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HEAT PRODUCTION AND EVAPORATIVE WATER LOSS OF DUNE LARKS FROM THE NAMIB DESERT¹

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Abstract. Dune Larks *Miafra erythrocephalus* are the only permanent residents living in the Namib Sand Sea, one of the driest regions on earth. For Dune Larks with an average body mass of 27.3 ± 1.8 g ($n = 12$), basal metabolic rate (BMR) equaled 36.0 kJ day⁻¹, a value near allometric predictions. Hence, I found no evidence that these birds have a reduced BMR. I suggest that because they live in a relatively cool environment in winter, which mandates significant metabolic machinery for thermogenesis, larks have an elevated BMR at this time. Below 30°C, total evaporative water loss (TEWL) varied little with ambient temperature (T_a), and averaged 66.0 mg H₂O hr⁻¹, or 1.58 g day⁻¹. The latter value was 21–44% lower than allometric predictions, supporting the idea that larks have a reduced TEWL, attributable, perhaps, to reduced cutaneous water loss. Metabolic water production may play a significant role in the water economy of larks in view of the fact that evaporative water losses are replaced at T_a s below 17.0°C.

Key words: avian energetics, basal metabolic rate, Dune Lark, desert, evaporative water loss, heat transfer coefficient, *Miafra erythrocephalus*, Namib.

The Namib sand sea, a 34,000 km² expanse of sand dunes situated along the southwestern coast of Africa, is among the driest regions in the world (Logan 1960, Teller and Lancaster 1985). Because of its proximity to the ocean and the cool Benguela current, ambient air temperatures (T_a) can be relatively cool across this region, especially in winter when T_a s often drop to <10°C at night (Lancaster et al. 1984). In contrast to

many other deserts, maximum T_a s rarely exceed 40°C. Among desert ecosystems where annual net primary production typically varies from 15–200 g dry mass m⁻² (Hadley 1979), the Namib sand sea has the lowest net primary production so far recorded, 5.7 g dry mass m⁻² (Seely and Louw 1980). Because this desert is geologically older than many others (Axelrod 1950, Schwarzback 1961), one might expect inhabitants to possess finely tuned behavioral and physiological adaptations that permit a desert existence. Several bird species frequent the Namib, but only one species has evolved the capacity to reside year-round in the Namib sand sea, the Dune Lark (*Miafra erythrocephalus*) (Willoughby 1971, Boyer 1988, Williams 1992).

Although the physiological prowess of small mammals that have evolved in deserts to minimize energy expenditure and rates of water loss is well known (Schmidt-Nielsen and Schmidt-Nielsen 1950, Schmidt-Nielsen 1964, MacMillen 1983), attempts to elucidate similar physiological attributes among species of arid-adapted birds have proven less fruitful. Reviewing nearly a decade of work, Bartholomew and Cade (1963) concluded that many avian species found in deserts do not possess unique physiological adaptations compared with their nondesert counterparts. These authors lamented the paucity of data on Old World desert species and suggested that these populations might be expected to show more conspicuous physiological adaptations to arid conditions than their ecological equivalents in the New World. The perception that birds inhabiting deserts are able to do so because of a suite of avian design characteristics possessed by all birds, rather than as a consequence of specific adaptation(s) to the desert environment, persists in the literature (Maclean 1996).

Several reports have appeared since the work of

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Bartholomew and Cade which have hypothesized that arid-zone birds may have evolved a reduced basal metabolic rate (BMR) (Dawson and Bennet 1973, Withers and Williams 1990, Schleucher et al. 1991). Advantages attributable to a diminution of BMR would include a lower overall energy demand, lower total evaporative water loss (TEWL) (the sum of respiratory and cutaneous water losses), and lower endogenous heat production which would have to be dissipated in a warm environment, often by evaporative means. Recently Williams and Tieleman (unpubl. data, available from author) have tested this hypothesis by comparing rates of basal metabolism for 23 species of birds from arid regions with 181 species from more mesic sites. Their analysis, based on traditional least-squares regression, and regressions based on phylogenetic independent contrasts, showed that, in general, desert birds have a BMR 25–50% lower than that of nondesert forms.

