

The influence of body mass, climate, and distribution on the energetics of South Pacific pigeons

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Abstract

Rate of metabolism and temperature regulation were studied in 16 species of South Pacific pigeons, which constitute 13 fruit-eaters, 1 seed-eater, 1 fruit/nut-eater, and 1 fruit/leaf-eater; 14 tropical and two temperate species; and ten mainland and six intermediate- or small-island species. The data presented here and those from 11 additional columbids indicate in an analysis of covariance that \log_{10} basal rate of metabolism is correlated with \log_{10} body mass ($P \leq 0.0001$), distribution ($P = 0.0023$), and climate ($P = 0.0016$). These factors account for 94.3% of the variation in \log_{10} basal rate of metabolism. In this analysis the lowest basal rates, corrected for body mass, are found in tropical pigeons living on small oceanic islands, whereas the highest basal rates are found in temperate species living on continents. The reduction of basal rate in large columbids facilitates their long-term persistence on small islands characterized by a limited resource base and unstable weather. Some small-island specialists have a smaller mass than their continental relatives, which further reduces resource requirements. The question whether a reduction in basal rate occurs in small columbids on small islands is unresolved. \log_{10} minimal thermal conductance is apparently correlated only with \log_{10} body mass ($P \leq 0.0001$); $r^2 = 89.4\%$. The mean nocturnal body temperature of columbids is 39.7°C . © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

Only a small fraction of the taxonomic and ecological diversity of birds has been incorporated into the study of avian energetics. Much of this diversity is found in the tropics, whereas most studies of avian energetics have concerned small, seed-eating, temperate passerines or polar seabirds. Few species that belong to families that are restricted to the lowland tropics, or that are tropical representatives of families that have a

climatically broad distribution, have been studied. Nevertheless, previous studies have suggested that basal rate in birds is correlated with body mass (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970; Reynolds and Lee, 1996), taxonomy (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970), food habits (McNab, 1988, 1994b; McNab and Bonaccorso, 1995), foraging style (McNab and Bonaccorso, 1995), climate (Weathers, 1979), plumage colour at low latitudes (Ellis, 1980), body composition (McNab, 1994a), and (for insular species) island size (McNab, 1994b).

A widespread, diverse family is the Columbidae (pigeons and doves), order Columbiformes. Columbids are found from cold-temperate to

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tropical environments and from forests to deserts. Their greatest diversity is in tropical rainforests: of the ≈ 300 species of pigeons and doves, 45 are found in New Guinea, more than any other island and even more than in Colombia (32 species). In contrast, only six living species are native in the United States and two in Canada. Columbids are diverse in the South Pacific today in spite of considerable anthropogenic extinction of the native avifauna (Steadman 1997).

Temperate and desert pigeons feed principally on seeds (Frith et al., 1976), whereas tropical species eat a variety of foods, ranging from seeds [when living in open habitats] to fruits [when living in forested habitats (Frith et al., 1967)]. Some species have distinctive food habits: the Nicobar pigeon, *Caloenas nicobarica*, feeds extensively on large nuts, as well as on fruits (Diamond et al., 1976; Coates, 1985), and the kereru, *Hemiphaga novaeseelandiae*, which lives in sub-tropical and temperate New Zealand, feeds on fruits and flowers in summer and on leaves in winter when fruits are unavailable (McEwan, 1978; Clout et al., 1986; pers. observ.). Columbids also show a diversity in body size, the smallest species being neotropical ground-doves of the genus *Columbina* (30–40 g) and the Australian diamond dove *Geopelia cuneata* (35 g), whereas the largest species is the New Guinean guria, or crowned pigeon (*Goura cristata*), at 2–3 kg — a 75-fold factor in body mass. Another source of diversity in pigeons is found in their patterns of distribution: in the South Pacific some species are limited to small islands, whereas others are limited to continents and large islands, with a few found in both environments.

The object of this study is to examine the factors that influence energy expenditure in pigeons and doves. Nearly all columbids that have had their rates of metabolism previously measured have a small mass, reside in temperate or desert environments on continents, and feed on seeds. Here I present data on 16 species of columbids from the South Pacific, including fruit-, seed-, nut-, and leaf-eating species; temperate and tropical species; small-island and continental species; and species that range in mass from 99 to 3050 g, a 34-fold range. I compare these data with those derived from the literature on ten other columbids and personal observations on the neotropical columbid *Columba leucocephala*.

2. Animals and methods

2.1. Animals

All 16 species of columbids studied were captives that had been maintained in large flight cages. The principal source of these birds was Simon Seeto, a pigeon fancier living near Madang City, Madang Province, Papua New Guinea. In the following list of studied species the source will be given if they came from other than Mr Seeto. The species were *Ptilinopus melanospila* (one male borrowed from the Lowry Park Zoo, Tampa, Florida); *P. perlatus* (one adult, Lowry Park Zoo); *Gymnophaps albertisii* (four individuals, two adults and two subadults, Rainforest Habitat, Technological University, Lae, PNG); *Columba vitiensis* (two adults, Rainforest Habitat); *Ducula pacifica* (four adults); *D. radiata* (two adults, Lowry Park Zoo); *D. rufigaster* (one adult, Lowry Park Zoo); *D. pistrinaria* (three adults); *D. rubricera* (1 adult); *D. zoeae* (two adults, one from Mr Seeto and one from Rainforest Habitat); *D. bicolor* (four adults); *D. pinon* (one adult and one subadult); *Hemiphaga novaeseelandiae* (three adults, Mt. Bruce Conservation Centre, Department of Conservation, New Zealand); *Leucosarcia melanoleuca* (four adults, Wellington Zoo, Wellington, New Zealand); *Caloenas nicobarica* (three adults); and *Goura cristata* (six adults, three from Mr Seeto and three from the National Museum and Art Gallery, NCD, PNG).

2.2. Methods

Rate of metabolism was measured in terms of oxygen consumption as a function of ambient temperature. Pigeons were placed in chambers that varied in size from 8.9 to 45.0 l, depending on the size of the pigeon. Ambient temperature was controlled by placing the chambers into a temperature-controlled refrigerator, modified to increase, as well as to lower, temperature. Room air was sucked continuously through the chamber and then through a column in which, sequentially, CO₂ (by colour-indicating soda lime) and water (by colour-indicating silica gel) were removed, air flow measured, and sent to an Applied Electrochemistry or a Beckman oxygen analyzer, the outputs of which were sent to a stripchart recorder. Air flow rates were sufficient to ensure that the calculated rate of metabolism was inde-

pendent of flow rate, which was demonstrated by varying the flow rate; i.e. flow rates were above a 'critical' value below which the calculated rate depends on flow rate, which in turn depends on chamber volume (McNab, in prep.). The period of exposure to a particular ambient temperature usually varied from 1.5 to 2.5 h to ensure a repeated estimate of the minimal rate of metabolism, which was used to estimate resting rate of metabolism at a defined temperature. The work reported here represents a total of 1851 h of measurements. Pigeon cloacal temperature was measured within 15 s of the end of each experiment with a thermocouple thermometer. The range in ambient temperature to which pigeons were exposed was chosen to define the zone of thermoneutrality and to estimate thermal conductance at temperatures below thermoneutrality, subject to limitations in obtaining low temperatures in New Guinea. Measurements made during the night were preferentially used because they represent the period of inactivity. A few daytime measurements were made in most species; if no difference was seen between daytime and nighttime measurements, these data were combined.

2.3. Data preparation

The rate of metabolism in thermoneutrality was analyzed to determine whether it differed among individuals. In eight of the 12 species that had two or more adults available to estimate basal rate, no difference in basal rate was found among the individuals. In two other species (*G. cristata*, *D. pinon*) the interindividual variation in basal rate was correlated with body mass; in these species no difference in basal rate was found among individuals when the rates were compared to the values expected from body mass. In *D. pistrinaria* and *C. nicobarica* a difference in basal rate among individuals was found that was not correlated with mass, but only in the latter was a large individual difference in basal rate found after the data were expressed relative to the fitted relationship between basal rate and body mass in columbids. Therefore, a sample size of one individual can be usually viewed as a reasonable first estimate of the basal rate of the species if the individual is measured > 5 times. Calculation of individual basal rates 1) clarify whether the basal rate suggested to be characteristic of a species is internally consistent; and 2) estimate the physiological diversity in

a population, thereby permitting a shift from a typological to a populational description of energy expenditure.

Thermal conductance was calculated as $C = \dot{V}_{O_2} / \Delta T$, where \dot{V}_{O_2} is the rate of metabolism and ΔT is the temperature differential between the body and environment (McNab, 1980). Attempts to separate thermoneutral from lower ambient temperatures and to define thermal conductance by a two-phase regression (Nickerson et al., 1989) are inappropriate when thermal conductance is not constant at temperatures below thermoneutrality because the slope of the fitted curve is not thermal conductance (McNab, 1980). Statistical data are given as mean \pm S.E. (n , measurements).

2.4. Statistics

A SuperANOVA© program was used to calculate the ANCOVA analyses presented here. In an attempt to determine the factors that influence basal rate or minimal thermal conductance, \log_{10} basal rate (or \log_{10} minimal conductance) were designated as the dependent variables and \log_{10} body mass, 'body size', food habits, climate, distribution, and genus were designated as the independent variables. The categorical variables included body size, which divides pigeons into two categories [small (< 200 g) and large (> 200 g)] to determine if a 'break' occurs in the scaling of basal rate; food habits (seeds, fruit, nuts, leaves); climate (desert, tropical, temperate); distribution (found on continents, intermediate-sized islands, or limited to small islands); and genus. Note that in the case of distribution, some pigeon species are found on mainlands (continents or large islands) and on adjacent small islands; those species were considered to be mainland species. Small-island species are defined as those limited in distribution to small islands. In a third, intermediate category, some species are only found on intermediate-sized islands, such as New Britain and New Ireland, whereas others are primarily located on small islands, but occasionally enter the coastal lowlands of a few large islands. The absence of a phylogeny for columbids (D.W. Steadman, pers. comm.) prevented any detailed analysis of the influence of phylogeny on the physiological characteristics of columbids, although their assignment to genus may be a weak substitute for such an analysis. Westoby et al. (1995), however, suggested that most recent at-

tempts to determine the impact of phylogeny on phenotypic characters are flawed by their assumption on the primacy of phylogeny as the determining factor and do not take character interaction into consideration.

