

Energy expenditure and water flux of free-living Dune Larks in the Namib: a test of the reallocation hypothesis on a desert bird

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Summary

1. Dune Larks (*Mirafra erythroclamys*) are the only avian species that has evolved the capability of surviving in the Namib Sand Sea, one of the driest regions in the world. Their field metabolic rate (FMR) and water flux, as measured by doubly labelled water, during the breeding and non-breeding season are reported here.

2. FMR is relatively constant over the annual cycle, which conforms to the 'reallocation hypothesis'. With data pooled for both seasons, males expended energy at a rate of 97.5 ± 20.4 kJ day⁻¹ (± 1 SD) and females at 87.5 ± 13.0 kJ day⁻¹. The data supported the hypothesis that Dune Larks do not possess a reduced FMR, a result attributable to their elevated basal metabolism. In a previous laboratory investigation, Dune Larks had a low rate of evaporative water loss despite their elevated basal metabolic rate (BMR). The present study demonstrated that this low evaporative water loss translates into a low water influx in the field.

3. The FMR of Dune Lark females equalled 88.1 ± 6.9 kJ day⁻¹ during incubation, and 88.5 ± 9.9 kJ day⁻¹ when they were feeding 8–10-day-old nestlings. These data do not support the idea that the incubation period is a time of low energy demand.

4. Dune Larks had a relatively constant water influx throughout the year. For sexes combined, mass-adjusted values of water influx averaged 0.59 ml H₂O/(day mass^{0.682}).

5. Calculations showed that neonates received 10 kJ day⁻¹ whereas towards the end of the nestling period, chicks were fed 75 kJ day⁻¹, the maximum gross energy intake for nestlings. During chick rearing, males increased the amount of food that they found by 57.7%, females by 64.3%, late in the nestling period.

6. Dune Larks foraged in the morning and late afternoon, but were constrained by their environment to seek shade at midday during the breeding season.

7. Metabolic water production plays a significant role in the water economy of Dune Larks. Assuming a mixed diet, 47% of their water intake comes from the oxidation of food stuffs.

Key-words: Desert, doubly labelled water, energetics, field metabolic rate, incubation, water flux

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Introduction

In order to understand the complex linkages between patterns of time allocation to various behaviours, 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 (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 & Daan 1980; Weathers & Sullivan 1993; Ricklefs 1996; Williams 1996b). An augmentation in parental energy expenditure is thought to be inversely correlated with survivorship, and ultimately has consequences for fitness, but the shapes of these functions are unclear (Masman 1986; Bryant 1991; Deerenberg 1999). Although the peak demand hypothesis is deeply rooted in concepts of avian life-history evolution, surprisingly few studies have measured daily energy expenditure at times other than the breeding season (Masman 1986; Weathers & Sullivan 1993; Weathers *et al.* 1999).

An alternative view, the 'reallocation hypothesis', espoused by West (1968) based on laboratory investigations on the Willow Ptarmigan (*Lagopus lagopus*) and supported by data on Yellow-eyed and Dark-eyed Juncos (*Junco phaeonotus* and *J. hyemalis*), suggests that field metabolic rate (FMR) is relatively constant over the annual cycle (Weathers & Sullivan 1993). Because birds breed when food supplies are at a maximum, and when ambient temperatures (T_a) are moderate, they experience decreases in energy costs for foraging and for thermoregulation, savings that can be reallocated to activities associated with breeding. Support has been proffered for both the peak demand hypothesis (Wijnandts 1984; Masman 1986; Gales & Green 1990), and for the reallocation hypothesis (Bryant & Tatner 1988; Weathers & 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. Data on seasonal variation in FMR for species from desert environments are lacking.

The Namib Sand Sea, a 34 000-km² expanse of dunes situated along the south-western coast of Africa, is among the driest regions on earth (Logan 1960; Teller & Lancaster 1985). As a consequence of hyper-aridity, the Namib has the lowest primary production recorded for any desert ecosystem (Seely & Louw 1980), and for its avian inhabitants, resources such as food or water are likely to be in short supply. Because of the Namib's austerity and, presumably, its rather stringent selection pressures, and because of its geological antiquity (Axelrod 1950; Schwarzbach 1961), one might expect inhabitants to possess a number of behavioural and physiological adaptations that permit a desert existence (Williams & Tieleman 2000a). Several bird species visit the Namib, but only one species has evolved the capability to reside year-round in the Sand Sea, the Dune Lark (*Mirafra erythroclamys* Strickland).

Natural selection has presumably shaped time and energy budgets such that they represent optimized solutions to the difficulties posed by the harsh desert environment (Williams & Tieleman 2000a). Information about birds that occupy such environments is important to our understanding of patterns of life history because many trade-offs in time allocation and in energy usage relevant to life-history evolution may not become apparent until resources are in short supply (Stearns 1992; Leroi, Bennett & Lenski 1994; Rose & Bradley 1998). Because such trade-offs are probably more pronounced in deserts, these environments offer opportunities for acquiring insights into the evolution of time and energy budgets. Although researchers have focused much of their thinking about life-history patterns around energy expenditure, water is also a critical resource in desert ecosystems, and a lack thereof may have a significant impact on fitness.

Although desert birds typically have a reduced basal metabolic rate (BMR) (Tieleman & Williams 2000;

Williams & Tieleman 2000a), Dune Larks had a BMR during the austral winter consistent with allometric predictions for all birds (Williams 1999). I suggested that Dune Larks living in the Namib expend considerable energy in the process of thermoregulation, especially during the winter. Maintenance of the organs necessary to process increased food intake and of the metabolic machinery for chemical heat production may result in an increase in BMR in Dune Larks, as has been documented for Hoopoe Larks *Alaemon alaudipes* in the Arabian desert (Williams & Tieleman 2000b). I predicted that Dune Larks do not have a reduced FMR, since BMR is often a significant component of FMR (Walsberg 1983). Dune Larks also had a total evaporative water loss 21–44% below predictions based on body size (Williams 1999). I suggested that they have evolved mechanisms that lower their water efflux, despite the absence of a reduced metabolic rate. This implies that Dune Larks have a reduced water flux in the field, a question to be addressed in this study.