Birds living in deserts often do not have access to drinking water and, as a result, must rely on preformed water in their diet, and on metabolic water, to supply their needs. Traits which might reduce TEWL could clearly be advantageous to them. In a vanguard study examining pulmocutaneous water loss for 13 species from 5 orders, Bartholomew and Dawson (1953) reported that, in the absence of temperature stress, rates of TEWL of desert and mesic birds did not differ. Williams (1996) recently collated rates of TEWL for 102 species ranging in size from hummingbirds to Ostriches (*Struthio camelus*) using both least-squares regression and regressions based on phylogenetic independent contrasts. Both approaches revealed that arid forms have a lower TEWL than species from more mesic environments.

Information on the metabolism and TEWL of avian species from Old World deserts is scant, especially species that occupy cool, coastal deserts such as the Namib. An understanding of species from these regions is especially important because, on the one hand, they are exposed to hyperarid conditions and, like many other desert-adapted birds, might be expected to exhibit a reduction in BMR and TEWL. On the other hand, they also are subjected to relatively cold temperatures, especially at night during winter, which requires shivering thermogenesis, and may result in an elevation in BMR because of the attendant up-regulation in their metabolic machinery (Dawson and O'Conner 1996). In this paper, I test the hypotheses that Dune Larks have a reduced BMR in response to desert conditions, and that they have a decreased TEWL in order to conserve water. In addition, I document the extent to which metabolic water production might replenish evaporative water losses in this species. Finally, I examine the idea that desert birds ought to minimize dry heat transfer when ambient temperature (T_a) exceeds body temperature (T_b) (Dawson and Bennett 1973, Tieleman and Williams 1999).

METHODS

STUDY ANIMALS

During the austral winter, June, 1990, I mist-netted 12 Dune Larks near the vicinity of Gobabeb, Namibia, a research station operated by the Desert Ecological Re-

search Unit of Namibia. As birds were captured, they were placed in temporary cages until they were transported by air to the University of Cape Town where they were housed in indoor holding facilities ($T_a = 18$ – 20°C). I fed them a diet of mixed bird seed, mealworms and other insects, and hard-boiled egg. Vitamins were added to their drinking water, which was provided ad libitum. Birds were in captivity three weeks before experiments were begun.

MEASUREMENT OF BODY TEMPERATURE

I measured core T_b immediately after the completion of metabolic rate measurements, by inserting a 36-gauge Teflon-coated copper-constantan thermocouple into the rectum. I recorded T_b when readings had stabilized and removal of the thermocouple by 1–2 mm brought about no change in measured T_b . The thermocouple and Westcor Thermometer (model TH-65) were calibrated against a mercury in-glass thermometer traceable to the National Institute of Standards and Technology ($\pm 0.1^\circ\text{C}$).

MEASUREMENT OF OXYGEN CONSUMPTION AND TOTAL EVAPORATIVE WATER LOSS

Rates of oxygen consumption (VO_2) and TEWL were determined for postabsorptive birds during their nocturnal phase (20:00–01:00), by standard flow-through respirometry and hygrometry methods (Gessaman 1987). My metabolism chamber was constructed from a 10 L stainless-steel canister with a circular brass flange welded to the top. A Plexiglas lid could be bolted to the top of the chamber rendering it air tight. The inner walls of the chamber were painted flat black to reduce reflectance of long-wave radiation (Porter 1969). The chamber was equipped with a wire-mesh platform on which the bird could stand over a layer of mineral oil into which excreta fell, excluding it as a source of water in my measurements. During each trial, I placed the chamber containing a lark in a temperature-controlled environmental cabinet that held temperature constant to $\pm 0.1^\circ\text{C}$. Air was drawn under negative pressure through columns of drierite, soda lime, and drierite to remove water and CO_2 from the air stream, and then through the chamber. Exiting air passed through a rotameter, a Hanna Thermohygrometer (model HI 8564) to measure relative humidity, then through another series of scrubbing columns before a subsample was routed through an Applied Electrochemistry oxygen analyzer to determine the fractional concentration of oxygen in dry, CO_2 -free air. The O_2 analyzer was zeroed with pure nitrogen and calibrated with dry CO_2 -free air. Flow rates were monitored continuously with a Brooks rotameter to assure constancy, but were measured several times during each trial with a bubble meter (Levy 1964). Flow rates varied from 600 to 2,000 mL min^{-1} depending on the T_a .