All factors were introduced simultaneously at the beginning of a covariant analysis. Factors were dropped sequentially as they failed to show significance in order from least significant to marginally significant until the largest number of significant factors were obtained (significance being defined as $P \leq 0.05$). Sometimes previously eliminated factors were brought back in the analysis to be sure that they were not eliminated because of interaction with other factors.

3. Results

Rate of oxygen consumption and body temperature were plotted as a function of ambient temperature in Figs. 1–6 for the 16 species studied. Nearly every experiment in which oxygen consumption was measured (indicated in the lower of the two panels for a species) has a body temperature (indicated in the upper panel). Here details of the physiology of individual species are described; an analysis of the general patterns found amongst columbids is addressed in Section 4.

3.1. *Ptilinopus melanospila*

One male of the sexually dimorphic black-naped fruit-dove, a species that is found at altitudes up to 1600 m from Java and the Philippines to Sulawesi and the Lesser Sunda Islands, was studied. The mean mass of this individual was 98.7 ± 0.65 g ($n = 44$). Thermoneutrality extended from 22 to 33°C (Fig. 1a) within which basal rate of metabolism was 1.17 ± 0.031 cm³ O₂/g·h ($n = 13$), which is 103% of the value expected from the fitted all-columbid basal-rate curve (see Section 4). The daytime rate of metabolism in thermoneutrality was 1.65 ± 0.206 cm³ O₂/g·h ($n = 4$). Minimal thermal conductance was 0.072 ± 0.0013 cm³ O₂/g·h°C ($n = 13$), which is 86% of the value expected from the fitted all-columbid minimal-conductance curve (see Section 4). Body temperature at night was 38.9 ± 0.19 °C ($n = 18$) at ambient temperatures below 27°C, whereas during daytime it was 41.2 ± 0.39 °C ($n = 6$). Occasionally body temperature fell to about 35°C when ex-

posed at night to cool temperatures; these lower body temperatures corresponded to lower rates of metabolism and a lower thermal conductance (0.057 ± 0.0020 cm³ O₂/g·h°C ($n = 3$)).

3.2. *Ptilinopus perlatus*

A single pink-spotted fruit-dove, a species widespread in lowland New Guinea up to 1200 m, was examined. Its mean mass was 196.0 ± 0.73 g ($n = 35$). Thermoneutrality extended from 24 to 32°C (Fig. 1b). Basal rate of metabolism was 0.971 ± 0.0210 cm³ O₂/g·h ($n = 16$), which is 112% of the value expected from the all-columbid curve; it includes measurements made during the day and at night because no difference between these measurements was seen (Fig. 1b). Minimal thermal conductance was found at ambient temperatures < 19°C, when it equaled 0.063 ± 0.0018 cm³ O₂/g·h°C ($n = 8$), which is 109% of the expected value and corresponded to the lower limit of thermoneutrality. A higher conductance, equal to 0.078 ± 0.0027 cm³ O₂/g·h°C ($n = 5$), was found between 19 and 24°C. Mean night-time body temperature at ambient temperatures < 25.5°C was 39.5 ± 0.38 °C ($n = 5$); during the day body temperature was 40.4 ± 0.18 °C ($n = 11$).

3.3. *Gymnophaps albertisii*

Four Papuan mountain-pigeons were measured, two adults and two subadults. This pigeon is widely distributed in New Guinea from sea level to 3350 m. The mean mass of the adults was 241.6 ± 1.14 g ($n = 29$). Thermoneutrality extended from 22 to 36°C (Fig. 1c) within which the pooled basal rate, measured at night, was 0.701 ± 0.0137 cm³ O₂/g·h ($n = 17$), which is 88% of the basal rate expected from mass. No difference was found in the basal rate between the two adults ($F = 0.35$; $P = 0.57$); they had basal rates that were 86(8) and 89(9)% of the expected values (the number of measurements for each individual in parentheses). During the day, the rate of metabolism in thermoneutrality was 0.884 ± 0.0170 cm³ O₂/g·h ($n = 6$). The lower limit of thermoneutrality was defined by a conductance equal to 0.040 cm³ O₂/g·h°C ($n = 1$), which is 78% of the expected value, whereas a somewhat higher conductance was usually encountered, namely 0.055 ± 0.0018 cm³ O₂/g·h°C ($n = 4$). Body temperature in the adults at night equaled $39.2 \pm$

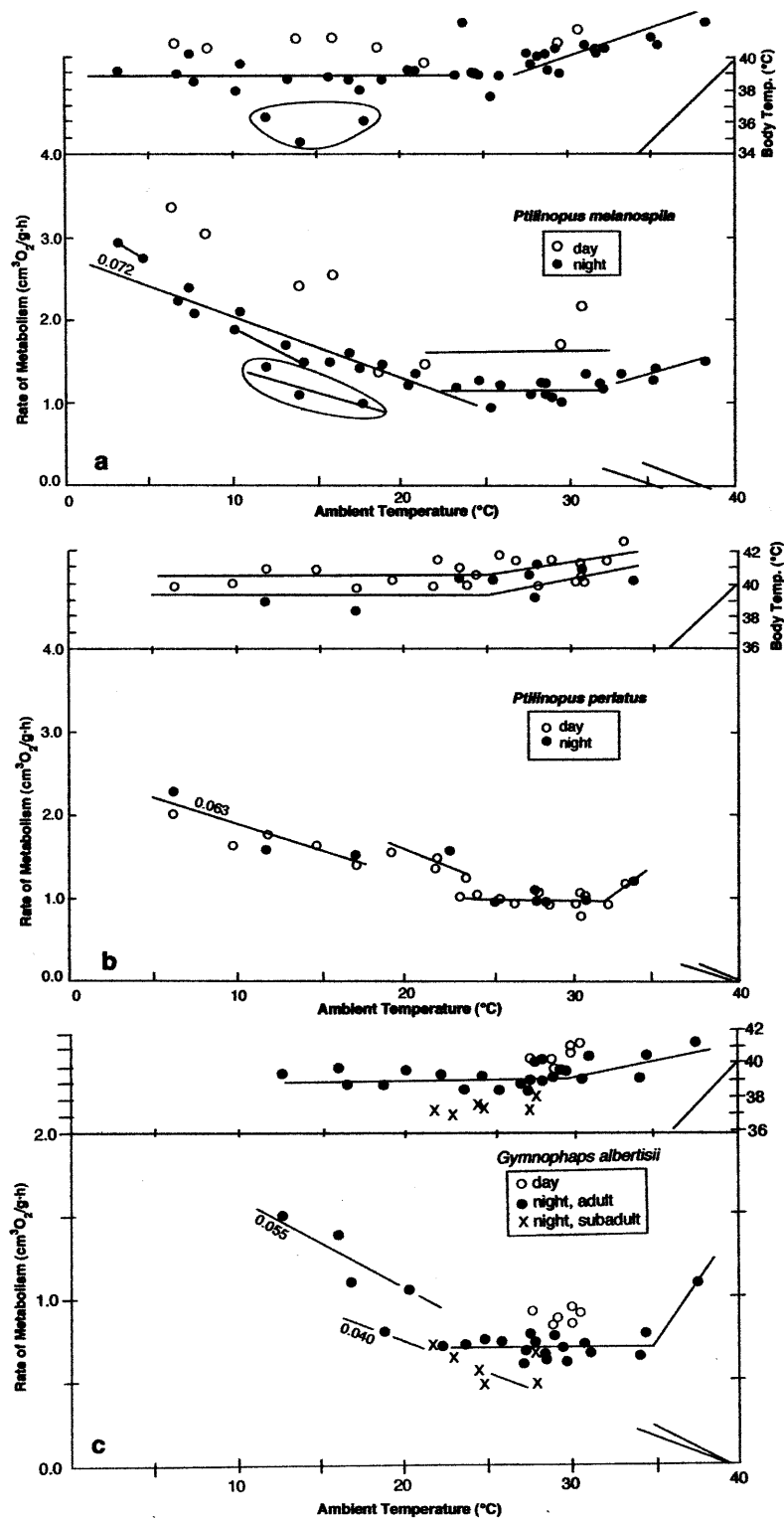


Fig. 1. Rate of oxygen consumption and body temperature as a function of ambient temperature in (a) one black-naped fruit-dove (*Ptilinopus melanospila*); (b) one pink-spotted fruit-dove (*Ptilinopus perlatus*); and (c) four Papuan mountain pigeons (*Gymnophaps albertisii*). Measurements with low body temperatures and rate of metabolism are circled.

0.16°C ($n = 13$) at ambient temperatures $< 28^{\circ}\text{C}$. Daytime body temperature was $40.1 \pm 0.22^{\circ}\text{C}$ ($n = 3$). Compared to adults, subadults had a

smaller mass ($178.0 \pm 1.53 \text{ g}$ ($n = 8$)), lower measurements in thermoneutrality ($0.552 \pm 0.0428 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 4$), or 61% of the columbid basal

