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Energetics and body temperature regulation in two convergent dove species from extreme habitats

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The small Australian Diamond Dove *Geopelia cuneata* (38 g) and African Namaqua Dove *Oena capensis* (36 g) live in desert and semi-desert habitats. They can be regarded as ecological counterparts on the two continents. They are both diurnal and active even throughout the hottest part of the day. Therefore, they regularly encounter extremely high temperatures (up to 60–70°C), especially when feeding on the hot ground. Metabolic rates (MR) of both species are 20–50% below expected values. This has been described for other desert pigeons before, while species from temperate regions have MR in the expected range of all birds. Both species tolerate elevated body temperatures (T_b; up to 44.8°C) under high external heat load. Additionally, they show effective heat loss mechanisms (panting, gular flutter) so that metabolic heat is dissipated as fast as it is produced by the organism without a further rise in body temperature. These physiological characteristics enable them to be active and forage on the ground throughout the day even when temperatures are highest. The two dove species are opportunistic breeders in adaptation to the unpredictable climatic conditions in their habitat. This can be seen from their fast pre- and postnatal development: The nestling time and total energy investment per juvenile are only 50% of the values expected for tropical birds. Thus, several broods can be raised under favourable conditions, especially when rainfall occurs.

1. Introduction

Endotherms adapt to their environment by varying their metabolic rates. However, only few studies have examined the influence of the habitat on the energetics of related species (Bennett & Harvey 1987, Reynolds & Lee 1996). Pigeons and doves (Columbiformes, Columbidae) are ideal for a comparative study of strategies in adaptation to various environmental conditions because they are cosmopolitan and occur in almost every habitat except for the polar and alpine regions. Of more than 300 existing species, only 8 had been investigated with regard to their metabolism and body temperature regulation (Reynolds & Lee 1996). Of special interest are the energy metabolism, thermoregulation and development of diurnal desert species, because they regularly face extreme environmental conditions, i.e. high ambient temperatures and intense solar radiation. Irregular precipitation and therefore unpredictable food and water supply in these zones also have a strong impact on the life history of the birds living there. This is especially prominent in the breeding season, when energetic demands are high. In this paper, I will especially stress the convergent features of two small desert adapted columbid species of genera that are not closely related within the family (Goodwin 1983).

2. Material and methods

Birds were obtained from private breeders and maintained in outdoor aviaries (2 × 2 × 2 m, Schleucher *et al.* 1991). 14 Diamond Doves (body mass M = 37.9 ± 1.5 g) and 5 Namaqua Doves (M= 36.4 ± 2.4 g) were used as a breeding stock in the years 1990 and 1991. Experiments with juveniles were conducted during the breeding season 1991 in Frankfurt, where the birds were kept in an outdoor cage (4 × 4 × 2 m). Nests were checked daily at the same time in the morning, and eggs as well as juveniles were marked individually. Freshly laid eggs were weighed (Sartorius PT 600, accuracy 0.1 g) and length and width measured (calliper rule, accuracy ± 0.05 mm). Body mass gain and development of morphological parameters in juveniles were measured daily. Only one egg or juvenile was removed from each nest at a time to ensure that the adults kept attending the nest. 32 nestlings of Diamond Doves and 8 of Namaqua Doves were used in the metabolic experiments.

Resting metabolic rates (RMR) were determined in adult birds as well as in juveniles in an open flow system with an O_2- and a CO_2- analyzer (Magnos 4 G, URAS 3K, Hartmann & Braun, Frankfurt). All experiments were carried out in insulated temperature-controlled rooms (± 1°C) at a light:dark cycle of 12:12 h for adults. Juveniles were measured in the dark in α (activity) phase and from day 40 on in ρ (rest) phase. The birds were placed in plexiglass respirometer chambers (volume 0.9–15 L depending on the size of the bird). Flow rate (measured with a flow-meter, ROTA) through the chamber was adjusted to 30L/h (ages 0–7 d) and 40 L/h (fledglings and adult birds). Gas volumes were corrected to STPD-conditions. RMR was calculated assuming that 1 mL O_2 equals 20 J.

Adult birds (6 Diamond Doves and 5 Namaqua Doves) were kept under experimental conditions continuously for 1 week at different ambient temperatures (T_a) with food and water provided *ad lib.* (for details, see Prinzinger 1988, Schleucher *et al.* 1991). Chicks were removed from their nests daily and tested under following T_a regimes: T_a = 20°C (cold stress, N = 2 on day 0, N = 7–8 on all following days in Diamond Doves, N = 2 in Namaqua Doves) and T_a = 34–36°C (TNZ of adult birds, N = 2 on day 0, 6–8 on all following days in Diamond Doves, N = 6 in Namaqua Doves). Two Diamond Dove chicks were additionally tested at 15°C to check whether the determined age of endothermy was dependent on the T_a chosen. An exposure time of 30 min was chosen because after 15–20 min the smallest chicks (ca. 2 g) had a very low body temperature close to T_a and a stable O_2 consumption, so that the last 10 min of the experiment were used for analyses. This procedure was applicable as a standard to all experiments, because the juvenile birds became very familiar with the experimental situation and settled down quickly. The dead space of the system (especially tubing) was reduced to a minimum so there was a stable O_2 reading no later than 10 min after the bird had been placed in the metabolic chamber.

