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Physiological Adaptation in Desert Birds

JOSEPH B. WILLIAMS AND B. IRENE TIELEMAN

We call into question the idea that birds have not evolved unique physiological adaptations to desert environments. The rate at which desert larks metabolize energy is lower than in mesic species within the same family, and this lower rate of living translates into a lower overall energy requirement in the wild. We argue that selection has reduced oxygen consumption at the tissue level under basal conditions for birds living in deserts. We document that total evaporative water loss—the sum of cutaneous water loss (CWL) and respiratory water loss—is reduced in desert birds, and present evidence that changes in CWL are responsible for this pattern. The diminution in CWL is attributable to changes in the lipid structure of the stratum corneum of the skin, the physical barrier to diffusion of water vapor. Finally, we show linkages between physiology and life-history attributes of larks along an aridity gradient; birds from deserts have not only a reduced rate of metabolism but also a small clutch size and slow nestling development. Hence, attributes of physiology are correlated with traits that directly affect reproductive success. Our hope is that we will prompt students to question the notion that birds do not possess physiological adaptations to the desert environment, and raise the specter of doubt about "preadaptation" in birds living in deserts.

Keywords: desert birds, basal metabolism, field metabolism, evolutionary physiology, cutaneous water loss

In 1932 John Philby, a British explorer, set off with 32 camels and several Bedu companions on a epic east–west journey across the Empty Quarter, or Rub 'al Khali, the largest desert sand sea in the world. Encompassing the southern third of the Arabian Pennisula, the Empty Quarter is more than 900 kilometers (km) long, 800 km wide, and home to sand dunes taller than the Eiffel Tower. When Philby pushed into the interior of this desert, it had not rained there for 30 years. Camels became weak, men short-tempered. Air temperatures fell below freezing in winter and soared to over 60 degrees Celsius (°C) in summer. In the interior of this desert region, Philby recorded in his journal that plants were scarce, and the ones he found were dead. He wrote, "Soon, the rolling sand dunes became bare, the hot sun blazed down on us, and the sand glared into our faces mercilessly." Amazingly, Philby recorded life in this desert. At the end of his book, *The Empty Quarter* (1933), he listed many of the animals that he had observed on his journey; one of the most common was a desert-dwelling lark, the hoopoe lark. How can birds endure such an extreme environment?

Desert regions experience intense solar radiation; extreme air temperatures; low relative humidity; scant, unpredictable rainfall; and meager primary productivity. For inhabitants of these environments, food supplies and drinking water can be scarce. In such extreme habitats, there may be strong selection pressures on the physiological attributes of animals that live there, especially adjustments that minimize rates of energy expenditure or water loss, or that enhance tolerance of high body temperature. For birds in deserts, the struggle for existence includes the often difficult tasks of balancing energy and water requirements with energy expenditure and water loss.

In current textbooks on animal physiology, students typically learn concepts of physiological adaptation to desert environments through discussions about arthropods, amphibians, reptiles, or mammals, but case studies for birds are rarely included (Willmer et al. 2000, Randall et al. 2002, Hill et al. 2004). For desert-dwelling arthropods, textbook examples include modifications of the waxy cuticle, a tactic to reduce integumentary water loss, or discontinuous ventilation, which ostensibly conserves respiratory water. Some arid-zone amphibians (e.g., arboreal frogs belonging to the genus *Phyllomedusa* or *Chiromantis*) secrete lipid mixtures on their skin, thereby minimizing cutaneous water loss (CWL; Jorgensen 1997). Perhaps the most often cited examples of physiological adaptation to deserts come from work by Schmidt-Nielsen and later by Walsberg on small mammals, kangaroo rats (*Dipodomys*; Schmidt-Nielsen 1979, Walsberg 2000). These small rodents reputedly have low CWL, low metabolism, the ability to recover respiratory water in their noses, and an unusual ability to concentrate their urine.

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Treatment of physiological adaptation in desert birds in current textbooks is short or absent, a result that apparently stems from early work by Bartholomew and colleagues on desert birds of the southwestern United States, a region that is relatively young on an evolutionary time scale (Bartholomew and Cade 1963, Dawson and Bartholomew 1968). After almost a decade of study, they concluded that desert birds lack physiological specialization. These authors lamented the paucity of data on Old World species and thought that these populations might show more conspicuous physiological adaptations to arid conditions than their ecological equivalents in the New World, because Old World deserts were geologically much older (Axelrod 1983). These speculations have for the most part been ignored, and many authors dismiss the idea that desert birds possess physiological adaptations to deserts, or they invoke "preadaptation" as an explanation of why birds lack such adaptations. In a comprehensive review of the physiological ecology of desert birds, Maclean (1996) wrote, "What seems to be adaptive in birds to the desert environment is in fact intrinsic to the avian condition" (p. 8). In their text *Animal Physiology,* Hill and colleagues (2004) promote this same view, "Birds occur in deserts, but if they need to drink, they can fly to watering places at some distance" (p. 712), implying little selection on desert birds for physiological specialization.

In Lewis Carroll's poem for children "The Hunting of the Snark," after landing on a imaginary island in a small boat, the captain says three times to the crew, "Just the place for a snark!" and then later says, "I have said it thrice: What I tell you three times is true." Even in the scientific community, once a message of "no adaptation in desert birds" is repeated often enough, it becomes etched in stone, and considered true however scant the evidence. Worse still, our students are taught this dogma with relatively few questions about its validity.

