

Ecological and Evolutionary Physiology of Desert Birds: A Progress Report¹

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SYNOPSIS. The adaptive significance of mechanisms of energy and water conservation among species of desert rodents, which avoid temperature extremes by remaining within a burrow during the day, is well established. Conventional wisdom holds that arid-zone birds, diurnal organisms that endure the brunt of their environment, occupy these desert climates because of the possession of physiological design features common to all within the class Aves. We review studies that show that desert birds may have evolved specific features to deal with hot desert conditions including: a reduced basal metabolic rate (BMR) and field metabolic rate (FMR), and lower total evaporative water loss (TEWL) and water turnover (WTO).

Previous work on the comparative physiology of desert birds relied primarily on information gathered on species from the deserts of the southwestern U.S., which are semi-arid habitats of recent geologic origin. We include data on species from Old World deserts, which are geologically older than those in the New World, and place physiological responses along an aridity axis that includes mesic, semi-arid, arid, and hyperarid environments.

The physiological differences between desert and mesic birds that we have identified using the comparative method could arise as a result of acclimation to different environments, of genetic change mediated by selection, or both. We present data on the flexibility of BMR and TEWL in Hoopoe Larks that suggest that phenotypic adjustments in these variables can be substantial. Finally, we suggest that linkages between the physiology of individual organism and its life-history are fundamental to the understanding of life-history evolution.

INTRODUCTION

Two evolutionary events that shaped current vertebrate life were the transition from water to land, and the development of endothermy (Freeman and Herron, 1998; Williams and Tieleman, 2001). When they invaded land, vertebrates were exposed to new ecological opportunities, while at the same time they faced the challenge of maintaining an aqueous internal milieu in a desiccating environment. With the development of endothermy, energy and water requirements of land animals escalated above ectothermic relatives, and problems of water loss were exacerbated because higher rates of metabolism are associated with increased evaporative and excretory water loss. As a result, endotherms make poor candidates for successful occupation of desert environments, regions where high ambient temperature (T_a) and low water availability limits primary productivity. Yet, despite these physiological limitations, birds and mammals reside in the hottest and driest deserts in the world (Williams and Tieleman, 2001).

Although the physiological prowess of desert mammals to minimize energy expenditure and water loss is well known (Schmidt-Nielsen and Schmidt-Nielsen, 1950; Schmidt-Nielsen, 1964; Walsberg, 2000), early attempts to elucidate similar physiological attributes among desert-dwelling birds were less fruitful. After nearly a decade of work on species from the semi-arid

Southwestern U.S., Bartholomew and Cade (1963) concluded that many avian species found in these deserts have not evolved unique physiological specializations that distinguish them from mesic counterparts. Bartholomew (1972) suggested that “most desert passerines appear to have a basal metabolic rate (BMR) appropriate to their size.” A widely held axiom is that birds inhabiting deserts are capable of doing so because of characters possessed by all birds, flight, excretion of uric acid, efficient evaporative cooling, behavioral avoidance of climatic extremes, rather than as a consequence of physiological design features to the desert environment (Maclean, 1996).

Previous work in Comparative Physiology, including our own, has classified species of birds as “desert” or “non-desert” for purposes of analyses. Climatologists have long recognized that deserts differ in their meteorologic parameters, and have emphasized that the environment of a given desert region depends on the interaction of a number of variables including T_a , amount and timing of rainfall, relative humidity, and wind (Thorntwaite, 1948; Meigs, 1953). These differences in environment likely influence the array of selection pressures imposed by each respective desert. Because not all deserts present the same environment, we recommend that in the future practitioners use the classification system of Meigs (1953), who categorized deserts along a continuum from semi-arid, to arid, to hyperarid. Meigs based his system on Thorntwaite’s (1948) index of moisture availability (I_m), a parameter incorporating the amount of rainfall, maximum T_a of the hottest month, and minimum T_a of the coldest month. In Meigs’ scheme, areas were characterized as

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hyperarid only if there was one documented occurrence of 12 consecutive months without rain.

In this review we explore whether birds have adjusted their rates of energy expenditure and water loss to desert environments. We examine the hypotheses that desert birds have a reduced BMR, total evaporative water loss (TEWL), cutaneous water loss (CWL), field metabolic rate (FMR), and water influx rate (WIR). We explore the idea that basal metabolism and evaporative water loss are flexible parameters that can be influenced by environment, especially T_a . Finally we identify linkages between the physiology of desert birds and their life-history.