Body temperatures T_b were measured telemetrically in 2 adult Diamond Doves by implanted miniature transmitters (for details, see Prinzinger *et al.* 1992). In juveniles and in 4 additional adults as well as in the Namaqua Doves the T_b was measured in the cloaca with a quick-responding calibrated NiCr-Ni digital thermometer (Testoterm 9300, accuracy 0.1°C). The measuring tip (diameter 1 mm) was inserted 0.5–1.0 cm depending on the age of the birds. Measurements were taken immediately (within 30 s) after the end of a metabolic experiment or after the chick had been removed from the nest. In adult birds, measurements were made at least 2 hours before the lights on in the temperature controlled room. Telemetric measurements took place continuously over periods of 3 weeks under aviary and experimental conditions.

The thermal conductance C [$J\ g^{-1}\ h^{-1}\ °C^{-1}$] was calculated by using the equation $M/(T_b - T_a)$ in the T_a-range below TNZ (< 32°C). For further discussion, see Schleucher (1999).

The evaporative water loss (EWL) was measured with a hygrometer measuring probe (Hygrotest Testoterm, Lenzkirch, Germany) inserted in an airtight tube at the air outlet of the metabolic chamber. Measurements took place simultaneously with the metabolic experiments in adult Namaqua Doves. In these experiments, no food and water were available to the birds over a period of 24 h. Breathing frequencies were measured by inserting a high-sensitive pressure transducer into the respirometer chamber. For further details, see Schleucher *et al.* 1991, however, no equipment for recording gular fluttering was available for the Namaqua Doves.

All data presented are means ± SD unless otherwise stated; n denotes the number of experiments at a given T_a, N represents the number of animals used. Care was taken that the individual birds were represented equally in the data set.

3. Results

3.1 Adult birds

Both species showed a typical diurnal rhythm of metabolism with lower values in the dark (ρ phase, Aschoff & Pohl 1970). During daytime (active = α phase) the birds were fully fed and not postabsorptive. Therefore, these data are regarded as RMR (Table 1, omitted in Fig. 1). However, the feeding procedure did not affect the MR in ρ phase, which could be determined by comparison of the values of Namaqua Doves in the different experimental setups. In the TNZ (range covered by equations II and IV in Fig. 1), there was no difference ($p > 0.05$) in MR between birds fed *ad lib.* (normal MR measurements, MR = 24.28 ± 2.52 J g^{-1} h^{-1}, n= 31) and those starved in the EWL measurements (MR = 22.56 ± 3.31 J g^{-1} h^{-1}, n = 10). This indicates that the experimental setup is well suited for exact BMR measurements in small birds. The physiological characteristics of both species are listed in Table 1. BMRs for both species are given as the means of all measurements in the TNZ.

The thermal conductance (C) was constant in the T_a-range between 10 and 32°C in both species. The values given in Table 1 are the means of the quotients $M/(T_b - T_a)$ calculated for each experimental run at T_a below TNZ.

The diurnal rhythm was also visible in the T_b-values over the whole range of T_a (Fig. 2). In the daytime values (Table 1), there were no significant differences between the values measured by telemetry and by hand in the Diamond Dove as well as between the two species ($p > 0.05$, see Table 1). Therefore, all daytime data were lumped together in Fig. 2. The mean daytime T_b for both species was 41.14 ± 0.74°C (n = 125), which is approximately 3°C above nighttime values. Maximum values recorded were 44.8°C in Diamond and 42.4°C in Namaqua Doves. The nighttime values were constant in the range of T_a = 12–32°C in both species (Fig. 2). At $T_a > 32$°C, T_b rose linearly with T_a to a maximum of 43.3°C (T_a = 41°C, Diamond Dove) and 40.8°C (T_a = 39°C, Namaqua Dove). For regression equations see Fig. 2. Again, there was no significant difference between data derived by telemetry in undisturbed birds and the measurements by hand in the cloaca. The telemetry experiments further showed that the level of T_b was independent of the time period over which the birds were exposed to the T_a. Especially in ρ, where no activity occurred, T_b was maintained at a stable level throughout the experiment.

The pulmocutaneous water loss was constant in the lower T_a-range (12 to 28°C, Namaqua Dove, and 12–35°C, Diamond Dove) and then rose exponentially in both species. In this high T_a-range, EWL correlates strongly with T_a. On a semilogarithmic plot, the relationship was linear (Fig. 3). Therefore, the birds were able to dissipate their metabolic heat completely by evaporation (Fig. 4) at high T_a.

The relationship between breathing frequency (F) and T_a was similar in the two species: F remained constant in a wide T_a range from 10–35°C. At T_as of 32–37°C, panting and normal breathing occurred intermittently. From 37°C on, doves showed almost only panting and synchronous gular fluttering.

3.2. Breeding parameters and ontogeny

As typical for Columbids, clutch size was 2 in all cases.

The breeding parameters (Table 2) were very similar in the two species. Juveniles grow extremely fast during the nestling period. The greatest absolute mass gain occurred between days 4 and 6 (maximum day 4: 2.5 ± 0.6 g d^{-1}, N = 40, Diamond Dove, and 2.6 ± 0.5 g d^{-1}, N = 11, Namaqua Dove), when M increases by up to 30% within a day. Growth levelled off during 9–11 d, the time

Table 1. Physiological parameters of Diamond and Namaqua Doves. Data of Diamond Doves with and without transmitters are arranged in two separate columns to demonstrate that there was no influence on physiological parameters caused by the implantation of the devices. N = number of birds, n = number of experiments, M = body mass, TNZ = thermoneutral zone, BMR = basal metabolic rate, RMR = resting metabolic rate, C = thermal conductance, T_b = body temperature, EWL = evaporative water loss, F = breathing frequency. Literature predictions from: 1) Aschoff & Pohl (1970), 2) Bennett & Harvey (1987), 3) Reynolds & Lee (1996), 4) Herreid & Kessel (1967), 5) Aschoff (1981), 6) Williams (1996).

