more diverse sample of species may permit altitude to be included with activity and the passerine/non-passerine dichotomy.

A similar adjustment can be attempted for the estimates derived from equation (16). However, even with activity dropped, altitude is not a significant correlate of BMR ($P=0.051$). This occurs because altitude correlates with the passerine/non-passerine dichotomy ($P=0.0031$): 15 of 33 non-passerines are limited to altitudes < 1000 m, whereas only 6 of 46 passerines have this limit (Appendix 1). Consequently, altitude cannot be retained in this sample of species in the presence of the dichotomy.

The conclusion, then, is that for an equation to approach a complete prediction of the basal rates of endotherms, it must include body mass and ecologically and behaviorally important factors. A comparison of equations (15) and (16) suggests that the latter is somewhat better overall, but the difference is not great. Equations (15) and (16), as reflected in their r^2 s, are much better descriptors of the energetics of the birds of New Guinea than equation (5), which reemphasizes that the analysis of complex sets of data is incomplete if only body mass is considered. Obviously, the interactions among the determinative factors in a diverse fauna are exceedingly complicated, which means that

many data from a diverse fauna must be available for these interactions to be clarified. The reliance on a narrow metabolism/mass analysis, which commonly occurs, represents no advance over the original Kleiberian analysis of 81 years ago. One might have hoped that an analytic approach to the numerical variation of the basal rates of birds (and mammals) would have made some progress over this time period. The analysis proposed here may be such an improvement.

THERMAL CONDUCTANCE

Data on thermal conductance (C) from 73 species of birds correlate with body mass ($P<0.0001$; Fig. 28). Then,

$$C (\text{mLO}_2\text{/h}^\circ\text{C}) = 0.46 \times m^{0.595 \pm 0.023} \quad (18).$$

This relationship accounts for 90.4% of the variation in conductance, but 65% of the conductances are less than expected from the general bird curve (equation 4), which might reflect that 18 of 33 non-passerines and 39 of 46 passerines have altitudinal limits to distribution > 1000 m. Log_{10} conductance also correlated with mass-independent basal rate ($P<0.0001$), but when incorporated into equation (18), the resulting relationship has an r^2 equal to 0.901, which is less than produced by equation (18). No other factor was found to correlate with conductance in the presence of body mass, including altitude ($P=0.22$). The complication with these data, as mentioned, was the inability to expose birds to cold enough temperatures to increase their rates sufficiently to get a good estimate of minimal thermal conductance, a problem most marked in larger species.

BODY TEMPERATURE

The regulated body temperatures of New Guinea birds are surprisingly variable, ranging from 35.4 to 41.4°C. What is responsible for such broad variation? Based on equation (1), several possibilities exist: body temperature might be expected to increase with mass and basal rate, but decrease with conductance. In fact, body temperature increases with mass ($P<0.0001$) (Fig. 29); $r^2 = 0.433$. A caution here is that some of the measurements of body temperature in the smallest species might be low as a result of a difficulty in

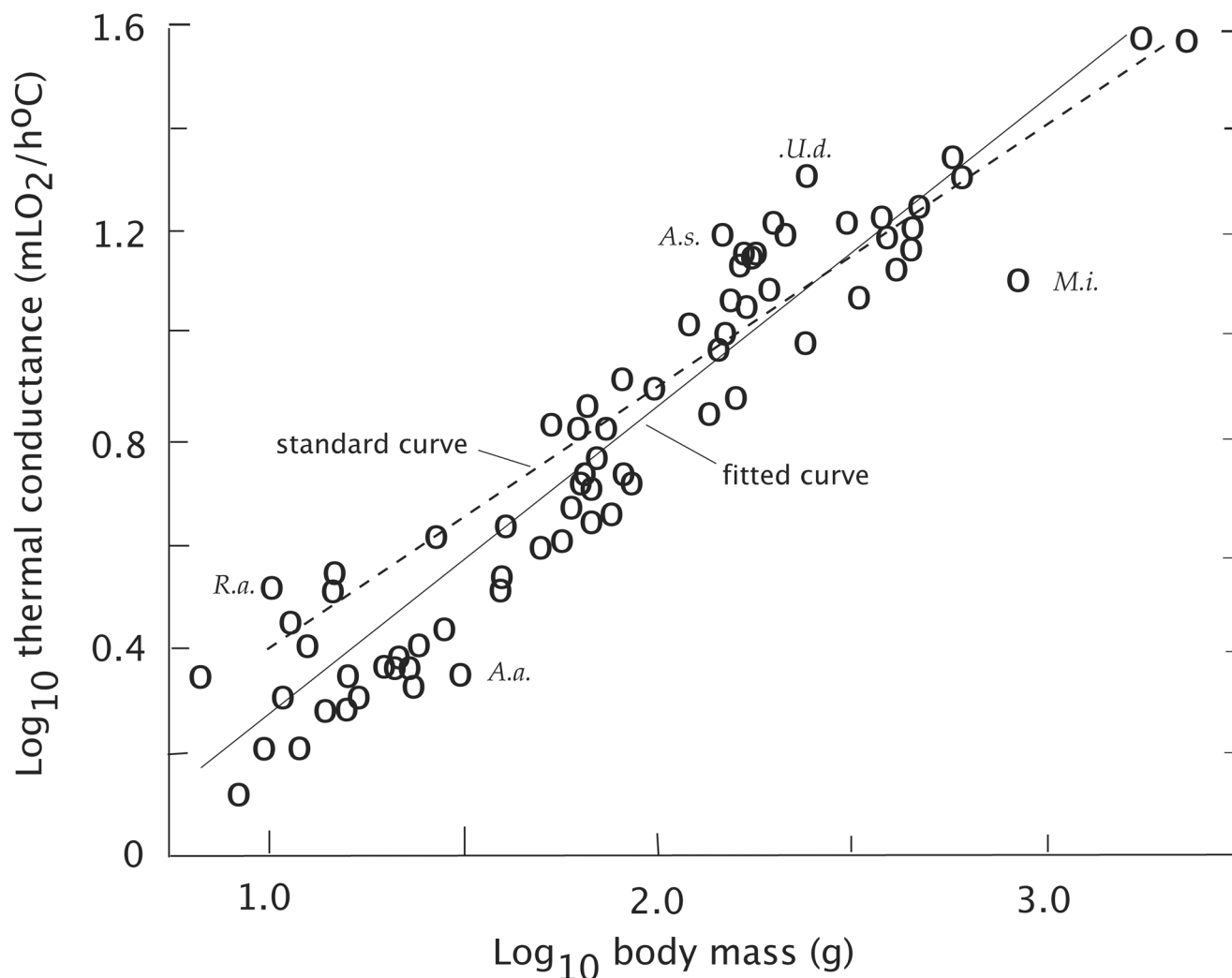


Figure 28. Log_{10} thermal conductance as a function of log_{10} body mass in 73 species of birds from New Guinea. A very low conductance in the New Guinea Flightless Rail (*Megacrex inepta*) is indicated.

penetrating their cloaca with a thermocouple. On the other hand, small species often have flexible body temperatures, as surely is the case in swifts (McNab & Bonaccorso 1995), which makes a definitive estimate of body temperature at their masses difficult. Body temperature does not correlate ($P=0.17$) with mass-independent thermal conductances derived from equation (18) or with mass-independent BMR ($P=0.70$).