In this overview, we call into question the idea that birds have not evolved unique physiological adaptations to desert environments. We present evidence that we have been gathering since 1996 on desert birds in general, and on Old World larks in particular, showing that the rate at which birds metabolize energy is lower in desert species, and that this lower rate of living translates into a lower overall energy requirement in the wild. Evidence thus far indicates that selection has reduced ATP (adenosine triphosphate) usage at the tissue level under basal conditions in these desert birds. We document that total evaporative water loss (TEWL), the sum of CWL and respiratory water loss, is reduced in desert birds, and present evidence that this diminution is attributable to changes in the lipid structure of the stratum corneum of the skin, the physical barrier to water vapor diffusion. Finally, we examine the linkages between physiology and life-history attributes of larks along an aridity gradient and find that birds from deserts not only have a reduced metabolism but also a small clutch size and slow nestling development. Hence, selection on physiological systems is correlated with attributes of reproduction.

What we mean by "adaptation"

The word *adaptation* is the centerpiece of Darwinian evolution, yet it is used in at least eight different ways in the literature, an unfortunate circumstance that can obscure, confuse, and complicate the communication of ideas (Mayr 1983, Bennett 1997). The historical view of adaptation maintains that an adaptation is a product and emphasizes past evolutionary history. Harvey and Pagel (1991) argued that "for a character to be regarded as an adaptation, it must be a derived character to a specific selective agent" (p. 13). The nonhistorical camp, by contrast, regards adaptation as a process and emphasizes current trait utility in the definition of adaptation. Reeve and Sherman (1993) called an adaptation "a phenotypic trait that results in the highest fitness among a specified set of variants in a given environment" (p. 9). In this article, we attempt to identify physiological adaptations, defined here as physiological traits that originated as a result of natural selection. These traits can continue to maintain the fitness of individuals within the population in the current environment. We have used the comparative method to discern evolutionary adaptation because we think that it increases our understanding of evolutionary process and illuminates the ecological context of evolutionary change.
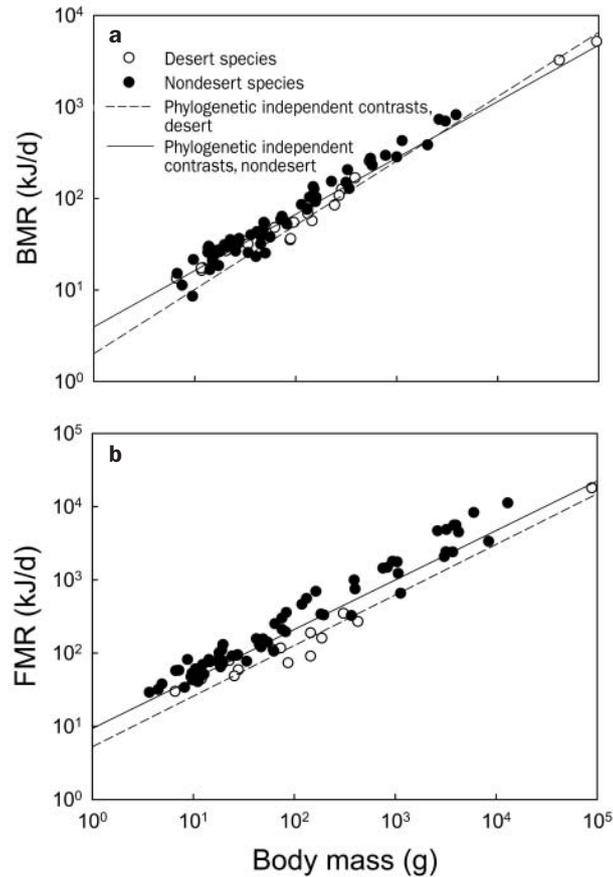
Energy

Because primary productivity is lower in deserts than in any other terrestrial environment, and because the mass-specific metabolism of birds is the highest of all vertebrates, natural selection potentially favors individual birds with reduced energy expenditure in desert environments (Williams and Tieleman 2001). Early work on a few species suggested that arid-zone birds had evolved a reduced basal metabolic rate (BMR), as measured in the laboratory on inactive, postabsorptive birds at thermally neutral temperatures during the rest phase of their circadian cycle (Dawson and Bennett 1973, Withers and Williams 1990). Selective advantages attributed to reduced basal metabolism include lower overall energy demand, lower respiratory water loss because of reduced ventilation frequency, and lower production of endogenous heat, which would have to be dissipated in a warm environment, often by evaporative means. To test the idea that desert birds have a reduced basal metabolism, we compared the basal metabolism of 21 species of birds from deserts with that of 61 species from more mesic areas (Tieleman and Williams 2000). Based on conventional least squares regression, and on regressions of phylogenetic independent contrasts (Felsenstein 1985), the analyses showed that, in general, desert birds had a BMR 17% to 25% lower than that of nondesert birds (figure 1a).