	Diamond Dove N = 4	Diamond Dove (telemetry) N = 2	Namaqua Dove N = 5
M [g]			
mean:	37.9 ± 1.52	35.3 ± 2.08	36.4 ± 2.04
range:	35.0–41.9	35.7–44.8	30.0–40.9
TNZ [°C]:	34–40°C	32–39°C	32–40°C
BMR (ρ phase)	23.85 ± 1.68	24.16 ± 2.89	24.38 ± 2.52
[J g^{-1} h^{-1}]	n = 13	n = 11	n = 31
% of predicted value (Diamond Dove: mean of rows 1 and 2)			
1)	78		80
2)	58		60
3)	51		52
RMR (α phase)	33.29 ± 4.24	30.5 ± 3.2	34.79 ± 4.66
[J g^{-1} h^{-1}]	n = 4	n = 6	n = 31
C [J g^{-1} h^{-1} °C], $T_a < 32$°C			
ρ phase	2.95 ± 0.36	2.75 ± 0.33	3.22 ± 0.50
α phase	3.99 ± 0.63	3.39 ± 0.73	3.89 ± 0.70
	n = 13	n = 11	n = 35
% of predicted value (ρ phase. Diamond Dove: mean of rows 1 and 2			
4)	108		115
5)	130		138
T_b [°C]			
ρ phase	38.58 ± 1.00	38.32 ± 0.42	38.43 ± 0.38
	n = 13	n = 11	n = 26
α phase	41.45 ± 1.11	41.31 ± 0.66	40.92 ± 0.77
	n = 25	n = 26	n = 74
EWL [mg H_2O g^{-1} h^{-1}]	2.3 ± 0.35[1]		1.37 ± 0.48
(T_a = 12–30°C)	n = 10		n = 8
% of predicted value (25°C)			
6) eq. (4)	78		46
6) eq. (7)	81		48
maximum	20.56 (T_a = 45°C)[1]		6.37 (T_a = 39°C)
F [min^{-1}], (T_a = 18–37°C)			
ρ phase	60 ±16[1]		55 ±14
	n = 37		n = 8
α phase	72 ±15[1]		64 ±10
	n = 37		n = 8
panting			
($T_a > 32$°C)	100–400[1]		210 – 300
	n = 18		n = 9
panting and synchronous gular flutter			
($T_a > 40$°C)	960 ± 40[1]		
	n = 3		

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[1] values from Schleucher *et al.* 1991.

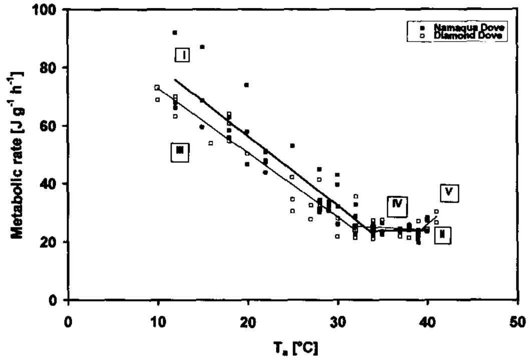

Fig. 1. Metabolic rate (ρ phase in Aschoff & Pohl 1970) versus ambient temperature T_a in Namaqua (N = 5, closed squares) and Diamond Doves (N = 6, open squares). The regression lines are described by the following equations: Namaqua Dove (thick lines): I (11–32°C): $M = 105.03 - 2.42\,T_a$, $n = 30$, $r = -0.89$, $p < 0.001$. II (32–40°C): $M = 22.0 + 0.05\,T_a$, $n = 22$, $r = 0.05$, n.s., $p > 0.05$. Diamond Dove (thin lines): III (10–32°C): $M = 95.4 - 2.23\,T_a$, $n = 27$, $r = -0.97$, $p < 0.001$. IV (32–39°C): $M = 30.8 - 0.17$, $n = 26$, $r = -0.16$, n.s., $p > 0.05$. V (39–41°C): $M = -75.23 + 2.53\,T_a$, $n = 12$, $r = 0.71$, $p < 0.01$. The TNZ was determined by computing the equations I and III with the highest r^2. n = number of experiments. Values for α (activity) phase were omitted for clarity, see Table 1 for details.