DISCUSSION

The analysis proposed here examines the extent to which the ecological and behavioral characteristics of birds in greater New Guinea influence their energy expenditures. The only comparably large

study of tropical birds was that of Wiersma et al. (2007), which concluded that body mass, a 'slow' lifestyle, and phylogeny determined the energetics of a Panamanian avifauna. Three problems exist with their analysis, one procedural and two with their conclusions that contradict those proposed here.

The procedural problem is with their classification of temperate birds with reference to their use or not of migration. Several passerines that migrate were said to be non-migratory, including the Northern Rough-winged Swallow (*Selgidopteryx ruficollis*), Northern House-wren (*Troglodytes aedon*), and the Northern Junco (*Junco hyemalis*), whereas some other species are

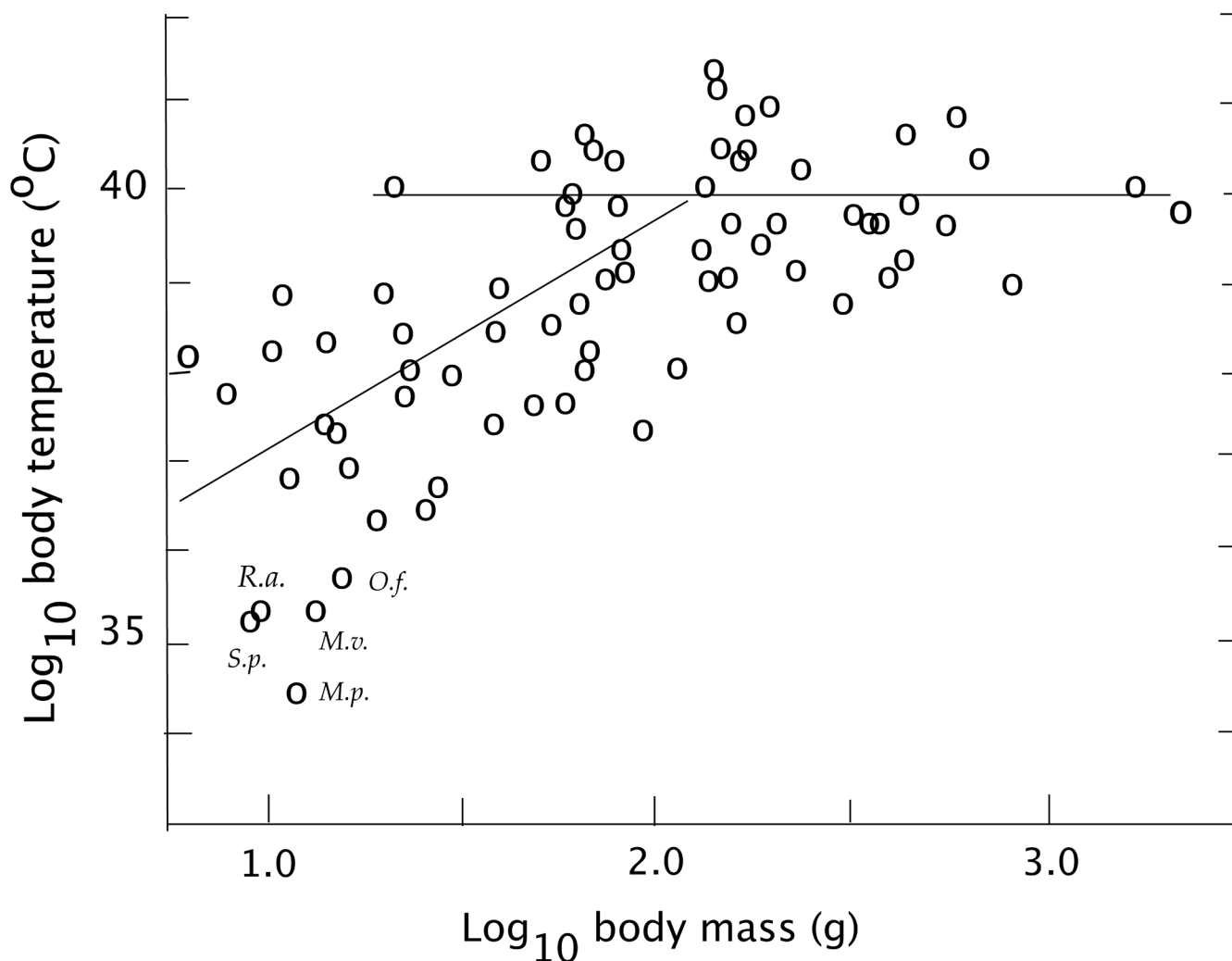


Figure 29. \log_{10} body temperature as a function of \log_{10} body mass in 79 species of birds of New Guinea. Low body temperatures were found in the Papuan Scrub-wren (*Sericornis perspicillatus*), Friendly Fantail (*Rhipidura albolimbata*), Canary Flycatcher (*Microeca papuana*), Fan-tailed Berrypecker (*Melanocharus versteri*), and Mountail Firetail (*Oreostruthus fuliginosus*).

partly migratory, including the American Robin (*Turdus migratorius*) and Eastern Phoebe (*Sayornis phoebe*), among others. All North American swallows are migratory. This raises the question whether energy expenditure is related to migratory habits and, if so, the extent to which differential migration influences energy expenditure.