BASAL METABOLISM

Several key issues in evolutionary physiology include attempts to understand the significance of the wide variation in basal metabolic rate of similar-sized species, the changes in metabolic machinery associated with this variation (Daan *et al.*, 1990; Konarzewski and Diamond, 1995), and the relationship between BMR and life-history traits (McNabb, 1988; Harvey *et al.*, 1991; Hayes *et al.*, 1992). Several reports have appeared since the work of Bartholomew and Cade (1963) that have hypothesized that arid-zone birds may have evolved a reduced BMR (Dawson and Bennett, 1973; Withers and Williams, 1990; Schleucher *et al.*, 1991). Selective advantages attributed to a diminution in BMR include a lower overall energy demand, lower total evaporative water loss (TEWL), and lower endogenous heat production which would have to be dissipated in a warm environment, often by evaporative means.

Evaluating the idea that desert birds have evolved a reduced BMR, Williams and Tieleman (2001) compared BMR for 21 species of birds from deserts with that of 61 species from more mesic areas. Our equation based on conventional least squares regression was $\log \text{BMR (kJ/d)} = 0.584 + 0.644 \log \text{Body mass (g)}$ for mesic birds, whereas among desert birds it was $\log \text{BMR (kJ/d)} = 0.505 + 0.644 \log \text{Body mass (g)}$. ANCOVA revealed that the y-intercepts differed significantly. Using phylogenetically independent contrasts (Felsenstein, 1985; Garland *et al.*, 1992), the equation for mesic birds was $\log \text{BMR (kJ/d)} = 0.595 + 0.616 \log \text{Body mass (g)}$, but for desert birds was $\log \text{BMR (kJ/d)} = 0.304 + 0.702 \log \text{Body mass (g)}$. Again statistical tests showed that desert birds had a significantly lower BMR. Both approaches suggest that desert birds have a BMR that is 17–25% lower than mesic birds.

The causes of a reduced BMR in desert birds remains unresolved. It may result from physiological acclimation, a reversible phenotypic response of an organism to different environments (Huey *et al.*, 1999), from genetic alteration resulting from natural selection, or from a combination of both (Williams and Tieleman, 2001). A complicating issue is that the capacity for acclimation could also be under genetic influence and therefore subject to selection (Schlichting and Pig-

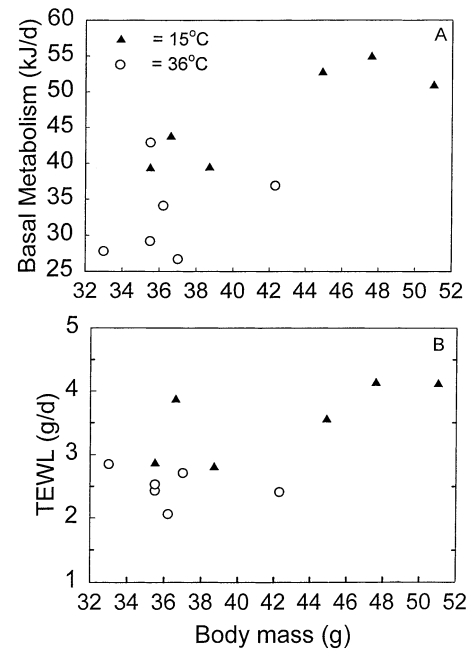


FIG. 1. (A) The relationship between basal metabolism (kJ/day) and body mass (g) in Hoopoe Larks from the Arabian desert. Open circles represent birds acclimated to 36°C, solid triangles represent birds acclimated to 15°C. (B) The relationship between total evaporative water loss (g H₂O/day) to body mass (g) in Hoopoe Larks from the Arabian desert. Symbols as in A.

liucci, 1998). Hudson and Kimzey (1966) reported that House Sparrows (*Passer domesticus*) from Houston, Texas, had a lower BMR than sparrows from more northerly populations, and proposed that these adjustments were genetically programmed, based on “common garden” experiments in the laboratory. However, in a review of 9 studies of temperate-zone species, Gelineo (1964) concluded that birds elevated their BMR by an average of $32 \pm 7.8\%$ when taken from a warm environment (29–33°C) and housed for 3–4 wk at colder temperatures (0–15°C).

