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Avian adaptation along an aridity gradient

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2002

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Tieleman, B. I. (2002). *Avian adaptation along an aridity gradient: Physiology, behavior, and life history*. s.n.

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PART III

Physiological mechanisms

CHAPTER 9

Flexibility in basal metabolic rate and evaporative water loss among Hoopoe Larks exposed to different environmental temperatures

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Journal of Experimental Biology 203: 3153-3159. 2000.

ABSTRACT

The "energy demand" hypothesis for short-term adjustments in basal metabolic rate (BMR) posits that birds adjust the size of their internal organs relative to food intake, a correlate of energy demand. We tested this hypothesis on Hoopoe Larks (*Alaemon alaudipes*), inhabitants of the Arabian Desert, by acclimating birds for 3 weeks at 15 °C and at 36 °C, then measuring their BMR and total evaporative water loss (TEWL). Thereafter we determined the dry masses of their brain, heart, liver, kidney, stomach, intestine, and muscles of the pectoral region. Though initially average body mass did not differ between the two groups, after 3 weeks, birds in the 15 °C group had gained mass (44.1 ± 6.5 g), whereas larks in the 36 °C group had maintained constant mass (36.6 ± 3.6 g).

Birds in the 15 °C group had an average BMR of 46.8 ± 6.9 kJ/d whereas birds in the 36 °C group had a BMR of 32.9 ± 6.3 kJ/d, values which were significantly different when we controlled for differences in body mass. When measured at 35 °C, larks in the cold-exposure group had a TEWL of 3.55 ± 0.60 g H_2O/d, whereas TEWL for birds in the 36 °C group averaged 2.23 ± 0.28 g H_2O/d, a 59.2% difference. Mass-independent TEWL differed significantly between groups.

Larks in the 15 °C group had a significantly larger liver, kidney, stomach, and intestine than larks in the 36 °C group. These increases in organ mass contributed 14.3% towards the total mass increment in the cold exposure group. Apparently increased food intake among larks in the cold group resulted in enlargement of some of the internal organs, and the increase in mass of these organs required higher oxygen uptake to support them. As oxygen demands increased, larks apparently lost more evaporative water, but the relationship between increases in BMR and TEWL remains unresolved.

ABSTRACT

Introduction

Studies of basal metabolism, the minimum metabolic rate of inactive, postabsorptive, endotherms while in their rest-phase and thermal neutral zone, have contributed significantly to our understanding of animal energetics (King and Farner 1961; Aschoff and Pohl 1970; Calder and King 1974; Hayssen and Lacy 1985; Reynolds and Lee 1996). Although animals in nature may only rarely function at basal levels of energy expenditure, this parameter has been useful as a physiological standard for assessing energy costs of thermoregulation (Dawson and O'Conner 1996), increments in energy expenditure due to activity in the wild (Drent and Daan 1980; Bryant and Tatner 1991; Ricklefs et al. 1996; Nagy et al. 1999), for investigating limits to maximum physiological performance (Peterson et al. 1990; Weiner 1993; Hinds et al. 1993; Chappel et al. 1999), in evaluating the role of body size and circadian phase on energy flux (Aschoff and Pohl 1970; Hayssen and Lacy 1985; Tieleman and Williams 2000), and in searches for evolutionary adjustments of metabolic rates to specific environments (Weathers 1979; Ellis 1984; Piersma et al. 1996; Williams and Tieleman 2001). Of the total ATP produced in the basal state, among mammals, most is used in protein synthesis or by ion pumps, with a smaller proportion being consumed by myosin ATPase, by gluconeogenesis, and by ureagenesis (Rolfe and Brown 1997). Although detailed studies that compartmentalize ATP usage in birds have yet to be done, it is likely that patterns for mammals and birds are similar.

