METABOLIC AND RESPIRATORY PHYSIOLOGY OF AN ARID-ADAPTED AUSTRALIAN BIRD, THE SPINIFEX PIGEON[1]

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Abstract. The thermal and respiratory physiology of the Spinifex Pigeon (*Geophaps plumifera*) is generally similar to that expected for a 90-g nonpasserine bird. The body temperature is 40.5 to 41.8°C except during thermal stress. The thermoneutral zone extends from about 35 to 45°C. The basal metabolic rate (0.85 ml O_2 g^{-1} hr^{-1}) is about 68% of the predicted nonpasserine value and 75% of the rate expected for a pigeon. Metabolic rate increases at $T_a < 35°C$ and $T_a > 45°C$. Dry thermal conductance is constant at 1.5 J g^{-1} hr^{-1} °C^{-1} for $T_a < 35°C$. Evaporative water loss increases exponentially with T_a, from <1 mg g^{-1} hr^{-1} at 0°C to >20 mg g^{-1} hr^{-1} at $T_a > 45°C$.

A number of physiological characteristics contribute to the remarkable thermal tolerance by Spinifex Pigeons of high ambient temperatures.

(1) The metabolic heat production is low.

(2) The pigeons become hyperthermic ($T_b = 43.4°C$) at $T_a > 40°C$, and this facilitates nonevaporative heat loss.

(3) The dry thermal conductance increases three- to fivefold at elevated T_a (>30°C), facilitating nonevaporative heat loss.

(4) Evaporative heat loss dissipates more than 100% of the metabolic heat production at $T_a > 40°C$.

Expired air temperatures are substantially lower than T_b at low T_a's; this reduces the respiratory evaporative water loss (REWL). The REWL increases exponentially with T_a, from about 0.30 mg g^{-1} hr^{-1} (0°C) to 1.0 (40°C). REWL is about 20% of total EWL, at all T_a's. Cutaneous EWL is about 80% of the total evaporative water loss. It increases from about 0.75 mg g^{-1} hr^{-1} (0°C) to 3.5 (40°C). The mechanism for increasing cutaneous evaporative water loss at high T_a is not clear.

Key words: Columbiformes; metabolism; body temperature; evaporative water loss; evaporative heat loss; Geophaps plumifera.

INTRODUCTION

The Spinifex Pigeon (*Geophaps plumifera*) inhabits rocky and stony areas of the semi-arid and arid regions of Northern Australia (Johnstone 1981). They are weak fliers and do not travel long distances to water, unlike the parrots which also inhabit these regions. Consequently, Spinifex Pigeons are typically found near permanent water, which they drink intermittently. They feed on seeds of spinifex (*Triodia*) and of other grasses and herbs (Frith and Baker 1975).

Spinifex Pigeons experience considerable water and heat stress. Their geographic range includes Marble Bar, one of the hottest places on earth with up to 160 days per year of shade air

temperatures exceeding 38°C (Dawson and Bennett 1973). Drinking and metabolic water production are the principal avenues for water gain, as preformed water intake from their seed diet is low. Maintenance of positive water balance is exacerbated by the necessity of evaporative cooling for thermoregulation at the remarkably high ambient temperatures which these birds routinely experience.

A previous study of the Spinifex Pigeon (Dawson and Bennett 1973) reported aspects of temperature regulation, metabolic rate, and evaporative water loss which were adaptive to their survival in a hot, dry environment. We investigate further the metabolic physiology and water balance of Spinifex Pigeons, with particular reference to body temperature and evaporative water balance at high ambient temperatures. Ventilation parameters were measured to calculate

the respiratory evaporative water loss, to determine the role of respiratory heat dissipation during thermoregulation at high ambient temperatures, and to partition total evaporative water (and heat) loss into its respiratory and cutaneous components.

MATERIALS AND METHODS

Spinifex Pigeons (Geophaps [= Lophophaps, Petrophassa] plumifera ferruginea) were captured at Mallina Station (21°S, 118°E) in the Pilbara region and airfreighted on the day of capture to Perth for laboratory study. Birds were maintained in outdoor aviaries and provided with mixed bird seed and water ad libitum. The mean mass of the nine Spinifex Pigeons studied was 89 ± 4.9 g (SD).