Here, I report on the first study that examines the FMR and water flux, as measured by doubly labelled water, of an arid-zone bird during both the breeding and non-breeding seasons. In addition to the above predictions about levels of FMR and water influx, questions are raised on whether patterns of energy expenditure between the breeding and non-breeding seasons for Dune Larks living in the hyper-arid Namib desert supported the peak demand hypothesis or the reallocation pattern. Based on the suggestion that Dune Larks forage mostly on insects during the breeding period, but to a large extent on seeds during the non-breeding season (Willoughby 1971), and on the observation that while incubating eggs and brooding small young, females typically spend time panting, a behaviour that requires considerable water, it is predicted that water influx of Dune Larks would be higher in the breeding season than in other times of the year. During the breeding season, parents must not only supply their own resource needs, but also those of their offspring. In order to estimate this increase in energy demand, I measured the energy expenditure and water flux of nestlings. I quantified partitioning of time to various behaviours during the breeding season in order to gain an appreciation of time allocation patterns and of how those patterns might be related to energy expenditure. Finally, to understand how the desert environment influences time-budgets of birds, and to obtain an idea of the thermoregulatory demands of larks, I measured their thermal environment using plumage-covered taxidermic casts (Bakken 1976).

Materials and methods

STUDY AREA

Dune Larks were studied in the Namib Sand Sea during December 1989, from January to July 1991, and from January to March 1993. The study area extended

from near Gobabeb (23°34' S, 15°03' E), a research station in the central Namib operated by the Desert Ecological Research Unit of Namibia, to Elephant valley, an interdune 'street' about 70 km to the south-west. The vegetation of this region has been described by Giess (1971) and Robinson (1976).

NATURAL HISTORY OF DUNE LARKS

The natural history of Dune Larks has received scant attention (Cox 1983; Boyer 1988). Aspects of their natural history relevant to this paper are briefly described here.

Somewhat larger in size than females but similar in appearance, males defend territories throughout the year, up to 10 ha. Dune Larks reportedly breed from November to April (Boyer 1988), but during the study, most individuals attempted to breed during the months of December to March. During the breeding season, males sing from elevated perches, or during their aerial display. Females build a domed nest, a task requiring 7–8 days, and then typically lay two eggs, which only she incubates. Females usually remain on their eggs during midday when T_a s are highest, panting intermittently to regulate both their body temperature (T_b) and the temperature of their eggs. During the nestling period, which spans 12–14 days, both sexes provide food to the young, mostly insects and spiders.

MACRO AND MICROCLIMATE

For each of the three field seasons, I obtained daily weather records from the weather station at Gobabeb. In addition, long-term weather records for this region were available from Lancaster, Lancaster & Seeley (1984). Operative temperature (T_e) represents an integrated measure of environmental temperature that reflects all external conductive, convective and radiative properties of an animal with no internal heat production or evaporative water loss (Bakken 1976). For larks, T_e was assessed by means of thermocouples centred inside plumage-covered copper casts manufactured according to Bakken *et al.* (1981). Air temperature (T_a) was measured 6 cm above the sand with a 38-gauge thermocouple surrounded by a cone of aluminium foil, and sand surface temperature (T_{sand}) was estimated using a 38 gauge thermocouple soldered to a 4-cm² piece of copper mesh buried about 1 mm below the sand surface. The output of each thermocouple was recorded every minute and averaged over each hour interval with the aid of a Campbell Scientific Data Logger, model 10X (Logan, UT, USA).

TIME–ACTIVITY BUDGETS

Time–activity budgets of six pairs of banded birds were quantified during the breeding seasons of 1989 and 1991 by recording activity and exposure to the sun every 15 s at a signal produced by an electronic metronome (Weins *et al.* 1970; Williams & Nagy 1984). During

the two seasons, 5456 point observations were recorded for males, and 1558 for females. Their activity was placed in one of the following categories: walk, peck, perch, stand, vocal, fly and other. As birds foraged, they walked briskly over the sand surface intermittently stopping to peck at food items on the surface, or to dig into the sand for food items (Cox 1983; Dean *et al.* 1992). Both activities were placed in the peck category. Birds were considered to be perching if they were standing above the sand surface on vegetation, typically a nara bush or clump of *Stipagrostis* sp. Both males and females vocalized, each repertoire sex-specific, but males often sang from exposed perches at the boundaries of their territory. Aerial displays of the male were included in the fly category.

DOUBLY LABELLED WATER

Measurements of FMR and water flux were obtained by means of the doubly labelled water (DLW) technique, in which the rate of decline of an isotope of hydrogen in the body water pool provides a measure of water flux (Nagy & Costa 1980), and the loss rates of both a hydrogen isotope and ¹⁸O yield an estimate of CO₂ production (Lifson & McClintock 1966; Nagy 1980; Speakman 1997). The procedures for using the DLW method have been detailed elsewhere (Williams 1987; Williams & Dwinell 1990; Williams & Du Plessis 1996). In brief, birds were mist-netted, injected with 0.15 ml of a mixture of tritiated water (1.1×10^4 Bq μl^{-1}) and 95 atom percentage ¹⁸O. After a 1-h period for equilibration of isotopes, a 60- μl blood sample was removed from the brachial vein. Birds were then weighed with a Pesola scale (Avinet, Dryden, NY, USA) that had been calibrated against a Metler P2100 laboratory balance (Metler-Toledo, Inc., Hightstown, NJ, USA), banded and released. Birds were netted 24 or 48 h later, had a second blood sample taken, were weighed and released. About 20% of the birds that were injected could not be re-netted. These birds were collected under permit with a 410-shotgun.

Blood samples or tissue samples were microdistilled to obtain pure water (Wood *et al.* 1975), then assayed in three separate 10- μl aliquots for tritium activity. The O¹⁸ content was measured in triplicate in the laboratory of K. Nagy, University of California, Los Angeles. Water influx was calculated using the equation of Nagy & Costa (1980) and rates of CO₂ production using the equation of Nagy (1980). Background levels of isotopes obtained from uninjected birds, three in summer and three in winter, were subtracted from values prior to calculations.