Basal metabolism varies widely between species of the same body mass, often by 200-300%, but the proximate and ultimate factors responsible for this variation remain an enigma (McNab 1988; Daan et al. 1990; Dawson and O'Connor 1996). Among temperate zone birds, seasonal adjustments in BMR have been documented with some species showing an elevated BMR in winter compared to summer (Pohl and West 1973; Cooper and Swanson 1994), and others displaying a reduced BMR in winter (Kendeigh 1969; Barnett 1970). Other species show no seasonal adjustments in BMR (Hart 1962; O'Conner 1995). Trends in BMR with habitat and/or latitude have been described for several subsets of birds (Weathers 1979; Hails 1983; Ellis 1984; Piersma et al. 1996), although exceptions are often found that complicate our understanding of environmental influences on BMR (Vleck and Vleck 1979; Williams 1999). It has been suggested that birds that live in deserts have a reduced BMR compared to species that live in more mesic areas (Hudson and Kimzey 1966; Withers and Williams 1990; Hinsley et al. 1993). The generality of this idea was recently explored by Williams and Tieleman (2001) who found that desert birds have a BMR 17-25% lower than that of non-desert forms. These differences could be derived from selection for genotypes with a reduced BMR in deserts, from phenotypic adjustment of BMR, or from a combination of both.

Trying to explain why species of shorebirds at high latitudes have a higher BMR than do shorebirds from tropical latitudes, Kersten and Piersma (1987) suggested that the former have a high daily energy expenditure, the result of high energy usage by the skeletal muscles, either from locomotory activity or thermogenesis, which in turn requires enlarged abdominal organs for support. Larger organ masses, according to them, mandate a high BMR. Later, also using interspecific comparisons, Daan et al. (1990) found a positive association between mass-independent measurements of BMR in birds, their heart and liver dry masses, and their field metabolic rate while caring for young. They hypothesized that natural selection adjusted the size of the internal organs to match energy requirements during parental care, the putative period of maximum energy expenditure, and that size-independent variation in BMR reflects the relative size of internal organs such as the liver, kidney, and heart which are thought to have high mass-specific rates of oxygen consumption (Krebs 1950; Martin and Fuhrman 1955). According to this idea, birds will posses organs that are fixed at some optimal size, a reflection of their energy needs during peak metabolic demand (Taylor et al. 1996; Weibel 1998). The idea that organ masses are invariant has been shown to be incorrect; some animals vary their organ sizes over short time periods in response to alterations in diet or environment (Toloza et al. 1991; Piersma et al. 1996; Piersma and Lindström 1997; Stark 1998).

Some birds increase their BMR when exposed to low temperatures in the laboratory, whereas other species show no acclimatory change in BMR. Hudson and Kimzey (1966) reported that House Sparrows (*Passer domesticus*) from Houston, TX, had a lower BMR than conspecifics from more northerly regions, and proposed that these differences were genetically programmed, because, when sparrows from Houston were subjected to the cold, their BMR did not change (see also West 1972). However, in a review of 9 studies of temperate-zone birds, Gelineo (1964) concluded that birds elevated their BMR by an average of 32 ± 7.8% when removed from a warm environment (29-33 °C) and kept at low temperatures (0-15 °C) for 3-4 weeks.

Less effort has been devoted to understanding the ecological and evolutionary significance of variation in total evaporative water loss (TEWL), the sum of respiratory water loss (RWL) and cutaneous water loss (CWL), than has been applied to questions about variation in BMR. Williams (1996) showed that desert birds have a reduced TEWL compared to mesic species using analyses of conventional least squares regressions, and regressions of phylogenetic independent contrasts. Both approaches supported the idea that birds from arid environments have a statistically lower TEWL than do birds from more mesic environments. In studies on small granivorous species, some individuals reduce their TEWL in response to water deprivation (Cade et al. 1965; Greenwald et al. 1967; Dawson et al. 1979), but the mechanism for this diminution remains unresolved. Finding a reduced TEWL in Zebra Finches (*Poephila guttata*) that were living without drinking water compared with individuals that had drinking water available, and ruling out changes in RWL for water-deprived individuals, Lee and Schmidt-Nielsen (1971) proffered the idea that the reductions in TEWL were likely attributable to a change in CWL. Menon et al. (1989) confirmed the observation that water-deprived Zebra Finches have a reduced CWL, and showed that these birds deposited more lipids in the intercellular spaces of the stratum corneum than did individuals with drinking water available. Presumably birds deposited lipids in the skin as an acclimatory response to enhance water conservation.

