

# Life in extreme environments: Investigations on the ecophysiology of a desert bird, the Australian Diamond Dove (*Geopelia cuneata* Latham)

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**Summary.** The Diamond Dove, *Geopelia cuneata*, is the world's second smallest (ca. 35 g) species of the columbid order. The Diamond Dove is endemic in the arid and semiarid Mulga and Spinifex regions of Central and Western Australia. It regularly encounters ambient temperatures ( $T_a$ ) in its habitat above +40°C, especially when foraging for seeds on bare ground cover, and may be found at up to 40 km from water. This entails extreme thermal stress, with evaporative cooling constrained by limited water supply. Energy metabolism ( $M$ ), respiration, body temperature ( $T_b$ ) and water budget were examined with regard to physiological adaptations to these extreme environmental conditions. The zone of thermal neutrality (TNZ) extended from +34°C to at least +45°C. Basal metabolic rate (BMR) was  $34.10 \pm 4.19 \text{ J g}^{-1} \text{ h}^{-1}$ , corresponding to the values predicted for a typical columbid bird. Thermal conductance ( $C$ ) was higher than predicted. *Geopelia cuneata* showed the typical breathing pattern of doves, a combination of normal breathing at a stable frequency (ca. 60  $\text{min}^{-1}$ ) at low  $T_a$  and panting followed by gular flutter (up to 960  $\text{min}^{-1}$ ) at high  $T_a$ . At  $T_a > +36^\circ \text{C}$ ,  $T_b$  increased to considerably higher levels without increasing metabolic rate, i.e.  $Q_{10} = 1$ . This enabled the doves not only to store heat but also to save the amount of water that would have been required for evaporative cooling if  $T_b$  had remained constant. The birds were able to dissipate more than 100% of the metabolic heat by evaporation at  $T_a \geq +44^\circ \text{C}$ . This was achieved by gular flutter

(an extremely effective mechanism for evaporation), and also by a low metabolic rate due to the low  $Q_{10}$  value for metabolism during increased  $T_b$ . At lower  $T_a$ , *Geopelia cuneata* predominantly relied on non-evaporative mechanisms during heat stress, to save water. Total evaporative water loss over the whole  $T_a$  range was 19–33% lower than expected. In this respect, their small body size proved to be an important advantage for successful survival in hot and arid environments.

**Key words:** Avian ecophysiology – Deserts – *Geopelia cuneata* – Thermoregulation – Respiration

The morphology, physiology and ethology of animals are related to their specific habitats and are therefore central topics of ecology. If any significant ecophysiological differences between animals exist, they would be expected to be most obvious in animals living under extreme environmental conditions. Morphology, physiology and ethology are also closely related, affecting each other independently of the influences of the habitat.

The large pigeon order (Columbiformes), with over 300 species, inhabits nearly all climatic zones of the world. Its members, although quite similar and “pigeon-like” in appearance, vary greatly in body mass (ca. 30–1500 g). This makes the order very interesting for comparative studies that stress the influences of abiotic habitat factors and of body size on the various physiological parameters such as energy metabolism, body temperature and breathing parameters.

This study provides insight into the complex relations between physiological factors that enable the Diamond Dove (*Geopelia cuneata*) to be one of the most successful inhabitants of Australia's hot centre. The Diamond Dove is the second smallest dove (ca. 35 g); only the South American Ground Dove *Columbina passerina* (ca. 30 g) is smaller, but it occurs in a less harsh environment.

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**Abbreviations and units:** Body Mass  $W$  (g), Ambient Temperature  $T_a$  (°C), Body Temperature  $T_b$  (°C), Thermoneutral Zone (TNZ), Metabolism  $M$  ( $\text{J g}^{-1} \text{ h}^{-1}$ ), Thermal Conductance  $C$ , wet Thermal Conductance  $C_{\text{wet}}$  ( $\text{J g}^{-1} \text{ h}^{-1} \text{ }^\circ \text{C}^{-1}$ ), Evaporative Water Loss EWL ( $\text{mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ ), Evaporative Heat Loss EHL ( $\text{J g}^{-1} \text{ h}^{-1}$ ), Breathing Frequency  $F$  (breaths  $\text{min}^{-1}$ ), Tidal Volume  $V_T$  (ml  $\text{breath}^{-1}$ ), Standard Temperature Pressure Dry STPD, Body Temperature Pressure Saturated BTPS, Respiratory Quotient RQ, n.s. = not significant ( $P > 0.05$ ),  $n$  = number of experiments