Estimates of water flux using isotopes of hydrogen are typically within $\pm 10\%$ of values obtained by standard laboratory methods (Nagy & Costa 1980) and estimates of CO₂ production as given by DLW are within 8–10% (Williams & Nagy 1984; Speakman 1997). Only a few validation studies of the DLW method have been performed on growing birds where the possibility

exists that isotopes could be differentially incorporated into growing tissues leading to substantial errors in estimates of CO₂ production (Williams & Nagy 1985; Klaassen *et al.* 1989; Gabrielsen *et al.* 1992). For chicks of the Arctic Tern (*Sterna paradisae*), estimates of CO₂ production as given by the DLW method differed from measurements using gas analysis by +10.3% on average (Klaassen *et al.* 1989). In a recent study on growing Black-tailed Godwits (*Limosa limosa*) and Northern Lapwings (*Vanellus vanellus*), H. Visser and H. Schekerman (unpublished data) found that the DLW method overestimated CO₂ production by 2.9%. In addition, these authors showed that a relative growth rate of 20% per day did not influence errors in the DLW method.

Energy expenditure can be calculated from CO₂ production when the composition of the diet is known (Gessamen & Nagy 1988; Weathers & Sullivan 1989). Following Williams & Du Plessis (1996), for adults a conversion factor of 23.3 J ml⁻¹ CO₂ was calculated based on a mixed diet of equal proportions of seeds

and invertebrates (Dean *et al.* 1992). For nestlings, a diet of insects was assumed and a conversion factor of 24.6 J ml⁻¹ CO₂ (Williams & Prints 1986).

STATISTICS

Computations were performed using SPSS 7.5 for Windows (SPSS, Chicago). Values are presented ±1 SD.

Results

CLIMATE

Along with the Atacama, and Peruvian deserts, the Namib is categorized as a hyper-arid, cool coastal desert (Meigs 1953, 1966). At Gobabeb mean daily T_a ranged from a high of around 25 °C during the austral summer to a low of about 17 °C in winter (Lancaster *et al.* 1984). Maximum T_as, recorded in a standard weather shelter, only occasionally exceeded 40 °C during summer, and during winter, the lowest minimum daily T_as were near freezing. Over the Namib, rainfall is localized, unpredictable and scant; sometimes an area will not receive rain for several years (Walter 1986). At Gobabeb, rainfall averages 27.2 mm yr⁻¹ with the highest likelihood of rain in March. Fog is common on the coast, but inland, around Gobabeb, fog only occurs 2–3 days per month (Lancaster *et al.* 1984). Estimates of fog precipitation at Gobabeb are around 30 mm yr⁻¹, although measurement of moisture input via fog into this ecosystem remains problematical (Walter 1986).

MICROCLIMATE

Although I recorded T_e during 1989, 1991 and 1993, I report here data for 1991 and 1993 only; patterns in 1989 mirrored other years. During January–February 1991 (n = 59 days), by midday all mounts exposed to the sun had reached an average T_e of around 46–50 °C, a temperature above the upper critical temperature for Dune Larks (Fig. 1; T_{uc} = 35.1; Williams 1999). T_{sand} varied from a low of 17 °C at night to a high of 60 °C, the latter a temperature that impedes the foraging of Dune Larks (see section on activity budgets). At night, T_e consistently fell below the lower critical temperature (T_{lc}) for Dune Larks in all locations.

Amid the austral winter, June–July 1991 (n = 61 days), the average T_e of a model in the shade did not exceed T_{uc} of Dune Larks, suggesting that they can find microsites during the winter that do not require substantial evaporative cooling to maintain their T_b (Fig. 1b). In general, T_e was below T_{lc} for about 16 h during the winter, and about 14 h during the summer.

During the breeding season of 1993 (n = 59 days), T_e of models exposed to the sun exceeded T_{uc} of Dune Larks for about 7 h per day, whereas T_e in the shade was typically below this value (Fig. 1c). Consistent with measurements of temperature during the breeding season of 1991, T_{sand} reached 60 °C during the afternoon.

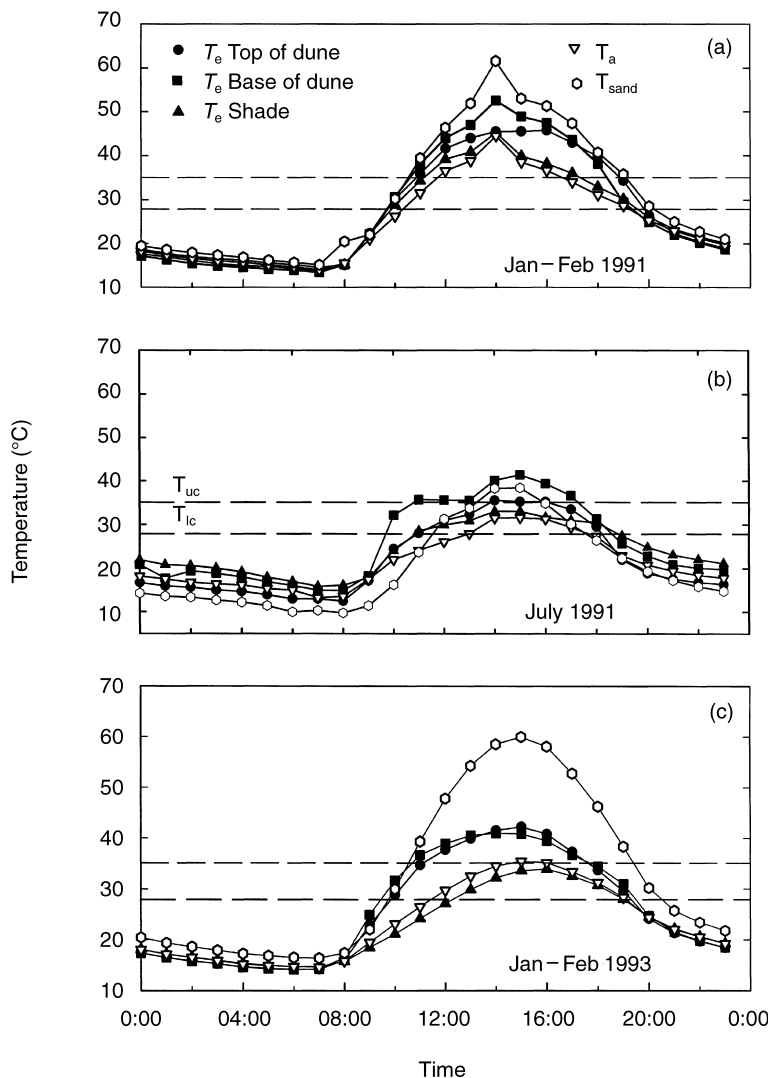


Fig. 1. Temperature of taxidermic mounts and of the sand surface at Khomabes, Namibia during 1991 and 1993. The upper dashed line represents the upper critical temperature of Dune Larks, and the lower dashed line represents the lower critical temperature. Each data point represents a mean for each hour of all days for the period shown.