In this study we examined the short-term plasticity of BMR, TEWL, and organ sizes, of Hoopoe Larks (*Alaemon alaudipes*). We test the "energy demand" hypothesis which postulates that organ sizes, BMR, and TEWL, are influenced by the amount of food consumed, which in turn parallels energy requirements. As energy demand increases because of lower ambient temperatures (T_a), or because of greater activity levels, birds ingest more food with the result that key organs involved in catabolism (stomach, intestine, and liver), in oxygen transport to tissues (heart and lungs), and in elimination of waste (kidneys), are stimulated to hypertrophy. Because these organs have high metabolic intensity, total oxygen demand under basal conditions increases as these structures become larger. When oxygen needs are elevated, ventilation rate increases with a concomitant increase in RWL.

Methods

Hoopoe Larks are distributed across most of the Sahara and throughout the Arabian Peninsula, including the hyperarid Rub 'Al Khali, one of the largest sand seas in the world (Cramp 1984; Lancaster 1989). Although similar in appearance to females, males tend to be larger, sometimes by as much as 20%. Hoopoe Larks typically establish permanent territories (± 1 km^2) along sandy wadis or on flat gravel plains where they forage for arthropods, lizards, and to a lesser extent seeds (Cramp 1984). During the spring, females lay 2-3 eggs; both sexes incubate eggs and feed the young. In the summer when T_as often exceed 45 °C, Hoopoe Larks avoid solar radiation during the middle part of the day by shading beneath clumps of grass, or by descending into lizard burrows (Williams et al. 1999).

We mist-netted 12 Hoopoe Larks in Mahazat as-Sayd, a reserve in the east-central Arabian Desert (22° 15' N 41° 50' E), and transported them to the National Wildlife Research Center, near Taif, Saudi Arabia. We randomly assigned individuals to two groups, 3 males and 3 females in each, verified that birds were similar in body mass in both assemblages, and placed one group in a constant temperature room at 15 ± 2.0 °C, the other in a room at 36 ± 2.0 °C. Birds were fed mealworms, cockroaches, crickets, and small seeds ad libitum. Both groups were exposed to a 12L:12D light regime.

After larks were exposed to either 15 °C or 36 °C for 3 weeks, we measured basal rates of oxygen consumption (VO_2) and TEWL for postabsorptive birds during their nocturnal phase by standard flow-through respirometry and hygrometry methods (Gessaman 1987). Because allometric equations for TEWL are based on measurements at 25 °C (Williams 1996), we also measured TEWL of Hoopoe Larks at this temperature. Birds were placed in water-jacketed steel metabolic chambers (24 cm x 20 cm x 28 cm) that had an air-tight Plexiglas lid. During measurements, T_a within the chamber was controlled by a Neslab circulating water bath (RTE-140) at 35 °C, a temperature previously determined to be within the thermal neutral zone of Hoopoe Larks (Tieleman et al. 2002c), or at 25 °C. Birds were placed on a wire-mesh platform over a layer of mineral oil which trapped feces, excluding it as a source of water in measurements. Air under positive pressure coursed through columns of drierite, soda lime, and drierite to remove water and CO_2 from the air stream, through a previously calibrated (Levy 1964) Brooks mass flow controller (model 5850 E) set at 700 ml/min, then through the chamber. Exiting air passed through a General Eastern Dewpoint Hygrometer (M4-DP) before a subsample was routed through an Applied Electrochemistry oxygen analyzer (S3A-II) to determine the fractional concentration of oxygen in dry, CO_2-free outlet air. After a 1 h equilibration period, we recorded the oxygen concentration and dew point of inlet and outlet air, the temperature of the dew point hygrometer, and T_a within the chamber, using a Campbell Scientific Data Logger model 21X, for 2 more h. Calculations of oxygen consumption were performed using equation 2 of Hill (1972). We used 20.08 J/ml O_2 to convert oxygen consumption to heat production (Schmidt-Nielsen 1997). When, during the third hour of measurements, the trace for oxygen consumption was stable for at least 10 min, we noted these times and used these data for calculations.