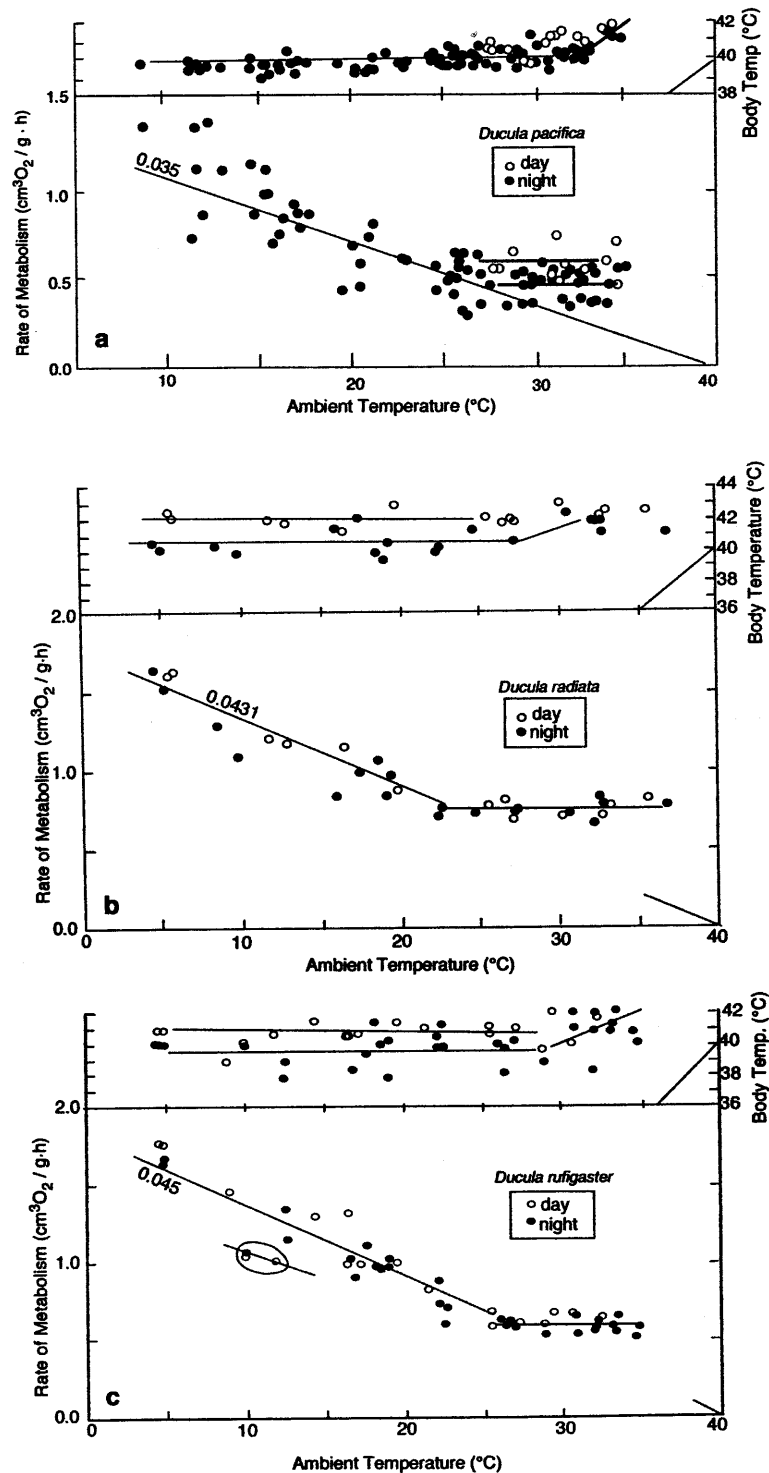


Fig. 2. Rate of oxygen consumption and body temperature as a function of ambient temperature in (a) four Pacific imperial-pigeons (*Ducula pacifica*); (b) two zone-tailed imperial-pigeons (*Ducula radiata*); and (c) one purple-tailed imperial-pigeon (*Ducula rufigaster*).

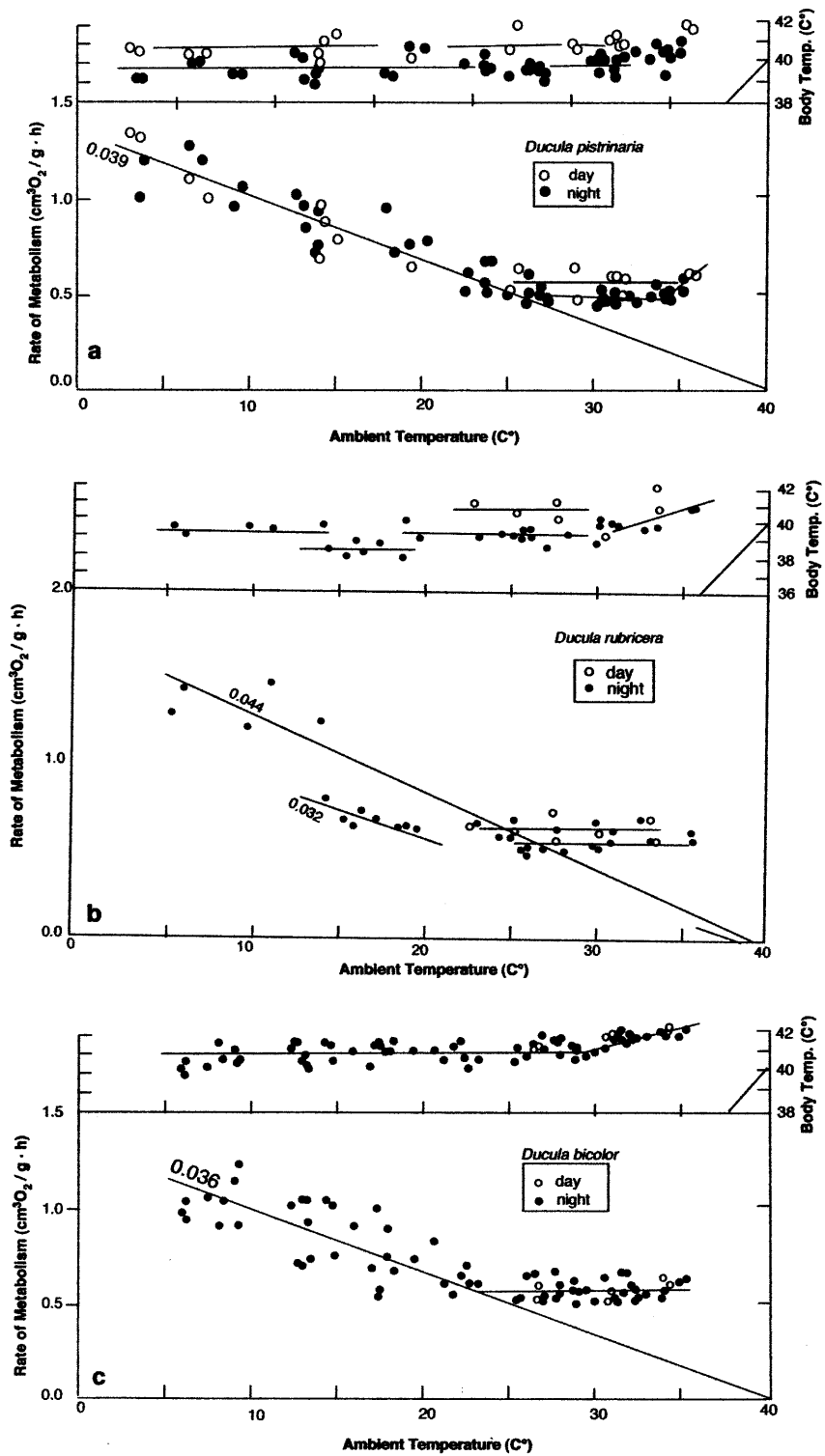


Fig. 3. Rate of oxygen consumption and body temperature as a function of ambient temperature in three grey imperial-pigeons (*Ducula pistrinaria*); (b) one red-knobbed imperial-pigeon (*Ducula rubricera*); and (c) four pied imperial-pigeons (*Ducula bicolor*).

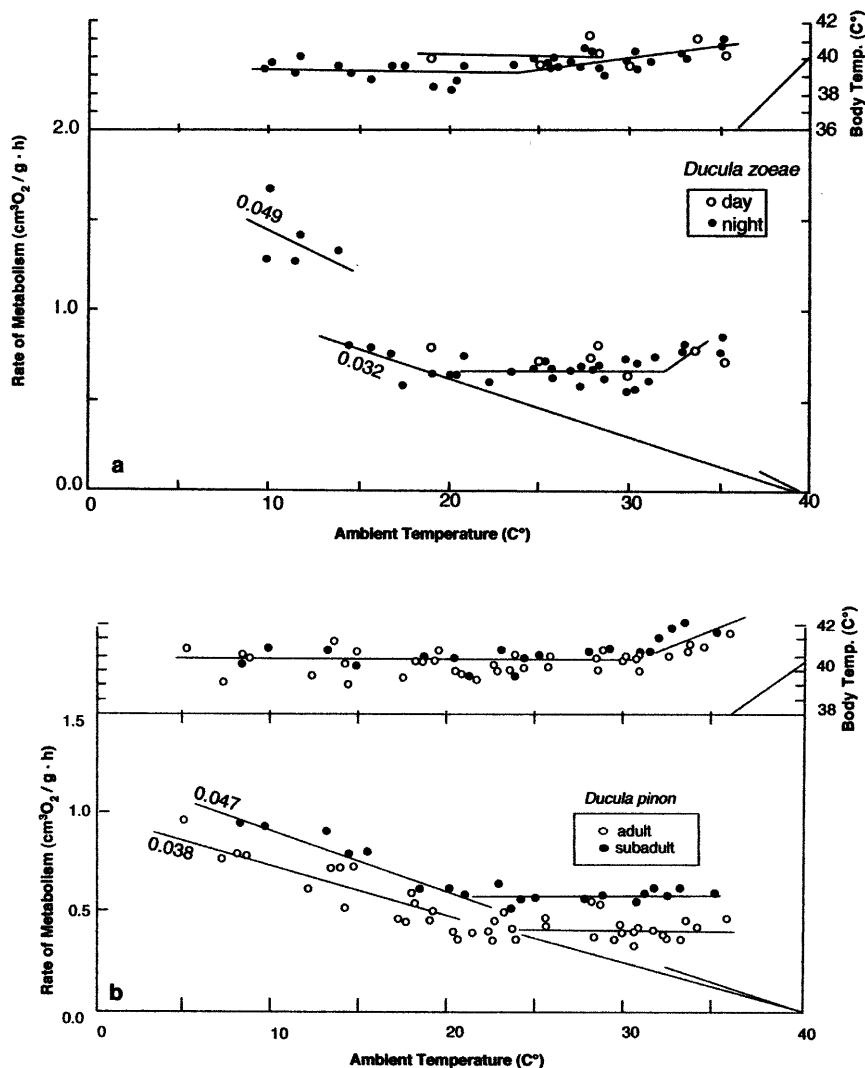


Fig. 4. Rate of oxygen consumption and body temperature as a function of ambient temperature in (a) two zoe imperial-pigeons (*Ducula zoeae*); and (b) two pinon imperial-pigeons (*Ducula pinon*).

standard), and a body temperatures that was about 2°C lower (Fig. 1c).