An important difference of interpretation is related to the implicit suggestion of Wiersma et al. (2007) that phylogeny is an importance determinant of basal rate of metabolism. The ability to account for the variation in the BMR of the 79 species from New Guinea depends on the factors used in the

analysis. Body mass accounted for 86.6% of the variation in basal rates (equation 5). The residual variation is principally associated with species having distinctive characteristics (equation 15). These include a flightless condition (*Megacrex*), island distribution (*Ducula*), high altitudinal distribution (*Rhipidura*, Paradisaeidae), and torpor (*Collocalia*, *Caprimulgus*, *Eurostopodus*). Mass-independent basal rates measured in these species varied from 0.51 to 1.89 times the values expected from the fitted mass curve, a ratio in residual variation equal to 3.7:1 (Fig. 21).

When these ecological/behavioral characters

are included in equation (15), altitude dropped and activity added, the residual variation in basal rate is reduced (Fig. 26) ($r^2 = 0.952$). Basal rate now varied from about 0.63 to 1.52 times the expected rates, i.e., a 2.4-fold ratio, a 35% reduction from that seen in Figure 21. Various groups with eccentric basal rates have moved closer to the fitted mean curve, including swifts, kingfishers, nightjars, fruit pigeons, the flightless rail, and birds-of-paradise.

When the passerine/non-passerine dichotomy is added to the four biological factors and body mass (Fig. 27), the range in residual variation is 0.83 to 1.85, a ratio of 2.2-fold variation of basal rate, a reduction of 40% of that seen in Figure 21, and a further reduction of 8% from that in Figure 26. Most of the values further approach the fitted curve and $r^2 = 0.967$.

The factors influencing BMR, other than body mass, principally depend on behavioral and ecological factors with a small input from the passerine/non-passerine dichotomy. The marked impact of this dichotomy, which raised r^2 from 86.6 to 94.7%, i.e., by 8.1%, when combined only with mass, stems principally from its correlation with ecological factors, which might be expected to prevent a combination of the dichotomy with these factors. That the dichotomy is a significant correlate with basal rate without dropping any of the four ecological factors in equation (15) implies that it was also correlated with factors that were not included in the analysis. But now its influence was greatly reduced in that its addition only increased r^2 from 95.2 to 96.7%, i.e., by 1.5%, only 19% of the impact when combined only with mass. The dichotomy thus represents at best only minor influences on basal rate.

A phylogenetic analysis does nothing to account for the *numerical* variation in basal rate, except as it correlates with ecological and behavioral factors that influence the variation. Thus, to state that the 'reason' that swifts have low basal rates is because they belong to the Apodidae and Apodiformes accounts neither for the reduction of their basal rates, nor for its basis; it represents circular reasoning. Furthermore, this approach completely ignores the physiological diversity

within clades that have species with distinctive behavioral characteristics. For example, why does *D. pacifica* have a much lower mass-independent basal rate than species of *Ducula* restricted to New Guinea? Whatever the answer is—the suggestion here being the evolution of a sedentary lifestyle on small islands—it cannot be “explained” simply by invoking phylogeny because phylogeny cannot predict the temporal accidents of history, including the accidental arrival on oceanic islands of volant rails from which evolved flightless endemics.

The insistence that the impact of phylogeny itself determines the level of basal rate and the precision of thermoregulation of swifts and nightjars almost implies that these characteristics are simply accidents of history that are transmitted through time without any reference to the ecology of these birds, a view that “...is, of course, totally incompatible with evolutionary thinking” (Mayr 1982, p. 304). Evolution is present in phylogenetic analyses, but natural selection has been lost. The analysis promoted here does not deny the importance of phylogeny. A phylogenetic analysis and that used here are addressing different questions. Phylogeny is preoccupied with the historical evolution of traits. The analysis promoted here concerns the numerical variation of energy expenditure, a response to a variety of ecological and behavioral factors as a result of the operation of natural selection. It can be seen in the responses of *D. pacifica* and *Gallirallus owstoni* to life on oceanic islands.

The fundamental difficulty in attempting to analyze the energetics of endotherms by a phylogenetic analysis is that the immediate basis of energetics is not evolutionary, but physiological. The appropriate question is: why to some species have higher basal rates at the same mass than others? This is a physiological/ecological question and, given its quantitative nature, needs a quantitative answer. The conclusion here is that the general correlation of the rate of metabolism with body mass essentially represents biological engineering, involving mass and surface area, whereas most of the residual variation in rate around the mass curve reflects responses to conditions in the environment

and the behavioral characteristics of species. This view of the residual variation is demonstrated by the observation that the species that fall above the metabolism/mass curve usually share some characteristics that they do not share with species that fall below the curve, and vice versa.

The second point of disagreement with the analysis of Wiersma et al. (2007) is their conclusion that tropical birds are characterized by a 'slow' lifestyle, as evidenced by low basal rates of metabolism. Lowland tropical passerines measured here and those reported by Wiersma et al. (2007) have average basal rates greater than expected from a general avian scaling curve (McNab 2009). That is, they do not have low basal rates. Temperate species simply have still higher basal rates. Tropical passerines may be 'slow', but the proposed 'slowness' is not demonstrated in their basal rates.

In New Guinea a slow lifestyle applies principally to lowland non-passerines, as was shown by the lower mass-independent basal rates in species with an altitudinal distribution < 1000 m (Fig. 24). These low rates are often associated with particular food habits or behaviors. Passerines in contrast have, with great variability, basal rates independent of altitude that average 1.11 times those of a standard bird curve (equation 3). Furthermore, all tropical environments are not lowland rainforests, as is the case at Gamboa, Panamá. Do birds in tropical environments other than lowland rainforests and cloud forests have distinctive patterns of energy expenditure?

Why do lowland rainforest passerines have lower basal rates than temperate species? Is it related to food supplies or compositions, the presence of high and the absence of low ambient temperatures, a seasonally equitable environment, or might it be associated with a sedentary lifestyle and a distinctive body composition, such as small pectoral muscle masses? Note that tropical island *Ducula* have low basal rates and small pectoral masses (Fig. 25) (N.A. Wright, pers. comm.). A similar pattern is seen in flightless rails (McNab & Ellis 2006) and in kiwis (McNab 1996) and sedentary ducks (McNab 2003a) that live in temperate New

Zealand. Wright and Steadman (2012) showed that seven species of birds, two hummingbirds and five passerines, have decreases in pectoral muscles in the transition from the larger island of Trinidad to the smaller island of Tobago. Mayr and Diamond (2001:307), when dealing with birds endemic to islands in the South Pacific, concluded that "[t]ropical birds are, on average, much more sedentary and much less prone to disperse over water than are bird species of the temperate zones." Therefore, the most likely explanation for the lower basal rates of lowland tropical passerines may, at this time, be associated with a sedentary lifestyle, which indeed is 'slow.'