To elucidate the mechanism(s) contributing to BMR among birds, we conducted an experiment on the flexibility of BMR and TEWL of Hoopoe Larks from the Arabian desert. We mist netted 12 individuals, and randomly assigned half of them (3 males and 3 females) to either a cold-exposure group (15°C) or a warm-exposure group (36°C). Initially the average body mass of birds in the two groups did not differ ($t = 1.2$, $P > 0.25$). After three weeks (12L:12D), larks in the 15°C group had gained on average 2.77 ± 0.8 g (SD), whereas body mass of birds in the 36°C group remained unchanged. In an ANOVA with BMR as the dependent variable, group as the main effect, and body mass as a covariate, we found that BMR differed significantly between groups (Fig. 1A). For Hoopoe Larks in the 15°C group, BMR averaged 46.8 ± 6.9 kJ/day (1.2 kJ/g-day), whereas BMR of larks from the 36°C group equaled 32.9 ± 6.3 kJ/day (0.98 kJ/g-day), a 42.2% difference. At the end of the experiment, we determined the dry mass of their brain, heart, liver,

kidney, stomach, small intestine, and left pectoral muscle. Birds from the 15°C group had a significantly larger liver (+43%), kidney (+37%), and small intestine (+66%), the tissues of which are known to have a high metabolic intensity (Martin and Fuhrman, 1955; Barnett, 1970; Daan *et al.*, 1990; Konarzewski and Diamond, 1995). The increase in mass attributable to the liver, kidney, and small intestine was 0.3 g, or 11% of the total mass increase in the cold-exposure group. Short-term flexibility in BMR seems to be large in this desert species, a result consistent with the general hypothesis that phenotypic variation is enhanced in stressful environments (Parsons, 1987). The possibility exists that mitochondrial density also increased in the organs of the cold-exposure group contributing to the elevation in BMR, a hypothesis in need of testing.

In the laboratory, heterozygotes of *Drosophila* sp. and of laboratory mice tend to have higher evolutionary fitness than their inbred homozygous parents when subjected to environmental extremes (Barnett and Colman, 1960; Parsons, 1996). Studies also suggest that heterozygote advantage may be a feature of polymorphisms in natural populations under extreme environments, and that the consequences of heterozygosity are environmentally dependent, becoming clearest under conditions of food limitation or other stressors (Hawkins, 1995; Parsons, 1995). If populations of desert birds experience episodes of high T_a s, and periods of low food and water availability, it could be that individuals heterozygous for a number of enzymes in metabolic pathways may be favored over those with less genetic heterozygosity. Species that have had a common evolutionary ancestor but have radiated to different environments may provide an appropriate system on which to test these ideas. BMR should decrease from cool mesic environments to hot desert environments, although the expected shape of this function remains ambiguous. Birds in arid environments should display more genetic heterozygosity than mesic counterparts and they should have the ability to down regulate their metabolism farther than mesic species.

BMR is, in part, determined by the sizes of internal organs such as the liver, kidney, and heart, which hypertrophy or atrophy depending on the level of food intake as dictated by energy expenditure, the "energy demand" hypothesis (Williams, 1999, 2001; Williams and Tieleman, 2000). As food intake decreases, because of decreased thermoregulatory demand, and perhaps reduced activity, organ sizes become smaller resulting in a lower level of metabolism at rest. Consistent with this hypothesis is the finding that some temperate birds have higher BMR in winter than during the spring (Dawson and O'Conner, 1996). Goldstein and Nagy (1985) documented but could not explain changes in BMR of Gambel's Quail (*Calipepla gambellii*) between years during the summer. However they did note that BMR was higher in this species during the summer when T_a s were much lower and thus thermoregulatory demands higher, an observation consistent with the "energy demand" hypothesis.