3.4. *Ducula pacifica*

Four Pacific imperial-pigeons were studied; they came from small islands along the north coast of Papua New Guinea. This supertramp species is limited in distribution to small islands from New Guinea to Tonga, Fiji, Samoa, and the Cook Islands. The mean body mass was 333.4 ± 2.90 g ($n = 104$). The zone of thermoneutrality extended from 27.5 to at least 35°C (Fig. 2a) within which the pooled basal rate of metabolism

(measured at night) was 0.427 ± 0.0141 cm³ O₂/g·h ($n = 31$), or 61% of the rate expected from mass. This is the lowest basal rate, compared to the all-columbid standard, of all the pigeons measured in this study; it is even lower compared to the Aschoff–Pohl (1970) nonpasserine standard, 51%. The basal rate in this species does not vary among the four individuals ($F = 0.64$; $P = 0.60$); their rates were 57(6), 58(6), 59(10), and 66(9)% of the expected values, the mean of which is 60%. Mean daytime rate of metabolism in thermoneutrality was 0.540 ± 0.026 cm³ O₂/g·h ($n = 11$), which still is only 77% of the expected basal rate and emphasizes the low basal rate found in this

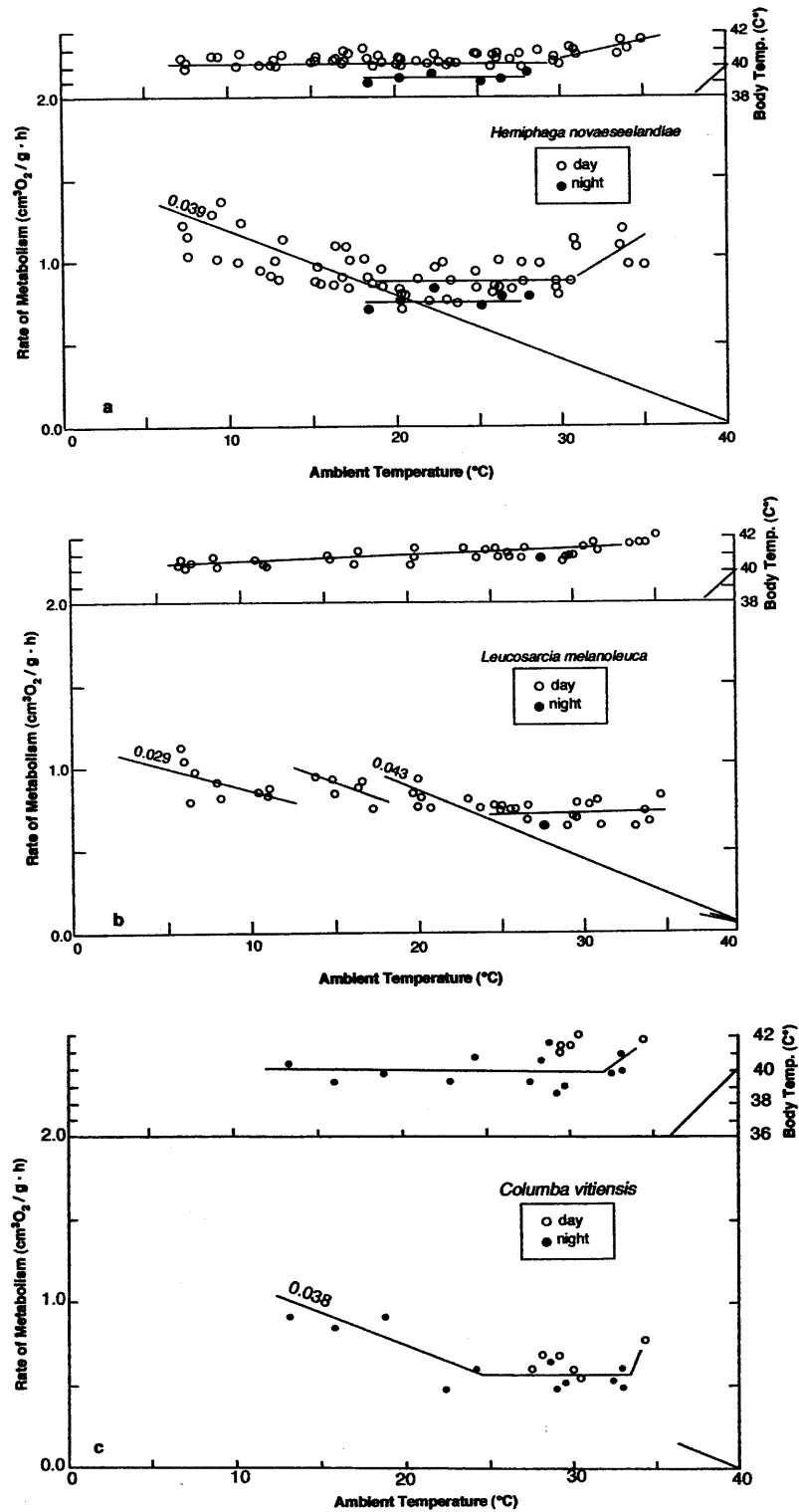


Fig. 5. Rate of oxygen consumption and body temperature as a function of ambient temperature in (a) three kereru (*Hemiphaga novaeseelandiae*); (b) four wonga pigeons (*Leucosarcia melanoleuca*); and (c) two white-throated pigeons (*Columba vitiensis*). Note that all experiments, but one, in the wonga were made during daylight hours and therefore probably do not represent 'standard' conditions.

species. An appreciable scatter is found in rate of metabolism below thermoneutrality, which does not reflect a variation in body temperature (Fig. 2a): the combined estimate of thermal conductance was $0.035 \pm 0.0012 \text{ cm}^3\text{O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 43$), which is 82% of the conductance expected from mass. Body temperature equaled $39.8 \pm 0.05^\circ\text{C}$ ($n = 69$) at ambient temperatures between 23 and 31.5°C during the night and tended to be slightly lower at $T_{a,s} < 23^\circ\text{C}$, when it equaled $39.6 \pm$

0.06°C ($n = 34$). Daytime body temperature was somewhat higher ($40.5 \pm 0.11^\circ\text{C}$ ($n = 4$)).

3.5. *Ducula radiata*

Two zone-tailed imperial-pigeons, a species found at altitudes between 200 and 2400 m in Sulawesi, were measured; they weighed $333.6 \pm 2.27 \text{ g}$ ($n = 35$). Their rate of metabolism in thermoneutrality, which extended from 22 to 37°C

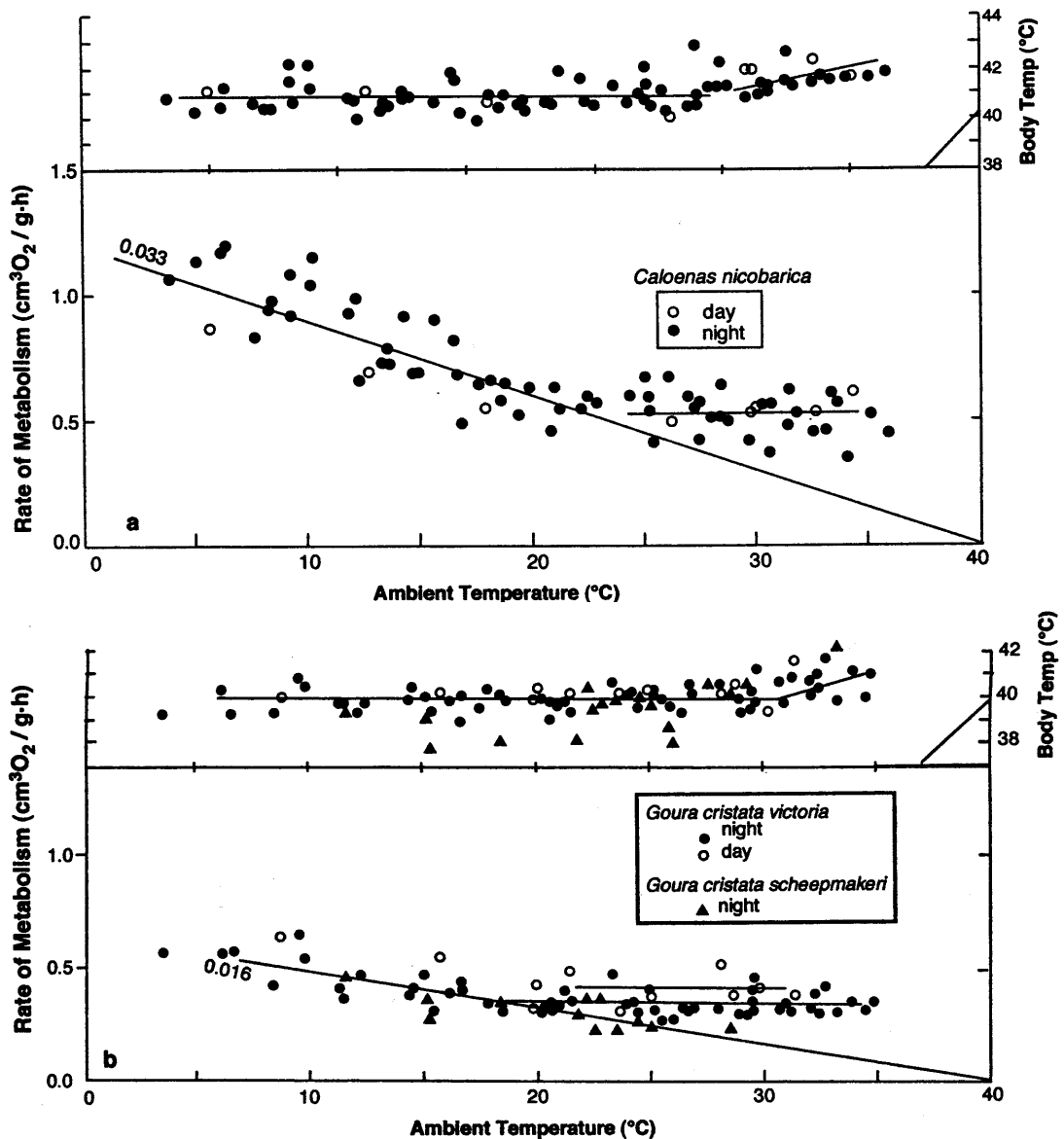


Fig. 6. Rate of oxygen consumption and body temperature as a function of ambient temperature in (a) three Nicobar pigeons (*Caloenas nicobarica*); and (b) six guria, or crowned pigeons (*Goura cristata*), representing two of the three described subspecies (see text).

(Fig. 2b), was the same in day and night. The pooled basal rate was $0.756 \pm 0.0109 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 17$), which is 107% of the expected rate. These individuals showed no difference in their basal rate ($F = 4.1 \times 10^{-4}$; $P = 0.98$); they had basal rates equal to 106(8) and 108(9)% of the expected values. Thermal conductance was $0.043 \pm 0.0009 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 13$), or 100% of expected. At ambient temperatures $< 28^\circ\text{C}$, nighttime body temperature was $40.6 \pm 0.21^\circ\text{C}$ ($n = 11$), whereas the daytime temperature was $42.0 \pm 0.15^\circ\text{C}$ ($n = 10$). Two experiments at temperatures below thermoneutrality produced slightly lower rates of metabolism and body temperatures (Fig. 2b).