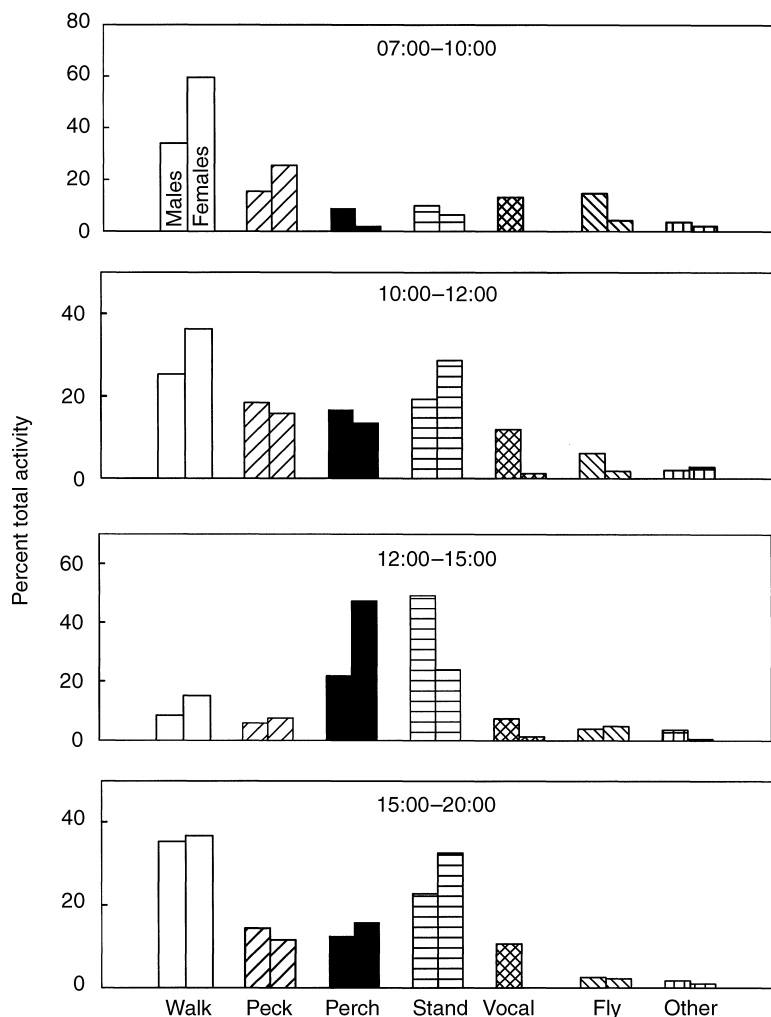


Fig. 2. Activity budgets of male and female Dune Larks during December to March. Sample sizes given in text.

ACTIVITY BUDGETS

During two breeding seasons 1989 and 1991, activity schedules for colour-marked Dune Larks differed between sexes (Fig. 2; $\chi^2 = 184.2$, $df = 6$, $P < 0.0001$). Overall, males tended to forage less than females, as indicated by their smaller percentage time spent walking and pecking; males also flew and vocalized more than females. A multidimensional contingency table showed that activity budgets also differed significantly between sexes among time periods during the day ($\chi^2 = 2.980$, $df = 42$, $P < 0.001$). Both sexes foraged in the mornings, but from 1200 to 1500 h, they perched or stood more of the time, typically in the shade. Birds were observed standing in the shade (shading) during midday on most days when T_a exceeded 36 °C.

BODY MASS OF ADULTS

Males averaged 29.0 ± 1.3 g ($n = 18$) during the breeding season, whereas females averaged 25.8 ± 1.2 g ($n = 16$), values significantly different ($t = 7.2$, $df = 32$, $P < 0.001$).

During the non-breeding season (June–July), males on average weighed 28.7 ± 2.2 g ($n = 8$), but females weighed 25.3 ± 0.8 g ($n = 9$) ($t = 4.1$, $df = 15$, $P < 0.001$). The percentage body water of eight adults that were collected and dried at 70 °C was 63.4 ± 1.0 , a value used in calculations of energy expenditure and water flux.

BODY MASS OF NESTLINGS

The logistic model that describes nestling growth for Dune Larks is

$$\text{mass (g)} = \frac{22.17}{1 + e^{-\left(\frac{x - 5.57}{3.26}\right)}}$$

where x is age in days and e is the base of natural logarithms (day of hatch = 0) ($n = 27$, $r^2 = 0.98$, $F = 766.0$, $P < 0.001$). When eggs hatch, nestlings weigh about 3.0 g, and by day 14, when they typically fledge, chicks have grown to nearly 23.0 g.

FIELD METABOLISM: ADULTS

Average values for FMR of 51 Dune Larks did not vary significantly when analysed by stages of the annual cycle (Fig. 3a; ANOVA, $F = 1.3$, $df = 50$, $P < 0.2$), or by stages within the breeding season ($F = 0.7$, $df = 35$, $P > 0.6$). With data pooled for both seasons, males expended energy at a higher rate than did females, 97.5 ± 20.4 kJ day⁻¹ vs 87.5 ± 13.0 kJ day⁻¹ ($t = 2.1$, $df = 49$, $P < 0.04$), a result attributable, at least in part, to the larger body mass of males. When measures of FMR were mass-adjusted by dividing this variable by $\text{mass}^{0.674}$, no statistically significant differences were found (Fig. 3b). The exponent 0.674 is the slope of the allometric equation relating FMR to body mass in desert birds (Williams *et al.* 1993). Rates of energy expenditure for females varied little during the breeding season. For example, incubating females had an energy expenditure of 88.1 ± 6.9 kJ day⁻¹ and, when feeding nestlings 8–10-days-old, they had an FMR of 88.5 ± 9.9 kJ day⁻¹. The percentage change in body mass between initial and final samples was small for all birds, averaging $0.26 \pm 3.0\%$ ($n = 51$).

FIELD METABOLISM: NESTLINGS

Between days 4 and 14, FMR of nestlings increased from 10 kJ d⁻¹ to around 40 kJ d⁻¹ (Fig. 4a). The logistic model that described these data was

$$\text{FMR(kJ/day}^{-1}) = \frac{44.04}{1 + e^{-\left(\frac{x - 6.5}{2.10}\right)}}$$

($r^2 = 0.71$, $F = 11.2$, $P < 0.003$), where x is age in days.