A reduction in basal metabolism, a laboratory measurement, gains ecological significance if it translates into a decrease in the field metabolic rate (FMR) of free-living animals, as measured by the doubly labeled water method. Again using two types of regression, we compared the FMR of 13 species of desert birds with that of 45 species from mesic regions; desert birds had a 49% lower field metabolism than nondesert
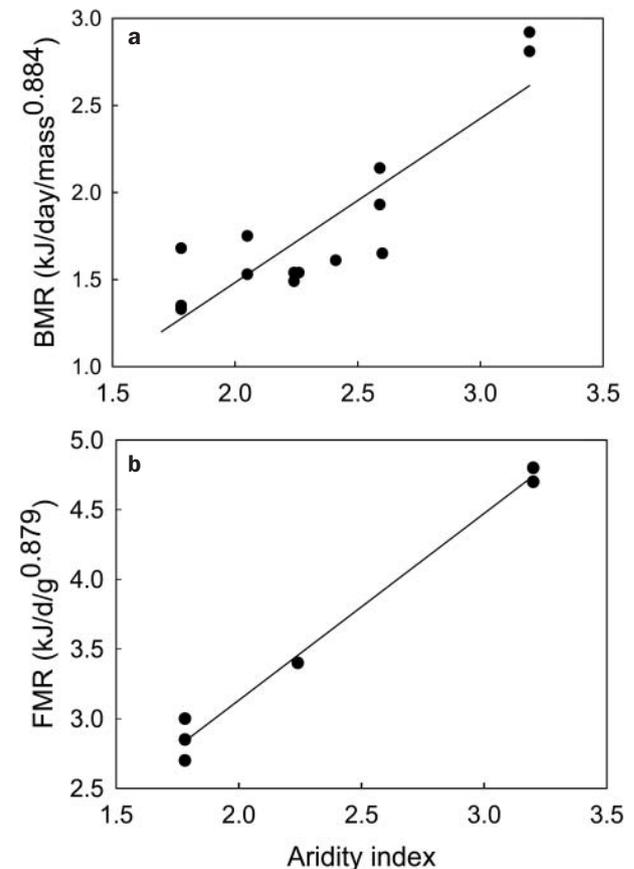
species (figure 1b; Tieleman and Williams 2000). Reductions in FMR could occur through changes in basal energy expenditure, in thermoregulatory requirements, or in activity levels. The finding of a 17% reduction in basal metabolism in desert birds suggests that the reduction in field metabolism may be only partly attributable to physiological differences. The relatively high air temperatures of deserts may reduce the costs of thermoregulation compared with those in nondesert areas, thereby contributing to a reduction in energy requirements. Also we have observed that some desert species rest in shade during the middle part of the day, and this inactivity could contribute to a lower FMR (Tieleman and Williams 2002a).

Broadscale comparisons among species have been criticized because species differ not only in environment but also in phylogenetic history, diet, and behavior (Leroi et al. 1994); comparisons of closely related species from different environments

may provide greater insights into how selection has influenced physiological adjustments to environment, without the complications of dissimilar historical background. Species within the family of larks (Alaudidae)—all ground-foraging birds with similar diets, similar behaviors, and a common phylogenetic history—represent a model system to test hypotheses of physiological adaptation, because different members of the family occur in environments ranging from the Arctic to deserts (Williams and Tieleman 2001). An examination of the BMR of 12 species of larks along an aridity gradient that extended from temperate grasslands of the Netherlands to the hyperarid deserts of Arabia indicated that basal metabolism decreased as the environment became more arid, a result consistent with the idea that natural selection has reduced metabolism of birds in arid environments (figure 2a; Tieleman and Williams 2000). Again, this reduction in basal metabolism was reflected in measurements of field metabolism on free-living larks along an aridity gradient. We and colleague Henk Visser collected data on the FMR of adults of seven species of larks feeding 5- to 8-day-old nestlings from the Netherlands and Saudi Arabia (Tieleman et al. 2003a,

Figure 1. (a) Basal metabolic rate (BMR, in kilojoules [kJ] per day [d]) of desert birds (open circles) and nondesert birds (filled circles) as a function of body mass (in grams [g]). Solid line represents the best-fit equation for nondesert species after correction for phylogeny; dashed line represents the best-fit equation for desert species. (b) Field metabolic rate (FMR, in kJ per d) of free-living birds as a function of body mass (in g). Solid line and filled circles represent nondesert species; dashed line and open circles represent desert species.

Figure 2. (a) Mass-corrected basal metabolic rate (BMR) of larks (in kilojoules [kJ] per day) along an aridity gradient. (b) Mass-corrected field metabolic rate (FMR) of larks (in kJ per day) along an aridity gradient. Low values of the aridity index characterize desert environments; high values characterize more mesic regions.

Tieleman et al. 2004). We found that field metabolism decreased as aridity increased; the mass-adjusted FMR of arid-zone species was 36% to 42% lower than that of mesic larks (figure 2b).

Interspecific phenotype–environment correlations can indicate either genetic differences brought about by natural selection or phenotypic plastic responses to environmental conditions. In a separate study, Tieleman and colleagues (2003b) showed that adjustments in basal metabolism could not be attributed to the acclimation of adults to thermal environment, food availability, or photoperiod. Hence, these physiological differences are probably the result of genetic differences, although we have not yet ruled out developmental plasticity during nestling development.