3.6. *Ducula rufigaster*

One purple-tailed imperial-pigeon was studied; this species is widely distributed in lowlands up to 600 m New Guinea and on a few adjacent islands. It weighed $376.7 \pm 6.01 \text{ g}$ ($n = 49$). Thermoneutrality extended from 26 to at least 35°C (Fig. 2c). Measurements of rate of metabolism were independent of time of day, so daytime and nighttime values were combined: basal rate was $0.606 \pm 0.0103 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 21$), which is 90% of the all-columbid basal rate. Thermal conductance in this pigeon was $0.045 \pm 0.0010 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 26$), which is 112% of the expected value. At ambient temperatures $< 29^\circ\text{C}$, nocturnal body temperatures equaled $39.7 \pm 0.21^\circ\text{C}$ ($n = 22$), whereas the mean diurnal body temperature was $40.6 \pm 0.17^\circ\text{C}$ ($n = 14$).

3.7. *Ducula pistrinaria*

Three grey imperial-pigeons were studied; they came from near or on Manus Island in the Admiralty Islands. This species is found on small islands at altitudes up to 250 m along the north coast of New Guinea eastward through the Bismarck Archipelago to the Solomon Islands. Mean body mass was $394.2 \pm 4.27 \text{ g}$ ($n = 71$). The zone of thermoneutrality extended from 27 to 35°C (Fig. 3a) within which the pooled basal rate of metabolism was $0.488 \pm 0.0062 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 23$). This rate is 74% of the all-columbid basal rate and 61% of the Aschoff–Pohl nonpasserine curve, the second lowest basal rate measured. A difference was found among the three individuals in their basal rates ($F = 4.87$;

$P = 0.019$), which not correlated with body mass ($F = 0.23$; $P = 0.64$): one individual had a basal rate that was different from the other two and was 77(7)% of the value expected from mass, whereas the other two had basal rates that were not significantly different ($t = 1.36$; $P = 0.19$) and equaled 71(14) and 74(2)%, the mean of the three individuals being 74%. During daylight hours, the rate in thermoneutrality equaled $0.562 \pm 0.0218 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 8$), which is still only 85% of the expected basal rate. Below thermoneutrality, rate of metabolism was independent of time of day. Thermal conductance equaled $0.039 \pm 0.0009 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 31$), which is 99% of the expected conductance. The body temperature in this pigeon at ambient temperatures $< 33^\circ\text{C}$ varied with time of day: the nocturnal temperature equaled $39.7 \pm 0.08^\circ\text{C}$ ($n = 38$), whereas the diurnal temperature was $40.8 \pm 0.11^\circ\text{C}$ ($n = 17$).

3.8. *Ducula rubricera*

One adult red-knobbed imperial-pigeon, which came from New Ireland and is limited in distribution to the Bismarck Archipelago and the Solomon Islands at altitudes up to 1000 m, was studied. This intermediate-island species had a mean mass of $418.8 \pm 1.04 \text{ g}$ ($n = 39$). Thermoneutrality extended from 24 to about 36°C (Fig. 3b) within which basal rate (measured at night) was $0.584 \pm 0.0150 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 18$). This rate is 91% of that expected from the all-columbid curve and 75% of the Aschoff–Pohl nonpasserine curve. During daytime the mean rate measured in thermoneutrality was $0.644 \pm 0.0225 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}$ ($n = 7$). No one thermal conductance describes rate of metabolism in this individual below thermoneutrality. The conductance that corresponds to the lower limit of thermoneutrality was $0.044 \pm 0.0016 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 8$), which corresponds to a body temperature of $39.4 \pm 0.09^\circ\text{C}$ ($n = 15$) at ambient temperatures $< 30^\circ\text{C}$. However, at ambient temperatures between 15 and 20°C , when body temperature equaled $38.4 \pm 0.16^\circ\text{C}$ ($n = 6$), thermal conductance was $0.032 \pm 0.0007 \text{ cm}^3 \text{ O}_2/\text{g}\cdot\text{h}^\circ\text{C}$ ($n = 8$). This lower conductance is 84% of the value expected from mass. Body temperature during the daytime equaled $40.8 \pm 0.23^\circ\text{C}$ ($n = 4$).

3.9. *Ducula bicolor*

Four pied imperial-pigeons were studied. They came from small islands off the north coast of Madang province, PNG, which some authors refer to *D. spilorrhoea*, but now is usually relegated to subspecific status (Beehler et al., 1986; Sibley and Monroe, 1990). Broadly defined, this species is found on small islands from the Andamans and Nicobars in the Indian Ocean through Indonesia eastward to New Guinea, the Torres Strait, and northern Australia, although it does limitedly invade the lowlands of New Guinea along some river courses and therefore is tentatively classified as an intermediate-island species (see Section 4). Mean body mass was 453.6 ± 3.85 g ($n = 72$). Thermoneutrality is found at ambient temperatures from 26 to 36°C (Fig. 3c). Rates of metabolism within thermoneutrality did not vary with time of day: pooled basal rate equaled 0.543 ± 0.0084 cm³ O₂/g·h ($n = 37$), which is 87% of the basal rate expected from the all-columbid curve and 71% of the Aschoff–Pohl nonpasserine curve. The basal rates of the four individuals were not different ($F = 0.70$; $P = 0.56$): they were 83(12), 86(6), 88(7), and 91(11)% of the values expected from mass, the mean of which is 87%. Rate of metabolism is variable at temperatures below thermoneutrality and independent of body temperature (Fig. 3c): the combined estimate for thermal conductance is 0.036 ± 0.0010 cm³ O₂/g·h°C ($n = 35$), which is 98% of the conductance expected from mass. The mean nocturnal body temperature at ambient temperatures < 31°C equaled 40.7 ± 0.07 °C ($n = 52$), whereas two measurements of daytime body temperature equaled 40.9°C.

3.10. *Ducula zoeae*

Two adult zoe imperial-pigeons, a resident of the lowlands and hills up to 1500 m in New Guinea, were studied. Most measurements were made on one individual, which weighed 456.6 ± 2.30 g ($n = 40$). Its zone of thermoneutrality ranged from 19 to 32°C (Fig. 4a) within which the basal rate of metabolism was 0.670 ± 0.0122 cm³ O₂/g·h ($n = 20$), which is 108% of the expected basal rate from the all-columbid curve. The second individual, which was measured only in thermoneutrality, had a mean mass of

602.3 ± 7.69 g ($n = 3$) and a mean rate equal to 0.609 ± 0.0035 cm³ O₂/g·h ($n = 3$), which is 109% of the all-columbid value. During the day, rate of metabolism in thermoneutrality was 0.750 ± 0.0215 cm³ O₂/g·h ($n = 7$). Rate of metabolism at ambient temperatures < 19°C was highly variable (Fig. 4a). The thermal conductance that defined the lower limit of thermoneutrality was 0.032 ± 0.0019 cm³ O₂/g·h°C ($n = 4$), or 88% of the value expected from the smaller individual, the only one measured at temperatures below thermoneutrality. Conductance was much higher at temperatures < 14°C (0.049 ± 0.0023 cm³ O₂/g·h°C ($n = 5$)). The smaller individual repeatedly showed a bout of shivering after being removed from an exposure to temperatures < 20°C. Mean body temperature at night in this species at ambient temperatures < 25°C was 39.3 ± 0.14 °C ($n = 14$); during the day body temperature equaled 40.2 ± 0.30 °C ($n = 5$).

3.11. *Ducula pinon*

Two pinon imperial-pigeons, one adult and one subadult, were studied. This species is widely distributed at altitudes below 800 m in New Guinea and on a few adjacent islands. The mean mass of the adult was 583.8 ± 2.11 g ($n = 42$) and the subadult was 449.7 ± 1.44 g ($n = 19$). All experiments were performed at night. Thermoneutrality in the adult extended from 23 to near 37°C (Fig. 4b), within which basal rate of metabolism was 0.547 ± 0.0117 cm³ O₂/g·h ($n = 25$), or 97% of the value expected from mass. In the subadult thermoneutrality had a similar temperature range, but basal rate equaled 0.789 ± 0.0127 cm³ O₂/g·h ($n = 12$), which is 126% of the expected rate. Thermal conductance in the adult was 0.038 ± 0.0010 cm³ O₂/g·h°C ($n = 15$), which is 119% of the expected value, whereas that of the subadult was 0.047 ± 0.0006 cm³ O₂/g·h°C ($n = 7$), or 129% of the expected value. The body temperature of the adult (39.7 ± 0.12 °C ($n = 31$)) at ambient temperatures < 32°C was slightly lower ($F = 4.63$; $P = 0.037$) than in the subadult (40.2 ± 0.19 °C ($n = 13$)). Why the subadult had a much higher standard rate of metabolism, a higher thermal conductance, and a higher body temperature is not clear; it was not obviously due to greater activity in the subadult.

3.12. *Hemiphaga novaeseelandiae*

Three adult kereru, or New Zealand pigeons, were studied. This species is found on the three main islands to an altitude of 1000 m and on the Chatham Islands. Their mean mass was 443.0 ± 5.92 g ($n = 64$). Thermoneutrality extended from about 20 to 30°C (Fig. 5a), a lower temperature range than was found in other species of a similar or smaller mass, as might be expected in a temperate species. Most of the measurements of rate of metabolism occurred during daytime. Within thermoneutrality the daytime pooled rate of metabolism was 0.870 ± 0.0168 cm³ O₂/g·h ($n = 25$), which is 138% of the basal rate expected in columbids. One individual had a higher daytime mass-specific rate in thermoneutrality than the other two ($F = 9.19$; $P = 0.0013$), in spite of its larger mass ($F = 424.03$; $P < 0.0001$), so that its higher rate was not due to scaling. The three individuals had rates in thermoneutrality that were 129(11), 131(7), and 160(7)% of the basal rates expected from mass, the mean of which is 140%. Measurements of basal rate at night were only made on one individual; its rate was 0.776 ± 0.0186 cm³ O₂/g·h ($n = 6$), which is 122% of the basal rate expected from its mass (435.6 g), down from the daytime rate that was 131% of expected. Mean thermal conductance in this species during the day was 0.039 ± 0.0008 cm³ O₂/g·h°C ($n = 28$), which is 105% of the value expected in columbids. Body temperature at ambient temperatures < 30°C during daytime was 40.4 ± 0.04 °C ($n = 52$), whereas at night it was 39.3 ± 0.08 °C ($n = 6$).