WATER INFLUX RATE: ADULTS

Water influx for Dune Larks did not vary significantly over the annual cycle (Fig. 5a; $F = 0.8$, $df = 50$, $P < 0.6$). When the comparison was restricted to the breeding

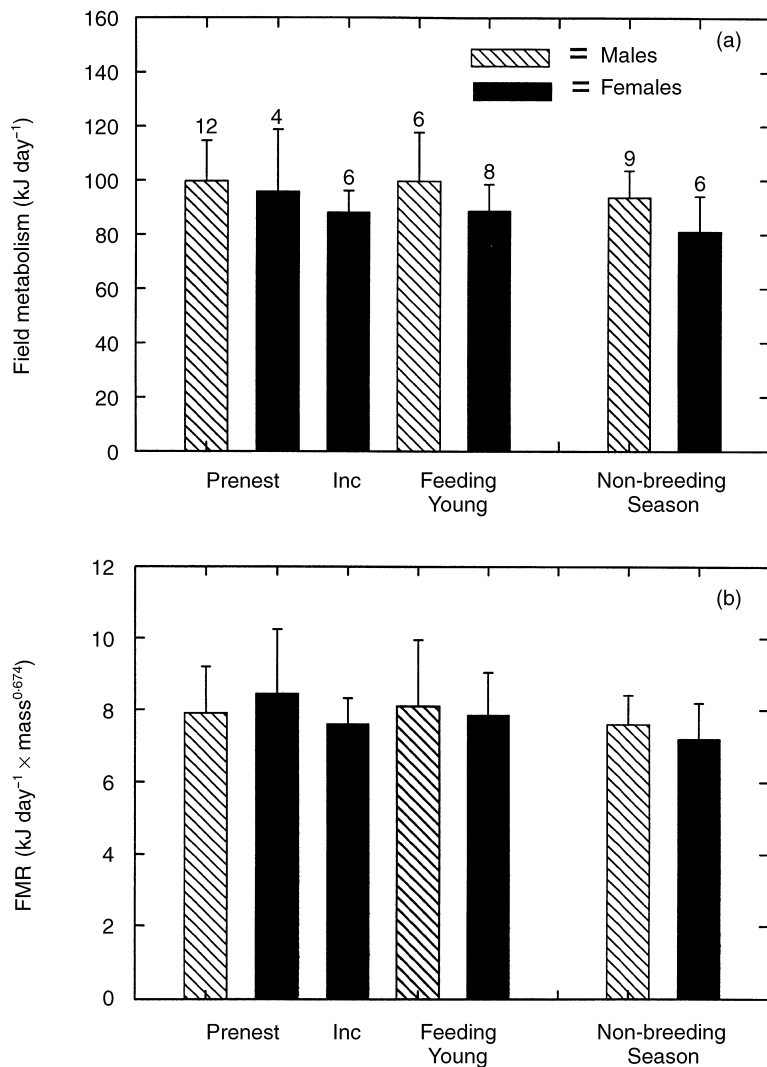


Fig. 3. (a) Field metabolic rate (kJ day⁻¹) and (b) mass-adjusted field metabolic rate (kJ day⁻¹) of Dune Larks prior to nesting, during incubation, while feeding nestlings 8–10-days-old, and during the non-breeding season.

season, males ingested significantly more water than females, 6.2 ± 1.0 ml H₂O day⁻¹ and 5.2 ± 1.3 ml H₂O day⁻¹, respectively ($t = 2.3$, $df = 32$, $P < 0.03$), but when values of water influx were adjusted for body mass, no significant differences between sexes were found (Fig. 5b). For sexes combined, mass-adjusted values of water flux averaged 0.59 ml H₂O/(day mass^{0.682}). The value 0.682 is the slope of the allometric relationship for water influx of desert birds (Williams *et al.* 1993).

WATER INFLUX: NESTLINGS

Water influx of nestlings was described as:

$$\text{Water influx (ml H}_2\text{O day}^{-1}\text{)} = \frac{5.3}{1 + e^{-\frac{(x-4.4)}{1.19}}}$$

($r^2 = 0.79$, $F = 17.5$, $P < 0.005$). These data suggest that influx was low during the first few days of nestling life, but by day 8, influx had reached an asymptote

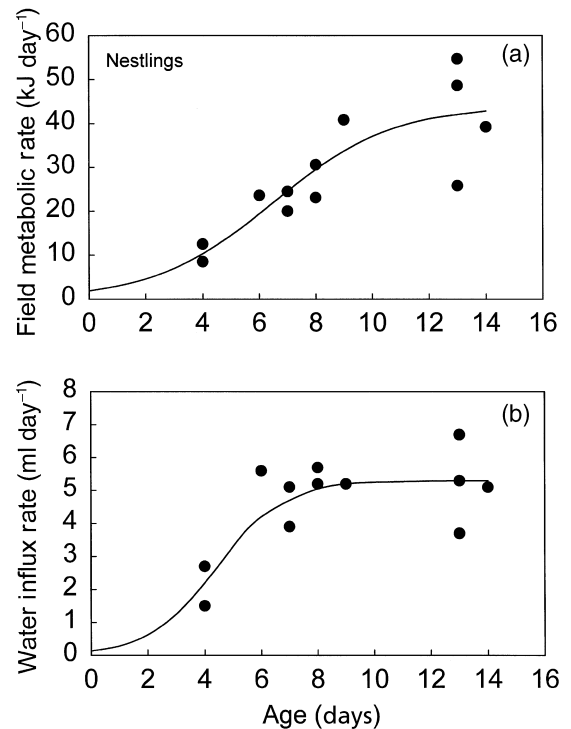


Fig. 4. The relationship between (a) field metabolic rate (kJ day⁻¹) and (b) water influx rate (ml day⁻¹) and age (days) of nestling Dune Larks.

around 5.0 ml H₂O day⁻¹ (Fig. 4b). If the water content of the arthropods supplied to the chicks as food remains reasonably constant, then parents supply about the same amount of food each day from day 8 to the end of the nestling period.