Rates of oxygen consumption ($\dot{V}_{O_2}$; ml O_2 g^{-1} hr^{-1}) and total evaporative water loss (TEWL; mg g^{-1} hr^{-1}) were determined for postabsorptive birds during the nocturnal phase by standard flow-through respirometry/hygrometry. The animals were placed in a small metal metabolic chamber (5,000 cm^3) over mineral oil to trap urine and feces. The metabolic chamber was in a temperature-controlled room; ambient air temperature (T_a; °C) was controlled from -5 to $+50$°C. In most experiments, the T_a was altered in <5°C steps, and held at each new temperature until $\dot{V}_{O_2}$ stabilized.

Water vapor was removed from ambient compressed air with drierite, and passed through the metabolic chamber at a constant rate (typically 1,200 ml min^{-1}) using a mass flow controller (Brooks model 5871A), to maintain about a 0.2% decrease in excurrent O_2 level and relative humidity of 10–20%. Excurrent air was passed through a dewpoint hygrometer (EG&G model DewAll 911) and then through a second desiccant column prior to passage through a paramagnetic oxygen analyzer (Servomex model OA184) or fuel cell oxygen analyzer (Applied Electrochemistry model S3A). The $\dot{V}_{O_2}$ and EWL were determined using the equations of Withers (1977). Water-vapor density of incurrent and excurrent air streams was calculated from dew point using the equations of Parrish and Putnam (1977). Air temperature within the chamber was monitored using a copper-constantan thermocouple in the metabolic chamber and a thermocouple meter (Wescor model TH-65). The body temperature (T_b; °C) of birds was determined immediately after the completion of a series of metabolic rate measurements, by inserting a copper-constantan thermocouple through the cloacal opening into the rectum.

The dry thermal conductance (C_{dry}; J g^{-1} hr^{-1} °C^{-1}) is the conductive/convective heat transfer coefficient, with evaporative heat loss subtracted from the metabolic heat production. It was calculated as:

$$C_{dry} = (20.1\ \dot{V}_{O_2} - 2.45\ \text{TEWL})/(T_b - T_a)$$

where 20.1 $\dot{V}_{O_2}$ is the metabolic heat production (J g^{-1} hr^{-1} assuming 20.1 J ml^{-1} O_2) and 2.45 TEWL is the total evaporative heat loss (J g^{-1} hr^{-1} assuming 2.45 J mg^{-1} water evaporated). T_b was not determined for every $\dot{V}_{O_2}$ and TEWL measurement. It was assumed to be constant at 40.5°C at T_a < 30°C, and to vary with T_a from 30–40°C (see Dawson and Bennett 1973). This assumption introduces a relatively small error so long as T_b is not close to T_a. At high T_a's (>40°C), thermal conductance was only calculated from $\dot{V}_{O_2}$ and TEWL data for which T_b was determined.

Ventilation frequency (f; min^{-1}), tidal volume (V_t; ml), and ventilation volume ($\dot{V}_I$; ml min^{-1}) were determined by whole body plethysmography (Bucher 1981, 1985; Chappell and Bucher 1987). A Grass pressure sensor (model PT5) and Beckman physiograph (model RS dynograph) were used to continuously record pressure fluctuations in the metabolic chamber due to ventilation. The f was directly calculated from the traces; V_t (at body temperature and pressure, saturated with water vapor; BTPS) was calculated after Malan (1973). The plethysmography system was calibrated by rapid injection of known air volumes into the respirometry chamber.

The oxygen extraction (E_{O_2}; %) was calculated as 100 STPD $\dot{V}_{O_2}/(0.2095$ STPD $\dot{V}_I)$ from -10 to 35°C in 5°C increments, from the regression equations for $\dot{V}_{O_2}$ and $\dot{V}_I$, and at 40°C from the data points at T_a from 37.5 to 42.5°C.

Expired air temperature (T_{exp}) can only be measured for birds that are restrained or anesthetized. Spinifex Pigeons were restrained by being loosely wrapped in a small piece of light cheesecloth and enclosed in a coarse wire-mesh tube; the birds were quite calm after 1 hr and could be approached without them becoming disturbed. This method of restraint was used to minimize effects on ventilation and cutaneous water loss. T_{exp} was measured at air temperatures from 2.5 to 37.5°c. The inspiratory-expiratory

temperature cycle was measured by holding a fine copper-constantan thermocouple (44 gauge) 1 mm inside the nasal opening, without touching the surrounding tissue. The time-constant of the thermocouple was 0.1 sec; the expired temperature cycle typically plateaued, indicating equilibrium with the thermocouple and expired air. The output of the thermocouple meter was continuously monitored using a BBC Acorn microcomputer and commercial software for data acquisition and data analysis. The peak expiratory cycle temperature was taken to be the T_{exp}. The average T_{exp} was calculated from five consecutive values for each pigeon at each T_a.