3.13. *Leucosarcia melanoleuca*

Four wonga pigeons, a seed-eating species from the woodlands of eastern Australia to an altitude of 900 m, were studied almost exclusively during daytime. Their mean mass was 466.1 ± 12.62 g ($n = 40$). The zone of thermoneutrality extended from 24 to 36°C (Fig. 5b), within which the pooled diurnal rate of metabolism equaled 0.734 ± 0.0129 cm³ O₂/g·h ($n = 20$), which is 119% of the basal rate expected from columbids. No differences were seen in the rate of metabolism among the three individuals measured in thermoneutrality ($F = 0.47$; $P = 0.63$); they had rates equal to 119(7), 120(6), and 120(7)% of the expected basal rates, the mean of which is 120%. Only one measurement was made at night in an

individual that had a diurnal rate equal to 120%; the nocturnal rate was 0.641 cm³ O₂/g·h, which is 104% of the basal rate expected from columbids (based on a mass equal to 468 g). Note that this rate is similar to the lowest rates measured in thermoneutrality during the day (Fig. 5b), which suggests that energy is expended during the day occasionally at the basal rate.

Thermal conductance in the wonga pigeon is not constant at temperatures below thermoneutrality (Fig. 5b). Two conductances are of interest: one defines the lower limit of thermoneutrality, 0.043 ± 0.0035 cm³ O₂/g·h°C ($n = 3$), which is 120% of the expected value, and the other is minimal, 0.029 ± 0.0008 cm³ O₂/g·h°C ($n = 9$), which is 81% of the conductance expected from body mass. Caution suggests, however, that even lower conductances might have been encountered if these pigeons had been exposed to ambient temperatures below 5°C. Daytime body temperature in this species tended to decrease slightly with a fall in environmental temperature (Fig. 4b), the mean being 40.7 ± 0.01 °C ($n = 9$) at air temperatures < 21°C. The one measurement of the nocturnal body temperature was 40.7°C.

3.14. *Columba vitiensis*

Two adult white-throated pigeons, collected from the PNG highlands (> 1200 m) near Mumeng (Morobe Province), were studied. This species is widespread from the Philippines, the Lesser Sundas, and the Moluccas through New Guinea, where it is found up to 2750 m, to Fiji and Samoa. Body mass in this species was 467.9 ± 5.91 g ($n = 16$). Thermoneutrality extended from 22 to 34°C (Fig. 5c). The pooled basal rate of metabolism, measured at night, was 0.555 ± 0.0204 cm³ O₂/g·h ($n = 9$), which is 90% of the basal rate expected from mass. No difference in basal rate was found between the two individuals ($F = 0.81$; $P = 0.78$); they had basal rates that were 88(5) and 92(4)% of the expected rates, the mean being 90%. During daytime, the rate of metabolism in thermoneutrality was 0.625 ± 0.0322 cm³ O₂/g·h ($n = 4$). The thermal conductance that defines the lower limit of thermoneutrality was 0.038 ± 0.0027 cm³ O₂/g·h°C ($n = 3$), which is 106% of the value expected from mass. At ambient temperatures < 30°C body temperature at night was 39.9 ± 0.30 °C ($n = 10$); during the day it was 41.6 ± 0.21 °C ($n = 4$).

3.15. *Caloenas nicobarica*

Three Nicobar pigeons were studied. This species is usually limited in distribution to altitudes below 400 m on small islands from the Nicobars in the Indian Ocean eastward to the Solomon Islands and Palau, but is also found in the lowlands of some intermediate islands, such as New Britain and New Ireland (Coates, 1985). The individuals studied came from small islands in Madang Province, PNG. Their mean mass was 613.0 ± 5.61 g ($n = 74$). Thermoneutrality extended from 25 to 37°C (Fig. 6a). Within this region pooled basal rate equaled 0.531 ± 0.0142 cm³ O₂/g·h ($n = 34$), which is 96% of the all-columbid rate and 75% of the Aschoff–Pohl non-passerine curve; no difference was found in rate of metabolism between day and night. However, a difference was found among the basal rates of the three individuals studied ($F = 6.12$; $P = 0.0057$); these individuals had basal rates equal to 80(7), 92(10), and 104(17)% of the expected values, the mean of which is 92%. This individual variation in basal rate, independent of mass, is greater than in any other species of pigeon studied, the causes of which are unknown. Thermal conductance at temperatures < 25°C was 0.033 ± 0.0008 cm³ O₂/g·h°C ($n = 39$), which is 108% of the expected value. Mean body temperature at ambient temperatures < 29°C was 40.9 ± 0.08 °C ($n = 54$), with no difference between day and night.

3.16. *Goura cristata*

Six individuals of the crowned pigeon, or guria, the largest living pigeon, were studied. Four individuals came from the Ramu river valley in Madang Province; they belonged to what is usually called the Victoria crowned pigeon, *G. victoria*. The other two crowned pigeons belonged to the southern crowned pigeon, *G. scheepmakeri* (see Beehler et al., 1986); they were obtained in the Owen-Stanley Mountains at altitudes less than 500 m. Sibley and Monroe (1990) recognized these populations as two of three subspecies that comprise one species of crowned pigeon, *G. cristata*. Data on energetics are presented for each subspecies, the specific identity for each population being retained in case they are considered separate species, and in combination, under the assumption that only one species of crowned pigeon exists.

Thermoneutrality in this species extended from 19 to 35°C, irrespective of subspecies affiliation (Fig. 6b). The pooled basal rate of metabolism in *G. c. victoria* was 0.344 ± 0.0074 cm³ O₂/g·h ($n = 38$), which is 102% of the value expected from a mean mass of 2187.2 ± 48.34 g ($n = 70$). Although one individual had a higher mass-specific basal rate than the other three ($F = 9.33$; $P \leq 0.0001$), it had a smaller body mass (1739.0 g). These four individuals had basal rates that were not different ($F = 3.61$; $P = 0.087$) when expressed relative to the rates expected from the all-columbid curve: 96(7), 101(11), 105(8), and 106(12)%, the mean of which is 103%. During daytime rate of metabolism in thermoneutrality was 0.406 ± 0.0225 cm³ O₂/g·h ($n = 9$). In *G. c. scheepmakeri* the pooled basal rate was 0.290 ± 0.0152 cm³ O₂/g·h ($n = 12$), which is 96% of the value expected from a mean mass of 2832.9 ± 60.63 g ($n = 17$). No difference was found in the basal rate between the two individuals that belonged to this subspecies ($F = 3.61$; $P = 0.09$); they had basal rates that were 91(7) and 102(5)% of the expected values. The pooled estimate of basal rate for *G. cristata*, combined for the two subspecies, was 0.331 ± 0.0208 cm³ O₂/g·h ($n = 50$), which is 101% of the value expected from a mean mass equal to 2313.4 ± 49.03 g ($n = 87$). When these populations are considered to be one species, they collectively have an appreciable range in individual basal rate, varying from 91 to 106% of the all-columbid curve, the most deviant value (91%) occurring in the largest individual (3053.3 g); the mean basal rate of these individuals is 100%.

Minimal thermal conductance in *G. c. victoria*, which corresponds to the lower limit of thermoneutrality (Fig. 6b), equaled 0.0168 ± 0.00065 cm³ O₂/g·h°C ($n = 18$), which is 109% of the value expected from a mass of 2166.3 g. The few measurements below thermoneutrality in *G. c. scheepmakeri* was 0.0154 ± 0.00105 cm³ O₂/g·h°C ($n = 4$), which is 115% of the value expected from a mass of 2832.9 g. When these data are combined, thermal conductance in *G. cristata* equaled 0.0160 ± 0.00045 cm³ O₂/g·h°C ($n = 22$), which is 107% of the value expected from 2313.4 g. Body temperature at ambient temperatures < 30°C in this species at night equaled 39.8 ± 0.08 °C ($n = 60$), whereas during the daytime body temperature equaled 40.3 ± 0.11 °C ($n = 10$).

4. Discussion

The fundamental parameters of pigeon energetics are the basal rate of metabolism, minimal thermal conductance, and body temperature, each of which will be examined in turn. The data available from 27 species of columbids are summarized in Table 1.

4.1. Basal rate of metabolism

4.1.1. Circadian variation

An examination of pigeons included in this study indicates a highly variable circadian variation in the thermoneutral rate of metabolism. Daytime:night-time ratio of thermoneutral rate of metabolism varied from 1.00 to 1.40, the mean of which is 1.12. This ratio is not known to correlate with any factor, including \log_{10} body mass ($F = 0.92$; $P = 0.35$).

4.1.2. Analysis of covariance

An analysis of covariance was made of basal rate in 27 species: \log_{10} basal rate is correlated with \log_{10} body mass ($P \leq 0.0001$, $r^2 = 0.873$). The ability to account for the variation in \log_{10} basal rate is improved when climate and distribution are added to \log_{10} mass. Then \log_{10} basal rate is correlated with all three factors ($F = 6.34$, $P = 0.0069$; $F = 6.41$, $P = 0.0067$; $F = 180.68$, and $P \leq 0.0001$, respectively); $r^2 = 0.948$. \log_{10} basal rate is correlated ($r^2 = 0.985$) with genus ($F = 4.31$, $P = 0.0108$) when coupled with \log_{10} mass ($F = 33.49$, $P \leq 0.0001$) and distribution ($F = 10.48$, $P = 0.0028$), as long as climate is not included in the analysis, which reflects a climate-based distribution of columbid genera. That is, *Geopelia*, *Scardafella*, and *Geophaps* are desert genera, or represented by desert species; *Ducula*, *Ptilinopus*, and *Goura* are tropical genera; and *Hemiphaga* is a temperate genus. \log_{10} basal rate is not correlated with food habits and is not correlated with 'body size', as long as \log_{10} body mass is included in the analysis.

4.1.3. Body mass

Body mass is the single most important factor setting the basal rate of metabolism in pigeons, as is always the case in endotherms when a marked range of body mass is present. In this case, basal rate is given by $\dot{V}_{O_2}(\text{cm}^3 \text{O}_2/\text{h}) = 6.95 \text{ g}^{0.606}$, when body mass is the only factor included in the

analysis. Because this curve has a higher intercept and a lower power than the Aschoff–Pohl (1970) nonpasserine curve, pigeons tend to have lower basal rates than other nonpasserines at masses greater than 70 g (Fig. 7).

4.1.4. Climate

The basal rate of metabolism of pigeons is correlated with climate (Fig. 7): desert and tropical pigeons have similar ($t = 1.31$, $P = 0.21$) basal rates, whereas temperate species have basal rates that are 22% greater ($t = 2.50$, $P = 0.021$) than tropical species and 40% greater ($t = 3.27$, $P = 0.0037$) than desert species.