The foregoing data suggest that natural selection has influenced the rate of living among desert birds compared to mesic species. Differences in metabolism among temperate-zone birds have been attributed to selection for larger size of organs with high metabolic intensity and relatively high oxygen consumption per unit tissue, such as the liver, kidney, and heart. These larger organs are thought to be required to maintain levels of energy expenditure during the period when parents care for nestlings, the putative time of peak energy demand (Kersten and Piersma 1987, Daan et al. 1990). However, when variation in body mass was taken into account, we could not show that organ sizes differ among larks from deserts and mesic regions (Tieleman et al. 2003b). At this point, we suspect that differences in FMR and basal metabolism among these species may be related to variation in tissue-specific metabolic rates, an avenue for future work.
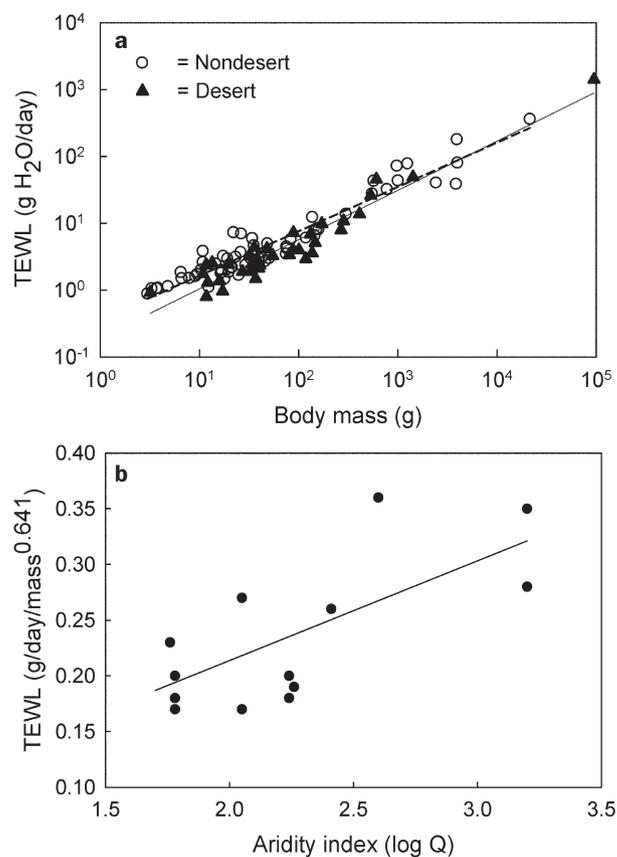
Water

Heralded by the journal *Science* as the most significant breakthrough of 2004 was the finding of two Rover missions that Mars was once warm, wet, and salty—a candidate environment for early life (Kargel 2004, Kennedy 2004). Pictures of this planet now reveal a dry, desertlike terrain, parts of which may have been sculpted by water at some time in the past. The question now is whether life has existed, or currently exists, on the red planet. Water can exist without life, but life as we know it cannot exist without water. Here on Earth, the hot air, intense sun, and scarcity of drinking water render deserts some of our harshest environments. Perhaps more than other vertebrates, desert birds face problems of dehydration in deserts because they are active during the day, most do not burrow as do some nocturnal desert rodents, and they have the highest mass-specific evaporative water loss of all terrestrial animals. One can imagine selection pressures that promote a frugal water economy in these environments.

Total evaporative water loss

Total evaporative water loss, the sum of evaporative water losses through the skin and from respiratory passages, is the major avenue of water efflux in birds, especially for small species in which TEWL is five times greater than urinary and fecal water loss (Dawson 1982). Given that water balance

is of central importance to the survival of desert birds, and that TEWL is a physiological trait under genetic influence (Furuyama and Ohara 1993), one might hypothesize that natural selection has reduced TEWL in desert species. Bartholomew and Dawson (1953) examined TEWL in 13 North American species of birds from mesic and arid habitats and concluded that TEWL did not differ between groups. Williams (1996) reassessed this hypothesis on the basis of data for 64 species from mesic environments and 38 species from deserts, using both conventional regressions and regressions based on phylogenetic independent contrasts, with the result that TEWL at moderate air temperature was lower in arid species than in mesic species, the decrease amounting to as much as 33% (figure 3a). This finding is consistent with the idea that natural selection has sculpted physiological phenotypes within desert environments to reduce their evaporative water losses.

We tested the idea that desert birds have reduced TEWL by measuring this parameter for 14 species of larks from the Netherlands (a mesic region), from semiarid Spain and South Africa, and from the arid deserts of Saudi Arabia (figure 3b).

Figure 3. (a) Total evaporative water loss (TEWL, in grams of water [H₂O] per day) as a function of body mass (in grams). Nondesert species are represented by open circles, desert species by filled triangles. (b) Mass-corrected TEWL of larks along an aridity gradient. Low values of the aridity index characterize desert environments; high values characterize more mesic regions.

In this figure, our aridity index is a complex parameter based on average rainfall and annual maximum and minimum air temperatures (Meigs 1953). Values of our aridity index are low for deserts, intermediate for semiarid areas, and high for mesic regions. Mass-adjusted TEWL correlated positively with environment when assessed by conventional least squares regression or by regressions based on phylogenetic independent contrasts. Rates of TEWL for mesic larks were nearly double those of species from the deserts of Saudi Arabia. In a separate study, we found that the decrease in TEWL among larks along our aridity gradient cannot be attributed to the acclimation of adults to thermal environment, food availability, or photoperiod (Tieleman et al. 2003b). We concluded that the most likely explanation is that natural selection has influenced TEWL in desert birds.

Hyperthermia

Some authors have suggested that hyperthermia, an elevation in body temperature of 2°C–4°C above normal, contributes to a reduction in TEWL among birds (Calder and King 1974, Withers and Williams 1990). Because birds have high rates of mass-specific metabolism, they have the highest body temperatures of all vertebrates, averaging about 41°C when the air temperature is moderate. One might predict that birds in deserts would have a lower body temperature than other birds because of their lower metabolism, which in turn would result in lower ventilation rates and hence lower respiratory water loss. When air temperature exceeds body temperature, the only avenue available to maintain body temperature below lethal limits (known to be around 46°C–47°C) is by increasing evaporative cooling, either from respiratory passages or through the skin. During bouts of high air temperature, birds will often elevate their body temperature several degrees. Hyperthermia is thought to benefit a bird's water economy because it increases the gradient between body and air temperature that drives nonevaporative heat loss, and because heat stored in tissues can be dissipated later by nonevaporative means; both of these effects decrease the need for evaporative cooling. We tested the idea that desert birds have a higher body temperature than nondesert species, both at moderate (25°C) and high (45°C) air temperatures, but found no significant differences in body temperatures between the two groups (Tieleman and Williams 1999). Therefore, we concluded that differences in TEWL between desert and mesic birds cannot be attributed to differences in the set point for body temperature. We constructed a model that showed that at air temperatures of 45°C, any bird could reduce TEWL by about 50% by becoming hyperthermic for bouts of 1 hour. For chronic episodes of high air temperature (5 hours), small birds continued to save about the same percentage of evaporative water by hyperthermia, but large birds were predicted to lose more water than they would if they maintained their body temperature at normothermic levels.