The respiratory evaporative water loss (REWL; mg g^{-1} hr^{-1}) was calculated from $\dot{V}_I$ and T_{exp} as;

$$REWL = 0.06(\chi_{exp} - \chi_a)\dot{V}_I/mass$$

where χ_{exp} and χ_a are the expired and ambient water vapor densities (mg H$_2$O liter^{-1}) i.e., χ at T_{exp} and T_a. In this manner, we can only calculate a maximum estimate of REWL for birds in the metabolism/hygrometry system (relative humidity of 10 to 20%) since T_{exp} was measured at a higher RH (40% at 30°C). We assume that T_{exp} would be lower in the drier air of the metabolic/hygrometric apparatus, and so REWL would be slightly lower.

Average values are presented as mean ± standard error (SE) with the sample size (n). All statistical tests are calculated after Zar (1984).

RESULTS

BODY TEMPERATURE

The T_b of Spinifex Pigeons was 40.5 ± 0.1°C (n = 6) at the end of metabolic experiments at low air temperatures (from −4 to −9°C), 41.8 ± 0.1°C (n = 5) at moderate T_a (40 to 42°C), and 43.4 ± 0.2°C (n = 8) at high T_a (47 to 51°C). These values are significantly different (ANOVA F (2, 16) = 130; $P < 0.001$). The values for T_b at low to moderate T_a fall within the range of values reported by Dawson and Bennett (1973).

OXYGEN CONSUMPTION RATE

The $\dot{V}_{O_2}$ was independent of T_a from a lower critical temperature of 35°C to an upper critical temperature of about 45°C (Fig. 1A). The basal $\dot{V}_{O_2}$ was 0.85 ± 0.024 ml O$_2$ g^{-1} hr^{-1} (n = 57) in this temperature range. There was a linear relationship between $\dot{V}_{O_2}$ and T_a's < 36°C; $\dot{V}_{O_2}$
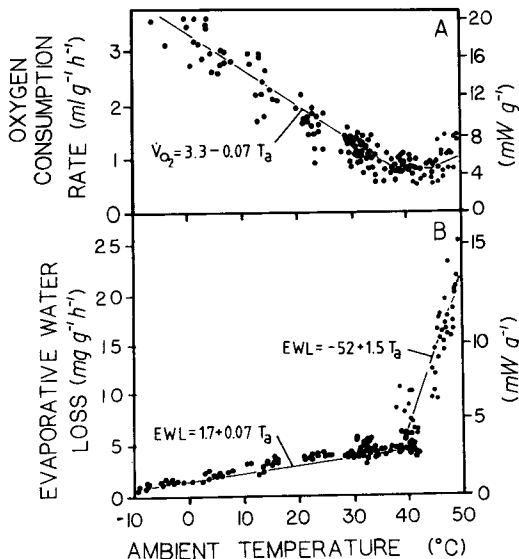

FIGURE 1. Relationship for the Spinifex Pigeon between ambient temperature and (A) oxygen consumption rate ($\dot{V}_{O_2}$; ml O$_2$ g^{-1} hr^{-1}) and metabolic rate (milliwatts g^{-1}) and (B) total evaporative water loss (EWL; mg H$_2$O g^{-1} hr^{-1}) and evaporative heat loss (mW g^{-1}).

= 3.31 − 0.069 T_a (n = 128; r^2 = 0.89; $P < 0.001$). The $\dot{V}_{O_2}$ increased at $T_a > 46°C$; $\dot{V}_{O_2}$ = −1.44 + 0.052 T_a (n = 43; r^2 = 0.13; $P > 0.05$).

TOTAL EVAPORATIVE WATER LOSS

Total evaporative water loss increased linearly with ambient temperature from <0 to 36°C (Fig. 1B); TEWL = 1.72 + 0.068 T_a (n = 106; r^2 = 0.71; $P < 0.001$). TEWL increased dramatically at $T_a > 36°C$; TEWL = −51.9 + 1.49 T_a (n = 64; r^2 = 0.85; $P < 0.001$).