During metabolism trials at temperatures of 40°C and below, I adjusted air flow rates so that relative humidity in the chamber was less than 15%. Above 40°C , my choice of flow rate was a compromise between maintenance of low water vapor pressures in the chamber (Lasiewski et al. 1966, Bernstein et al. 1977), and the desire to maintain a ΔO_2 of at least 0.05%, in order to minimize errors in my measurement of metabolism. Above 40°C , relative humidity varied be-

tween 35–40%. Although it is possible that I did not measure maximum TEWL at these high temperatures (Bernstein et al. 1977), the data of Lasiewski et al. (1966) suggest that this is unlikely. For Painted Quail *Excalfactoria chinensis*, these authors showed that, at 40°C, TEWL was unaffected by water vapor pressures ranging from 10–40 mm Hg. In my study, water vapor pressure in metabolism chambers ranged from 20–25 mm Hg at T_{as} above 40°C. I calibrated the hygrometer over LiCl and NaCl standards on a weekly basis; adjustments did not exceed 1%.

Air temperature within the chamber was monitored with a 28-gauge thermocouple and Wescor digital thermometer. Because downstream air-flow rates were measured before removal of CO_2 , I used equation 4b of Withers (1977) to calculate VO_2 . Rates of TEWL were calculated as the difference in water vapor density between excurrent and in current air times the flow rate. After birds remained at a given temperature for at least 1 hr, I recorded the fractional oxygen concentration of the air stream with the aid of a BBC Acorn computer and commercially available data acquisition software (Lighton 1985). When the trace on the computer screen was constant for at least 15 min, I recorded both variables. I used $20.08 \text{ J (mL O}_2\text{)}^{-1}$ to convert oxygen consumption into heat production, $2.427 \text{ J (mg H}_2\text{O)}^{-1}$ to convert TEWL into dissipated heat, and $0.528 \text{ mg H}_2\text{O (mL O}_2\text{)}^{-1}$ to relate metabolic water production to oxygen consumption (Calder and King 1974, Schmidt-Nielsen 1997).

DRY HEAT TRANSFER COEFFICIENT

The dry heat transfer coefficient is a function of several properties of the bird, some fixed such as body size and surface to volume ratio, others variable such as the degree of vasodilation of capillaries in the skin and the extent of piloerection (Burton 1934, Calder and King 1974):

$$h = \frac{H_m - H_e}{T_b - T_a}$$

where H_m represents metabolic heat production, H_e heat loss by means of evaporation, and T_b and T_a are as defined previously. The heat transfer coefficient ($\text{J sec}^{-1}\text{ }^\circ\text{C}^{-1}$) should not be confused with heat loss to or heat gain from the environment (J sec^{-1}), the latter calculated by multiplying the heat transfer coefficient by the temperature gradient. At higher T_{as} , calculations of h often show considerable scatter because, as T_a approaches T_b , small errors in measurements translate into large errors in estimation of h . Moreover, at the point where $T_a = T_b$, the equation is undefined, yet the properties of the bird that characterize the heat transfer coefficient remain intact. To examine the trends in changes in h at high T_{as} , I have calculated h at the upper critical temperature (T_{uc}), at the temperature of equality where $T_a = T_b$, and at $T_a = 45^\circ\text{C}$. For the first and last of these three values, I calculated h using values for H_m , H_e , and T_b from equations presented in this study that describe these variables relative to T_a for Dune Larks. To calculate h at $T_a = T_b$, I have applied l'Hopital's rule (Apostol 1967), a differentiation technique that provides a polynomial approximation of h when both numerator and denominator are zero (Tie-

leman and Williams 1999). Here, I assume that T_b remained constant during my steady state measurements.