Respiratory water loss

Another factor that has been suggested as a cause of reduced TEWL in desert birds is a decrease of respiratory water loss as result of counter-current heat exchange in their nasal passages (Schmidt-Nielsen et al. 1970). The nasal cavity of birds contains turbinates (Bang 1971), cartilaginous structures that are thought to have as one of their functions water recovery from exhaled air. Inhaled air is filtered, warmed, and humidified (presumably to saturation) by the evaporation of water from turbinal mucosa before reaching the lungs. On inhalation, convective heat exchange and evaporation cool the epithelial tissues along the turbinates; on exhalation, as warm air passes over these nasal membranes, it cools, condensing water on them and thus making moisture available for the next inspiration (Schmidt-Nielsen 1981). Measurements of the temperature of exhaled and inhaled air are thought to allow indirect estimates of the amount of water that is recovered from the inhaled air stream on exhalation. This measure has been used to characterize the importance of nasal turbinates for water economy, although, by itself, it does not allow quantification of the reduction in respiratory water loss solely attributable to turbinates. To estimate a reduction in RWL requires additional information on tidal volume, respiratory frequency, and the temperature of exhaled air in the absence of turbinates.

Schmidt-Nielsen (1981) proposed that desert animals are likely to have more complex nasal turbinates that allow cooling of air to temperatures below those of nondesert species, resulting in a larger reduction in respiratory water loss in desert animals. To date, there exists no evidence to support this idea. Hillenius (1992) compared the respiratory water loss of five species of mesic mammals when they were forced to breathe through their mouth and when they breathed through their nasopharyx at an air temperature of 15°C. He did not measure any arid-zone mammals. All species recovered significant amounts of water in their nose, despite being species from mesic environments. These results led Hillenius to conclude that turbinates did not evolve as an adaptation to environment; rather, he proposed that turbinates evolved early in mammalian radiation in response to the development of high ventilation rates needed for endothermy.

We and colleagues from Israel examined the hypothesis that counter-current heat exchange in the nasal passages reduced the TEWL of crested larks (*Galerida cristata*), a species found in semiarid areas, and desert larks (*Ammomanes deserti*), found in arid deserts, over a range of air temperatues (Tieleman et al. 1999). We reasoned that if nasal turbinates significantly reduce TEWL, then occluding nares and forcing birds to breathe through their open bill should result in a marked increase in TEWL. When the nasal apertures in the bills of crested larks and desert larks were occluded with rubberized plastic, changes in TEWL were insignificant for desert larks (the arid-zone species), but for crested larks, TEWL was 27%, 10%, and 6% higher at air temperatures of 15°C, 25°C, and 35°C, respectively, than when birds could breathe through their open nasal passages. For the latter species, though differ-

ences in TEWL between open and closed nares were statistically significant, water recovery in the nares was small. Hence, water recovery in the nares does not appear to explain the large differences in TEWL between desert and mesic species. Direct measurements of respiratory water loss in crested larks indicated that it increased by 38%, 47%, 29%, and 2% at air temperatures of 15°C, 25°C, 35°C, and 45°C, respectively, when the nares were occluded. These comparisons suggest that direct measurements are the only way to ascertain the effect of nasal turbinates on reductions of respiratory water loss and TEWL. Found in both birds and mammals, nasal turbinates appear to be a feature of endothermy, but they do not seem, at this point, to be an adaptation to desert environments.

Cutaneous water loss

In combination, our results led us to explore the idea that desert birds could reduce their TEWL by decreasing the rate of water loss through their skin compared to mesic species (Williams 1996, Williams and Tieleman 2001). Early investigators surmised that most evaporative cooling took place in the respiratory passages, but later work showed that CWL is an important avenue of water loss in thermoregulatory processes, at least at air temperatures below body temperature (Bernstein 1969, Webster and Bernstein 1987, McKechnie and Wolf 2004).

Cutaneous water loss is a function of (a) the water vapor gradient between skin and air and (b) the total resistance to water vapor diffusion across skin, feathers, and boundary layer (Webster et al. 1985). A model that describes this relationship is

CWL (grams [g] H_2O per square meter [m^2] per second [s]) = $(\rho_s - \rho_a) / r_t$,

where ρ_s is water vapor density (g H_2O per m^3) just below the surface of the skin (assumed to be saturated at skin temperature), ρ_a is water vapor density of external air, and r_t (s per m) is total resistance to vapor diffusion. Transport of water across the skin, feathers, and boundary layer is called conductance [CWL / $(\rho_s - \rho_a)$], and can be visualized as the slope of the equation that relates CWL (g H_2O per m^2 per s) to the vapor density gradient between skin and air (g H_2O per m^3) (Williams and Tieleman 2001). If conductance is thought of as the velocity of water molecules moving from skin to air per unit of gradient [(g H_2O per m^2 per s) / (g H_2O per m^3) = m per s], then the reciprocal (1/conductance) provides insight into the time required for water molecules to move across a unit of space, a parameter referred to as resistance (s per m). Values of resistance are preferred over measures of conductance because they can be used in calculations involving parallel resistances, analogous to resistances in electrical circuits. Total resistance (r_t) varies interspecifically from 25 to 250 s per m depending on skin temperature, the degree to which feathers are fluffed, and species; the mechanisms that drive this variation are largely unknown. Components of r_t in birds include the parallel resistances of skin, feathers, and

boundary layer; skin resistance accounts for 75% to 90% of total resistance, at least at moderate air temperatures. To understand CWL, we need to appreciate these resistances and factors that influence them.