## Materials and methods

### Laboratory investigations in the Federal Republic of Germany

Eight captive-raised Diamond Doves (6 ♂, 2 ♀, ages unknown), were used in the experiments. The birds were housed together in an indoor aviary (ca. 1.5 × 2 × 2 m) at  $T_a$  of 20–25°C with a light-dark cycle of 12:12 (L:0900–2100 hours). They were maintained on commercial bird seed, water and fresh green food *ad lib*. Before and during the experiments mean body mass ( $W$ ) was 34.4 ± 3.4 g (range 30.4–40.8 g).

The equipment and experimental protocol for measurement of  $M$  (via oxygen consumption and carbon dioxide production),  $F$  and  $T_b$  are described in detail in Prinzinger (1988). During measurements, the doves were kept in plexiglass respirometer chambers (ca. 30 × 15 × 25 cm, ca. 11.25 l). For gular flutter, the whole-body plethysmography equipment was supplemented by a pressure transducer with a range of ±2 mbar (Furness Controls Ltd. Type FC 011), and a rapid-response oscillograph (Tectronix, Type 654). These instruments allowed the recording of high-frequency, small-amplitude pressure fluctuations.  $F$  was also monitored visually using a one-way mirror, without disturbing the birds. In each metabolism measurement, frequencies were recorded up to 10 times during both day and night. Night-time values were not taken before 2200 hours or after 0700 hours to ensure that the birds were sleeping. Experiments were made on 6–7 consecutive days to make sure the birds were familiar with the experimental situation.  $T_b$  was determined in the cloaca after the end of each metabolism experiment at noon.

### Calculations

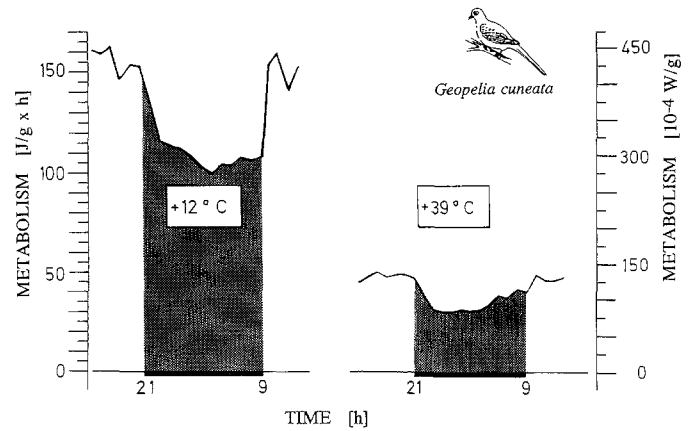
Gas volumes were corrected to STPD, and lung volumes additionally to BTPS. All values are means ± SD. Linear regressions were calculated by the method of least squares. Calculations of  $M$  and  $V_T$  were made according to Prinzinger (1988). Periods of panting and gular flutter were excluded from calculations of lung parameters.

Water savings by increased  $T_b$  were calculated using the following equations (Calder and King 1974): specific heat capacity of animal tissue  $Q = 3.35 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ , stored heat  $Q_s = \Delta T_b \times Q$  ( $\text{J g}^{-1}$ ), and total heat storage =  $Q_s \times W$  ( $\text{J}$ ).  $\Delta T_b$  is the difference between normal and increased  $T_b$ .

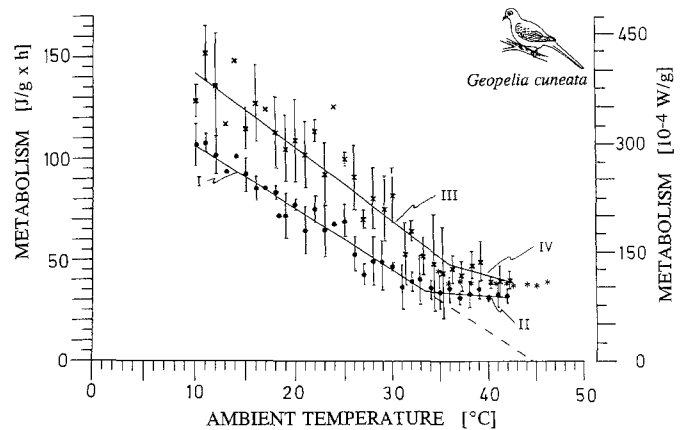
We assumed that 1 ml  $\text{O}_2 = 20 \text{ J}$ . The energy units may be converted by the equation  $1 \text{ J h}^{-1} = 2.87 \times 10^{-4} \text{ W}$ .