TOTAL EVAPORATIVE WATER LOSS

Because birds living in deserts often do not have access to drinking water, they must rely on preformed water in the diet and metabolic water to supply their needs. Traits that reduce water losses might be expected to be under strong selection. Examining pulmonary water loss for 13 species from 5 orders, Bartholomew and Dawson (1953) reported that, in the absence of temperature stress, TEWL of desert and mesic birds did not differ. Williams (1996) collated rates of TEWL for 102 species ranging in size from hummingbirds to Ostriches using both conventional analysis of covariance and regressions based on phylogenetic independent contrasts. Both approaches revealed that arid forms have a lower TEWL than species from more mesic environments. This suggests that natural selection may have sculpted phenotypes within desert environments to reduce their evaporative water losses.

However, as we have pointed out, variation in physiological performance may be a result, at least in part, of acclimation. An experiment on Hoopoe Larks showed that TEWL varies significantly with acclimation temperature (Fig. 1B; Williams and Tieleman, 2000). For larks in the 15°C group, TEWL averaged 3.6 ± 0.6 g H₂O/day whereas TEWL for larks in the 36°C group equaled 2.2 ± 0.3 g H₂O/day. TEWL correlated positively with BMR: TEWL (g H₂O/day) = $-0.21 + 0.078$ BMR (kJ/day) ($r^2 = 0.83$, $F = 50.4$, $P < 0.001$). One might argue that these difference in TEWL are attributable to the fact that a higher BMR mandates increased ventilation resulting in an elevated respiratory water loss (RWL). In a separate study, we determined that RWL accounts for 31.7% of TEWL at 35°C, and that cutaneous water loss (CWL) accounts for the remaining 68.3% (Tieleman and Williams, unpublished). Assuming that the increase of 42.2% in BMR is correlated with a parallel increase in RWL and no change in CWL, TEWL should have increased by 13.4%. Our finding that TEWL increased by 59.2% suggests that birds in the cold-exposure group altered the permeability of their skin to water vapor diffusion.

We think that TEWL, like BMR, decreases along an aridity gradient, and we predict that arid-zone birds have a greater degree of flexibility in TEWL than do birds from mesic environments.

CUTANEOUS WATER LOSS

The physiological mechanisms that have evolved to reduce TEWL in desert birds remain obscure, although several candidates have been proposed: hyperthermia (Calder and King, 1974; Weathers, 1981; Dawson, 1984), a countercurrent heat exchange system in the nasal passages that lowers RWL (Schmidt-Nielsen *et al.*, 1970), and adjustment of the lipid structure in the skin to reduce CWL (Menon *et al.*, 1989, 1996; Ophir *et al.*, 2000). Previously, we explored the role of hyperthermia (Tieleman and Williams, 1999) and of countercurrent water recovery in the nasal turbinates

in reducing TEWL (Tieleman *et al.*, 1999). Based on this work we concluded that these factors could not account for the difference in TEWL between desert and non-desert forms.

Desert birds could reduce their TEWL by decreasing their CWL (Menon *et al.*, 1989, 1996; Williams, 1996; Ophir *et al.*, 2000). Although early investigators surmised that most evaporative cooling took place in the respiratory passages (Rawles, 1960; Bartholomew and Cade, 1963; Mount, 1979), later work showed that CWL was an important avenue of water loss in the thermoregulatory process, at least at T_{as} below T_b (Smith, 1969; Bernstein, 1969; Dawson, 1982; Webster and Bernstein, 1987; Webster and King, 1987; Wolf and Walsberg, 1996). We were unable to identify any significant differences for CWL at thermally neutral T_{as} for species from desert and mesic environments (Williams and Tieleman, 2001). However, conclusions were tentative because data were few ($n = 8$ mesic, $n = 8$ desert) and obtained using a variety of methods.

Few studies have investigated CWL at high T_{as} when T_b must be regulated below lethal limits solely by evaporative water loss, from skin and from respiratory passages (Marder and Ben-Asher, 1983; Wolf and Walsberg, 1996). Some species, especially members of the Columbiformes, seem to rely primarily on CWL when T_a exceeds T_b , whereas other species employ a combination of CWL and RWL, the latter facilitated by panting or gular flutter (Bouverot *et al.*, 1974; Wolf and Walsberg, 1996; Tieleman *et al.*, 1999; Williams and Tieleman, 2001). Our understanding of CWL and RWL at high T_{as} , and how these variables are partitioned, remains rudimentary.