STATISTICAL ANALYSES

Data were analyzed by means of a SPSS statistical package (SPSS 1997). I determined linear relationships by least-squares regression (Zar 1984). Because I measured oxygen consumption repeatedly on the same individuals, my data are not strictly independent. To assure that individuals did not significantly differ from each other, I calculated regressions for each individual and tested for differences among individuals by analysis of covariance for data below the T_{lc} (Snedecor and Cochran 1980). For data within the thermal neutral zone (TNZ), I tested for differences among individuals using ANOVA. Finding no differences, I pooled data for all individuals. The sample size (n) represents the number of measurements made on 12 birds. I rejected the null hypothesis at $P = 0.05$. Means are presented \pm SD, unless otherwise noted.

RESULTS

LABORATORY METABOLISM

Because larks were captured during the nonbreeding season, sexes could not be distinguished, although I often netted pairs of birds which likely consisted of a male and female. Body masses of larks averaged $27.3 \pm 1.8 \text{ g}$ ($n = 12$) during laboratory trials.

Between T_{as} of -3.9 to 35°C , T_b did not vary significantly with T_a and averaged $40.8 \pm 0.9^\circ\text{C}$ (Fig 1a; $r^2 = 0.10$, $F_{1,18} = 1.9$, $P > 0.18$, $n = 20$). Above 35°C , T_b increased linearly with T_a ; $T_b = 35.1 + 0.2(T_a)$ ($r^2 = 0.91$, $F_{1,19} = 87.4$, $P < 0.001$, $n = 11$).

The temperature of equality, where $T_b = T_a$, can be determined from the latter equation: $T_{b=a} = 43.9^\circ\text{C}$. At T_{as} below this value, the thermal gradient between a lark and its environment is positive, resulting in heat flux from the bird to the environment. Above $T_{b=a}$, larks gain heat from the environment, and therefore must rely on evaporative cooling to regulate their T_b .

The basal metabolic rate of Dune Larks was $74.7 \pm 6.9 \text{ ml O}_2 \text{ hr}^{-1}$ (Fig. 1b; $n = 16$), or 36.0 kJ day^{-1} . Below thermal neutrality, $\text{ml O}_2 \text{ hr}^{-1} = 201.95 - 4.56(T_a)$ ($r^2 = 0.91$, $F_{1,33} = 335.3$, $P < 0.001$, $n = 35$). This equation intersects the x-axis at 44.3°C . Above the TNZ, oxygen consumption was described as: $\text{ml O}_2 \text{ hr}^{-1} = -118.1 + 5.5(T_a)$ ($r^2 = 0.72$, $F_{1,13} = 33.5$, $P < 0.01$, $n = 15$).

The intersection of the above equations and basal metabolism provides an estimate of the upper (T_{uc}) and lower (T_{lc}) critical temperatures; $T_{uc} = 35.1$, and $T_{lc} = 27.9$, respectively.

Below 30°C , TEWL loss varied little with T_a ($r^2 = 0.04$, $P = 0.3$) and averaged $66.0 \text{ mg H}_2\text{O hr}^{-1}$, or 1.58 g day^{-1} (Fig 1c; $n = 32$). Above 30°C , TEWL was best described by: $(\text{mg H}_2\text{O hr}^{-1}) = e^{-0.164 + 0.161(T_a)}$; ($r^2 = 0.93$, $F_{1,32} = 382.3$, $P < 0.001$, $n = 34$).

Multiplying the equation for oxygen consumption by $0.528 \text{ mg H}_2\text{O (mL O}_2\text{)}^{-1}$, the factor that relates O_2 consumption to water production during fat catabolism (Schmidt-Nielsen 1997), yields an equation for metabolic water production below the T_{lc} , metabolic water (mg hr^{-1}) = $106.6 - 2.41(T_a)$. At a T_a of 16.9°C , metabolic water production ($66.0 \text{ mg H}_2\text{O hr}^{-1}$) equals