### Investigations in Australia

Field observations were carried out during September 1988 in the Hamersley Ranges in Western Australia. Laboratory measurements of  $M$  and water balance were performed in Perth with six birds mist-netted in the Pilbara region of Western Australia. Mean  $W$  of the wild-captured doves was 35 ± 3.5 g (range 28–40 g, ages and sexes unknown). The birds were housed in a 3 × 2 × 1.5 m outdoor aviary under natural light and climate conditions. Air temperatures did not exceed +25°C during the 6-week measuring period. Experimental equipment was similar to that described above; the metabolism chamber was equipped with an ondina oil bath to collect excreta (Withers and Williams 1990). Doves were not provided with food or water during measurements. Thus, each experiment lasted only 24 h with several intervening days of recovery. A Servomex oxygen analyzer model OA 184 and a Vaisala HMI 33 hygrometer with measuring probe HMP 31 UT were used. Amounts of water evaporated were converted into J by assuming 1 mg water evaporated = 2.4 J. Temperature-controlled rooms allowed  $T_a$  to be regulated up to +46°C.



**Fig. 1.** Examples of diurnal cycles in energy metabolism  $M$  ( $\text{J g}^{-1} \text{ h}^{-1}$ ) at  $T_a = +12^\circ\text{C}$  (left) and  $T_a = +39^\circ\text{C}$  (right). Dark phase (shaded) from 2100 to 0900 hours



**Fig. 2.** The relation between energy metabolism  $M$  ( $\text{J g}^{-1} \text{ h}^{-1}$ ) and ambient temperature  $T_a$  ( $^\circ\text{C}$ ). Crosses represent daytime values (0900–2100 hours) of the aviary birds in Frankfurt, asterisks represent daytime values of the wild birds in Perth, dots represent nighttime values (2100–0900 hours). Each symbol ( $\pm$ SD) represents the mean of 3–6 periods of 12-h measurements. Where no SD is given only one measurement was made. The corresponding regression lines are described by the following equations (see numbers in the figure):

$$I: M = 136.82 - 3.04 T_a, r = -0.94, P < 0.001, n = 72$$

$$II: M = 46.91 - 0.40 T_a, r = -0.26, \text{ n.s.}, n = 36$$

$$III: M = 178.70 - 3.62 T_a, r = -0.91, P < 0.001, n = 87$$

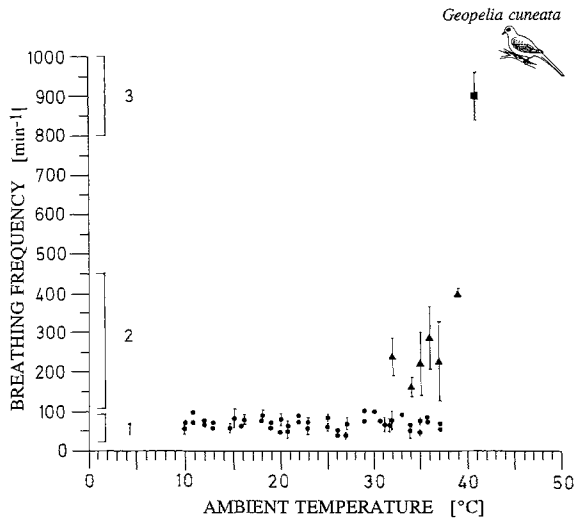
$$IV: M = 97.02 - 1.35 T_a, r = -0.44, \text{ n.s.}, n = 21$$

## Results

### Metabolism

At each  $T_a$  measured, the doves showed a diurnal rhythm of  $M$  with higher values during the day (Fig. 1). The TNZ of *Geopelia cuneata* ranged from a lower critical temperature of about +34°C to at least +46°C (Fig. 2). In the TNZ, daytime levels of  $M$  were 128% of the nighttime values.