4.1.5. Distribution

The restriction of fruit pigeons belonging to the genus *Ducula* to small offshore islands is associated with a low basal rate of metabolism (Figs. 7 and 8): they have basal rates that are 66% of species found on continents or large islands ($t = 3.56$; $P = 0.0018$), although species that are found on intermediate islands have basal rates that are indistinguishable from those of mainland species ($t = 0.56$; $P = 0.58$). The allocation of species to an intermediate island size, however, is often difficult: for example, *D. bicolor* usually is limited to small islands offshore of large islands, although it occasionally invades some of the lowland river courses in New Guinea, such as the Sepik and Fly Rivers. This species was tentatively designated as an intermediate-island species. Equally, *C. vitiensis* is difficult to classify by island size because, although it is found (sparcely at higher altitudes) in New Guinea, it is also found on small islands in the central South Pacific as far east as Fiji and Samoa. This species too was designated as an intermediate-island species. The white-crowned pigeon from the Caribbean is found on small islands in the Florida Keys, the Bahamas, and the Lesser Antilles, but occurs on the large islands of the Greater Antilles (Raffaele et al. 1998), so here is classified as an intermediate-island species.

One way to avoid some of the ambiguity between the intermediate-island and large-island/continental categories is to combine them and contrast this combination with the narrowly defined small-island specialists. Then the analysis indicates (with only two categories of climate, temperate and tropical/desert) that \log_{10} is correlated with \log_{10} body mass ($F = 369.22$, $P \leq 0.0001$), climate ($F = 12.85$, $P = 0.0016$), and

Table 1
Energetics and ecological variables in pigeons and doves

| Species | Mass (g) | Basal rate of metabolism (cm ³ O ₂ /h) | Minimal thermal conductance | Body temp. (C°) | Size ^a | Food | Climate | Distribution ^b | Source |
|----------------------------------|----------|--|-----------------------------|-----------------|-------------------|--------------|-----------|---------------------------|----------------------------------|
| <i>Geopelia cuneata</i> | 35.0 | 59.7 | 7.0 | — | s | Seeds | Desert | Main | Schleucher et al., 1991 |
| <i>Scardafella inca</i> | 41.5 | 48.7 | 4.6 | 38.3 | s | Seeds | Desert | Main | MacMillen and Trost, 1967 |
| <i>Geophaps plumifera</i> | 89.0 | 75.7 | — | 40.5 | s | Seeds | Desert | Main | Withers and Williams, 1990 |
| <i>Zenaida macroura</i> | 91.0 | 117.4 | — | — | s | Seeds | Temperate | Main | Hudson and Bush, 1964 |
| <i>Ptilinopus melanospila</i> | 98.7 | 115.5 | 7.1 | 38.9 | s | Fruit | Tropical | Main | This study |
| <i>Streptopelia senegalensis</i> | 108.0 | 152.3 | — | — | s | Seeds | Desert | Main | Kendeigh et al., 1977 |
| <i>Ptilinopus superbus</i> | 120.4 | 138.5 | 10.5 | 38.1 | s | Fruit | Tropical | Main | Schleucher, 1999 |
| <i>Streptopelia turtur</i> | 154.0 | 203.3 | — | — | s | Seeds | Temperate | Main | Kendeigh et al., 1977 |
| <i>Geophaps lophotes</i> | 166.0 | 137.8 | — | 39.0 | s | Seeds | Desert | Main | Dawson and Bennett, 1973 |
| <i>Streptopelia decaocto</i> | 187.0 | 228.1 | — | — | s | Seeds | Temperate | Main | Kendeigh et al., 1977 |
| <i>Ptilinopus perlatus</i> | 196.0 | 190.3 | 12.3 | 39.5 | s | Fruit | Tropical | Main | This study |
| <i>Gymnophaps albertisii</i> | 241.6 | 169.4 | 9.7 | 39.2 | l | Fruit | Tropical | Main | This study |
| <i>Columba leucocephala</i> | 251.9 | 241.1 | 14.8 | 42.0 | l | Fruit | Tropical | Interm | Pers. observ. |
| <i>Columba livia</i> | 314.6 | 311.5 | 13.8 | 39.7 | l | Seeds | Temperate | Main | Calder and Schmidt-Nielsen, 1967 |
| <i>Ducula pacifica</i> | 333.4 | 142.4 | 11.8 | 39.8 | l | Fruit | Tropical | Small | This study |
| <i>Ducula radiata</i> | 333.6 | 252.2 | 14.4 | 40.6 | l | Fruit | Tropical | Main | This study |
| <i>Ducula rufigaster</i> | 376.7 | 228.3 | 17.0 | 39.7 | l | Fruit | Tropical | Main | This study |
| <i>Ducula pistrinaria</i> | 394.2 | 192.4 | 15.4 | 39.7 | l | Fruit | Tropical | Small | This study |
| <i>Ducula rubricera</i> | 418.8 | 244.6 | 13.4 | 39.1 | l | Fruit | Tropical | Interm | This study |
| <i>Hemiphaga novaeseelandiae</i> | 435.6 | 338.0 | 17.0 | 39.3 | l | Fruit/leaves | Temperate | main | This study |
| <i>Ducula bicolor</i> | 453.6 | 246.3 | 16.2 | 40.7 | l | Fruit | Tropical | Interm | This study |
| <i>Ducula zoeae</i> | 456.2 | 305.7 | 14.6 | 39.3 | l | Fruit | Tropical | Main | This study |
| <i>Columba vitiensis</i> | 467.9 | 259.1 | 17.8 | 39.9 | l | Fruit | Tropical | Interm | This study |
| <i>Leucosarcia melanoleuca</i> | 468.0 | 300.0 | — | — | l | Seeds | Temperate | Main | This study |
| <i>Ducula pinon</i> | 583.8 | 319.3 | 22.0 | 39.7 | l | Fruit | Tropical | Main | This study |
| <i>Caloenas nicobarica</i> | 613.0 | 325.5 | 20.4 | 40.9 | l | Fruit/nuts | Tropical | Interm | This study |
| <i>Goura cristata</i> | 2313.4 | 765.7 | 37.0 | 39.8 | l | Fruit | Tropical | Main | This study |

^a Size: s, small (<200 g); l, large (>200 g).

^b Distribution: main, mainland; small, small islands; interm, intermediate islands (see text).

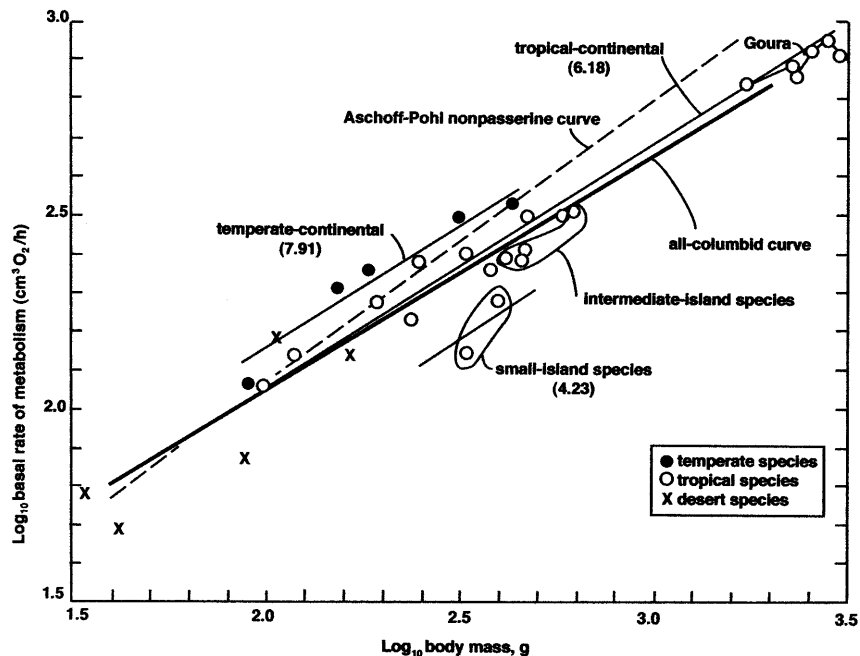


Fig. 7. Log_{10} total basal rate of metabolism as a function of log_{10} body mass in pigeons and doves (data from Table 1). In all species, mean values are used, except in *G. cristata* in which the data for each individual is indicated (and connected). The standard nonpasserine curve of Aschoff and Pohl (1970) and four fitted curves for columbids (see text) are indicated (the coefficients for the equations that include mass, climate, and distribution are placed in parentheses).

distribution ($F = 11.70$, $P = 0.0023$); $r^2 = 0.943$. Species that are small-island specialists have basal rates that are 69% those of other columbids. In other words, the use of one or the other of the groupings of pigeons by island size makes no difference for the conclusion that basal rate in fruit pigeons is correlated with island size.

The effect of island size on basal rate is especially prominent in fruit-pigeons belonging to the genus *Ducula* in which little overlap, even among individual basal rates (corrected for body size), occurs among mainland, intermediate-island, and small-island species (Fig. 8). Fruit pigeons belonging to other genera, especially those found in mainland areas, have basal rates similar to those found in *Ducula*. Yet, the appreciable residual variation of basal rate in mainland genera and species indicates that some factors other than scaling, climate, and island size are present. The possible nature of these factors is explored under generic affiliation and phylogeny (Section 4.1.6.).

The correlation of basal rate with island size in large-bodied *Ducula* raises the question whether small-bodied birds have the same correlation of basal rate with island size. For example, the genus *Ptilinopus* includes many small-bodied, small-is-

land specialists, none of which has been measured. The reason why pigeon size might be important for the impact of island size to be shown is that island size represents a (crude) measure of resource availability and pigeon size represents a (crude) measure of resource requirements (see McNab, 1994b). Small pigeons might require smaller islands than large pigeons for a reduction in basal rate to occur. Nevertheless, Sailer (1999) showed in the genus *Ptilinopus* that those species endemic to South Pacific islands without avian predators have smaller pectoral girdles and muscle masses than species endemic to continents and islands that have both mammalian and avian predators; *Ptilinopus* species restricted to islands with only avian predators have intermediate muscle masses. This pattern may correspond to a variation in basal rate. At a size extreme, small passerines may find most islands to be large: only the smallest islands might require the smallest passerines to adjust their use of resources.