CWL is a function of the water vapor gradient between skin and air, and the total resistance to water vapor diffusion across skin, feathers, and boundary layer (Appleyard, 1979; Webster and King, 1987; Wolf and Walsberg, 1996). Resistance to vapor diffusion across the skin accounts for 75 to 90% of the total resistance, at least at moderate T_{as} (Tracy, 1982; Marder and Ben-Asher, 1983; Webster *et al.*, 1985). For resistance across the skin to change, birds must vary the diffusion path length, or alter the permeability of the skin to water vapor. The skin of birds is composed of an epidermis and a well vascularized dermal layer (Lucas and Stettenheim, 1972). During heat stress, birds can reduce the diffusion path length by vasodilation of the dermal capillary bed, effectively increasing CWL (Peltonen *et al.*, 1998). Rock Doves (*Columba livia*) under heat stress not only increase perfusion of capillaries but also increase the permeability of the skin to water vapor (Smith, 1969; Arieli *et al.*, 1995; Peltonen *et al.*, 1998). In response to dehydration, changes in epidermal lipid conformation within the stratum corneum may reduce the permeability of avian skin to water vapor, although data are few (Menon *et al.*, 1988, 1989, 1996). When Denda *et al.* (1998) maintained hairless mice at high (>80%) or low (<20%) humidities for two weeks, they found that an-

imals living in dry environments altered their transepidermal water loss by 31%. These phenotypic adjustments were accomplished by an increase in the number of lamellar bodies in the stratum granulosum, by an increase in the number of layers of cells in this region, and by an increase in the total lipids in the epidermis.

Our working hypothesis is that CWL, at thermal neutral temperatures, decreases among birds along an aridity axis. The mechanism(s) that impede water loss through the skin, especially of desert birds, remains unresolved, although changes in lipid deposition and epidermal thickness are likely candidates.

ENERGY EXPENDITURE AND WATER INFLUX IN THE FIELD

Laboratory studies provide insights into potentially important physiological mechanisms that enable birds to live in deserts, but these results achieve ecological and evolutionary meaning only if patterns correlate with attributes of organisms in their natural environment. Since the advent of the doubly labeled water method it has been possible to measure the field metabolic rates (FMR) and water influx rates (WIR) of free-living birds with reasonable accuracy (Lifson and McClintock, 1966; Nagy, 1980; Williams and Nagy, 1984; Williams, 1985; Speakman, 1997).

Nagy *et al.* (1999) showed that FMR in desert birds is 48% lower than in non-desert forms, a result derived from conventional ANCOVA. We confirmed this conclusion using both conventional analysis and regressions based on phylogenetic independent contrasts (Fig. 2A; Tieleman and Williams, 2000). Factors that might lead to a conservative FMR in desert birds include a reduced BMR, although the relationship between BMR and FMR is unresolved (Ricklefs *et al.*, 1996), less energy devoted to thermoregulation, or less time spent in energy demanding activities.

Patterns for WIR in desert birds compared with other birds are less clear. An analysis using least-squares regression suggested that WIR rates for species from deserts are 59% lower than those from mesic habitats ($n = 17$ desert species, 41 species from mesic habitats), a statistically significant difference, but a stepwise multiple regression using phylogenetic independent contrasts disclosed no statistically significant effect (Fig. 2B; Tieleman and Williams, 2000). A reduced WIR of desert birds in the field would correspond with low TEWL rates for desert birds in the laboratory (Williams, 1996), and would suggest several physiological and behavioral mechanisms that potentially have evolved in desert species to reduce TEWL and WIR.

ENERGY EXPENDITURE AND LIFE-HISTORY

Measurements of FMR integrate a complex set of design functions, some that relate physiological factors to an organism's BMR, others that involve behavioral and physiological adjustments in energy expenditure relative to the environment, and ultimately bridge the