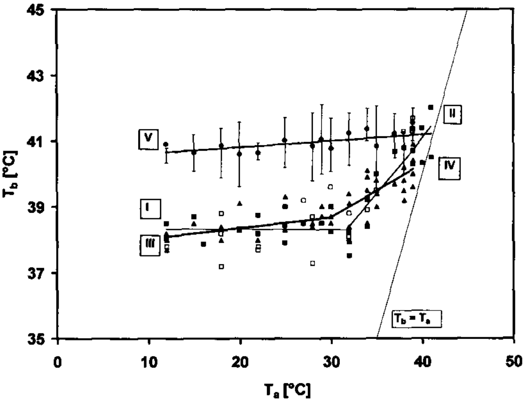

Fig. 2. Body temperature T_b versus ambient temperature T_a in Namaqua and Diamond Doves. Closed triangles: Namaqua Dove, hand measurements (ρ). Closed squares: Diamond Dove, hand measurements (ρ), open squares: Diamond Dove, telemetry measurements (ρ). Each datum represents a T_b measurement taken at the end of a 24 h experiment at the respective T_a. Telemetry values represent the mean of a continuous measurement at a given T_a. SD are omitted for clarity. Closed circles: mean T_b in α (= active) phase for both species (for details, see Results). The regression equations are I: $T_b = 38.4 - 0.002\,T_a$ (T_a = 12–32°C), $n = 36$, $r = -0.03$, n.s., $p > 0.05$, and II: $T_b = 26.3 + 0.37\,T_a$ ($T_a > 32°C$), $n = 26$, $r = 0.91$, $p < 0.001$ (thin lines, Diamond Dove combined telemetry and hand measured data). III: $T_b = 37.7 + 0.03\,T_a$ (T_a = 12–30°C), $n = 25$, $r = 0.50$, $p < 0.05$, and IV: $T_b = 33.8 + 0.16\,T_a$ ($T_a > 30°C$), $r = 0.74$, $p < 0.001$, $n = 24$ (thick lines, Namaqua Dove). V: $40.35 + 0.02\,T_a$, $n = 125$, $r = 0.22$, n.s., $p > 0.05$, (T_a = 12 to 41°C, all birds in α phase).

at which the nestlings left the nest (10.8 ± 1.1 d, N = 36, Diamond Dove, 12.6 ± 0.5 d, N = 6, Namaqua Dove). Mean body mass at leaving the nest was 20.1 ± 1.59 g, N = 32 (53% of adult M, Diamond Dove) and 22.4 ± 1.93 g, N = 7 (60% of adult mass, Namaqua Dove). The young were fed by the adults for another 10 d outside the nest. Adult mass was attained by Diamond Doves at an age of 50 d, and at 60 d by Namaqua Doves.

On the first days, the nestlings were almost naked with only a few downy quills (Fig. 5a). By day 3 the quills of the contour feathers as well as the flight feathers (primaries and secondaries, tail) broke through the skin. During these days, juveniles were constantly brooded by at least one adult. On day 7 (Diamond Doves) and day 8 (Namaqua Doves), young were completely covered with feathers (Fig. 5e). From this day on, adults left the nest for short periods.

In the first days after hatching, juveniles of both species showed typical ectothermic reactions, their MR and T_b being strongly dependent on T_a (Figs. 6 and 7). According to the ectothermic state of hatchlings, RMR varied directly with T_a in the first days of life (Fig. 6). 1 d old nestlings had RMR approximately 3 times as high at T_a of 35°C as at 20°C. RMR increased rapidly in the first days of life in all tested T_a to a maximum value at day 7. From then on, it decreased slowly towards adult values (Fig. 6a and b). The transition to endothermy occurred on day 5, when RMR under cold stress was higher than under thermoneutral conditions (Figs. 6a and b, and 7 a). Beyond this age, RMR correlated inversely with T_a (endothermic reaction). Fig. 7a and b demonstrates the transition to endothermy. They are given for Diamond Doves only, as Namaqua Doves show identical results.

The T_b of juveniles taken from the nests with a sibling as well as of birds kept at TNZ in the

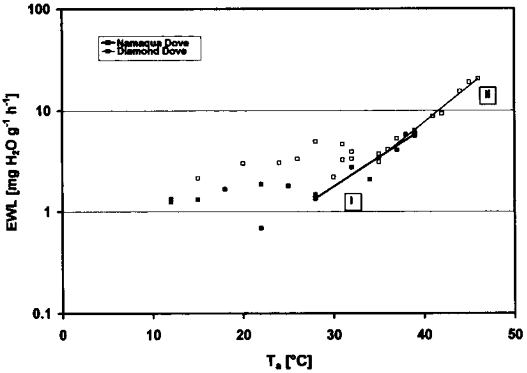

Fig. 3. Evaporative water loss (EWL) versus ambient temperature T_a in Diamond and Namaqua Doves. The regression lines are described by the following equations: I: log EWL = – 1.48 + 0.058 T_a ($r = 0.97$, $p < 0.001$, $n = 9$, $T_a = 28–39°C$; thick line and closed symbols; Namaqua Dove). II: log EWL = – 1.95 + 0.071 T_a ($r = 0.99$, $p < 0.001$, $n = 10$, $T_a = 35–44°C$; thin line and open symbols; Diamond Dove).

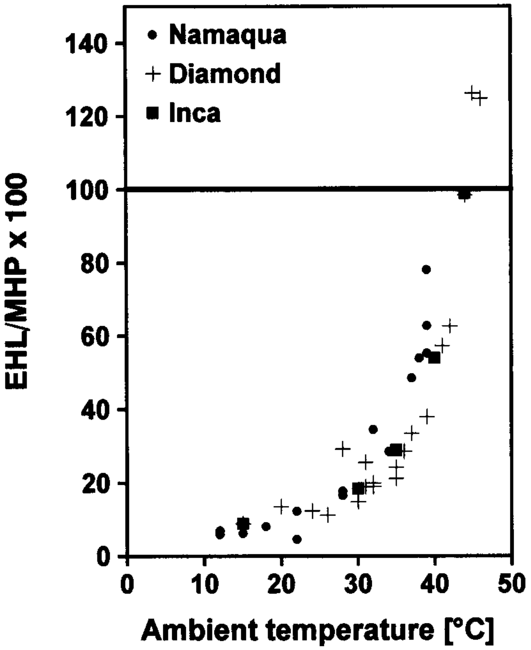

Fig. 4. Heat loss efficiency in 3 xerophilous dove species from 3 different continents. Each point represents the ratio of evaporative heat loss (EHL) and metabolic heat production (MHP) measured simultaneously. EHL was calculated by assuming that 2.4 kJ are required per ml H_2O evaporated. Data for Diamond Dove are from Schleucher *et al.* 1991, Inca Dove data are from MacMillen & Trost 1967, with permission from Elsevier Science.