Evaporative water loss was calculated using the equation, TEWL (g/day) = $[(V_e \rho_{out} - V_i \rho_{in})] \times 1.44 \times 10^{-3}$, where ρ_{in} and ρ_{out} is the absolute humidity (g H_2O/m^3) of inlet air and outlet air, respectively, V_i is the flow rate (ml/min) of air entering the chamber as given by the mass flow controller, and V_e is the flow rate of exiting air. Absolute humidity (ρ) was determined using the equation ρ (g H_2O/m^3) = $216.7 (e_s)/T_{dp} + 273.15$ where e_s is the saturation vapor pressure at a given dew point and T_{dp} is the temperature of the dew point hygrometer (List 1951). We calculated V_e as $V_e = V_i - [V_{O2} (1- RQ)] + V_{H2O}$. In this equation, V_i (ml/min), the flow rate into the chamber, and oxygen consumption (V_{O2}; ml/min), are known, R.Q. is assumed to equal 0.71 (King and Farner 1961), and V_{H2O} is calculated as $V_{H2O} = \rho(V_i + V_{CO2} - V_{O2})/(1-\rho)$. The latter equation is derived from the fact that $\rho = V_{H2O}/(V_i + V_{CO2} - V_{O2} + V_{H2O})$, the fraction of water in air flowing through the dew point hygrometer.

After measurements, we sacrificed birds, and dissected out their brain, heart, liver, kidney, stomach, intestine, and muscles of the pectoral region (pectoral and supracoracoideus) on the right side of the body. Internal organs and muscles were dried to constant mass for 3 days at 75 °C, and weighed on a Sauter scale (model RE 1614) to ± 0.1 mg.

Statistics were performed using SPSS 9.0 (1999). Means are presented ± SD. In making simultaneous multiple comparisons, like we have done on organ sizes between groups, the probability of a Type I error escalates rapidly. To compare organ sizes between groups, we used t-tests after a sequential Bonferroni correction in the level of significance was made (Hochberg and Tamhane 1987; Rice 1989).

Results

Body mass

At the beginning of the experiment, birds that were assigned to the 15 °C group averaged 41.3 ± 7.0 g ($n = 6$), and those placed in the 36 °C group averaged 37.2 ± 4.7 g ($n = 6$), values which did not differ significantly ($t = 1.2$, $P > 0.25$). After 3 weeks, birds in the 15 °C group were significantly heavier (44.1 ± 6.5 g) than birds in the 36 °C group (36.6 ± 3.6 g) ($t = 2.5$, $P < 0.04$). Birds in the 15 °C group gained on average 2.77 ± 0.8 g, an increase that was significantly different from zero ($t = 8.7$, $P < 0.001$), but birds in the 36 °C group decreased in mass by -0.57 ± 1.2 g, a value indistinguishable from zero ($t = 1.2$, $P > 0.3$).

Basal metabolism

Basal metabolism of Hoopoe Larks from the 15 °C group averaged 46.8 ± 6.9 kJ/d, whereas BMR of larks from the 36 °C group equaled 32.9 ± 6.3 kJ/d. Larks in the 15 °C group had a BMR that was 42.2% higher than birds in the warmer group. In an ANOVA with BMR as the dependent variable, group as a main effect, and body mass as a covariate, we found that BMR differed significantly between groups ($F = 6.2$, $P < 0.03$; Fig. 1A). In addition we compared measures of BMR relative to tarsus length, the latter a proxy for structural size, independent of organs, that might contribute disproportionately to BMR. The ratio of BMR (kJ/d) to tarsus length (mm) averaged 1.35 ± 0.11 for the 15 °C group and 0.99 ± 0.18 for the 36 °C group ($t = 4.18$, $P < 0.002$).