The mean ratio of TEWL to $\dot{V}_{O_2}$ increased from <1 mg H$_2$O/ml O$_2$ at the lowest T_a's to over 20 at the highest T_a's (Fig. 2A); ln (TEWL/ $\dot{V}_{O_2}$) = −0.874 + 0.0717 T_a (n = 172; r^2 = 0.90; $P < 0.001$) although the EWL/$\dot{V}_{O_2}$ values at $T_a > 40°C$ were generally higher than predicted by this relationship. Total evaporative heat loss was equivalent to metabolic heat production (i.e., 100% heat dissipation) at a T_a of about 40°C.

THERMAL CONDUCTANCE

The slope of the relationship between $\dot{V}_{O_2}$ and T_a (−0.069 ± 0.002 ml O$_2$ g^{-1} hr^{-1} °C^{-1}) at $\dot{V}_{O_2}$ below the lower critical temperature is an average wet thermal conductance (C_{wet}); the average C_{wet} is equivalent to 1.3 J g^{-1} hr^{-1} °C^{-1}. This rela-
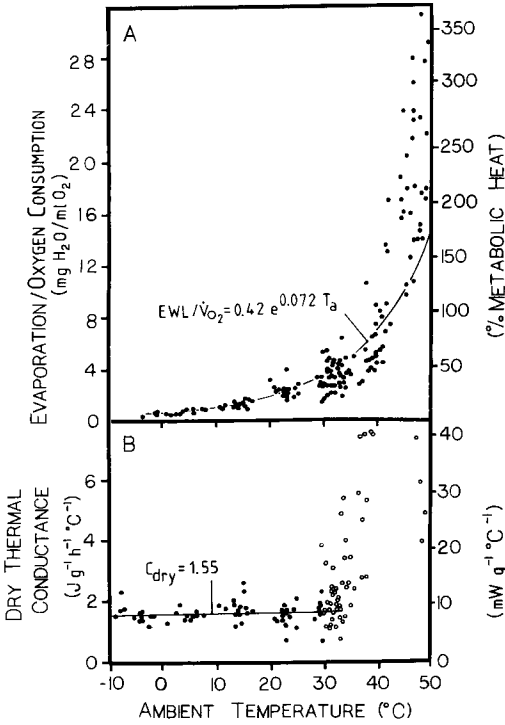
FIGURE 2. Relationship between ambient temperature and the ratio of TEWL to (A) $\dot{V}_{O_2}$ and (B) dry thermal conductance for the Spinifex Pigeon. Open symbols for C_{dry} were excluded from the linear regression analysis.

tionship does not intercept the T_a axis at T_b, but at 48°C, indicating that C_{wet} alters with T_a. Dry thermal conductance is independent of EWL, hence is less dependent on T_a than is C_{wet}. C_{dry} was independent of $T_a < 30$°C at $1.55 - 0.001$ T_a ($n = 67$; $r^2 = 0.001$; $P < 0.001$), but increased three- to fourfold at higher T_a (Fig. 2B).

VENTILATION PARAMETERS

Frequency declined with T_a from about 65 min^{-1} at -10°C to about 37 min^{-1} at 30°C (Fig. 3A). f was quite variable at $T_a > 30$°C; these high values presumably reflect mild thermal stress and possible intermittent hyperventilation. The relationship between f and T_a at <30°C was; $f = 58.2 - 0.71\ T_a$ ($n = 27$; $r^2 = 0.70$; $P < 0.001$).

The V_t (BTPS) was independent of T_a (Fig. 3B). The mean V_t was 1.29 ($\pm$ 0.10) ml BTPS.