experimental situation were 34–36°C on days 0 (freshly hatched) and 1 (n = 32). On day 3, mean T_b was 38.0 ± 0.75°C (99% of adult values, effective endothermy). Under experimental conditions, the ectothermy of the semi-altricial juveniles in the first days of life was obvious (Fig. 7a and b). The dependency of T_b on T_a decreased with age. On day 7, juveniles of both species were able to regulate T_b in the range of adults (Fig. 6b) independent of the T_a chosen: at $T_a = 20°C$, T_b was 39.1 ± 0.49, N = 8, at $T_a = 15°C$ T_b was 39.0 ± 0.64, N = 2.

4. Discussion

4. 1. Adult birds

Although the allometry of MR has been described in various publications over the last decades, there is still no consistency in the way the data sets are being dealt with (e.g. Reynolds & Lee 1996). Because the data sets of the various authors were obtained and selected under different conditions, it is difficult to judge which is the most suitable. Therefore, I compared the Diamond and Namaqua Dove data with the most common and recent reviews about the allometry of MR (Table 1). Independent of the equation chosen, BMR of both species are clearly (20–49%, Table 1) below the predicted levels. Equally low metabolic rates have been found in other xerophilic doves, the Inca Dove *Scardafella inca* (30–50% below prediction, MacMillen & Trost 1967), the Spinifex Pigeon *Lophophaps ferruginea* (30–66%, Withers & Williams 1990), and the Crested Pigeon *Ocypaps lophotes* (20–44%, Dawson & Bennett 1973). In pigeons that had been acclimated to heat over long periods of time, the metabolic rates decreased even further (e.g. Marder & Gavrieli-Levin 1987). Unlike the parrots (Williams *et al.* 1991), reduced BMR seems to be a common characteristic of desert-adapted pigeons and doves (Dawson & O'Connor 1996). Low metabolic rates are correlated with low internal heat production, which is of advantage in the hot and arid environment. At the same time, the high thermal conductances facilitate the heat flow from the bird to the environment, especially when $T_b > T_a$.

Furthermore, the internal heat can be dissipated by effective means of evaporation (Figs. 3 and 4). One of these mechanisms is the gular flutter (Schleucher *et al.* 1991), which has also been described for the Inca Dove (MacMillen & Trost 1967, Lasiewski & Seymour 1972). It is very likely that this mechanism is working as a resonant system, hence its energy cost is very low when operating at maximal efficiency as a heat dissipating mechanism. Because only a small area in the throat is moved at low muscle activity, the system is more advantageous than panting.

The amount of water evaporated is another indicator for the thermoregulatory ability of birds under heat stress. However, the amount of water lost is not a measure of 'quality' of thermoregulation *per se*, but rather the balance between heat loss and heat gain. In Diamond and Namaqua Doves, pulmocutaneous water loss is considerably (20 – 60%) lower than expected for both species in the T_a-range below TNZ (Fig. 3, Table 1). Thus, the birds minimise water loss during the desert nights and other times of day when T_a is relatively low. This has also been found in other desert birds, for instance parrots and larks (Williams *et al.* 1991, Williams 1996, Tieleman *et al.* 1999). However, in the high T_a-range the birds are able to dissipate all the internally produced heat by evaporation (Fig. 4). This seems to be a common mechanism for many small desert-adapted birds (Lasiewski & Seymour 1972). The similarity in the regulatory mechanisms in the different small dove species and also in other desert birds such as the budgerigar (Weathers & Schoenbaechler 1976) as well as the larger pigeons (Marder & Gavrieli-Levin 1987) is striking and indicates the strong impact of abiotic factors on the physiological characteristics of these species.

The body temperatures in both species are in the expected range (Prinzinger *et al.* 1991) for T_a= 12 to 32 °C. Above this T_a, the doves show elevated T_b so that T_b is kept above T_a. This does not indicate a breakdown of thermoregulation, but is clearly a regulated phenomenon. This could be shown in the telemetry studies, where the T_b was constant throughout a measuring period of 24 h at each given T_a. By using controlled hyperthermia the doves store an amount of heat equivalent to 52% of one hour's metabolic heat production and save 197 mg of water. This controlled hyperthermia was also found to be an efficient heat defence mechanism in other small heat-adapted birds (Weathers 1981, Withers & Williams 1990, Tieleman & Williams 1999).

The combination of these physiological features enables the doves to be active throughout the day even when temperatures are at their maximum. Diamond Doves even tolerate T_a of 60 to 70°C for at least 1 h when foraging on the ground (Schleucher 1993).

Table 2. Comparison of egg and breeding parameters of Diamond and Namaqua Doves. N = number of individual eggs/birds.