The RQ was independent of  $T_a$  and time of day with a mean of  $0.82 \pm 0.04$ . Within the TNZ, mean resting  $M$  averaged  $34.10 \pm 4.19 \text{ J g}^{-1} \text{ h}^{-1}$  ( $n = 36$ ). Daytime values of the wild doves were lower than those of the individuals



**Fig. 3.** The relationship between breathing frequency  $F$  and  $T_a$  for (1) normal breathing, ( $\bullet$ ,  $n=45$ : day/ $n=37$ : night), (2) panting, ( $\blacktriangle$ ,  $n=18$ ) and (3) gular flutter, ( $\blacksquare$ ,  $n=3$ ). Each symbol ( $\pm$ SD) represents the mean of 2–6 experimental periods (each up to 10 single measurements) at a given  $T_a$ . Where no SD is shown symbol dimensions exceed SD. No differentiation was made between day- and nighttime values in the graph. For values, regression equations and details see text

raised in captivity ( $37.71 \pm 2.09 \text{ J g}^{-1} \text{ h}^{-1}$ ,  $n=25$ , in the wild doves vs.  $44.06 \pm 3.57 \text{ J g}^{-1} \text{ h}^{-1}$ ,  $n=30$ , in the captive birds).

$C$ , as calculated from the slope of the regression line of  $M$  versus  $T_a$ , was 3.04 (night) and  $3.62 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$  (day), respectively. The wet thermal conductance ( $C_{\text{wet}}$ ), calculated from the ratio  $M/(T_b - T_a)$  was  $4.02 \pm 0.47$  (night) and  $5.94 \pm 0.95 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$  (day).

### Breathing parameters

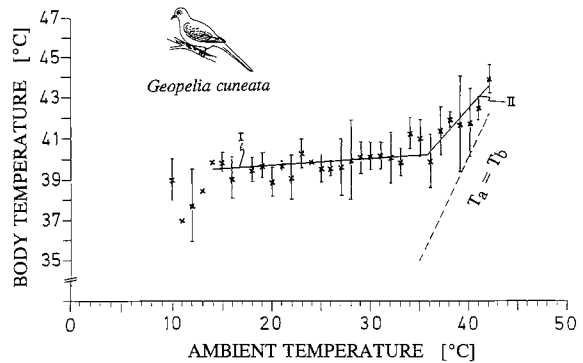
The frequency of normal breathing (mean for all  $T_a$ s) was  $59.5 \pm 15.7 \text{ min}^{-1}$  (night) and  $72 \pm 15.1 \text{ min}^{-1}$  (day). There was a slight, but not significant, decrease in  $F$  with increasing  $T_a$ . The corresponding regression equations are: Night:  $F = 62.99 - 0.15 T_a$ ,  $r = -0.08$ , n.s.; Day:  $F = 81.27 - 0.37 T_a$ ,  $r = -0.21$ , n.s. (Fig. 3). At  $T_a > +32^\circ\text{C}$  the doves used normal respiration alternating with panting. Panting rates ( $F > 100 \text{ min}^{-1}$ ) rose sharply with increasing  $T_a$ , to a maximum of  $400 \text{ min}^{-1}$ . Gular fluttering with a nearly stable frequency ( $960 \pm 40 \text{ min}^{-1}$ ) occurred at  $T_a > +40^\circ\text{C}$ . During normal breathing  $V_T$  was  $0.34 \text{ ml BTPS}$  ( $0.27 \text{ ml STPD}$ ) in the TNZ, increasing to  $1.23 \text{ ml BTPS}$  ( $0.98 \text{ ml STPD}$ ) at  $T_a = +10^\circ\text{C}$  (see Table 1).

### Body temperature

At  $T_a$ s from  $+14$  to  $+36^\circ\text{C}$ , mean daytime  $T_b$  was stable at  $+39.8 \pm 0.48^\circ\text{C}$ . At  $T_a < +14^\circ\text{C}$ ,  $T_b$  slightly decreased to a minimum of  $+37.0^\circ\text{C}$ . At  $T_a > +36^\circ\text{C}$ ,  $T_b$  rose significantly (Fig. 4). The highest  $T_b$  value record-

**Table 1.** Metabolic rate  $M$ , breathing rate  $F$  and tidal volume  $V_T$  (in ml STPD) of resting birds at different  $T_a$ s.  $V_T$ s are derived from the values of the regression equations of  $M$  and  $F$  versus  $T_a$ . Therefore no  $n$  and no SD are given (for details see Materials and methods and the legend to Fig. 2)