A lesson from this analysis is that ecological and environmental factors should be included *before* bringing phylogenetic factors into the analysis. No analysis can ignore the great impact of body mass on energy expenditure, which is why it must be included in all phylogenetic analyses of energy expenditure. If phylogenetic analyses of energy expenditure are so central to its understanding, why must body mass be included? After all, body mass is correlated with phylogeny. The necessity to add body mass to all phylogenetic analyses of basal rates is an admission that at least one factor other than history is important in determining their level in endotherms. The modest argument here is simply that factors other than mass must be included, even if their effects are much more subtle than that of mass. However, the preferential use of phylogeny, after accounting for the impact of mass, hides the subtle effects of factors that are correlated with phylogeny and therefore prevents their influence on the phenotype from being identified. If factors other than body mass are brought into an analysis before the addition of phylogenetic factors and if they, along with mass, cannot account for all of the variation in a quantitative character, that might facilitate the identification of other factors that are potentially responsible for the remainder of the variation through their correlation with phylogeny. This may be the case with the addition of the passerine/non-passerine dichotomy and apply to the 3.5% of the variation in the basal rate of metabolism unaccounted for in the 79 species.

IMPLICATIONS

The analysis of the ecological, behavioral, and physiological characteristics of the avifauna of New Guinea is itself of value, but also as an important, if not exclusive (Mayr & Diamond 2001, Filardi & Smith 2005, Steadman 2006), source for the terrestrial avifauna of islands in the South Pacific. For an extended discussion of the dispersal of birds in the South Pacific, see Steadman (Chapter 17). For example, two species complexes of monarch flycatchers belonging to the genus *Monarchus* in the Solomon Islands may have been derived from Australian species (Filardi & Smith 2005). However, the New Guinea avifauna sets a standard against which the characteristics of small-island endemics can be judged to determine the extent to which they have made an adjustment to island life. Such adjustments have been clearly made in the sedentary behavior of small-island endemics and the evolution of a flightless condition, a flightless condition being the epitome of a sedentary lifestyle. The Guam Island Rail, *Gallirallus owstoni*, which is flightless, has a basal rate that is 86% of the value expected from the mean avian curve, or 85% from equation (5), i.e., low by any standard (McNab & Ellis 2006).

The movement of birds from New Guinea, the Philippines, and Australia to the islands of the South Pacific raises the question as to whether adjustments occur relative to the distance from an immediate or ultimate source. What is the significance of the observation that the evolution of a flightless condition in rail genera varies with geography? Does island size influence the evolution of a flightless condition? Is the ability to withstand the presence of people by species endemic to islands related to the level of their energy expenditure (and possibly related to their reproductive output)?

A species of much interest is the Island Thrush (*Turdus poliocephalus*) because of its complex response to island life. It has radical adjustments in coloration and altitudinal limits to distribution. This species occurs at altitudes in which forest communities have no more than 30 species (Mayr and Diamond 2001). This requires ascending to higher altitudes on larger islands, i.e., > 2500 m

in New Guinea, > 1400 m on Bougainville, but at sea level on the smaller islands of Vanuatu. In New Guinea this species has a basal rate equal to 123% of the value expected from mass (by an all-avian standard) at altitudes between 2500 and 4100 m. Does its basal rate vary with altitude and geographical isolation, especially in populations that have been isolated long enough to evolve distinctive color morphs? The Bronze Ground-dove also is found at higher altitudes on larger islands; it has a basal rate equal to 79% of the value expected from body size at an altitude of 2000 m in New Guinea. The difference in basal rate between the thrush and dove possibly reflects the passerine/non-passerine dichotomy, whatever its basis might be, potentially including activity, and diet. Similar altitudinal patterns of distribution in relation to island size and altitude occur in the thrush *Zoothera [dauma]*, the warbler (*Phylloscopus trivirgatus*), and the fantail (*Rhipidura [rufidorsa]*) in the Bismarcks (Mayr & Diamond 2001). (The brackets around the species names represent superspecies complexes.)

Obviously, much work needs to be done on the ecological energetics of birds in Australasia, work that should be done before we have lost through extirpation and extinction even more of the fauna endemic to islands in the South Pacific than has already occurred. New Guinea is a pivotal location for this exploration because of its location, size, and species diversity. This monograph is the first attempt at such an analysis: much more needs to be done.

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Appendix 1. The Energetics of New Guinea Birds