Using a mask to separate respiratory water vapor from water vapor lost through the skin, we examined CWL and respiratory water loss in hoopoe larks (*Alaemon alaudipes*) and Dunn's larks (*Eremalauda dunni*) from the Arabian Desert, and skylarks (*Alauda arvensis*) and woodlarks (*Lullula arborea*) from temperate grasslands in the Netherlands (Tieleman and Williams 2002b). The contribution of CWL to TEWL in larks ranged from 50% to 70% at moderate air temperatures, but at high temperatures, respiratory water loss dominated (figure 4). CWL per unit surface area at 25°C was 29% lower in arid-zone species than in mesic larks, suggesting that a reduction in CWL was a primary determinant of the lower TEWL in desert birds. When acclimated to different environments for 3 weeks, 15°C-acclimated hoopoe larks increased CWL by 22% compared with 35°C-acclimated birds, but other species of desert birds or temperate-zone larks did not change CWL. However, even with the increase in CWL of hoopoe larks, rates did not equal those predicted for a mesic species of the same body size. Our data are consistent with the idea that larks from deserts have a reduced CWL at moderate air temperatures, but provided no support for the notion that at high air temperatures, larks from arid regions rely more on CWL than larks from mesic environments. We could not attribute these interspecific differences in CWL to acclimatory responses of adults to environmental temperature, and we think that the most likely explanation is that they are the result of genetic differences due to natural selection. Hence we suggest that natural selection has operated on CWL in desert birds, and that this is the factor responsible for their reduced TEWL.

Our finding that water loss through the skin is reduced in desert birds prompted us to investigate possible mechanisms that would produce this result. The skin of birds is com-
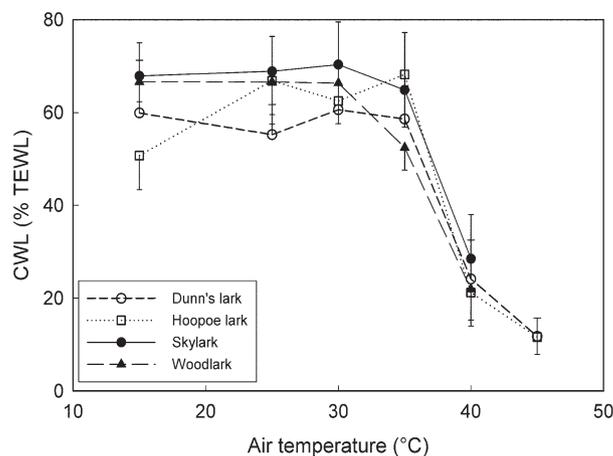
Figure 4. Cutaneous water loss (CWL) as a percentage of total evaporative water loss (TEWL) of larks at air temperatures ranging from 15 degrees Celsius (°C) to 45°C.
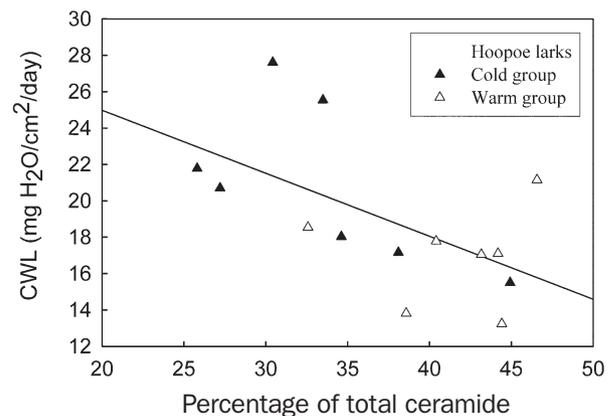
posed of a thin outer nonvascular epidermis and a thicker inner vascularized dermis (Lucas and Stettenheim 1972). One component of the epidermis is an outer cornified layer of nonliving, flattened cells embedded in a lipid matrix. This layer, called the stratum corneum, is thought to form the barrier to water vapor diffusion from animal to environment (Elias et al. 1981, Blank et al. 1984, Bouwstra 1997). There is considerable evidence to support the idea that lipids of the stratum corneum form the barrier to water vapor diffusion, at least in mammals (Scheuplein and Blank 1971, Elias et al. 1981, Grubauer et al. 1989, Elias and Menon 1991). Working on birds from the wild for the first time, Mike Haugen (a graduate student working with J. B. W. and B. I. T.) examined the relationship between lipids of the stratum corneum and the CWL of species of larks along an aridity gradient, and discovered that free fatty acids, cholesterol, and ceramides (large lipid molecules containing a sphingoid base linked to a fatty acid via an amide bond) were the major constituents of lipids of the stratum corneum, just as in mammals (figure 5; Haugen et al. 2003a). For five species of larks, two from the Netherlands and three from Saudi Arabia, the data did not
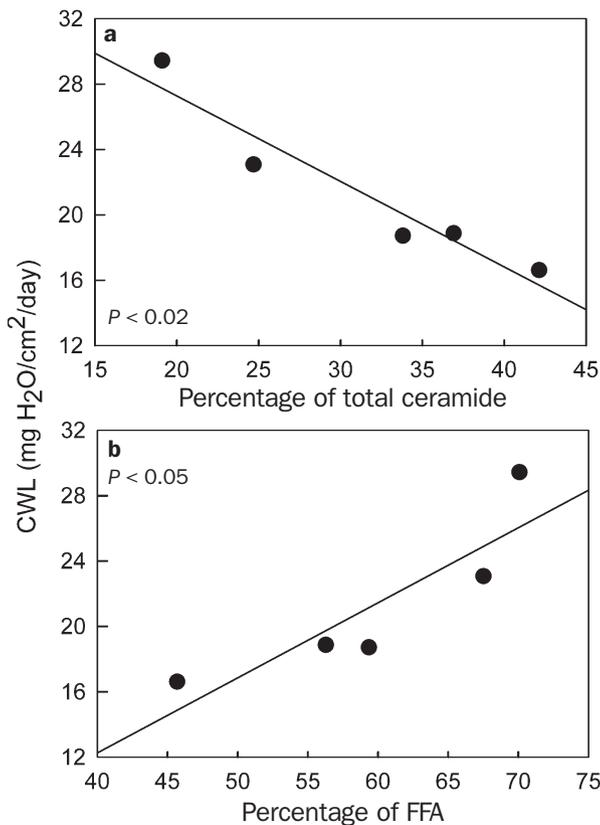
support the hypothesis that birds from deserts had larger quantities of lipids per unit area of skin, as we originally supposed. Instead, we discovered that larks from desert environments had a higher proportion of ceramides and a smaller proportion of free fatty acids in their stratum corneum, an adjustment that apparently increased skin resistance to water vapor diffusion (figure 5). This is an exciting result, because it appears that subtle changes in the ratios of lipid classes can alter the movement of water vapor through the skin. We hypothesized that desert birds have a higher proportion of ceramides in their stratum corneum and a lower proportion of free fatty acids because this combination allows the lipid layers to exist in a more highly ordered crystalline phase and consequently elevates skin resistance to water vapor diffusion.