$T_a$ ( $^\circ\text{C}$ )	$M$ ( $\text{J g}^{-1} \text{ h}^{-1}$ )	$F$ (breaths $\text{h}^{-1}$ )	$M/F$ ( $\text{J g}^{-1} \text{ breath}^{-1}$ )	$V_T$ (ml)
10	106.43	3689	28.80	0.98
12	100.36	3671	27.30	0.93
14	94.28	3653	25.80	0.88
16	88.20	3635	24.30	0.83
18	82.12	3617	22.70	0.77
20	76.05	3599	21.10	0.72
22	69.97	3581	19.50	0.66
24	63.89	3563	17.90	0.68
26	57.81	3545	16.30	0.55
28	51.74	3527	14.67	0.50
30	45.66	3509	13.00	0.44
32	39.58	3491	11.30	0.39
34	33.51	3473	9.60	0.32
36	27.43	3455	7.90	0.27

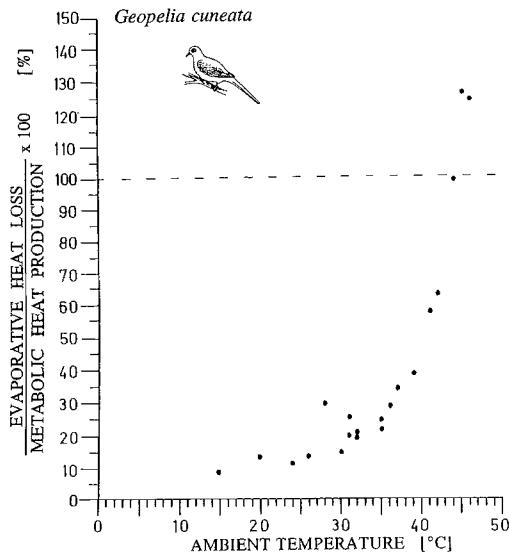


**Fig. 4.** The relationship between body temperature  $T_b$  and ambient temperature  $T_a$ . Each symbol represents the mean of 2–6 measurements. All values are daytime measurements after 24 h exposure to the given  $T_a$ . The corresponding regression lines are described by the following equations: I:  $+14^\circ\text{C} \leq T_a \leq +36^\circ\text{C}$ :  $T_b = 39.10 + 0.032 T_a$ ,  $r = 0.21$ , n.s.,  $n = 79$ ; II:  $T_a \geq +36^\circ\text{C}$ :  $T_b = 21.07 + 0.54 T_a$ ,  $r = 0.79$ ,  $P < 0.05$ ,  $n = 25$

ed was  $+44.8^\circ\text{C}$  ( $T_a = +42^\circ\text{C}$ ) without any obvious harm to the bird. This gives a maximum  $\Delta T_b$  between mean and increased  $T_b$  of  $5^\circ\text{C}$ . The total maximum heat storage of a bird experiencing this  $\Delta T_b$  ( $566 \text{ J}$ ) is equivalent to 50% of 1 h of metabolic heat production in the TNZ (ca.  $1100 \text{ J h}^{-1}$ ) and confers a water saving of up to  $236 \text{ mg}$  per bird.

### Evaporative water loss

Over a  $T_a$  range of  $+15$  to  $+35^\circ\text{C}$ , EWL remained nearly constant, the mean being  $3.00 \pm 0.35 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ . At  $T_a > +35^\circ\text{C}$ , EWL rose exponentially to  $20.56 \text{ mg g}^{-1} \text{ h}^{-1}$  at the highest  $T_a$  measured. Figure 5 shows the relation between heat lost by evaporation and the heat produced by  $M$  at the various  $T_a$ s. At a  $T_a$



**Fig. 5.** The ratio of evaporative heat dissipation and metabolic heat production at various  $T_a$ s ( $n=47$ ). 100% of the heat produced by  $M$  is dissipated by evaporation at  $T_a = +43^\circ\text{C}$  (broken line)

of  $+44^\circ\text{C}$ , the amount of heat dissipated by evaporation is equal to that produced by the bird's metabolism.