Total Evaporative Water Loss

For larks in the 15 °C group, TEWL averaged 3.55 ± 0.60 g H_2O/d, whereas TEWL for birds in the 36 °C group averaged 2.23 ± 0.28 g H_2O/d, a 59.2% difference. In an ANOVA with TEWL as the dependent variable, group as a main effect, and body mass as a covariate, we found that TEWL, measured at 35 °C, differed significantly between groups ($F = 17.1$, $P < 0.003$; Fig. 1B). Birds with a higher BMR tended to have a higher TEWL, a relationship described by TEWL

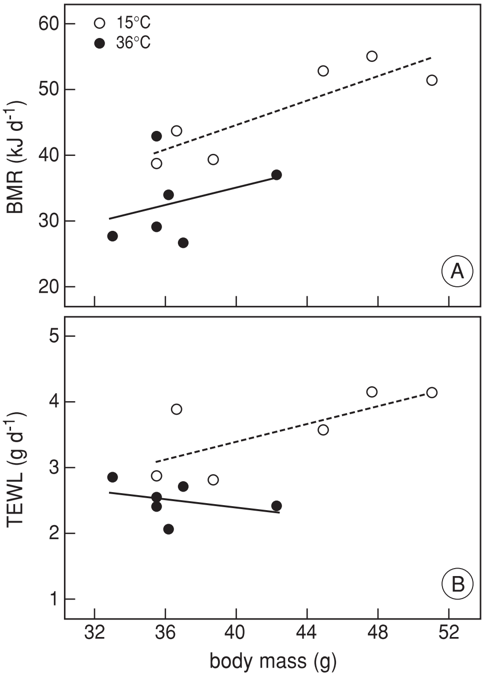

Figure 1. (A). The relationship between basal metabolism (kJ/d) and body mass (g) in Hoopoe Larks from the Arabian Desert. Solid circles represent birds acclimated to 36 °C, open circles represent birds acclimated to 15 °C. (B) The relationship between total evaporative water loss (g H_2O/d) to body mass (g) in Hoopoe Larks from the Arabian Desert. Symbols as in A.

(g H_2O/d) = -0.21 ± 0.078 BMR (kJ/d) ($r^2 = 0.83$, F = 50.4, $P < 0.001$). When measured at 25 °C, TEWL of larks in the 15 °C group averaged 3.11 ± 0.4 g H_2O/d, whereas larks in the 36 °C group averaged 2.17 ± 0.7 g H_2O/d, values significantly different (t = 3.3, $P < 0.008$).

Organ masses

After 3 weeks, larks acclimated to 15 °C had a significantly larger liver, kidney, and intestine than larks in the 36 °C group (Table 1). Although the stomach was not significantly heavier among birds in the 15 °C group, it was nearly so (P = 0.016; minimum level for significance = 0.013). The total increase in organ mass, exclusive of changes in pectoral muscle, amounted to 403 mg (Table 1), representing 14.3% of the mass gain in the cold group. Masses of internal organs were positively associated with basal metabolism (Fig. 2). We also calculated partial correlation coefficients for BMR and organ mass for our entire data set while controlling for body size, using tarsus length as an index of body size (Hayes and

TABLE 1. Dry masses (mean ± 1 SD; mg) of organs and muscle of Hoopoe Larks after 3 weeks at 15 °C or 36 °C.

Category	15 °C	36 °C	% Change	Probability [a]
Brain	213.6±17.4	203.4±22.2	5.0	0.39
Heart	122.0±13.3	111.9±13.6	9.0	0.22
Liver	345.5±66.4	241.2±16.8	43.2	0.004*
Kidney	108.2±10.3	78.9±7.0	37.2	0.001*
Stomach	253.3±54.3	181.6±26.4	39.5	0.016
Intestine	445.9±78.4	268.5±51.6	66.1	0.001*
Pectoral muscle[b]	939.9±152.1	914.8±95.2	2.7	0.74

[a] statistical significance determined by t-test after sequential Bonferroni correction (Rice 1987).

[b] pectoral muscle includes the supracoracoideus muscle.

* indicates significance after Bonferroni correction.