Previous research showed that hoopoe larks from the Arabian Desert reduced CWL when acclimated to 35°C for 3 weeks, compared with individuals of the same species at 15°C; but skylarks and woodlarks from the Netherlands, and Dunn's larks, also from Arabia, did not (Tieleman and Williams 2002b). If lipids influence CWL, then after 3 weeks of acclimation to 35°C, hoopoe larks ought to have changed the lipid structure of their skin, and thus their skin resistance. Haugen and colleagues (2003b) tested the idea that hoopoe larks acclimated to 35°C would alter the lipid composition of their stratum corneum, resulting in an increase in skin resistance and a decrease in CWL. Results showed that hoopoe larks that were acclimated to 35°C for 3 weeks had lower CWL and higher proportions of ceramides, but lower proportions of free fatty acids and sterols, in their stratum corneum (figure 6). This demonstrates that adjustments in ratios of lipid classes in the stratum corneum are associated with changes in CWL in hoopoe larks.

Figure 5. Cutaneous water loss (CWL) in larks (in milligrams water [H₂O] per square centimeter per day) as a function of the percentage of lipids in the stratum corneum that were (a) ceramides and (b) free fatty acids (FFA). Desert birds had higher percentages of lipids and lower percentages of free fatty acids than did mesic larks.

Figure 6. Cutaneous water loss (CWL) in larks (in milligrams water [H₂O] per square centimeter per day) as a function of the percentage of lipids in the stratum corneum that were ceramides. Filled triangles represent hoopoe larks that were acclimatized to 15 degrees Celsius (°C) for 3 weeks; open triangles represent hoopoe larks that were acclimatized to 35°C for 3 weeks.

Linkages between physiology and life history

There have been a number of attempts to understand the connections between an organism's life history—the attributes of an individual that directly influence the number of young it produces, such as clutch size or the growth rate of nestlings—and its physiology (Drent and Daan 1980, Ricklefs and Wikelski 2002). Most of our understanding about this nexus is based on limited data from birds in tropical and temperate regions, with data on tropical species coming mostly from the New World. Birds in the tropics are thought to have high adult survival but low reproductive success, accompanied by low rates of metabolism, whereas birds living in temperate regions are considered to have lower adult survival but higher reproductive success and higher rates of metabolism. Hence, for birds, the rate of living in temperate areas tends to be fast, whereas in the tropics it tends to be slow. We think that an appreciation of the evolutionary optimization of physiological traits, and of their coupling to life-history attributes, will be enhanced when studies include species from the Old World that live in other environments. Only then will we be able to begin to map physiological traits onto some sort of environmental template in the context of life history. As we have pointed out, basal metabolism, TEWL, and field metabolism all vary among larks along an aridity gradient, with species that live in deserts having low values (figures 2, 3); a low FMR indicates that parental effort while raising nestlings is markedly reduced in desert environments. Species in deserts utilized 27% less energy to raise young than mesic species, after taking into account mass differences among species (Tieleman et al. 2003a). Moreover, water influx, a proxy for food intake, decreased among these species of larks with increasing aridity when they were raising young (figure 7). The decrease in parental effort for larks in arid areas might reflect a lower fitness value of a single brood for desert species, suggesting that the probability of adult survival is higher in arid than in mesic areas among larks of the Old World, if patterns are congruent with those of birds in the New World.