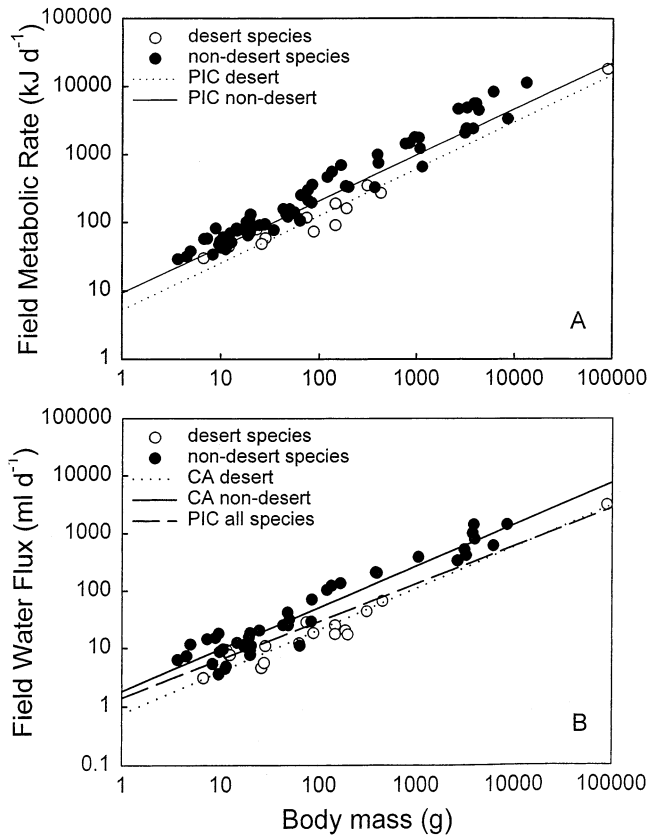


FIG. 2. (A) Logarithmic plot of field metabolic rate in desert birds (unfilled circles) and nondesert birds (filled circles) versus body mass. The allometric equations obtained by the method of phylogenetically independent contrasts are plotted for desert birds (dotted line) and nondesert species (solid line). (B). Logarithmic plot of field water flux in birds from deserts (unfilled circles) and nondesert birds (filled circles) versus body mass. The allometric equations generated with conventional least squares regression analysis are plotted for desert (dotted line) and nondesert species (solid line). The equation for all birds obtained with the method of phylogenetically independent contrasts is represented by the dashed line.

hiatus between individual physiological performance and avian life-history. Evolutionary interpretation of life-history variation requires a link between attributes of the individual, such as physiology and behavior, with evolutionary fitness (Ricklefs, 2000). As a corollary to the hypothesis that species from arid regions have reduced FMRs, we suggest that increasing aridity results in lower levels of reproductive effort and reduced annual fecundity, important components of avian life-history. Support for this idea comes from a comparison of clutch size and number of broods per year among larks that live in mesic, semi-arid, and arid regions (Table 1). Mesic species have large clutch size and raise multiple broods during the breeding season, whereas larks from the desert have small clutch size and typically only raise one clutch per year. In addition, we have found that during some years when rainfall is poor, larks in the Arabian desert do not breed. Ricklefs (2000) reported a strong positive relationship between annual fecundity and annual adult mortality among species of temperate and tropical birds. Because desert larks appear to have low reproductive rates, it may be that they also have low mortality rates compared with larks in more mesic environments, an idea we are currently testing.

To understand the complex linkages between patterns of time allocation to various behaviors, their costs in terms of energy expenditure, and their influence on life-history parameters, information about variation of allotments of time and energy over the annual cycle is necessary (King, 1974; Roff, 1992; Stearns, 1992). One prevalent idea is that energy expenditure is substantially elevated during the breeding season, the so called "peak demand hypothesis," especially during the phase when parents are feeding dependent young (Drent and Daan, 1980; Weathers and Sullivan, 1993; Ricklefs *et al.*, 1996; Williams, 1996, 2000). An augmentation in parental energy expenditure is thought to be inversely correlated with survivorship, and ultimately has consequences for fitness, but the shapes of

TABLE 1. Clutch size and number of clutches per year of larks along an aridity gradient.

Species ^a	Habitat	Clutch size	# Clutches/yr	Breeding regularity
Sskylark (<i>Alauda arvensis</i>)	Mesic	3.9	3–4	Annual
Woodlark (<i>Lullula arborea</i>)	Mesic	4.0	2–3	Annual
Calandra Lark (<i>Melanocorypha calandra</i>)	Semi-arid	4.2	2	Annual
Short-toed Lark (<i>Calandra brachydactyla</i>)	Semi-arid	3.5	2	Annual
Lesser Short-toed Lark (<i>Calandrella rufescens</i>)	Semi-arid	3.3	2	Annual
Dune Lark (<i>Mirafra erythrochlamys</i>)	Hyperarid	2.0	1	Annual
Dunn's Lark (<i>Eremalauda dunnii</i>)	Arid	2.8	1	<Annual
Hoopoe Lark (<i>Alaemon alaudipes</i>)	Arid-Hyperarid	2.0	1	<Annual

^a Sources Cramp (1988); Williams (2000).