Shonkwiler 1996). In these calculations BMR was significantly related to liver mass (P = 0.03), to kidney mass (P = 0.04), to stomach mass (P = 0.025), but only marginally so to intestine mass (P = 0.06).

Discussion

Our data are consistent with the “energy demand” hypothesis for short-term adjustments in BMR (Williams 1999). When exposed to a T_a of 15 °C during 3 weeks of acclimation, larks expended more energy in thermoregulation than did the control birds housed at thermally neutral temperatures. At 15 °C, the resting metabolic rate of hoopoe larks is 98.7 kJ/d, whereas at 36 °C, the BMR is 32.9 kJ/d, a three-fold difference (Tieleman et al. 2002c). We fed larks in the cold group about 420 g/d of our insect mixture, about 140 g/d for birds in the warm group. Birds in the 15 °C group consumed more food, which apparently stimulated the enlargement of organs like the liver, kidney, intestine, and perhaps the stomach. Based on histological measurements, Brugger (1991) reported that absorptive cells of the gut (enterocytes) increased in size and number in hyperphagic Red-winged Blackbirds (*Agelaius phoeniceus*). The increase in mass of the intestine that we have documented, 66%, is among the largest so far reported for birds (Karasov 1996; Piersma et al. 1999; Battley et al. 2000). Because some of these organs, such as the liver and kidney, have high mass-specific metabolic rates (Krebs 1950), these morphological adjustments translate into higher mass-independent BMR in birds exposed to colder T_as.

We have not located other studies on birds that have examined variation in organ masses as a consequence of acclimation to temperature and in conjunction with changes in BMR, but some investigations have been performed on mammals. Konarzewski and Diamond (1995) acclimated nude house mice (*Mus musculus*) at either 23 °C or 30 °C for 8 days, measured their BMR, and then deter-

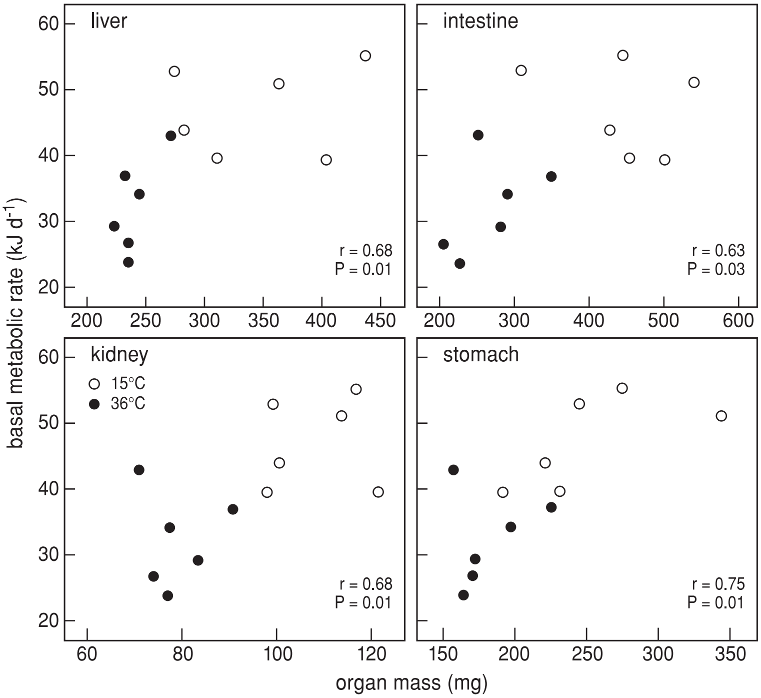

Figure 2. The relationship between organ mass and basal metabolism in Hoopoe Larks from the Arabian Desert. Solid circles represent birds acclimated to 36 °C, open circles represent birds acclimated to 15 °C.

mined the dry masses of their internal organs. The lower acclimation temperature resulted in mice having a significantly higher mass-independent BMR than mice exposed to the higher T_a, and cold-exposed mice had a significantly larger liver, intestine, kidney, and heart. Working with haired strains of mice, Toloza et al. (1991) also found that when mice were exposed to colder temperatures, animals elevated their BMR and enlarged their organs.