## Discussion

### Basal metabolic rate

In Diamond Doves metabolism remained at the basal level from  $+34^\circ\text{C}$  to at least  $+46^\circ\text{C}$ . An upper critical  $T_a$  could not be obtained from the range of  $T_a$ s tested. Such a wide TNZ is an excellent adaptation to hot and arid conditions. TNZs at similar high  $T_a$ s have been observed only in a few desert birds: Paradise Whydah *Steganura paradisea* ( $+34$  to  $+38^\circ\text{C}$ , King and Farner 1961), Spinifex Pigeon *Petrophassa plumifera* ( $+34$  to ca.  $+44^\circ\text{C}$ , Dawson and Bennett 1973; Withers and Williams 1990), Rock Pigeon *Columba livia* ( $+35$  to  $+42^\circ\text{C}$ , Marder and Arieli 1988), and Sandgrouse (Pteroclididae) ( $+32$  to  $+46^\circ\text{C}$ , Thomas 1984).

The expected BMR for a typical nonpasserine the size of the Diamond Dove is  $31.70$  (Aschoff and Pohl 1970) or  $34.80\text{ J g}^{-1}\text{ h}^{-1}$  (Lasiewski and Dawson 1967). Although metabolic rates lower than these have often been observed in desert birds (e.g. Dawson and Bennett 1973), the measured BMR of Diamond Doves ( $34.10\text{ J g}^{-1}\text{ h}^{-1}$ ) is not lowered. Indeed, it is 11% higher than the value predicted for all birds by Bennett and Harvey (1987) of  $30.60\text{ J g}^{-1}\text{ h}^{-1}$ .

The metabolic rates of Diamond Doves may reflect their behavior in their natural habitat: field studies of the seed-eating Diamond Doves indicated that they are often active during the hottest times of the day, exposed to the intense heat of solar radiation (see also Immelmann 1970). This may be related to competition and predation in the low-productivity desert habitat. Obviously, heat loss mechanisms of Diamond Doves are able to compensate for intense heat load.

The thermal conductance (night) of Diamond Doves is 20% higher than predicted by Lasiewski and Calder (1971) and Aschoff (1980). The daytime value is 6% higher than predicted. These results are consistent with the suggestion of Aschoff (1980) that desert birds have a high conductance. This is even more obvious from the  $C_{\text{wet}}$  values; the daytime  $C_{\text{wet}}$  value is 67%, and the nighttime value is 74% higher than that predicted. High  $C_{\text{wet}}$  facilitates heat loss by non-evaporative mechanisms.

### Breathing parameters

$F$  and  $V_T$  of the Diamond Dove are well within the expected range given by Lasiewski and Calder (1971). Breathing frequency  $F$  was constant over a broad range of  $T_a$  ( $+10$  to  $+32^\circ\text{C}$ ). Circadian differences in oxygen demand and  $T_a$ -dependent variations in metabolic rate were mainly (up to 90%) met by changes in  $V_T$  rather than  $F$ .

At  $T_a > +32^\circ\text{C}$ , regular breathing and panting occurred alternately. There was a rapid elevation in  $F$  up to 14 times the normal value. At  $T_a > +40^\circ\text{C}$  the Diamond Doves used gular flutter, a mechanism extremely advantageous for efficient thermoregulation. It enables the bird to dissipate heat at much lower energetic cost than can be achieved by panting (Lasiewski and Bartholomew 1966).

An identical pattern of breathing over a wide  $T_a$ -range has also been described for the Inca Dove (*Scardafella inca*, Lasiewski and Seymour 1972). This dove is an inhabitant of Southern American steppe regions; it is nearly the same size as the Diamond Dove. The similarity in the physiology of these different species, apparent in their  $T_b$  regulation and EWL (MacMillen and Trost 1967), indicates that similar environmental conditions lead to the same physiological adaptations.

### Body temperature

The normal  $T_b$  of Diamond Doves was within the expected range for a bird of the Columbidae order (Prinzinger et al. 1991). At high  $T_a$ , Diamond Doves showed an impressive tolerance of high  $T_b$ . Within the TNZ, metabolism remained constant despite the increase in  $T_b$ . That is, the  $Q_{10}$  is 1, presumably due to a compensatory reduction of blood flow in the alimentary tract. Such compensation has also been found in mammals (Dawson, T.J., pers. comm.). It allows the bird to take advantage of the elevated  $T_b$ . The resulting greater difference  $T_b - T_a$  promotes passive non-evaporative heat dissipation and reduces evaporation, which saves water. Keeping the body temperature at lower levels would require extra energy and thus result in a counterproductive increase in heat production and water loss. A low  $Q_{10}$  has also been observed by Weathers (1981) in various birds weighing less than 100 g exposed to heat stress.