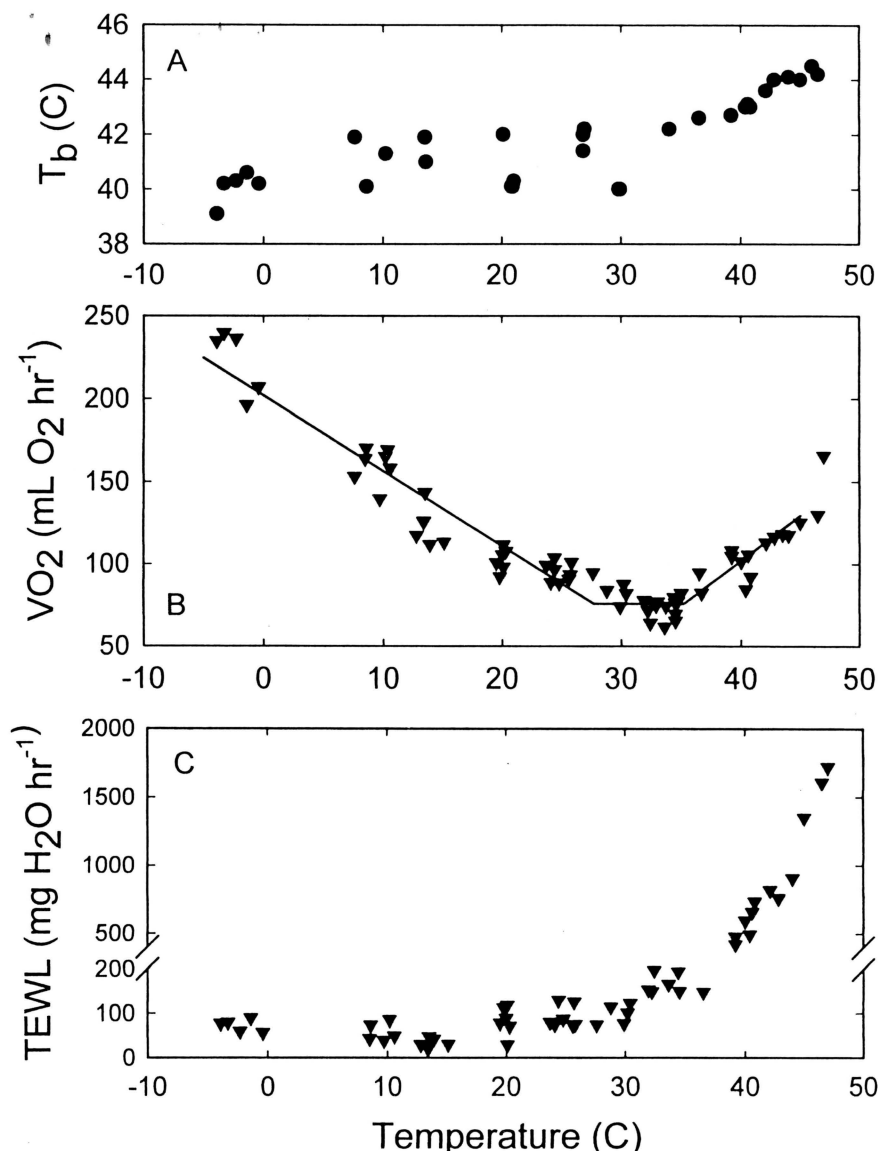


FIGURE 1. (A) body temperature, (B) oxygen consumption, and (C) total evaporative water loss of Dune Larks as a function of air temperature.

evaporative water loss, and below this value, metabolic water production offsets evaporative water losses.

For Dune Larks, h was not significantly related to T_a for ambient temperatures below 30°C, and averaged $94.0 \pm 10.8 \text{ J hr}^{-1} \text{ } ^\circ\text{C}^{-1}$ ($n = 27$; Fig. 2). Above 30°C, h increased as T_a increased; $h \text{ (J hr}^{-1} \text{ } ^\circ\text{C}^{-1}) = -1,152.0 \pm 36.0 (T_a)$ ($r^2 = 0.30$, $F_{1,21} = 10.5$, $P < 0.004$, $n = 23$).

One might predict that a lark should increase h as T_a increases in the TNZ to some maximum value, and then, as T_a approaches T_b and exceeds it, the lark should make whatever adjustments possible to reduce h to a minimum, thereby reducing heat gain from the environment. To test this idea I calculated h using equations for H_m , H_e , and T_b as functions of T_a (Calder and King 1974). At T_{uc} , $h = 157.3 \text{ J hr}^{-1} \text{ } ^\circ\text{C}^{-1}$, and at T_{47} , the highest temperature for which I have data, $h = 495.0 \text{ J hr}^{-1} \text{ } ^\circ\text{C}^{-1}$ (Fig. 2). At the point of thermal

equality, $T_{b=a}$, $h = 356.9 \text{ J hr}^{-1} \text{ } ^\circ\text{C}^{-1}$. Apparently Dune Larks increase their heat transfer coefficient up to an ambient temperature of 47°C.