Species	Mass (g)	BMR (mLO ₂ /h)	%*	Conductance (mLO ₂ /h°C) % ⁺	Tb (°C)	Distribution	Altitude (km) (level)	Food	Substrate	Source	
Gruiformes											
Rallidae											
<i>Megacrex inepta</i>	856.6	240.7	41	12.8	54	39.0	NG	0-0.3 (1)	invert	terrest	McNab & Ellis 2006
Columbiformes											
Columbidae											
<i>Gallicolumba beccarii</i>	68.8	90.8	79	5.1	75	40.7	NG/island	1.4-2.8 (3)	fruit/insect	terrest	this study
<i>Ptilinopus superbus</i>	120.4	138.5	84	10.5	117	38.1	NG/island	0-1.4 (2)	fruit	arboreal	McNab 2000
<i>Ptilinopus perlatus</i>	196.0	190.3	84	12.3	108	39.5	NG/island	0-1.2 (1)	fruit	arboreal	McNab 2000
<i>Gymnophaps albertsii</i>	241.6	169.4	65	9.7	77	39.2	NG/island	0-3.4 (4)	fruit	arboreal	McNab 2000
<i>Ducula pacifica</i>	333.4	142.4	49	11.8	80	39.8	Small island	0-0.2 (1)	fruit	arboreal	McNab 2000
<i>Ducula rufgaster</i>	376.7	228.3	66	17.0	108	39.7	NG/island	0-1.2 (1)	fruit	arboreal	McNab 2000
<i>Ducula pistrinaria</i>	394.2	192.4	54	15.4	96	39.7	Small island	0-0.2 (1)	fruit	arboreal	McNab 2000
<i>Ducula rubricera</i>	418.8	244.6	66	13.4	81	39.1	Large island	0-1.0 (1)	fruit	arboreal	McNab 2000
<i>Ducula bicolor</i>	453.6	246.3	63	16.2	94	40.7	Large island	0-0.9 (1)	fruit	arboreal	McNab 2000
<i>Ducula zoeae</i>	456.2	305.7	78	14.6	84	39.3	NG/island	0-1.5 (2)	fruit	arboreal	McNab 2000
<i>Columba vitiensis</i>	467.9	259.1	65	17.8	102	39.9	NG/island	0-1.5 (2)	fruit	arboreal	McNab 2000
<i>Ducula pinon</i>	583.8	319.3	69	22.0	113	39.7	NG/island	0-0.5 (1)	fruit	arboreal	McNab 2000
<i>Caloenas nicobarica</i>	613.0	325.5	68	20.4	102	40.9	Large island	0-0.5 (1)	fruit/nut	terrest	McNab 2000
<i>Goura victoria</i>	2313.4	765.7	68	37.0	96	39.8	NG	0-0.3 (1)	fruit	terrest	McNab 2000
Psittaciformes											
Psittacidae											
<i>Psittacella brehmii</i>	99.8	141.7	97	7.9	96	37.4	NG	1.6-2.8 (3)	fruit/seed	arboreal	this study
Strigiformes											
Tytonidae											
<i>Tyto tenebricosa</i>	710.0	477.8	91	--	--	40.4	NG	0-4.0 (4)	vert	arboreal	this study
Strigidae											
<i>Ninox theomacha</i>	151.4	187.7	98	10.1	101	41.2	NG/island	0-2.5 (3)	insect	arboreal	this study
<i>Uroglaux dimorpha</i>	245.3	262.5	100	20.4	160	40.3	NG	0-1.5 (2)	vert	arboreal	this study
Caprimugiformes											
Podargidae											
<i>Podargus papuensis</i>	314.6	191.9	62	16.5	115	38.8	NG	0-1.0 (1)	insect	aerial	McNab & Bonaccorso 1995
<i>Podargus ocellatus</i>	145.0	101.5	55	--	--	36.2	NG	(2)	insect	aerial	Lasiewski et al. 1995

Appendix 1. The Energetics of New Guinea Birds (continued)

Species	Mass (g)	BMR (mLO ₂ /h)	%* (mLO ₂ /h°C) ⁺	Tb (°C)	Distribution	Altitude (km) (level)	Food	Substrate	Source	
Caprimugiformes (cont.)										
Caprimulgidae										
<i>Caprimulgus macrurus</i>	68.6	55.6	49	4.4	65	(38.1) NG/island	0-1.7 (2)	insect	aerial	McNab & Bonaccorso 1995
<i>Eurostopodus mystacalis</i>	162.0	86.0	43	7.6	73	(39.1) NG	0-1.5 (2)	insect	aerial	McNab & Bonaccorso 1995
Apodiformes										
Apodidae										
<i>Collocalia esculenta</i>	6.8	14.6	58	2.2	101	(38.2) NG/island	0-4.0 (4)	insect	aerial	McNab & Bonaccorso 1995
<i>Collocalia vanikorensis</i>	11.6	21.5	60	2.8	99	(38.9) NG	0-0.5 (1)	insect	aerial	McNab & Bonaccorso 1995
Coraciiformes										
Alcedinidae										
<i>Ceyx lepidus</i>	14.9	32.6	77	3.2	98	38.4 NG/island	0-1.3 (2)	insect	arboreal	this study
<i>Alcedo azurea</i>	31.5	42.8	62	2.2	47	38.0 NG/island	0-1.0 (1)	fish/crust	arboreal	this study
Halcyonidae										
<i>Todiramphus sanctus</i>	41.5	55.6	67	4.3	81	39.0 winter NG	0-1.7 (2)	invert	arboreal	this study
<i>Tanyseptera galatea</i>	50.7	51.2	55	3.9	66	37.7 NG/island	0-0.3 (1)	insect/invert	arboreal	this study
<i>Tanyseptera sylvia</i>	63.1	77.6	72	6.6	101	37.7 Large island	0-1.5 (2)	insect/lizard	arboreal	this study
<i>Melidora macrorrhina</i>	84.9	74.9	57	--	--	39.4 NG/island	0-0.8 (1)	insect/frog	arboreal	this study
<i>Dacelo gaudichaud</i>	138.5	103.9	58	7.1	74	39.4 NG/island	0-1.0 (1)	invert/vert	arboreal	this study
Brucerotiformes										
Bucerotidae										
<i>Rhyticeros plicatus</i>	1781.6	814.3	85	37.4	111	40.1 NG/island	0-1.2 (1)	fruit	arboreal	McNab 2001
Passeriformes										
Pittidae										
<i>Pitta versicolor</i>	83.1	101.5	78	5.4	72	39.9 winter NG	0-0.3 (1)	invert	terrest	this study
Muscicapidae										
<i>Turdus poliocephalus</i>	66.1	137.5	123	5.4	81	39.7 NG/island	2.7-4.1 (4)	fruit/insect	arboreal	this study
Cinclosomatidae (Eupetidae?)										
<i>Ifrita kowaldi</i>	28.9	61.3	94	2.7	61	(36.8) NG	0-2.6 (3)	insect	arboreal	this study

Appendix 1. The Energetics of New Guinea Birds (continued)