The $\dot{V}_I$ (ml BTPS min^{-1}) altered with T_a in similar fashion as f; $\dot{V}_I$ was inversely related to $T_a < 30$°C; $\dot{V}_I = 77.9 - 0.96\ T_a$ ($n = 22$; $r^2 = 0.58$; $P < 0.001$).
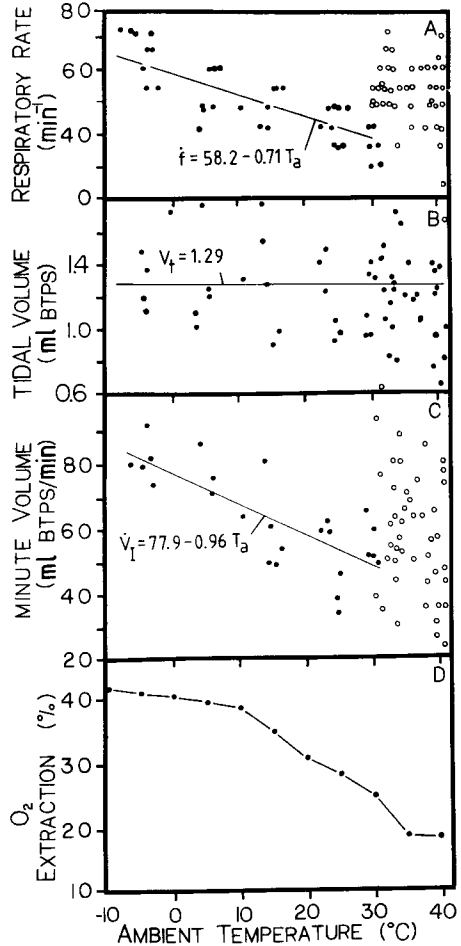

FIGURE 3. Relationship between ambient temperature and (A) respiratory frequency, (B) tidal volume, (C) minute volume, and (D) oxygen extraction efficiency for the Spinifex Pigeon. Open symbols were excluded from the linear regression analysis.

The oxygen extraction efficiency declined from 42.9% of inspired O_2 at $T_a = -10$°C to 19.1% at $T_a = 35$°C (Fig. 3D).

EXPIRED AIR TEMPERATURE

The expired air (T_{exp}) was generally warmer than air temperature and cooler than body temperature; it was linearly correlated with T_a (Fig. 4); $T_{exp} = 11.6 + 0.69\ T_a$ ($n = 36$; $r^2 = 0.97$; $P < 0.001$).

DISCUSSION

Results of this and a previous study (Dawson and Bennett 1973) indicate that the Spinifex Pi-

geon is remarkably tolerant of high ambient temperatures. The upper critical temperature of the thermoneutral zone is about 45°C, and the birds tolerate higher air temperatures in the laboratory without obvious stress. Birds in the field at air temperatures of 45°C and operative temperatures of 60°C do not appear to be heat stressed (i.e., do not gular flutter) even under these extreme conditions (Williams, unpubl. observ.). A variety of physiological attributes contribute to this remarkable thermal tolerance of Spinifex Pigeons.

The thermal, metabolic, and respiratory parameters of the Spinifex Pigeon show some consistent deviations from expected values that partly explain their remarkable thermal tolerance (Table 1). Spinifex Pigeons, like other birds, have a relatively high body temperature of 40 to 42°C, depending on T_a. The high T_b of birds preadapts them to living at high T_a because it facilitates nonevaporative heat loss (Miller 1963). Spinifex Pigeons become hyperthermic at T_a greater than 40°C, and this further facilitates nonevaporative heat loss. Basal oxygen consumption rate is about 68% of the expected value for a nonpasserine bird (Lasiewski and Dawson 1967), in agreement with previous determinations of the basal metabolic rate for the Spinifex Pigeon (Dawson and Bennett 1973). Columbiform birds in general have a low basal metabolic rate, about 80% of that predicted by the Lasiewski-Dawson equation (Bennett and Harvey 1987), but the Spinifex Pigeon has an even lower-than-expected $\dot{V}o_2$ for a pigeon (about 77% of expected). A low basal metabolic rate minimizes the need for heat dissipation, and is commonly observed for arid-adapted mammals and some birds (Hart 1971, Dawson and Bennett 1973, Calder and King 1974, Kendeigh et al. 1977). The dry thermal conductance of Spinifex Pigeons at $T_a < 35$°C is in accord with expected values, but increases by three- to fourfold at higher T_a's, thereby increasing nonevaporative heat dissipation. Total evaporative water loss at 25°C is 30% higher than predicted, thus facilitating heat dissipation. The TEWL values reported here are higher than those previously measured for Spinifex Pigeons (Dawson and Bennett 1973) but the reason for this is not obvious. It may reflect either methodological differences (gravimetric measurement vs. hygrometric measurement) or perhaps a different physiological (acclimation) condition of the birds. The ratio of evaporative water loss to metabolic
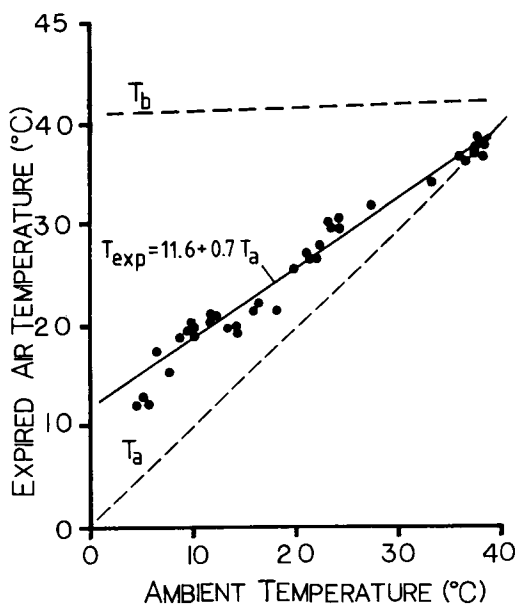