DISCUSSION

Basal metabolism, the minimal rate of heat production of postabsorptive, inactive endotherms in the rest phase of their daily cycle, is an important parameter in the physiology of these animals, often used as a baseline for comparisons among species (Dawson and O'Conner 1996). Such comparisons are viewed as a tool that can lead to insights about general principals of design by natural selection for animals that have evolved in different habitats and environments. Several studies have proposed that desert-adapted birds have a reduced BMR compared to species that occupy more mesic habitats (Hudson and Kimsey 1966, Root et al. 1991, Hinsley et al. 1993).

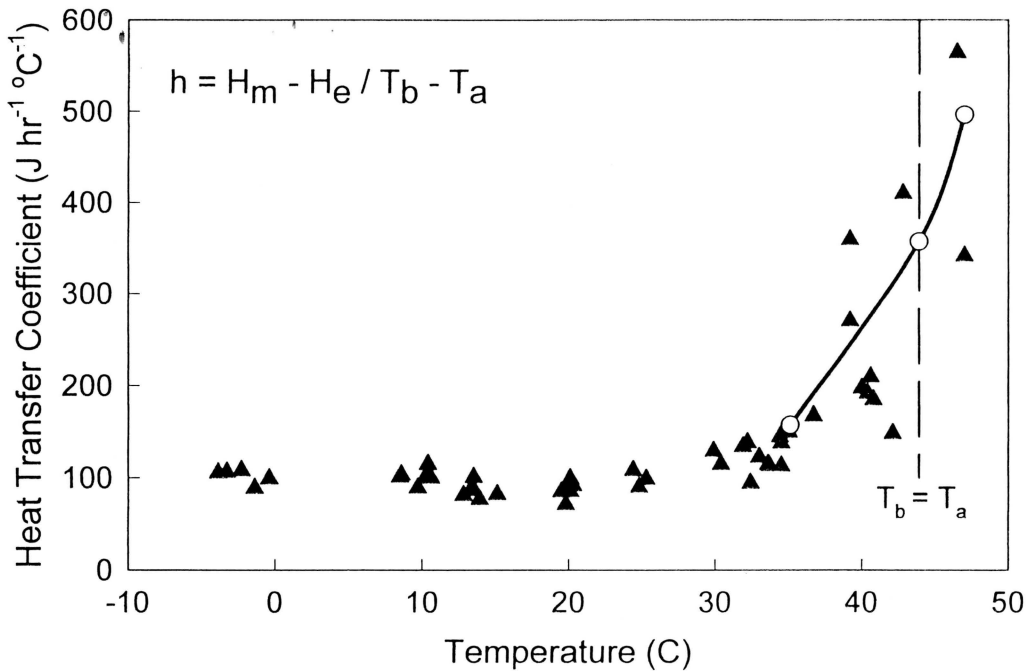


FIGURE 2. The heat transfer coefficient of Dune Larks as a function of air temperature. The dashed vertical line represents the point at which air temperature and body temperature are equal.

The prediction that Dune Larks have a reduced BMR is not supported by my data. The equation of Aschoff and Pohl (1970) predicts a BMR of 35.2 kJ day⁻¹ for a Dune Lark of 27.3 g, nearly the same as my estimate of 36.0 kJ day⁻¹. Recently, Reynolds and Lee (1996) reported that passerines and nonpasserines do not differ in levels of BMR, and published a single phylogenetically-adjusted equation for the basal metabolism of birds:

$$\log \text{BMR (W)} = 1.311 + 0.635 \log \text{body mass (g)}$$

Judging from the 95% confidence interval for the intercept (-1.525 to -1.113), this value should be negative instead of positive as reported. With the intercept corrected (-1.311), this equation yields a BMR of 34.5 kJ day⁻¹. Hence, I find no evidence that Dune Larks have a reduced BMR, at least during the winter.