We wondered how these alterations in the physiology of desert birds would relate to life-history traits such as clutch size, the number of clutches laid in a season, and the rate of growth of nestlings. We assessed nestling growth by using the growth constant of the logistic equation fitted to daily measurements of nestling mass. High values of K, the growth constant, indicate rapid growth; low values indicate slow growth. Desert birds laid fewer eggs and had fewer clutches in a breeding season than did mesic larks (figure 8). We have documented that during some years in Saudi Arabia, when it does not rain, resident desert birds forego breeding entirely, whereas this does not occur in mesic areas that receive rain. Nestlings of desert birds grow more slowly than their mesic counterparts, a trend that cannot be attributed to predation because predation on lark nests is actually higher in the desert than in the Netherlands (Tieleman et al. 2004). The slow growth of nestlings in deserts is more a consequence of short food supplies than of predation pressure. Hence, desert birds have characteristics similar to those of tropical birds: slow
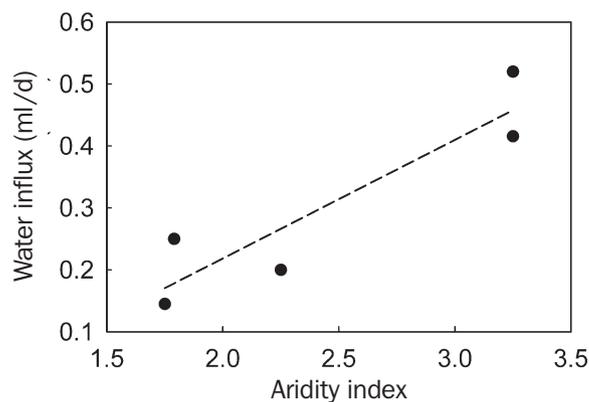

Figure 7. Water influx (in milliliters per day) of free-living larks feeding nestlings 6 to 8 days old, as a function of aridity.
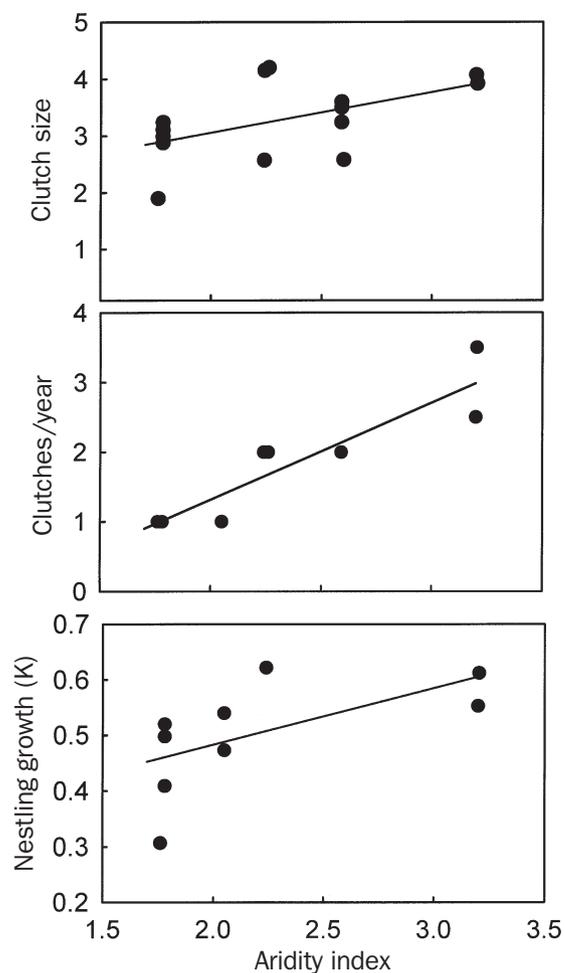

Figure 8. Clutch size, number of clutches per year, and nestling growth rate (K) of species of larks along an aridity gradient.

nestling growth, small clutch size, and low metabolism. We do not know whether this slow pace of life is related to longevity, but our prediction is that adult birds in deserts live longer than mesic species. The ecological factors associated with this congruence of physiological and life-history traits would seem different between tropical and desert environments. A major task for researchers will be to find commonalities in these ecological factors that might select for the same coevolved suite of traits.

Summary

We call into question the idea that birds have not evolved unique physiological adaptations to desert environments. For desert larks, we have shown that their rate of energy metabolism is lower than in mesic species within the same family, and that this lower metabolic rate translates into a lower overall energy requirement in the wild. Evidence thus far suggests that selection has reduced oxygen consumption at the tissue level under basal conditions for birds living in deserts. We have documented that TEWL, the sum of CWL and respiratory water loss, is reduced in desert birds, and presented evidence that changes in CWL are responsible for this pattern. The diminution in the rate of water loss through the skin is attributable to changes in the lipid structure of the stratum corneum, the physical barrier to water vapor diffusion. Finally, we have shown linkages between physiology and life-history attributes of larks along an aridity gradient; birds from deserts have not only reduced metabolism but small clutch size and slow nestling development. Hence, attributes of physiology are correlated with traits that directly affect reproductive success. Our hope is that we will prompt students to question the notion that birds do not possess physiological adaptations to the desert environment, and that we will raise the specter of doubt about "preadaptation" in birds living in deserts. When the teacher lands his or her boat in the desert and says, "A snark doesn't have adaptations to live here," if a student responds, "I'm not so sure," our article will have served its purpose.

Acknowledgments

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