	Diamond Dove	N	Namaqua Dove	N
Egg length ± SD [cm]	2.00 ± 0.80	45	1.94 ± 0.06	14
Min/max [cm]	1.80/2.17		1.84/2.06	
Egg width ± SD [cm]	1.53 ± 0.05		1.51 ± 0.07	
Min/max [cm]	1.46/1.66		1.30/1.57	
Egg mass ± SD [g]	2.54 ± 0.22	39	2.42 ± 0.15	12
Min/max [g]	2.20/3.00		2.10/2.60	
Mean incubation time ± SD [d]	12.00 ± 0.80	40	13.50 ± 0.50	14
Mean hatching mass ± SD [g]	1.95 ± 0.22	13	1.94 ± 1.16	9
Min/max [g]	1.70/2.40		1.70/2.20	
Nestling time ± SD [d]	10.80 ± 1.10	36	12.60 ± 0.50	6
Mean body mass at leaving the nest ± SD	20.10 ± 1.59	32	22.4 ± 1.93	7
% adult mass at fledging	53.0		60.0	

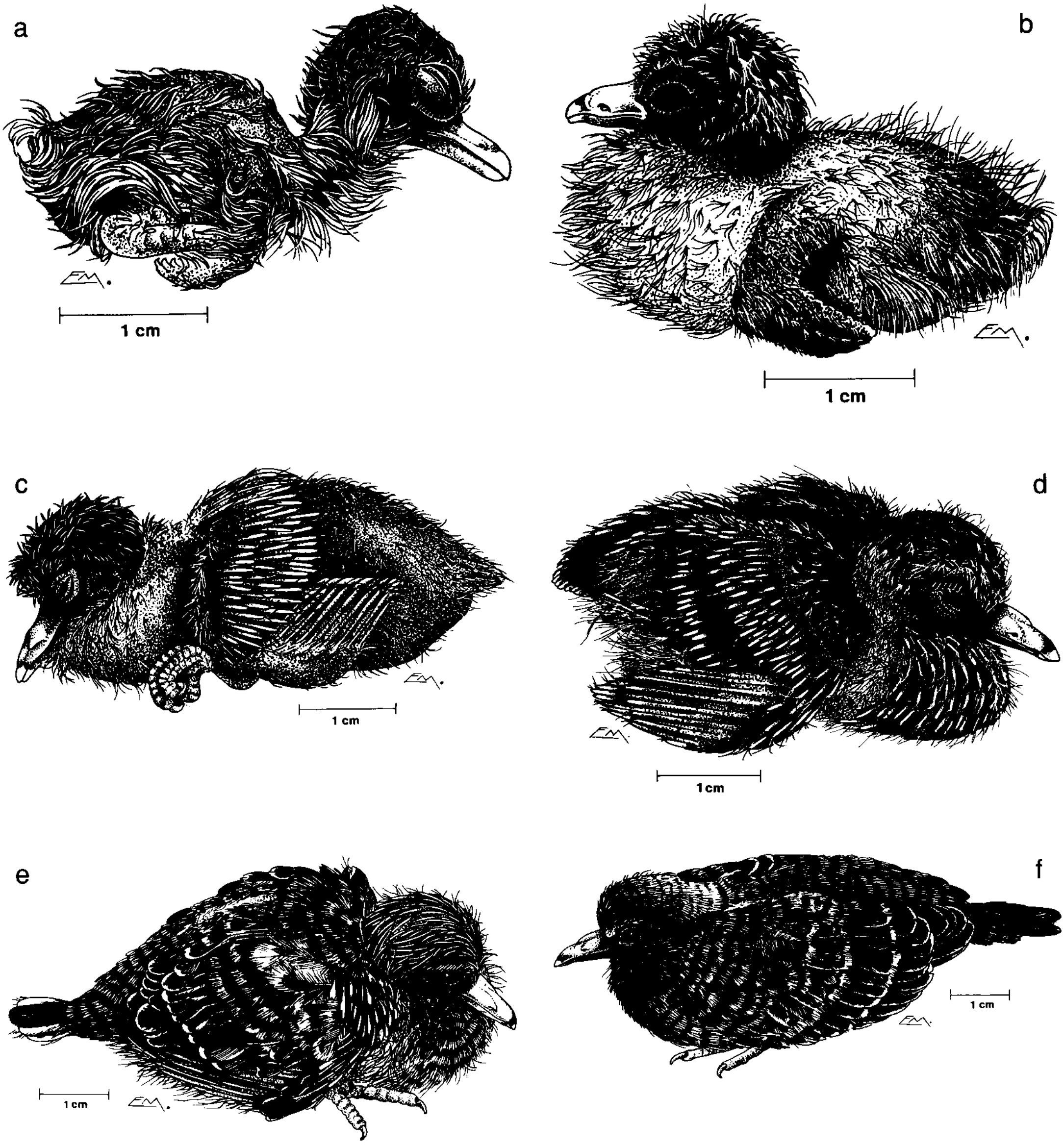

Fig. 5. Phenology of postnatal growth of Diamond and Namaqua Doves. — a: Namaqua Dove immediately after hatching (= day 0). — b: Diamond Dove one day old (= day 1). — c: Namaqua Dove on day 4. — d: Diamond Dove on day 5 (day of transition to endothermy). — e: Diamond Dove on day 7, T_b regulated at a fully stable level. — f: Diamond Dove on day 9, earliest time at which nest is left.