FIGURE 4. Relationship between expired air temperature (T_{exp}) and ambient air temperature (T_a) for the Spinifex Pigeon. The approximate relationship between body temperature (T_b) and T_a is also indicated.

rate is 2.0 mg H_2O/ml O_2 at $T_a = 25$°C; this is equivalent to an evaporative dissipation of 24% of the metabolic heat production. Evaporation dissipates 100% of the metabolic heat load at about $T_a = 40$°C. The remarkable thermal tolerance of Spinifex Pigeons is a combination of low heat production, the ability to increase nonevaporative heat loss by hyperthermia and elevated dry thermal conductance, and a relatively high evaporative water loss.

Enhanced respiratory heat loss by panting or gular flutter is an important mechanism for body temperature regulation by many birds when heat stressed. Ventilation parameters, particularly frequency and minute volume, can change dramatically even within the thermoneutral zone (Bucher 1985). Birds less thermally tolerant than Spinifex Pigeons such as Chukars, *Alectoris chukar* (Chappell and Bucher 1987), Linneated Parakeets, *Bolborhynchus lineola* (Bucher 1981), Green-cheeked Amazon Parrots, *Amazona viridigenalis* (Bucher 1985), and Fairy Penguins, *Eudyptula minor* (Stahel and Nicol 1988) have a markedly increased evaporative water loss at T_a greater than about 35°C. The Monk Parrot (*Myiopsitta monachus*) uses open-mouthed panting coupled with lingual flutter (rather than

TABLE 1. A comparison of resting thermal, metabolic, water loss and respiratory parameters of the Spinifex Pigeon (body mass = 89 g) with values predicted for a nonpasserine bird of the same body mass.

	Spinifex Pigeon	Predicted
Body temperature (°C)	40.5–41.8	39–42[a]
Basal metabolic rate (ml O_2 g^{-1} hr^{-1}; STPD)	0.85	1.3 (nonpasserine)[b]
		1.1 (pigeon)[c]
Dry thermal conductance (J g^{-1} hr^{-1} °C^{-1})	1.5 ± 0.08	1.1–1.9[d]
Ventilation frequency (min^{-1}; 30°C)	37	22.3[e]
Tidal volume (ml; BTPS; 30°C)	1.29	1.33[f]
Minute volume (ml BTPS g^{-1} hr^{-1}; 30°C)	49	30[g]
Oxygen extraction (%; 30°C)	25%	≈25%[e]
Evaporative water loss: (mg g^{-1} hr^{-1}; 25°C)		
Total	3.4	2.54[h]
Cutaneous	2.55	
Respiratory	0.85	
Metabolic-specific water loss (mg H_2O/ml O_2; 25°C)	≈2.5	

[a] King and Farner (1961).
[b] Aschoff and Pohl (1970); Lasiewski and Dawson (1967).
[c] Estimated from Bennett and Harvey (1987).
[d] Herreid and Kessel (1967); Drent and Stonehouse (1971).
[e] Bucher (1985).
[f] Bech et al. (1980).
[g] $V_t \cdot f$.
[h] Crawford and Lasiewski (1968).

gular flutter) to enhance evaporative heat dissipation at $T_a > 35°C$ (Weathers and Caccamise 1975). The ventilatory frequency of the Spinifex Pigeon is higher and more variable at ambient temperatures greater than 30°C (i.e., at about the lower critical temperature) but does not increase dramatically or precipitously. Spinifex Pigeons occasionally, but only intermittently, gular fluttered at T_a's up to 45°C. Gular flutter occurred more at T_a above 45°C, but was still not continuous. Enhanced respiratory water loss is apparently not the primary mechanism for high temperature tolerance by the Spinifex Pigeon.

