FLEXIBILITY IN BASAL METABOLIC RATE AND EVAPORATIVE WATER LOSS AMONG HOOPOE LARKS EXPOSED TO DIFFERENT ENVIRONMENTAL TEMPERATURES

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Summary

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. Although mean body mass did not differ initially 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 a constant mass (36.6±3.6 g; means ± S.D., N=6).

Birds in the 15 °C group had a mean BMR of 46.8±6.9 kJ day^{-1}, whereas birds in the 36 °C group had a BMR of 32.9±6.3 kJ day^{-1}, values that 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$_2$O day^{-1}, whereas TEWL for birds in the 36 °C group averaged 2.23±0.28 g H$_2$O day^{-1}, a difference of 59.2 %. Mass-independent TEWL differed significantly between groups.

Larks in the 15 °C group had a significantly larger liver, kidney and intestine than larks in the 36 °C group. The total increase in organ mass contributed 14.3 % towards the total mass increment in the cold exposure group. Increased food intake among larks in the cold group apparently resulted in enlargement of some of the internal organs, and the increase in mass of these organs required a higher rate of 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.

Key words: phenotypic plasticity, hoopoe lark, *Alaemon alaudipes*, Arabian desert, basal metabolic rate, total evaporative water loss, energy demand.

Introduction

Studies of basal metabolic rate, 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 function only rarely at basal levels of energy expenditure, this variable has been useful as a physiological standard for assessing the energy costs of thermoregulation (Dawson and O'Conner, 1996) and 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; Chappell 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, 2000). 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 carried out, it is likely that patterns for mammals and birds are similar.

Basal metabolic rate 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 with 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'Connor, 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 with 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 (2000), 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 from thermogenesis, which in turn requires enlarged abdominal organs for support. Larger organ masses, according to Kersten and Piersma (1987), 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 possess 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 periods in response to alterations in diet or environment (Toloza et al., 1991; Piersma et al., 1996; Piersma and Lindstrom, 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, Texas, 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 nine 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 with 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 probably 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 values of ambient temperature (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 the tissues (heart and lungs) and in the elimination of waste (kidneys) are stimulated to hypertrophy. Because these organs have a high metabolic intensity, total oxygen demand under basal conditions increases as these structures become larger. When oxygen requirements are elevated, ventilation rate increases, with a concomitant increase in RWL.

Materials and methods

Hoopoe larks (*Alaemon alaudipes*; Sibley and Monroe, 1990) 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, 1988; 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 (approximately 1 km^2) along sandy wadis or on flat gravel plains, where they forage for arthropods, lizards and, to a lesser extent, seeds (Cramp, 1988). During the spring, females lay 2–3 eggs; both sexes incubate the eggs and feed the young. In the summer, when T_a often exceeds 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, three males and three females in each, verified that the birds were similar in body mass in both assemblages, and placed one group in a constant-temperature room at 15±2.0 °C and the other in a constant-temperature room at 36±2.0 °C. Birds were fed mealworms, cockroaches, crickets and small seeds *ad libitum*. Both groups were exposed to a 12 h:12 h L:D light regime.

After the larks had been exposed to either 15 °C or 36 °C for 3 weeks, we measured basal rates of oxygen consumption ($\dot{V}_{O_2}$) and TEWL for postabsorptive birds during their nocturnal phase using 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×20 cm×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 (B. I. Tieleman and J. B. Williams, unpublished results), or at 25 °C. Birds were placed on a wire-mesh platform over a layer of mineral oil which trapped feces, excluding this 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^{-1}, then through the chamber. Exiting air passed through a General Eastern dew point 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 a further 2 h. Calculations of rates of oxygen consumption were performed using equation 2 of Hill (1972). We used 20.08 J ml^{-1} 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:

$$\text{TEWL} = [(\dot{V}_e \rho_{out} - \dot{V}_i \rho_{in})]1.44 \times 10^{-3}, \qquad (1)$$

where TEWL is in g day^{-1}, ρ_{in} and ρ_{out} are the absolute humidity (g H_2O m^{-3}) of inlet air and outlet air, respectively, $\dot{V}_i$ is the flow rate (ml min^{-1}) of air entering the chamber as given by the mass flow controller, and $\dot{V}_e$ is the flow rate (ml min^{-1}) of exiting air. Absolute humidity (ρ; g H_2O m^{-3}) was determined using the equation:

$$\rho = 216.7(e_s/T_{dp}) + 273.15, \qquad (2)$$

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 $\dot{V}_e$ as:

$$\dot{V}_e = \dot{V}_i - [\dot{V}_{O_2}(1 - \text{RQ})] + \dot{V}_{H_2O}. \qquad (3)$$