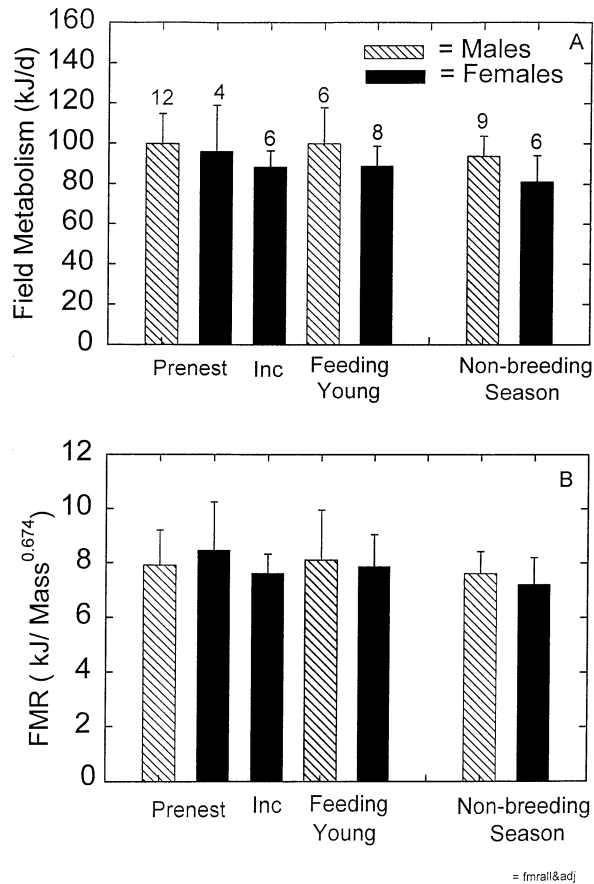


FIG. 3. (A) Field metabolic rate (kJ/day) and (B) mass-adjusted field metabolic rate (kJ/day) of Dune Larks prior to nesting, during incubation, while feeding nestlings 8–10 days old, and during the non-breeding season.

these functions are unclear (Masman *et al.*, 1988; Bryant, 1991; Deerenberg, 1999).

An alternative view, the “reallocation hypothesis,” suggests that field metabolic rate (FMR) is relatively constant over the annual cycle (West, 1968; Weathers and Sullivan, 1993; Weathers *et al.*, 1999). Because birds breed when food supplies are at a maximum, and when ambient temperatures are moderate, they experience decreases in energy costs for foraging and for thermoregulation, savings which can be reallocated to activities associated with breeding. Support has been proffered for both the peak demand hypothesis (Wijnandts, 1984; Masman *et al.*, 1988; Gales and Green, 1990), and for the reallocation hypothesis (Bryant and Tatner, 1988; Weathers and Sullivan, 1993). Generalizations about the ecological circumstances that influence patterns of energy expenditure have been hampered by the relatively small number of studies that have compared FMR during the breeding and non-breeding season.

In a recent study, Williams (2001) found that FMR is relatively constant over the annual cycle for Dune Larks (*Mirafra erythroclamys*), a resident of the Namib, which supports to the “reallocation hypothesis”

(Fig. 3). For desert birds, there exists no evidence that a peak in energy expenditure occurs during the breeding season, a pattern which conflicts with those found for some species in temperate climates (Masman *et al.*, 1988; Bryant and Tatner, 1988; Gales and Green, 1990). Moreover, some authors have proposed that the incubation period represents a time of reduced energy demand owing to reduced activity, and to lower thermoregulatory demands because of the insulation provided by the nest (Drent and Daan, 1980; Walsberg, 1983; Bennet and Harvey, 1987). The FMR of Dune Lark females equaled 88.1 kJ/day during incubation, 88.5 kJ/day when they were feeding 8–10 day old nestlings. There is no support for the idea that female larks work harder during the chick rearing period compared with the incubation period.

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