Discussion

Time-budgets are a useful tool in deciphering the decision-making process used by animals as they interact with their environment (King 1974; Goldstein 1988; Krebs & Davies 1997). During the breeding season, male Dune Larks spent 38.4% of their time foraging, the combination of walking and pecking, whereas females spent 46%. These are conservative estimates of the amount of time spent finding food because as birds forage they pause to survey their environment, a behaviour that appears in their time-budget as standing. In addition, these estimates are summed over the entire day, but Dune Larks often stand in shade for long periods during the middle part of the day, presumably to avoid excessive heat from the sun. Examination of their time-budget during the morning hours shows that males forage 50% of their time during this period, and females 85% (Fig. 2). On hot days during the breeding season, Dune Larks seek shade to avoid the midday sun (J. B. Williams, unpublished data). Such behaviour constricts the foraging niche of larks, and probably constrains their energy and water intake in an environment where supplies may already be low. As the morning progresses, T_c increases until it becomes

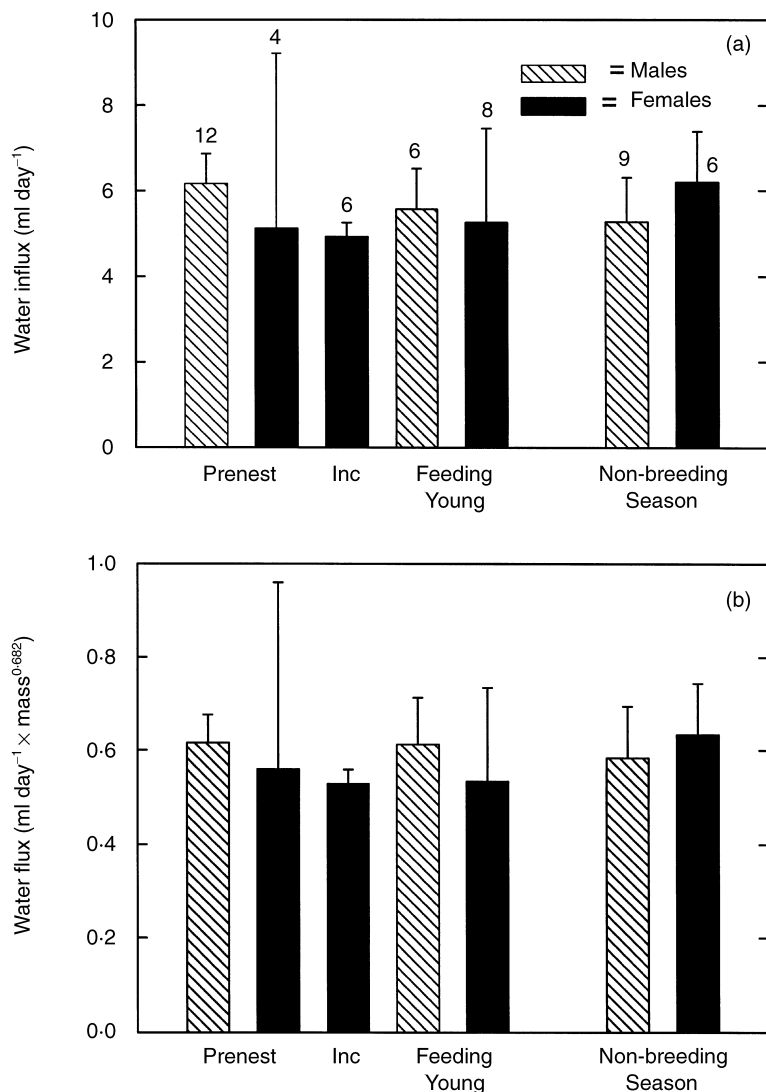


Fig. 5. (a) Water influx (ml day^{-1}) and (b) mass-adjusted water influx of Dune Larks prior to nesting, during incubation, while feeding nestlings 8–10-days-old, and during the non-breeding season.

disadvantageous to continue foraging in the direct sunlight, so birds stand in the shade; birds would lose more water by evaporative cooling, if they remained exposed to the sun, than they could obtain in the food that they find (Williams, Tieleman & Shobrak 1999).

Among birds, FMR is thought to be positively associated with levels of BMR (Daan *et al.* 1990; Koteja 1991), but the determinants of this linkage remain unclear. If natural selection has had an impact on the energy budgets of birds, a basic assumption underlying much of life-history theory, then it becomes an important exercise to identify design features that covary with levels of FMR to gain insights into the selective pressures that have created the trajectory for development of current physiological traits. The association between levels of BMR and FMR has been attributed to selection for the metabolic machinery required to maintain levels of energy expenditure during the purported time of peak energy demand, the nestling period, when parents are caring for young (Daan *et al.* 1990; Ricklefs 1996).

The hypothesis that the FMR of Dune Larks is not reduced owing to their elevated BMR is supported by the data of this study (Williams 1999). Estimates of FMR equalled 97.5 and 87.5 kJ day^{-1} , for males and females, respectively, values that exceed expectation based on body mass by $+7.5\%$ and $+4.4\%$ (Tieleman & Williams 2000). These authors also constructed an allometric equation for FMR for birds from desert environments; values of FMR for Dune Larks exceeded predictions for desert birds by 53.9% for males, and 54.3% for females. These data are consistent with the idea that their relatively high BMR translates into a high FMR in the field.

The factors responsible for the relatively high metabolic rates of Dune Larks compared with other species of desert birds remain unclear. The uniform FMR during stages of the breeding cycle, and during the non-breeding season, does not lend credence to the idea that levels of BMR reflect the maintenance of the necessary metabolic machinery to sustain high rates of metabolism during the chick-rearing period (Daan *et al.* 1990; Ricklefs 1996). I have proposed that the level of BMR is influenced by thermoregulatory demand in desert birds (Williams 1999). Because of their high T_{ic} , around $27.9 \text{ }^\circ\text{C}$, nearly $10 \text{ }^\circ\text{C}$ higher than allometric predictions (Kendeigh, Dolnik & Gavrilov 1977), and of the cool Namib environment with minimum T_a s averaging $9.1 \text{ }^\circ\text{C}$ in winter and $16.5 \text{ }^\circ\text{C}$ during March, the hottest month (Lancaster *et al.* 1984), Dune Larks expend considerable energy in thermoregulation. The increase in food consumption required to meet increased energy needs mandates larger organ sizes which in turn influences their BMR (Williams & Tieleman 2000b). Birds with lower overall thermoregulatory demands, such as in summers of hot deserts, should have a lower BMR at this time, attributable to smaller organs for food processing and to tissues that support thermogenesis, such as the pectoral muscle (Dawson & O'Connor 1996). Because BMR is a significant component of FMR (Walsberg 1983), the latter should be correlated with the former.