Species	Mass (g)	BMR (mLO ₂ /h)	%*	Conductance (mLO ₂ /h°C) % ⁺	Tb (°C)	Distribution	Altitude (km) (level)	Food	Substrate	Source
Passeriformes (cont.)										
Acanthizidae										
<i>Sericornis perspicillatus</i>	8.5	29.3	100	1.3	39	NG	1.5-2.5 (3)	insect	arboreal	this study
<i>Sericornis papuensis</i>	9.8	29.6	92	1.6	61	NG	2.0-3.5 (4)	insect	arboreal	this study
<i>Sericornis nouhuysi</i>	16.1	46.7	105	1.9	57	NG	1.4-3.0 (3)	insect	arboreal	this study
<i>Crateroscelis robusta</i>	17.3	47.3	102	2.0	58	NG	18-3.6 (4)	insect	arboreal	this study
Rhipiduridae										
<i>Rhipidura albolimbata</i>	10.3	53.9	163	3.3	124	NG	1.8-3.6 (4)	insect	arboreal	this study
<i>Rhipidura atra</i>	11.0	46.2	133	2.0	72	NG	1.0-2.4 (3)	insect	arboreal	this study
Petroicidae										
<i>Microeca papuana</i>	12.9	37.3	97	2.5	84	NG	1.8-3.5 (4)	insect	arboreal	this study
<i>Peneothello sigillatus</i>	21.1	56.5	107	2.3	60	NG	2.5-3.9 (4)	insect	arboreal	this study
<i>Peneothello cyanus</i>	23.8	62.6	109	2.1	52	NG	1.5-2.4 (3)	insect	arboreal	this study
Pachycephalidae										
<i>Pachycephala schlegelii</i>	22.0	52.1	94	2.4	62	NG	1.7-3.7 (4)	insect	arboreal	this study
<i>Pachycephala soror</i>	23.4	65.1	115	2.3	57	NG	1.0-2.0 (2)	insect	arboreal	this study
<i>Pachycephala rufinucha</i>	40.0	80.4	100	3.2	61	NG	1.8-2.6 (3)	insect	arboreal	this study
<i>Ptilinopus nigrescens</i>	70.5	149.5	129	5.8	84	NG	1.6-2.2 (3)	fruit/insect	arboreal	this study
Meliphagidae										
<i>Lichmera indistincta</i>	10.1	38.1	116	--	--	NG/island	0-0.5 (1)	nectar/insect	arboreal	Vitali et al. 1999
<i>Ptiloprora guisei</i>	20.2	51.3	100	2.3	62	NG	1.8-2.5 (3)	insect	arboreal	this study
<i>Ptiloprora perstriata</i>	24.7	62.0	108	2.5	61	NG	2.5-3.8 (4)	nectar/insect	arboreal	this study
<i>Melidectes fuscus</i>	27.4	54.3	87	4.1	95	NG	3.0-3.7 (4)	nectar/insect	arboreal	this study
<i>Melipotes fumigatus</i>	57.4	126.3	124	4.0	64	NG	1.0-3.4 (4)	fruit/insect	arboreal	this study
<i>Melidectes rufocristatus</i>	63.9	145.1	133	5.2	79	NG	1.4-2.8 (3)	nectar/insect	arboreal	this study
<i>Melidectes belfordi</i>	66.8	133.2	119	7.3	109	NG	1.6-3.8 (4)	nectar/insect	arboreal	this study
<i>Philemon buceroides</i>	140.5	293.6	161	--	--	NG/island	0-1.0 (1)	nectar/insect	arboreal	this study
Melanochartidae										
<i>Toxorhamphus poliopterus</i>	12.2	31.7	86	1.6	55	NG/island	0.5-2.5 (3)	nectar	arboreal	this study
<i>Melanochartus versteri</i>	14.3	47.0	115	1.9	60	NG	1.8-3.7 (4)	fruit	arboreal	this study
Paramythiidae										
<i>Oreocharis arfaki</i>	22.3	57.5	105	--	--	NG	2.2-2.7 (3)	fruit	arboreal	this study
<i>Paramythia montium</i>	40.3	74.6	92	3.4	65	NG	2.5-3.8 (4)	fruit	arboreal	this study

Appendix 1. The Energetics of New Guinea Birds (continued)

Species	Mass (g)	BMR (mLO ₂ /h) %*	Conductance (mLO ₂ /h°C) % ⁺	Tb (°C)	Distribution	Altitude (km) (level)	Food	Substrate	Source
Passeriformes (cont.)									
Estrildidae									
<i>Erythrura trichroa</i>	15.1	55.0	129	37.5	NG/island	1.0-3.0 (3)	seed	arboreal	this study
<i>Oreostruthus fuliginosus</i>	16.2	33.0	74	35.8	NG	2.8-3.7 (4)	seed	arboreal	this study
Artamidae									
<i>Artamus maximus</i>	61.2	113.2	107	39.9	NG	0.6-2.6 (3)	insect	aerial	this study
Cnemophilidae									
<i>Cnemophilus loriae</i>	75.2	112.0	92	39.7	NG	1.8-2.4 (3)	fruit	arboreal	this study
<i>Cnemophilus macgregorii</i>	78.1	118.7	96	38.6	NG	1.8-2.4 (3)	fruit	arboreal	McNab 2005
<i>Cnemophilus macgregorii</i>	87.1	133.3	100	39.2	NG	2.4-3.5 (4)	fruit	arboreal	this study
Ptilonorhynchidae									
<i>Archiboldia papuensis</i>	171.3	234.7	113	38.6	NG	2.6-2.9 (3)	fruit	arboreal	this study
Paradisaeidae									
<i>Cicinnurus regius</i>	54.0	104.8	107	40.4	NG	0-0.3 (1)	fruit/insect	arboreal	McNab 2005
<i>Lophorina superba</i>	74.6	129.8	108	40.5	NG	1.5-1.8 (2)	insect	arboreal	McNab 2005
<i>Cicinnurus magnificus</i>	82.3	141.6	110	40.4	NG	0.4-1.2 (1)	fruit/insect	arboreal	McNab 2005
<i>Parotia lawesii</i>	144.9	205.8	111	39.1	NG	1.2-1.9 (2)	fruit	arboreal	McNab 2005
<i>Astrapia stephaniae</i>	148.2	289.0	153	41.4	NG	1.5-2.8 (3)	fruit/insect	arboreal	McNab 2005
<i>Paradisaea rudolphi</i>	156.1	273.2	140	40.5	NG	1.3-1.8 (2)	fruit/insect	arboreal	McNab 2005
<i>Parotia wahnesi</i>	164.2	231.5	115	39.7	NG	1.1-1.7 (2)	fruit	arboreal	McNab 2005
<i>Manucodia keraudrenii</i>	170.7	215.1	104	40.4	NG	1.0-2.0 (2)	fruit	arboreal	McNab 2005
<i>Manucodia chalybata</i>	177.2	246.3	116	40.5	NG	0.6-1.5 (2)	fruit	arboreal	McNab 2005
<i>Ptiloris magnificus</i>	179.4	269.1	126	40.9	NG	0.6-1.2 (1)	insect	arboreal	McNab 2005
<i>Epimachus meyeri</i>	202.7	330.4	143	41.0	NG	2.0-3.0 (3)	insect	arboreal	McNab 2005
<i>Paradisaea raggiana</i>	215.7	336.5	140	39.7	NG	0-1.5 (2)	fruit/insect	arboreal	McNab 2005