The expired air temperature of Spinifex Pigeons was substantially less than body temperature at low T_a's (e.g., 5°C) but approached T_b at high T_a (e.g., 40°C). The relationship between T_{exp} and T_a for Spinifex Pigeons is similar to that for other birds (Schmidt-Nielsen et al. 1970, Kaiser and Bucher 1985). The relatively low T_{exp} results in a considerable countercurrent recovery of water and heat from the expired air. For example, at $T_a = 30°C$ there is a 41% recovery of the water vapor evaporated into the inspired air by nasal cooling of the expired air to 32.3°C, for the Spinifex Pigeon.

Total evaporative water loss is commonly determined in physiological studies, but it is not usually partitioned into its respiratory and cutaneous components due to technical difficulties. Consequently, the quantitative contributions of respiratory and cutaneous water loss to water and thermal balance are not known for most birds. In this study, the respiratory component of total evaporative water loss (REWL) was determined by calculation from V_t and T_{exp}. The REWL increased exponentially with T_a (Fig. 5), from 0.3 to 1.0 mg g^{-1} hr^{-1}. This is considerably lower than the REWL calculated if air was expired at body temperature, particularly at lower T_a, reflecting the importance of countercurrent recovery of respiratory water. The REWL was about 20% of the total evaporative water loss over the entire range of T_a's investigated here. Kaiser and Bucher (1985) also calculated REWL for Prairie Falcons (*Falco mexicanus*) in a similar fashion, and reported values from 0.43 mg g^{-1} hr^{-1} (at 2°C) to 4.5 (at 40°C). In contrast to the results for Spinifex Pigeons, the REWL of Prairie Falcons was not a constant fraction of the total EWL; it varied from about 80% of TEWL at low T_a to as little as 25% of TEWL at about 30°C, and accounted for more than the TEWL at high T_a, indicating that expired air was not 100% saturated.

Cutaneous evaporative water loss (CEWL) was calculated as the difference between TEWL and REWL. The CEWL of Spinifex Pigeons increased with elevated T_a from about 0.75 (at 0°C) to 3.5 mg g^{-1} hr^{-1} (at 40°C), but was a constant fraction (about 0.7 to 0.8) of the TEWL over the range of T_a investigated here. The CEWL of Spi-

TABLE 2. Comparison of the cutaneous evaporative water loss (CEWL; mg cm^{-2} hr^{-1}) for the Spinifex Pigeon and other birds.

Species	Temperature	CEWL
Spinifex Pigeon[a]	0–40	0.47–2.2
Rock Pigeon[b]	27–47	2.6–19.1
Mourning Dove[c]	25–35	1.26–4.3
Palm Dove[d]	20–45	2.5–5.9
Collared Dove[d]	20–45	2.0–8.2
Quail[d]	20–40	0.55–2.1
Partridge[d]	20–40	0.51–1.9
Painted Quail[e,f]	25–35	0.7–1.1
Zebra Finch[f]	30	1.3
Budgerigar[f]	30	1.7
Village Weaver[f]	30	1.2
Poorwill[g]	35	1.1
Roadrunner[g]	30–35	0.9–1.0
Ostrich[h]	≈30	1.0
Prairie Falcon[i]	2–40	0.1–4.5

[a] Present study.
[b] Marder and Gavrielli-Levin (1986).
[c] Webster and Bernstein (1987).
[d] Marder and Ben-Asher (1983).
[e] Bernstein (1971a).
[f] Bernstein (1971b).
[g] Lasiewski and Bernstein (1971).
[h] Withers (1983).
[i] Kaiser and Bucher (1985).

nifex Pigeons is equivalent to 0.47 (at 0°C) to 2.2 mg cm^{-2} hr^{-1} (40°C), assuming a surface area of 200 cm^2 (calculated from the modified Meeh equation; cm^2 = 10 g$^{0.667}$; Walsberg and King 1978). These values are similar to those reported for other birds (Table 2).