The peak demand hypothesis suggests that energy expenditure is substantially elevated during the breeding season, especially during the period when parents are delivering food to young in the nest (Drent & Daan 1980; Walsberg 1983; Bennet & Harvey 1987). This idea has become entrenched in discussions about avian life-history evolution, wherein a trade-off is thought to exist between current reproductive effort and future parental survival (Stearns 1992). With increases in clutch size, and attendant increases in energy expenditure, especially when parents are feeding nestlings, adult birds experience a decline in survival, referred to as the cost of reproduction (Williams 1966; Bryant 1979; Resnick 1992). In contrast to the nestling period, energy expenditure during incubation is considered to be low owing to reduced activity, and to lower thermoregulatory demands because of the insulation provided by the nest (Walsberg 1983). The FMR of

Dune Lark females equalled 88.1 kJ day^{-1} during incubation, 88.5 kJ day^{-1} 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 other stages of the nesting cycle (Williams 1987; Williams & Dwinell 1990; Williams 1996b).

For Dune Larks, FMR does not vary among stages within the breeding cycle, after adjusting for differences in body mass, nor does it vary between the breeding and non-breeding seasons, a pattern dissonant with the peak demand hypothesis, and one in harmony with the re-allocation hypothesis. It appears that Dune Larks have an optimal level of energy expenditure, and that energy demanding activities such as moult, breeding and thermoregulation are temporally spaced in such a way that FMR is invariant over the annual cycle.

The energy requirements of altricial nestlings constitute an integral component of the reproductive performance of parent birds (Ricklefs 1974; Williams & Prints 1986; Weathers 1992). An estimate of the additional quantity of food that parents must procure above their own needs can be obtained by constructing energy budgets for their young along with reasonable assumptions about their efficiency of assimilation (AE). Gross energy intake (GEI) of nestlings can be calculated as:

$$\text{GEI (kJ day}^{-1}\text{)} = [\text{FMR (kJ day}^{-1}\text{)} + \text{Production (kJ day}^{-1}\text{)}] / \text{AE}$$

where FMR includes heat production as a result of maintenance metabolism, the energy cost of biosynthesis, the heat increment of feeding, the energy cost of thermoregulation, and the energy cost of activity (Williams & Prints 1986; Weathers 1996). I do not have information on the energy accumulated in tissues of Dune Lark nestlings, but estimates of production can be obtained from the equation

$$\text{kJ g}^{-1} \text{ wet mass} = 3.51 + 4.82u,$$

where u is the proportion of adult mass achieved (Weathers 1996). Because production represents less than 20% of the total energy metabolized during the course of the nestling period, use of this equation will cause only small errors in the calculation of GEI, usually less than 5% (Weathers 1996). The energy accumulated in tissues was calculated on a daily basis from data on nestling growth (J. B. Williams, unpublished data), and these estimates of production were combined with FMR to obtain the daily metabolizable energy intake per nestling (Fig. 6). Dividing by 0.65, the average AE for House Sparrow nestlings (*Passer domesticus*) (Blem 1975; Kendeigh *et al.* 1977), yields GEI. My calculations show that neonates received about 10 kJ day^{-1} whereas towards the end of the nestling period, chicks were fed about 75 kJ day^{-1} , the maximum gross energy intake. For adult males, GEI is around 130 kJ day^{-1} , assuming an AE of 0.75 (Williams & Hansell 1981), and for females, it is $116.7 \text{ kJ day}^{-1}$.

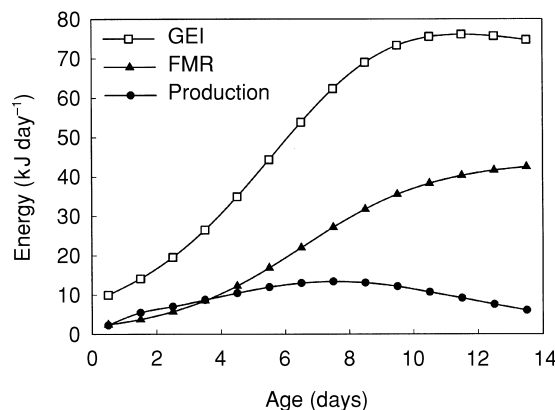


Fig. 6. The relationship between gross energy intake, field metabolic rate, production and age in nestling Dune Larks.

Hence if each parent supplies half of the brood's requirements, assuming a clutch size of two, then males must increase the amount of food that they find by 57.7%, females by 64.3%, late in the nestling period.

The maximum energy demand placed on parents by altricial young, a parameter that may have implications for brood productivity (Bryant & Hails 1983) and that ultimately is related to fitness, may occur toward the end of the nestling period (but see Weathers & Sullivan 1989). If a relationship between peak energy demand and brood productivity does exist, then interspecific variation in peak daily metabolizable energy intake of nestlings should provide clues about the capacity of parents to find food in a given environment, and how natural selection has modulated growth rates and clutch size to maximize fitness. In environments with low primary production, such as deserts, where parents may have difficulty finding food, it is predicted that clutch size and/or growth rates of altricial young are altered in such a way as to reduce peak energy requirements. To test this hypothesis for Dune Larks, an allometric curve was used that predicts peak daily metabolizable energy intake of nestlings using mass at fledging and the time interval to fledging as the independent variables (Weathers 1992; Weathers 1996). This equation explained 97% of the variation in peak energy demand among the 30 species included in Weathers' data set. For Dune Larks, assuming an asymptotic mass of 22.17 g for nestlings, and a nestling period of 14 days, Weathers' equation predicts a peak energy demand of 63 kJ day^{-1} . In actuality, peak daily metabolizable energy intake for Dune Lark nestlings was 50 kJ day^{-1} during the last few days of the nestling period, 21% less than predictions. These data are consistent with my prediction that natural selection has adjusted nestling growth rates of desert birds such that peak energy demands placed on parents are lower than for species from other more productive environments. Despite rather high rates of energy expenditure and presumably of respiratory water loss due to frequent lung ventilation to meet oxygen demands, total evaporative water loss (TEWL) of Dune Larks, the sum of respiratory

and cutaneous water losses, averaged only 1.58 ml H₂O day⁻¹ when measured at $T_{a,s}$ less than 30 °C, a rate of evaporation 44% less than would be expected based on body size (Williams 1996a, 1999). It is suggested that this species has evolved mechanisms that lower water efflux, probably involving an increase in resistance to water vapour across the skin, and predicted that water flux in the field would also be reduced. The present study has demonstrated that Dune Larks have a remarkably low water influx rate throughout the annual cycle, an average of 5.86 ml H₂O day⁻¹ for males, 5.41 ml H₂O day⁻¹ for females. Dune Larks had a water influx about 72.0% less than expectation for mesic birds based on body size (Tieleman & Williams 2000). Allometric predictions based on an equation for 17 species of birds from deserts equal 8.56 ml H₂O day⁻¹ for male larks, and 7.87 ml H₂O day⁻¹ for females (Tieleman & Williams 2000). Measured values for Dune Larks are about 31% less than predictions for desert birds.