Of the species studied here, the species most committed to a small-island existence is *D. pacifica*, which is a supertramp (Diamond, 1974; Steadman et al., 1990) that widely moves between

islands in the central South Pacific. It is found on very small islands [e.g. Anuta (0.4 km²) and Tikopia (4.6 km²); (Steadman et al., 1990)], but whether it has self-sustaining populations on these small, remote islands is unclear. Its ability to persist on the smallest islands may be facilitated by having the lowest basal rate of all the species studied, although some intraspecific differentiation of basal rate might occur in populations depending on island size and isolation. Another way to consider the low basal rate (61%) in this 333 g pigeon is to realize that it has a basal rate (142.4 cm³ O₂/h) equivalent to a 'standard' non-passerine that weighs 133 g, or a 'standard' columbid that weighs 146 g. Thus *D. pacifica* has a mass that is 2.2–2.5 times that expected from its basal rate of energy expenditure: a larger size increases the period of time for tolerance of fasting and a shortage of resources (Millar and Hickling, 1990), which may facilitate persistence on South Pacific islands affected by El Niño, La Niña, and cyclonic events. Nevertheless, *D. pacifica* is one of the smallest species in its genus,

which can be interpreted as an additional response to a small-island existence. For example, femur length in pigeons is a measure of body size (J. Sailer, pers. comm.): *Ducula pacifica* and *D. poliocephala* (a Philippine mainland species) have similar femur lengths (46.7 vs. 47 mm, respectively), but they differ in body mass (333 vs. 510–564 g, respectively). This may imply an evolutionary reduction in mass and an even greater reduction in basal rate as a response to life on small islands.

The other small-island specialist studied is *D. pistrinaria*, which has a larger mass and a higher basal rate than *D. pacifica* (Fig. 8). Does this mean that it has a reduced commitment to a small-island existence than *D. pacifica*? In fact, *D. pistrinaria* apparently feeds during the daytime in the lowlands of intermediate islands, like New Britain and New Ireland, but returns to small offshore islands to roost and breed (Coates 1985), a behaviour unknown in the Pacific imperial-pigeon. The correlation of basal rate and island size may be more refined than indicated in Fig. 8.

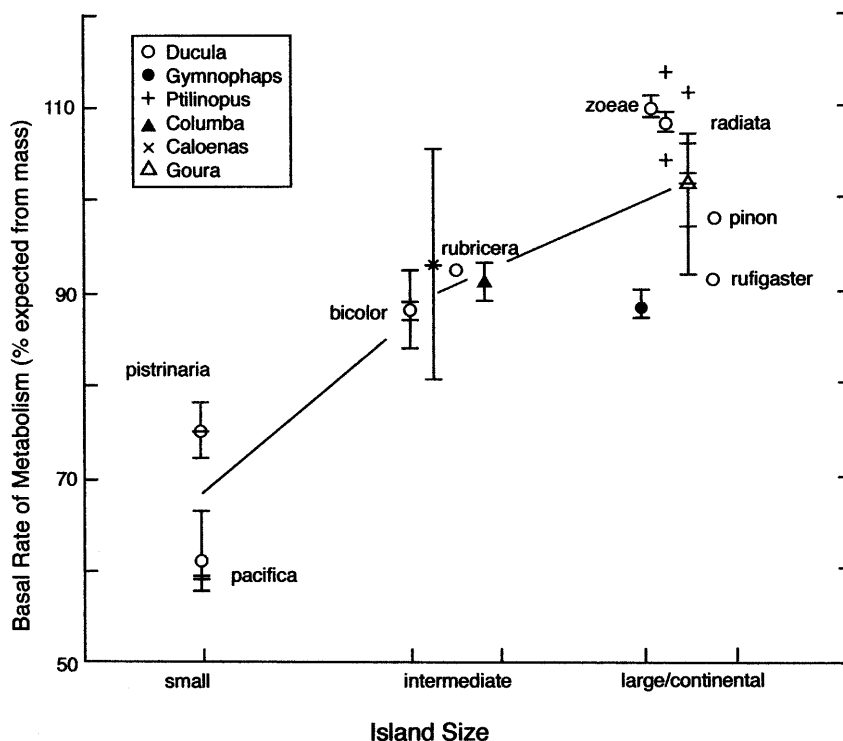


Fig. 8. Basal rate of metabolism, corrected for body mass using the all-columbid curve, in adult tropical, South Pacific, frugivorous pigeons as a function of the size of the land areas in which they are found. The individual estimates of basal rate of metabolism are indicated by horizontal bars in species that had more than one individual measured in thermoneutrality. The generic symbol indicates the mean of the individual estimates, or an individual estimate, if only one individual is available.

4.1.6. Phylogeny

Another factor potentially influencing basal rate of metabolism is phylogeny. A difficulty preventing its examination here is that no rigorous phylogeny is available for columbids (D.W. Steadman, pers. com.). The use of genus as a substitute for phylogeny was unsuccessful because of the interaction between genus and climate. Some differences among columbids, however, are not accounted for by the combination of mass, climate, and distribution (see Fig. 8). For example, frugivory among neotropical columbids is found in the genus *Columba*, whereas it mainly occurs in *Ducula* and *Ptilinopus* in the South Pacific. Measurements of energetics in a Neotropical frugivorous pigeon, *C. leucocephala*, indicate a basal rate greater than was found in any other tropical frugivorous pigeon (ca. 123% of the all-columbid curve), even though the white-crowned pigeon lives on small and intermediate islands in the Caribbean. *Columba leucocephala* is appreciably smaller (250 g) than the smallest *Ducula* (ca. 325 g). The only *Columba* found in most of the South Pacific, the larger (450 g) white-throated pigeon (*C. vitiensis*) has a lower basal rate; it may not be as frugivorous as some other columbids (Steadman and Freifeld, 1999). These data raise the question whether the physiological responses of *C. leucocephala* to frugivory and island life are different from those of *Ducula*, whether they can be accounted for by consideration of other ecological factors, or whether the evolutionary history of this species may account for its higher basal rate. Many more data on the energetics of columbids, including neotropical species, are required before these questions can be answered.

4.1.7. Conclusion

Basal rate of metabolism in pigeons is complexly related to many, often interacting, factors, including, at least, body mass, climate (using only temperate and tropical/desert climates), and distribution on land masses of various sizes (using only small islands and mainlands), while neglecting generic affiliation (because of its complexity and interaction with climate). Thus, high basal rates are found in pigeons that are large and live in temperate climates on continents or large islands. Those with the lowest basal rates are small, live in tropical or desert climates, and are restricted in distribution to small oceanic islands. This pattern can be summarized by the following

equation when climate and island size are included:

$$\dot{V}_{\text{O}_2}(\text{cm}^3 \text{ O}_2/\text{h}) = 4.23(C \cdot D)g^{0.623},$$

where *C* and *D* are dimensionless coefficients reflecting the occurrence of columbids in various climates and having various distributions, respectively. The values of these coefficients are:

| Climate (<i>C</i>) | | Distribution (<i>D</i>) | |
|----------------------|------|---------------------------|------|
| Tropical/desert | 1.00 | Small islands | 1.00 |
| Temperate | 1.28 | Mainlands | 1.46 |

These coefficients lead to a series of equations (Fig. 7), the extremes of which are for tropical, small-island specialists, when the coefficient is 4.23 (1.00×1.00) = 4.23, and for temperate, continental specialists, when the coefficient is 4.23 (1.28×1.46) = 7.91. A common condition is found in tropical, continental/large-island species in which the coefficient is 4.23 (1.00×1.46) = 6.18. Notice that the power of mass in the correlation with basal rate has changed from 0.606, when only mass is included in the analysis, to 0.623, when mass, climate, and distribution are included. This shift demonstrates that the fitted power is influenced by the factors other than mass that are correlated with basal rate, which throws doubt on the value of extended discussions of the 'true' value of this or that power when only body mass is considered. Data on more small fruit-eating pigeons, small-island pigeons, and large seed-eating pigeons are needed to clarify further these relationships and interactions.

4.2. Minimal thermal conductance

In an analysis of covariance, minimal thermal conductance appears to be correlated only with body mass ($F = 142.74$, $P < 0.0001$; $r^2 = 0.894$), when $C(\text{cm}^3 \text{ O}_2/\text{h}^\circ\text{C}) = 1.04 g^{0.452}$, a relationship that is similar to, but slightly lower than that described by Lasiewski et al. (1967) for birds (Fig. 9). No other factor, including the most likely (climate ($F = 0.21$; $P = 0.82$)), when combined with \log_{10} mass, has an impact on minimal conductance.

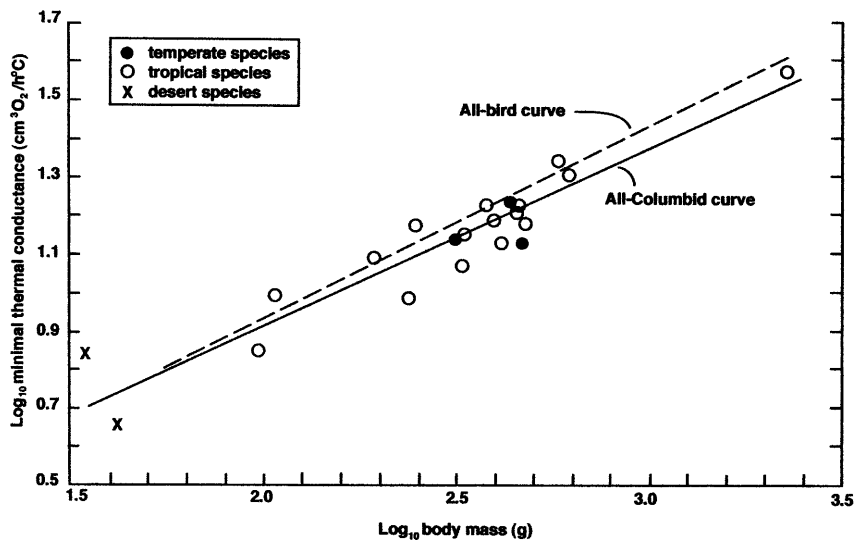


Fig. 9. Log_{10} total minimal thermal conductance as a function of log_{10} body mass in pigeons and doves (data from Table 1). The standard curve of Lasiewski et al. (1967) and the fitted curve for columbids are indicated.

4.3. Body temperature

The mean nocturnal body temperature found in columbids is $39.7 \pm 0.19^\circ\text{C}$ ($n = 22$ species). Body temperature is not correlated with log_{10} basal rate ($F = 3.43$, $P = 0.079$), as might be expected. Body temperature during the daytime in pigeons is approximately 1.1°C higher than at night.

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