Recent studies in comparative ecophysiology, ones that attempt to eliminate historical bias by incorporating adjustments for phylogeny, often assume that physiological traits are invariant, and that physiological adaptation can be deduced from interspecific comparisons (Huey 1987; Garland et al. 1997). However, the phenotypic flexibility that we have found in BMR and TEWL within Hoopoe Larks prompts caution when interpretations of differences in physiological traits among species are made. Presumably BMR and TEWL are optimized within the phenotype for a given set of environmental circumstances (Lewontin 1969; Feder 1987), an equilibrium that has both a genetic and a phenotypic component. These facts should be borne in mind when making broad scale comparisons among species, and have significance when making interpretations based on phylogenetic independent contrasts (Felsenstein 1985a). Traits measured on individuals at different times of the year or from different geographic locations may vary not because of genetic differences, but rather because of acclimatization.

Tieleman and Williams (2000) produced an equation that relates BMR to body mass among 21 species of desert birds which predicts a BMR of 32.5 kJ/d for a 36.6 g lark. Our measurement of 32.9 kJ/d for birds at 36 °C corresponds closely to this prediction, and may lead one to speculate that BMR shows adaptation to environment in this species (Weathers 1979). Similarly, TEWL for Hoopoe Larks in the 36 °C group, measured at 25 °C, was 36.9% below allometric predictions for desert birds (Williams 1996) which may suggest evolutionary specialization that reduces evaporative water loss. However, if we measured these traits for larks during the winter when they were exposed to colder temperatures, we may have found that their BMR and TEWL were above allometric predictions for desert birds, as we have found in the cold-exposure group.

We found that, in the group acclimated to 15 °C, TEWL, measured at 35 °C, increased by 59.2% and BMR increased by 42.2%. However, the nature of the relationship between BMR and TEWL is unclear. One might predict that higher metabolic rates mandates increased ventilation, accomplished by increasing breathing frequency or by increasing tidal volume, resulting in an elevated respiratory water loss (RWL). In a separate study on Hoopoe Larks, we determined that RWL accounts for 31.7% of TEWL at 35 °C, and that CWL accounts for the remaining 68.3% (Tieleman and Williams, 2002b). Assuming that the increase of 42.2% in BMR is correlated with a parallel increase in RWL and no change in CWL, one would predict an increase in TEWL of 13.4%. Our finding that TEWL increased by 59.2% suggests that the birds in the cold-exposure group may have altered the permeability of their skin to water vapor diffusion.

Parsons (1987) posited that phenotypic and genotypic variability tend to be high in organisms that live in conditions of severe environmental stress, especially for quantitative traits important in survival. Although consensus has not emerged on this issue (Via et al. 1996), we use this as a working hypothesis for phenotypic flexibility in terrestrial birds, especially those that live in deserts. These individuals survive for long periods on scant resources, before an unpredictable pulse of rain occurs, stimulating a shift in resource abundance. The necessity of minimizing energy expenditure and water needs is paramount in order to survive long periods of heat and drought. During periods when energy demand is increased, such as in winter or when breeding after a pulse of rain, we envision that the birds eat more food, increase their organ sizes, and elevate their BMR and their FMR. One can imagine that in more mesic environments at higher latitudes, selection pressures for down regulation of internal organs may not be as great, and as a result the physiological phenotype will not be as variable. If Parsons is correct, then we predict that the phenotypic flexibility in BMR and TEWL among desert birds is greater than genetically similar birds that live in mesic areas.

Acknowledgments

We thank Patrick Paillat, Abdulrahman Khoja, Stephane Hemon, Stephane Ostrowski, Phil Seddon, and the staff of the National Wildlife Research Center, Taif, Saudi Arabia for their help during all aspects of this study. This project would not have been possible without the financial support of the National Wildlife Research Center (JBW), and of the Schuurman Schimmel van Outeren Foundation, The Netherlands (B.I.T.). We thank S. Daan and T. Piersma for their critical comments on a previous version of the manuscript.