* % = $100 \times (BMR/7.25m^{0.652})$ + % = $100 \times (C/0.85 m^{0.492})$

Appendix 2. Estimates of BMR. $c/m = (\text{calculated BMR})/(\text{measured BMR})$

Species	Ecological characteristic	mass g	measured BMR mLO ₂ /h	5 ¹ mLO ₂ /h (c/m)	Calculated BMR Equations		
					15 ² mLO ₂ /h (c/m)	16 ³ mLO ₂ /h (c/m)	17 ⁴ mLO ₂ /h (c/m)
Part 1. Non-passeromes							
<i>Megacrex inepta</i>	flightless	856.6	240.7	445.6 (1.85)	234.8 (0.96)	189.3 (0.79)	259.9 (1.23)
<i>Collocalia esculenta</i>	torpor	6.8	14.6	26.8 (1.85)	12.9 (0.89)	9.9 (0.68)	17.3 (1.18)
<i>Collocalia vanikorensis</i>	torpor	11.6	21.5	36.6 (1.69)	18.2 (0.85)	14.2 (0.67)	20.3 (0.94)
<i>Caprimulgus macrurus</i>	torpor	68.6	55.6	102.8 (1.84)	56.7 (1.02)	48.0 (0.86)	69.6 (1.25)
<i>Eurostopodus mystacalis</i>	torpor	162.0	86.0	169.3 (1.96)	98.3 (1.14)	86.2 (1.00)	116.7 (0.72)
c/m mean ± s.e. (n)				1.84 ± 0.055 (4)	0.98 ± 0.066 (4)	0.80 ± 0.079 (4)	1.02 ± 0.121 (4)
<i>Ducula pacifica</i>	small island	333.4	142.4	257.5 (1.81)	123.8 (0.87)	112.0 (0.79)	186.5 (1.31)
<i>Ducula pistrinaria</i>	intermediate island	394.2	192.4	283.8 (1.47)	239.7 (1.24)	195.8 (1.02)	319.7 (1.66)
<i>Ducula rubricera</i>	intermediate island	418.8	244.6	294.0 (1.20)	249.2 (1.02)	204.0 (0.83)	331.6 (1.36)
<i>Ducula spilorrhoa</i>	intermediate island	453.6	246.3	308.0 (1.25)	262.3 (1.06)	215.4 (0.87)	347.9 (1.41)
<i>Caloenas nicobarica</i>	intermediate island	613.0	325.5	366.9 (1.12)	318.0 (0.98)	264.4 (0.81)	417.1 (1.28)
c/m mean ± s.e. (n)				1.26 ± 0.075 (4)	1.08 ± 0.057 (4)	0.88 ± 0.048 (4)	1.43 ± 0.082 (4)
<i>Todiramphus sanctus</i>	migratory	41.5	55.6	76.7 (1.39)	56.8 (1.02)	42.3 (0.76)	98.2 (1.77)
<i>Tanyiptera sylvia</i>	migratory	63.1	77.6	97.9 (1.26)	74.2 (0.96)	56.2 (0.72)	126.3 (1.63)
<i>Pitta versicolor</i>	migratory	83.1	101.5	114.9 (1.14)	88.5 (0.87)	96.9 (0.95)	125.3 (1.23)
c/m mean ± s.e. (n)				1.26 ± 0.072 (3)	0.95 ± 0.044 (3)	0.81 ± 0.071 (3)	1.54 ± 0.162 (3)

¹BMR = $8.81 \times m^{0.581}$ ²BMR = $3.30 \times (V \times I \times M \times S) m^{0.640} (V [n = 1.00, y = 0.59]), (I [s = 1.00, Li = 1.74]), (M [R = 1.00, O = 0.66]), (S [a = 1.00, n = 1.38])$ ³BMR = $3.01 \times (V \times I \times M \times S \times P) m^{0.681} (V [n = 1.00, y = 0.57]), (I [s = 1.00, Li = 1.56]), (M [R = 1.00, n = 0.82]), (S [a = 1.00, np = 0.70])$ ⁴BMR = $3.52 \times (V \times I \times T \times A) m^{0.602} (V [n = 1.00, y = 0.58]), (I [s = 1.00, Li = 1.55]), (T [n = 1.91, y = 1.00]), (A [l = 0.84, 234 = 1.00])$

Appendix 2. Estimates of BMR (continued).