In this equation, $\dot{V}_i$ (ml min^{-1}), the flow rate into the chamber, and the rate of oxygen consumption ($\dot{V}_{O_2}$; ml min^{-1}) are known, the respiratory quotient (RQ) is assumed to equal 0.71 (King and Farner, 1961) and $\dot{V}_{H_2O}$ is calculated as:

$$\dot{V}_{H_2O} = \rho(\dot{V}_i + \dot{V}_{CO_2} - \dot{V}_{O_2})/(1 - \rho). \qquad (4)$$

The latter equation is derived from the fact that $\rho = \dot{V}_{H_2O}/(\dot{V}_i + \dot{V}_{CO_2} - \dot{V}_{O_2} + \dot{V}_{H_2O})$, the fraction of water in air flowing through the dew point hygrometer.

After measurements, we killed the birds and dissected out their brain, heart, liver, kidney, stomach, intestine and the 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.

Statistical analyses were performed using SPSS 9.0 (1999). Values are presented as means ± S.D. In making simultaneous multiple comparisons, as we have done for 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 had been made (Hochberg and Tamhane, 1987; Rice, 1989).

Results

Body mass

At the beginning of the experiment, the mass of birds that were assigned to the 15 °C group averaged 41.3±7.0 g (*N*=6) and the mass of those placed in the 36 °C group averaged 37.2±4.7 g (*N*=6), values that 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 metabolic rate

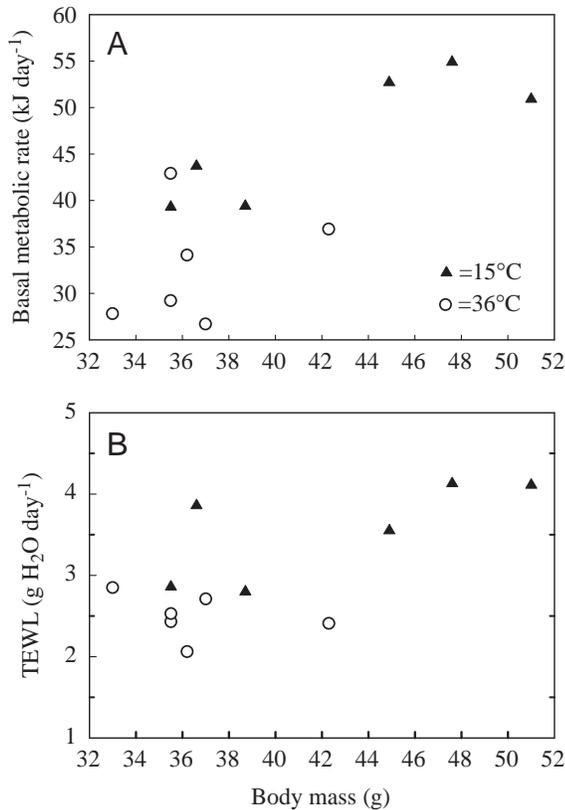The basal metabolic rate of hoopoe larks from the 15 °C group

Fig. 1. (A) The relationship between basal metabolic rate (kJ day^{-1}) and body mass (g) in hoopoe larks from the Arabian desert. Filled triangles represent birds acclimated to 15 °C; open circles represent birds acclimated to 36 °C. (B) The relationship between total evaporative water loss (TEWL; g H$_2$O day^{-1}) and body mass (g) in hoopoe larks from the Arabian desert. Symbols as in A.