Cutaneous heat dissipation is the predominant avenue of evaporative heat loss for the Spinifex Pigeon, although nonevaporative heat loss is a greater fraction of the total heat loss at T_a up to 35°C (Fig. 6). The CEWL dissipates about 3% (at low T_a) to 40% (high T_a) of metabolic heat production. The CEWL of other birds dissipates about 15% to 50% of heat production, increasing at higher T_a (see Webster and Bernstein 1987).

Pigeons and doves have considerable capacity to modulate cutaneous evaporative cooling (Marder and Ben-Asher 1983, Webster et al. 1985, Webster and Bernstein 1987). The Spinifex Pigeon also appears to modulate cutaneous evaporative water loss as an important avenue for maintaining thermal balance at high ambient temperatures. The mechanisms controlling cutaneous water loss are not clear. Cutaneous evaporation may be enhanced at high T_a by an elevated skin temperature, increased air flow over the skin, increased water content of the skin, or decreased resistance of the skin barrier to evaporation by a steric change in the epidermal lipids
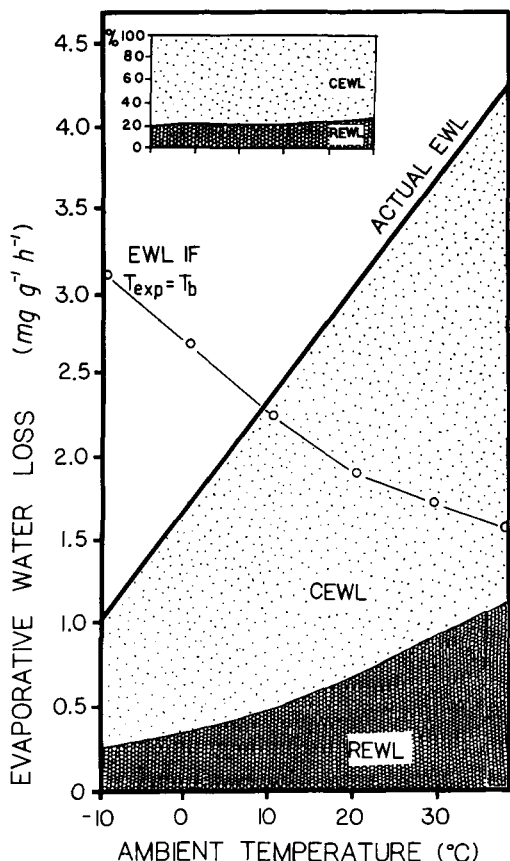

FIGURE 5. Partitioning of total evaporative water loss (TEWL) into respiratory (REWL) and cutaneous (CEWL) components, at air temperatures from −10°C to 40°C for the Spinifex Pigeon. The open circles indicate magnitude of the respiratory evaporative water loss if respiratory air was expired at body temperature. The inset shows the partitioning of REWL and CEWL expressed as a percentage of TEWL.

(Webster and Bernstein 1987). Skin temperature does not alter sufficiently to explain the enhanced CEWL of Mourning Doves at high T_a (Webster and Bernstein 1987). Convective air flow through the feathers might be enhanced at elevated T_a by ptiloerection. We commonly observed ptiloerection, particularly of the dorsal feathers, by Spinifex Pigeons at elevated T_a but the potential significance of this to enhanced CEWL or elevated dry thermal conductance is not known. Increased blood flow to the skin, or a thermally induced phase transition of the epidermal lipids may also contribute to elevated CEWL at high T_a.
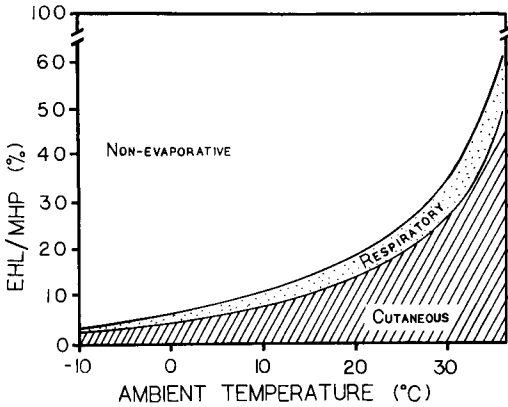
FIGURE 6. Partitioning of metabolic heat production into nonevaporative and evaporative (respiratory and cutaneous) heat loss for the Spinifex Pigeon at ambient temperatures from −10 to 40°C.

ACKNOWLEDGMENTS

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