Species	Ecological characteristic	mass g	measured BMR mLO ₂ /h	5 ¹ mLO ₂ /h (c/m)	Calculated BMR Equations		
					15 ² mLO ₂ /h (c/m)	16 ³ mLO ₂ /h (c/m)	17 ⁴ mLO ₂ /h (c/m)
Part 1. Non-passeromes (cont.)							
<i>Ceyx lepidus</i>	invert/vert	14.9	32.6	42.3 (1.30)	29.4 (0.90)	21.0 (0.64)	52.9 (1.62)
<i>Alcedo azurea</i>	invert/vert	31.5	42.8	65.4 (1.53)	47.4 (1.11)	35.0 (0.82)	69.7 (1.63)
<i>Tanyptera galeata</i>	invert/vert	50.7	51.2	86.2 (1.68)	64.3 (1.26)	48.4 (0.95)	92.8 (1.81)
<i>Melidora macrorrhina</i>	invert/vert	84.9	74.9	116.3 (1.56)	89.7 (1.20)	68.8 (0.76)	127.0 (1.70)
<i>Dacelo gaudichaud</i>	invert/vert	146.2	111.1	159.5 (1.43)	127.1 (1.14)	99.6 (0.90)	176.0 (1.58)
c/m mean ± s.e. (n)				1.50 ± 0.064 (5)	1.12 ± 0.061 (5)	0.81 ± 0.054 (5)	1.67 ± 0.040 (5)
<i>Ninox theomacha</i>	carnivore	151.4	187.7	184.4 (0.98)	196.9 (1.05)	124.4 (0.66)	213.9 (1.14)
<i>Uroglaux dimorpha</i>	carnivore	245.3	262.5	215.5 (0.82)	268.1 (1.02)	172.8 (0.66)	286.0 (1.09)
<i>Tyto tenebricosa</i>	carnivore	710.0	477.8	399.5 (0.83)	349.4 (0.73)	292.2 (0.61)	542.4 (1.14)
c/m mean ± s.e.. (n)				0.88 ± 0.052 (3)	0.93 ± 0.010 (3)	0.64 ± 0.017 (3)	1.12 ± 0.017 (3)
<i>Gallicolumba beccarii</i>	frugivore	68.8	90.8	102.9 (1.13)	78.7 (0.87)	59.6 (0.66)	111.8 (1.23)
<i>Psittacella brehmii</i>	frugivore	99.8	141.7	127.8 (0.90)	150.8 (1.06)	97.5 (0.69)	166.5 (1.17)
<i>Ptilonopus superbis</i>	frugivore	120.4	138.5	142.5 (1.03)	112.7 (0.81)	87.2 (0.63)	156.6 (1.13)
<i>Ptilonopus perlatus</i>	frugivore	196.0	190.3	189.1 (0.99)	153.3 (0.81)	121.6 (0.64)	209.9 (1.10)
<i>Gymnophaps albertsii</i>	frugivore	241.6	169.4	213.6 (1.26)	175.3 (1.03)	140.2 (0.83)	238.4 (1.44)
<i>Ducula rufigaster</i>	frugivore	376.7	228.3	276.5 (1.20)	232.9 (1.02)	231.5 (1.01)	311.5 (1.36)
<i>Ducula zoeae</i>	frugivore	456.2	305.7	309.0 (1.01)	263.2 (0.86)	263.7 (0.86)	415.6 (1.36)
<i>Columba vitiensis</i>	frugivore	467.9	259.1	313.6 (1.21)	267.5 (1.03)	219.8 (0.85)	422.0 (1.63)
<i>Ducula pinon</i>	frugivore	583.8	319.3	356.6 (1.11)	308.2 (0.97)	255.8 (0.80)	405.5 (1.27)
<i>Rhyticeros plicatus</i>	frugivore	1781.6	814.3	681.9 (0.84)	629.5 (0.77)	666.8 (0.82)	793.8 (0.97)
<i>Goura victoria</i>	frugivore	2313.4	765.7	793.6 (1.04)	744.1 (0.97)	652.8 (0.85)	927.4 (1.21)
c/m mean ± s.e. (n)				1.07 ± 0.040 (11)	0.93 ± 0.032 (11)	0.79 ± 0.035 (11)	1.26 ± 0.042 (11)
c/m mean ± s.e. (n)				1.15 ± 0.059 (19)	0.98 ± 0.034 (19)	0.77 ± 0.028 (19)	1.35 ± 0.057 (19)

Appendix 2. Estimates of BMR (continued).

Species	Ecological characteristic	mass g	measured BMR mLO ₂ /h	Calculated BMR Equations			
				5 ¹ mLO ₂ /h (c/m)	15 ² mLO ₂ /h (c/m)	16 ³ mLO ₂ /h (c/m)	17 ⁴ mLO ₂ /h (c/m)
Part 2. Passerines							
<i>Lichmera indistincta</i>	low altitude	10.1	38.1	33.8 (0.89)	34.8 (0.91)	28.1 (0.74)	35.2 (0.92)
<i>Cicinnurus regius</i>	low altitude	54.0	104.8	89.4 (0.85)	101.8 (0.97)	88.1 (0.84)	96.6 (0.92)
<i>Cicinnurus magnificus</i>	low altitude	82.3	141.6	114.2 (0.81)	133.3 (0.94)	117.4 (0.83)	124.5 (0.88)
<i>Philemon buceroides</i>	low altitude	140.5	293.6	155.9 (0.53)	187.7 (0.64)	168.9 (0.58)	171.8 (0.59)
<i>Ptiloris magnifus</i>	low altitude	179.4	269.1	179.7 (0.67)	219.5 (0.82)	199.5 (0.74)	199.1 (0.74)
c/m mean ± s.e. (n)				0.75 ± 0.066 (5)	0.86 ± 0.060 (5)	0.75 ± 0.047 (5)	0.81 ± 0.064 (5)
<hr/>							
<i>Rhipidura albolimbata</i>	high altitude	10.3	53.9	34.2 (0.63)	36.1 (0.67)	28.5 (0.53)	45.5 (0.84)
<i>Pachycephala soror</i>	high altitude	23.4	65.1	55.0 (0.85)	59.6 (0.92)	49.8 (0.77)	69.5 (1.07)
<i>Peneothello cyanus</i>	high altitude	23.8	62.6	55.6 (0.88)	60.2 (0.96)	50.4 (0.81)	70.1 (1.12)
<i>Cicinnurus regius</i>	high altitude	54.0	104.5	89.4 (0.85)	101.8 (0.97)	88.1 (0.84)	114.8 (1.10)
<i>Artamus maximus</i>	high altitude	61.2	113.2	96.2 (0.85)	110.3 (0.97)	77.4 (0.68)	123.8 (1.09)
<i>Turdus poliocephalus</i>	high altitude	66.1	137.5	100.6 (0.73)	115.8 (0.84)	101.1 (0.74)	141.1 (1.03)
<i>Melidectes belfordi</i>	high altitude	66.8	133.2	101.2 (0.76)	116.6 (0.88)	101.8 (0.76)	142.0 (1.07)
<i>Lophorina superba</i>	high altitude	74.6	129.8	107.9 (0.83)	125.2 (0.96)	109.8 (0.85)	139.5 (1.07)
<i>Astrapia stephaniae</i>	high altitude	148.2	289.0	160.8 (0.56)	194.2 (0.67)	175.2 (0.61)	230.7 (0.80)
<i>Paradisaea rudolphi</i>	high altitude	156.1	273.2	165.7 (0.61)	200.8 (0.73)	181.5 (0.66)	181.5 (0.66)
<i>Parotia wahnesi</i>	high altitude	164.2	231.5	170.7 (0.74)	207.4 (0.90)	187.8 (0.81)	254.6 (1.06)
<i>Archiboldia papuensis</i>	high altitude	171.3	234.7	174.9 (0.75)	213.1 (0.91)	193.3 (0.82)	252.0 (1.07)
<i>Epimachus meyeri</i>	high altitude	202.7	330.4	192.9 (0.58)	237.3 (0.72)	216.8 (0.66)	279.2 (0.84)
<i>Paradisaea raggiana</i>	high altitude	215.7	336.5	200.0 (0.60)	246.9 (0.73)	226.2 (0.67)	299.0 (0.86)
c/m mean ± s.e. (n)				0.73 ± 0.031 (14)	0.85 ± 0.031 (14)	0.73 ± 0.026 (14)	0.98 ± 0.039 (14)
X 1.29 (equation [13])				— —	1.10	— —	— —
X 1.19 (equation [17])				— —	1.01	— —	— —

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