Because of the scarcity of drinking water in deserts, together with relatively high $T_{a,s}$, desert animals are more likely to be exposed to physiological problems of water shortage than animals living in mesic habitats. Dehydration leads to physiological problems associated with ionic imbalance, and to problems of delivery of oxygen and nutrients to tissues because of altered blood flow. Because Dune Larks rarely drink, they rely on preformed water in their food, and on water produced in the process of oxidative phosphorylation to fulfil their needs. Seeds contain only small amounts of preformed water, 3–10% by mass (Kendeigh 1959; Goldstein & Nagy 1985), whereas insects are composed of 65–75% water (Redford & Dorea 1984). Given their purported dietary shift from mostly insects during the breeding season to largely seeds in winter, and given their reliance on panting to maintain T_b during the breeding season, but not during winter, it is predicted that water influx of Dune Larks would be higher in the

breeding season compared to other times of the year. However, the water influx of Dune Larks was statistically indistinguishable between the two seasons. Thus the data do not support the idea that Dune Larks shift their dietary items between seasons.

Based on the fact that, for Dune Larks in the laboratory, ratios of oxidative water production to evaporative water loss were greater than 1.0 at moderate $T_{a,s}$, it is argued that metabolic water production (MWP) plays a significant role in the water economy of Dune Larks (Williams 1999). Depending on the type of substrate catabolized, MWP varies, from 26.3 mg H₂O kJ⁻¹ for the oxidation of fats and of proteins to 31.1 mg H₂O kJ⁻¹ for carbohydrates (Schmidt-Nielsen 1984). Assuming seeds contain 13.5% protein, 5.1% lipid, and 81.4% carbohydrate, the composition of millet (MacMillen 1990), then 30.1 mg H₂O would be produced per kJ energy expended. A similar calculation for insects, assuming they contain 62% protein, 14.9% lipid and 15.0% carbohydrate (Williams & Prints 1986), showed that 27.2 mg H₂O is produced per kJ expended. If Dune Larks have an FMR of 92.4 kJ day⁻¹ ($n = 51$), and if they eat a diet of insects and seeds in equal proportions, then they generate 2.65 g metabolic H₂O day⁻¹, 47% of their total water influx (= 5.58 g H₂O day⁻¹).

Total water influx for Dune Larks can be evaluated from estimates of MWP and from calculations of preformed water in their foods. The amount of preformed water in the diet of Dune Larks is given by:

$$\text{g preformed H}_2\text{O} = \frac{\text{GEI} \times P_w}{E_d \times (1 - P_w)},$$

where GEI is calculated as FMR/AE (assimilation efficiency), P_w is the proportion of total mass that is water, and E_d is the energy density of the food type (kJ g⁻¹ dry mass).

One can use the above equation to estimate the total preformed water that Dune Larks obtain in their diet. If they consume only insects with an $E_d = 23.0$ kJ g⁻¹ dry mass (Kale 1965; Cummins & Wuycheck 1971), and if $P_w = 0.65$ (Williams & Hansell 1981; Goldstein & Nagy 1985), and assuming an AE of 0.75 (Williams & Hansell 1981), then they must eat 16.74 g of live insects to meet their energy needs, 92.4 kJ day⁻¹. This quantity of insects would provide 9.95 g of preformed H₂O, in excess of what larks actually obtain (5.58 g H₂O day⁻¹). Similar calculations for a seed diet, assuming that $E_d = 17.7$ kJ g⁻¹ dry mass (Kendeigh *et al.* 1977), $P_w = 0.10$ (Kendeigh 1959) and an AE of 0.69 (Williams & Hansell 1981), showed that they would obtain 0.84 g H₂O day⁻¹ by eating seeds to supply their energy needs, substantially less than 5.58 g H₂O day⁻¹. When the percentage of energy supplied by seeds in the diet was varied and the amount of water supplied from seeds, from insects, and from metabolic water, was solved for the results suggested that Dune Larks would obtain about 5.58 g H₂O day⁻¹ in their diets when they were eating a mixed diet of somewhere around 20–30% insects (Fig. 7).

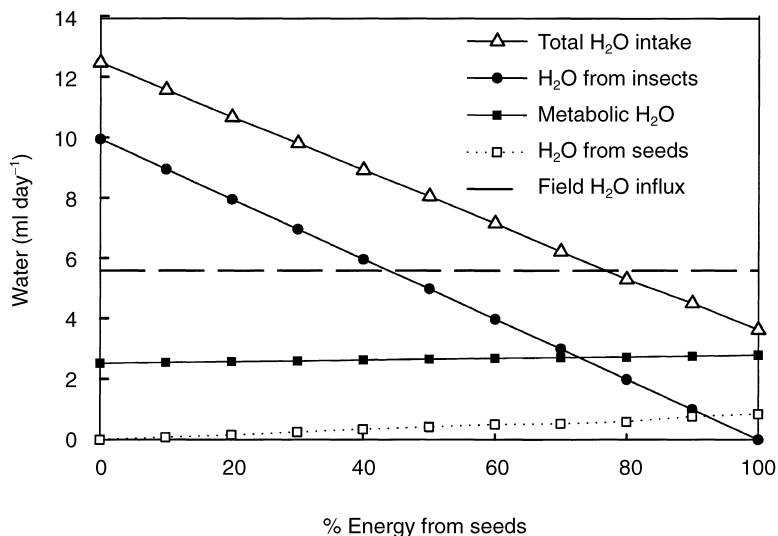


Fig. 7. A model of water intake of Dune Larks with varying proportions of insects and seeds in their diet.

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