### Water balance

Given their capacity for passive heat dissipation it is not surprising that the EWL of Diamond Doves was lower than predicted by Crawford and Lasiewski (1968) and

Calder and King (1974), by 19% at  $T_a$  from +15 to +35° C and as much as 33% at +46° C. Nevertheless, under severe heat load ( $T_a > +44°$  C), the birds dissipate more heat by evaporation than they produce by metabolism. Therefore the total amount of water evaporated alone is not a good measure of heat tolerance. This has also been found by several other authors (e.g. Dawson 1958; Lasiewski and Bartholomew 1966; Lasiewski and Seymour 1972). On the contrary, lowering the amount of water required for thermoregulation by other effective water-saving mechanisms such as increased  $T_b$  and a moderate level of metabolism is an ecophysiological advantage in desert birds with low water supply.

## Conclusion

Small body size (high surface/volume ratio) and high conductive heat loss, in combination with tolerance of high  $T_b$ , moderate levels of metabolism, and effective means of water loss, enable the Diamond Dove to be one of the most common and successful inhabitants of Australia's hot arid environment. This study clearly shows that it is not a single adaptation but a combination of different physiological adaptations that enables this species to live in a hot and arid habitat throughout the year.

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## References

- Aschoff J (1980) Thermal conductance in mammals and birds: Its dependence on body size and circadian phase. *Comp Biochem Physiol* 69A: 611-619
- Aschoff J, Pohl H (1970) Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J Ornithol* 111: 38-47
- Bennett PM, Harvey PH (1987) Active and resting metabolism in birds: allometry, phylogeny and ecology. *J Zool* 213: 327-363
- Calder WA, King JR (1974) Thermal and caloric relations of birds. In: Farner DS, King JR (eds) *Avian biology*, vol 4, Academic Press, New York, pp 260-413
- Crawford EC, Lasiewski RC (1968) Oxygen consumption and respiratory evaporation in the Emu and Rhea. *Condor* 70: 333-339
- Dawson WR (1958) Relation of oxygen consumption and evaporative water loss to temperature in the Cardinal. *Physiol Zool* 31: 37-48
- Dawson WR, Bennett AF (1973) Roles of metabolic level and temperature regulation in the adjustment of Western Plumed Pigeons (*Lophophaps ferruginea*) to desert conditions. *Comp Biochem Physiol* 44A: 249-266
- Immelmann K (1970) *Im unbekanntem Australien*. Verlag Helene, Pfungstadt
- King JR, Farner DS (1961) Energy metabolism, thermoregulation and body temperature. In: Marshall AJ (ed) *Biology and comparative physiology of birds*, vol 2, Academic Press, New York, pp 215-279
- Lasiewski RC, Bartholomew GA (1966) Evaporative cooling in the Poor-will and the Tawny Frogmouth. *Condor* 68: 253-262
- Lasiewski RC, Calder WA (1971) A preliminary analysis of respiratory variables in resting birds. *Respir Physiol* 11: 152-166
- Lasiewski RC, Dawson WR (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23
- Lasiewski RC, Seymour RS (1972) Thermoregulatory responses to heat stress in four species of birds weighing approximately 40 grams. *Physiol Zool* 45: 106-118
- MacMillen RE, Trost CH (1967) Thermoregulation and water loss in the Inca Dove. *Comp Biochem Physiol* 20: 263-273
- Marder J, Arieli Y (1988) Heat balance in acclimated pigeons exposed to temperatures up to 60° C. *Comp Biochem Physiol* 91A: 165-170
- Prinzinger R (1988) Energy metabolism, body-temperature and breathing parameters in nontorpid Blue-naped Mousebirds (*Urocolius macrourus*). *J Comp Physiol B* 157: 801-806
- Prinzinger R, Preßmar A, Schleucher E (1991) Body temperature in birds. *Comp Biochem Physiol* 99A: 499-506
- Thomas DH (1984) Adaptations of desert birds: Sandgrouse (Pteroclididae) as highly successful inhabitants of Afro-Asian arid lands. *J Arid Environ* 7: 157-181
- Weathers WW (1981) Physiological thermoregulation in heat-stressed birds: Consequences of body size. *Physiol Zool* 54: 345-361
- Withers PC, Williams JB (1990) Metabolic, respiratory and hygric physiology of an arid adapted Australian bird, the Spinifex Pigeon. *Condor* 92: 961-969