4. 2. Breeding parameters and ontogeny

The habitat of both Diamond and Namaqua Doves is characterized by (a) extreme abiotic conditions such as air temperatures T_a up to 45–50°C and high solar radiation and (b) erratic rainfall and therefore unpredictable food and water supply. In spite of this climatic background, both species are present in the desert and semi-desert regions of Australia and Africa throughout the year (Goodwin 1978, Blakers *et al.* 1984). For successful reproduction in these zones it would be adaptive if the birds were able to respond quickly to favourable conditions. This is clearly reflected by the

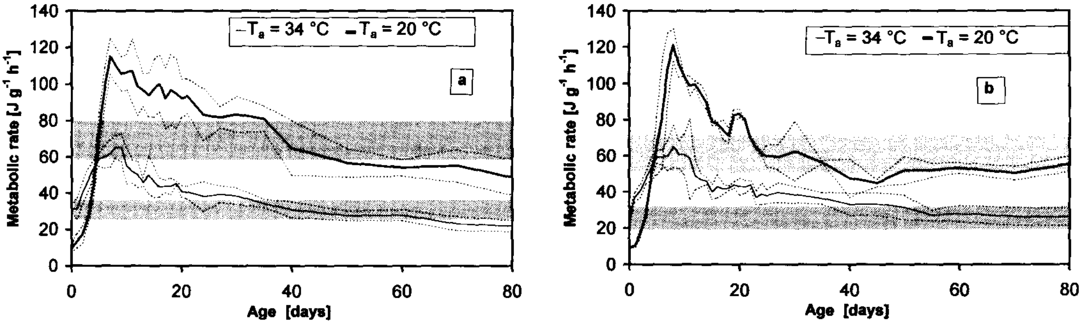

Fig. 6a and b. Ontogeny of metabolism in Diamond (a) and Namaqua Doves (b) at T_a of 20 (cold stress) and 34°C (TNZ). The thicker lines represent the mean (N = 2–8), the broken lines indicate SD. The hatched areas denote the range of metabolic rates in adult birds at the given T_a.

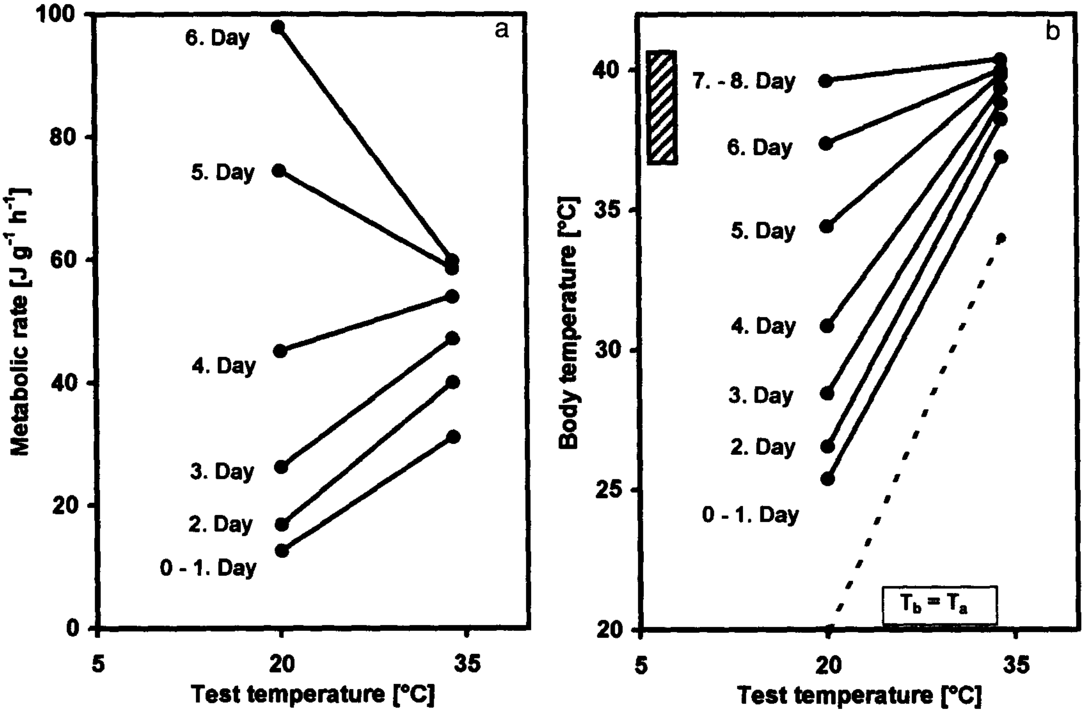

Fig. 7a and b. RMR (a) and T_b (b) at different test temperatures in Diamond Doves. Namaqua Doves show similar results, therefore graphs are given for Diamond Doves only to save space. The transition to endothermy (increasing MR at decreasing T_a) occurs on day 5. On day 6, juveniles are able to regulate T_b in the adult range (hatched box). On day 7, T_b is stable. At the test temperature 15°C, T_b is 5–6°C lower than in the test group at 20°C on days 0–5. The difference decreases rapidly between days 6 and 7. On day 7, T_b is stable as well.

high gonadic activity in Australian desert-adapted pigeons throughout the year (Frith *et al.* 1976). Monogamic pair bonds further facilitate the quick start of a breeding cycle (Frith 1982, own observations).

As in all pigeons, the energy expenditure for the typical nest construction is small in Diamond and Namaqua Doves. Nests are fragile platforms constructed of only few twigs. However, they gain stability with age of the nestlings because faeces is deposited within the nest material. Clutch size is also small, and egg mass equals 6–7% of the mass of the female bird. This is average for a columbid, but at the low end of the scale for altricial birds (4–10%, Bezzel & Prinzinger 1990, Prinzinger *et al.* 1997).