Why do Dune Larks not show the same reduction in metabolism as other arid-adapted birds? Although this problem remains unresolved, the answer may be linked to their thermoregulatory requirements during winter. The Namib is a cool desert, especially during the winter, with a mean daily temperature around 17°C at this time, and a mean daily minimum temperature of around 9°C (Lancaster et al. 1984, see Evenari 1985 for a comparison with other deserts). With a T_{lc} of 27.9°C, Dune Larks expend considerable energy in the process of chemical heat production during winter. Because they must maintain the metabolic machinery to produce heat by shivering, this may result in a higher basal metabolism. Seasonal adjustments in BMR in birds are well known with wintertime basal rates often exceeding summer values (Pohl and West 1973, Cooper and Swanson 1994, Dawson and O'Conner 1996). It remains to be determined whether larks seasonally adjust their BMR in response to temperature changes.

Despite their level of basal metabolism, Dune Larks have a reduced TEWL compared to more mesic species. I have published equations that relate TEWL to body mass using both traditional least-squares regression, and regression of phylogenetically independent contrast data (Williams 1996). The former predicts a water vapor efflux of 2.0 mL day⁻¹, the latter, 2.82 mL day⁻¹, values 21% and 44% higher, respectively, than what I have measured in Dune Larks (1.58 mL day⁻¹). Thus, Dune Larks utilize some mechanism to retard water loss while at the same time possessing a BMR higher than predicted for a desert bird. If BMR is not lower than expected, and, as a consequence, respiratory variables not reduced, it seems reasonable to suggest that this species may have evolved a relatively low cutaneous water loss, perhaps because of alteration of the lipid content of their skin. Indeed, during bouts of water deprivation, Zebra Finches (*Poephila guttata*) can reduce transepidermal water loss by over a factor of two, primarily by bolstering the lipid content of the interstices of skin cells (Webster et al. 1985, Menon et al. 1989).

An examination of metabolic water production relative to TEWL can provide insights into the contribution that oxidative water makes towards replenishing evaporative water losses (MacMillen 1990). For example, among a small coterie of birds that can survive in the laboratory solely on a diet of air-dried seeds, Zebra Finches have a metabolic water production equivalent to TEWL when T_a equals 22.9°C (Cade et al. 1965). Although these relationships do not provide a complete assessment of a bird's water balance in its natural environment, they approach ecological significance when one considers that TEWL in small birds represents >70% of total H₂O losses including losses in urine and feces (Bartholomew 1972, MacMillen

1990, MacMillen and Baudinette 1993). Comparisons of metabolic water production and TEWL indicate that Dune Larks produce more metabolic water than is lost by means of evaporation during winter nights when T_a drops below 17°C. In this situation, Dune Larks may achieve a positive water balance, thereby accumulating H_2O that can be drawn upon during daylight hours when T_a s are higher. Because these calculations are based on the catabolism of fats, they are conservative. Assuming larks were catabolizing carbohydrates instead of fats, then they would produce 0.65 mg H_2O mL⁻¹ oxygen consumed (Schmidt-Nielsen 1997), and their rate of water production would equal their TEWL at a T_a of 22.0°C. This analysis suggests that metabolic water production plays a significant role in the water economy of Dune Larks.

Below the T_{ic} , h is often assumed to be minimal, but as T_a increases, the TNZ is reached, in which a bird dissipates metabolic heat over a decreasing gradient. Because of adjustments in ptiloerection and vasodilation, one could predict that h should increase in the TNZ to a maximum at the T_{uc} . At T_a s above $T_b = T_a$, where the bird is gaining heat from the environment, it could be argued that the bird should adjust attributes of its thermal shell so as to produce the lowest h possible. In this temperature range, the bird would be expected to minimize heat gain because regulation of T_b comes at the expense of losing considerable water. Dune Larks do not adjust properties of their thermal shell such that h returns to some minimum value. In this species, values for h increased monotonically at higher T_a s, a pattern consistent with Black-rumped Waxbills (*Estrilda troglodytes*), Black-throated Sparrows (*Amphispiza bilineata*), and Monk Parakeets (*Myiopsitta monachus*) (Cade et al. 1965, Weathers and Caccamise 1975, Weathers 1981).

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