Table 1. *Dry masses of organs and muscle of hoopoe larks after 3 weeks at 15 or 36 °C*

| | Dry mass (mg) | | | |
Category	15 °C	36 °C	% Change	*P*
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	939.9±152.1	914.8±95.2	2.7	0.74

Statistical significance was determined by *t*-test after sequential Bonferroni correction (Rice, 1989). An asterisk indicates a significant difference after Bonferroni correction.
Values are means ± S.D., *N*=6.
Pectoral muscle includes the supracoracoideus muscle.

tended to have a higher TEWL, a relationship described by TEWL=−0.21+0.078BMR (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$_2$O day^{-1}, whereas that of larks in the 36 °C group averaged 2.17±0.7 g H$_2$O day^{-1}, values that are 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-acclimated group. The masses of the liver, kidneys intestine and stomach were positively associated with basal metabolic rate (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 Shonkwiler, 1996). In these calculations, BMR was significantly related to liver mass (*P*=0.03), to kidney mass (*P*=0.04) and to stomach mass (*P*=0.025), but only marginally so to intestine mass (*P*=0.06).

averaged 46.8±6.9 kJ day^{-1}, whereas BMR of larks from the 36 °C group was 32.9±6.3 kJ day^{-1} (*N*=6). Larks in the 15 °C group had a BMR that was 42.2 % higher than birds in the warmer group. In an analysis of variance (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 day^{-1}) to tarsus length (mm) averaged 1.35±0.11 kJ day^{-1} mm^{-1} for the 15 °C group and 0.99±0.18 kJ day^{-1} mm^{-1} 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$_2$O day^{-1}, whereas TEWL for birds in the 36 °C group averaged 2.23±0.28 g H$_2$O day^{-1} (*N*=6), a difference of 59.2 %. 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

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 day^{-1}, whereas at 36 °C, the BMR is 32.9 kJ day^{-1}, a threefold difference. We fed larks in the cold-acclimated group about 420 g day^{-1} of our insect mixture,
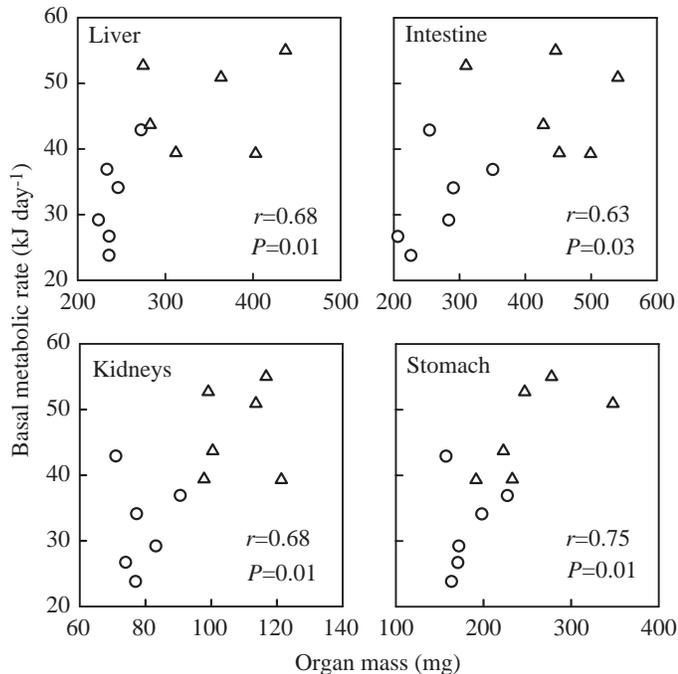
Fig. 2. The relationship between organ mass (mg) and basal metabolic rate (kJ day⁻¹) in hoopoe larks from the Arabian desert. Open circles represent birds at 36 °C and open triangles birds at 15 °C.

about 140 g day⁻¹ for birds in the warm-acclimated group. Birds in the 15 °C group consumed more food, which apparently stimulated the enlargement of organs such as the liver, kidney, intestine and, possibly, the stomach. On the basis of 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 kidneys, have high mass-specific metabolic rates (Krebs, 1950), these morphological adjustments translate into higher mass-independent BMR in birds exposed to colder T_a values.

We have not located other studies on birds that have examined variations in organ mass 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 determined 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, they elevated their BMR and enlarged their organs.

Recent studies in comparative ecophysiology, those 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., 1992). 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. BMR and TEWL are presumably 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, 1985). 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 for 21 species of desert birds which predicts a BMR of 32.5 kJ day⁻¹ for a lark weighing 36.6 g. Our measurement of 32.9 kJ day⁻¹ 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 had measured these traits for larks during the winter when they were exposed to colder temperatures, we might 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 mandate 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 % (B. I. Tieleman and J. B. Williams, unpublished results). 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., 1995), 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 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 field metabolic rate. 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 (1987) is correct, then we predict that the phenotypic flexibility in BMR and TEWL among desert birds will be greater than that among genetically similar birds that live in mesic areas.

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