The development of juvenile Diamond and Namaqua Doves is extremely rapid, as it was previously described for other columbids (Arad 1989). Compared to the predictions after Weathers (1992), the nestling time is 57% (Diamond Dove) and 33% (Namaqua Doves) shorter. The duration of the nestling period is closely related to the development of thermoregulation (Ricklefs & Hainsworth 1968, Prinzinger & Siedle 1988, Arad 1989). Species with short nestling periods show relatively early onset of thermoregulation in relation to their mass gain (Ricklefs & Hainsworth 1968). Transformation of the dove data according to the growth index introduced by Ricklefs (1967, 1983) shows that the two dove species have a pattern of thermoregulatory development that is similar to that of passerines (accelerated nestling growth). According to this transformation, the development of thermoregulation is completed after 70–75% of the nestling time in the doves, while comparable species with longer nestling periods can thermoregulate not earlier than at 90–95% of the nestling time (Ricklefs & Hainsworth 1968). At the time of onset of thermoregulation (day 5) the body feathers are still in the protective sheaths and do not form an insulative cover on the body (Fig 5d). Obviously, the feather quality is not the deciding factor for the transition to endothermy. This has also been found in mousebirds (Finke *et al.* 1995). It is likely that the development of metabolically active organs such as the skeleton muscles, liver and heart has progressed far enough to supply sufficient energy, but the surface/volume ratio is still high so the T_b can not be regulated at adult level (Fig. 7a and b). From the day at which the thermal insulation (feather cover) is fully developed, T_b is effectively regulated and adults stop constant brooding (day 7, Figs. 7b and 5e). The rapid development of thermoregulatory abilities in the juveniles combined with the behavioural mechanisms of the adults enable these desert species to reproduce under extreme climatic conditions. This was previously demonstrated for the larger Rock Pigeon (Arieli *et al.* 1988).

To estimate the energetic costs of reproduction, RMRs were calculated for 3 stages of the nestling time according to equation (7) in Weathers and Siegel (1995). In both species, RMRs were lower than predicted at hatching (20% in Diamond and 33% in Namaqua Doves), but 20% higher at day 5 (maximum growth). At the time when the young left the nest, RMRs were as predicted. This indicates that the energetic demands of the extremely rapid growth are high and that nestling metabolism is in fact affected by growth rate (for critical review, see Weathers 1996). Maximum effort is put into the quick development of young in order to take advantage of favourable breeding conditions in an unpredictable environment. However, the shorter nestling time decreases the total metabolized energy per nestling produced (TME, Weathers 1992) by 65% (Diamond Dove) and 40% (Namaqua Dove).

The energetic demands of pair formation, nest construction, egg production as well as the TME for raising the young are small and enable the doves to raise several broods in short intervals if conditions are good. Although the egg composition and embryonic development of the Diamond Doves do not indicate direct influences of the environment on the embryonic phase (Prinzinger *et al.* 1997), they are pre-adaptive for survival in the hot and arid environment. Therefore, these columbids are typical opportunistic breeders in adaptation to the desert environment. Pigeons and doves have no effective defence mechanisms against predators of their nests such as burrows or strong aggressive behaviour, etc. Their nests are normally easily visible and accessible. However, eggs and chicks lost can be replaced quickly due to the low energy investment. Obviously, the strategy of doves is clearly low investment and quick response to favourable conditions which leads to successful reproduction in the extreme habitat.

5. Conclusions

Diamond and Namaqua Doves can be considered as direct ecological pendants in their respective habitats on the African and Australian continents. Although not directly related within the Columbid family (Goodwin 1983), they show a very close resemblance in their morphology (body size and general habitus), physiology (temperature regulation, metabolic rates, water budget) as well as their reproductive biology. The study presents evidence for a strong influence of extreme abiotic conditions on the biology of these species.

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Selostus: **Äärioloshteissa elävien kyyhkyjen ruumiinlämmön ja energiatalouden säätely**

Pienet australialaiset timanttikyyhkyt *Geopelia cuneata* (38 g) ja afrikkalaiset naamiokyyhkyt *Oena capensis* (36 g) elävät aavikoilla, puoliaavikoilla ja kuivilla aroalueilla. Niitä voidaan pitää näiden kahden mantereen ekologisina vastinlajeina. Molempien lajien aineenvaihdunta-arvot ovat 20–50% samankokoisten lintujen odotettuja arvoja alempana, kun yleensä kyyhkyslajien aineenvaihdunta-arvot ovat lintujen normaalitasolla tai jopa korkeampia. Erittäin kuumissa oloissa molemmat lajit sietävät elimistön lämpötilan kohoamista (jopa 44,8°C:een), mikä vähentää aktiivisen lämmönpoiston tarvetta. Lisäksi niillä on tehokkaita haihtumiseen perustuvia lämmönpoistomekanismeja (esim. läähätys, kurkun leyhytys). Niiden avulla linnut voivat poistaa lämpöä yhtä nopeasti kuin elimistön oma aineenvaihdunta sitä tuottaa. Nämä fysiologiset ominaisuudet mahdollistavat kokopäiväisen aktiivisuuden jopa ympäristön lämpötilan ollessa korkeimmillaan. Molemmat lajit ovat sopeutuneet elintilojensa vaikeasti ennustettaviin ilmasto-oloihin opportunistisella haudontakäyttäytymisellä. Poikasten tuotto on voimakkaasti nopeutettu: sekä pesimisaika että energiavarojen käyttö jokaista kasvatettua poikasta kohti on vain 50% samankokoisille tropiikin linnuille odotetuista arvoista. Näin ne voivat kasvattaa suotuisissa sääoloissa (erityisesti sadekuurojen aikaan) nopeasti useampia pesueita peräkkäin.

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