

Variation in allocation of time, water and energy in Hoopoe Larks from the Arabian Desert

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Summary

1. Patterns of resource allocation in different times of the year can provide insights into the effects of simultaneous environmental constraints on reproduction and survival of desert birds. Field metabolic rate (FMR), water influx rate (WIR) and patterns of time allocation of Hoopoe Larks (*Alaemon alaudipes* Desfontaines) were investigated during spring, when larks were rearing offspring, and during summer, presumably the harshest time for desert birds, in the Arabian Desert.

2. FMR was 45% below allometric predictions in spring (1.83 times basal metabolic rate, BMR) and 58% below predictions in summer (1.37 times BMR). WIR was 37% lower than predicted during the nestling period and 55% lower than predicted during summer.

3. Activity patterns during spring and summer were bimodal, with birds foraging in the early morning and late afternoon and resting in the shade or attending the nest during midday. Foraging time was similar in spring (32.0% of total daytime) and summer (33.6% of total daytime), despite higher energy and water intakes for parents and offspring in spring, suggesting that food availability was higher in spring. The non-foraging time was entirely spent resting in summer, while in spring half of this time was allocated to caring for offspring and the other half to resting in the shade. Hoopoe Larks fed their offspring 55 times per day and shaded their chicks about 5 h per day to protect them from solar radiation.

4. High T_a s combined with low and unpredictable food availability in deserts may constrain reproduction by limiting the amount of time, water and energy that parents can devote to rearing offspring.

Key-words: Desert, Hoopoe Lark, metabolic rate, resource allocation, water influx rate

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Introduction

Studies of resource allocation, mostly carried out in temperate environments, have traditionally focused on time and energy as critical factors in reproduction and survival of organisms (King 1974; Tinbergen & Dietz 1994). In deserts, characterized by high ambient temperatures (T_a), limited food availability and low rainfall, a third crucial resource for reproduction and survival is water (Williams & Tieleman 2001). For birds in deserts, water and energy come in single packages of food because drinking water is usually absent. High T_a s during the middle part of the day constrain the time that desert birds can spend on activities such

as foraging, thereby limiting water and energy intake. Food intake and activity time are mutually dependent, because water provides the means for evaporative cooling, the only source of cooling when T_a exceeds body temperature. Thus, an increased water intake provides a larger capacity to avoid overheating and thereby can increase time spent active (Tieleman & Williams 2002). Patterns of resource allocation in different times of the year can provide insights into the effects of simultaneous environmental constraints, such as food availability and thermal environment, on reproduction and survival of desert birds.

During the reproductive season, birds devote time, energy and water to the production of offspring. The energy and water requirements for rearing young may constrain current reproduction through limited availability of resources and future reproduction through deleterious effects of energy expenditure on parental condition and survival (Hails & Bryant 1979; Drent & Daan 1980; Daan *et al.* 1990a, 1996). In some species,

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parent birds elevate their energy and water requirements to provide care for their young (Wijnandts 1984; Bryant & Tatner 1988; Masman *et al.* 1988; Gales & Green 1990), whereas in others they do not increase their energy expenditure and water loss during the breeding season and apparently 'reallocate' resources from other activities to reproduction (Weathers & Sullivan 1993; Williams 2001). In general, parental investment in reproduction may be low in environments where resources are scarce and unpredictable, and species have evolved a slow pace of living in response to these circumstances (Stearns 1976; Tieleman, Williams & Visser 2004).

In north temperate areas, winter is thought to be the critical period for survival because foraging time is limited by short days, food availability is reduced, and energy needs for thermoregulation are elevated because of low T_a s. In deserts, in contrast, summer may present the largest challenge for survival. During summer, birds in deserts are confronted with increased water demands for evaporative cooling, while foraging time is constrained by high T_a s (Goldstein 1984; Nagy 1988; Tieleman & Williams 2002). Yet, our knowledge of optimal allocation patterns of water, energy and time during summer in deserts is limited to several species of galliforms and sandgrouse, which all had access to drinking water (Alkon *et al.* 1982; Alkon *et al.* 1985; Goldstein & Nagy 1985; Carmi-Winkler *et al.* 1987; Kam *et al.* 1987; Nagy 1988; Hinsley 1994), and only two passerine birds (Anava *et al.* 2000, 2002; Williams 2001).

We investigated field metabolic rate (FMR), water influx rate (WIR) and patterns of time allocation of Hoopoe Larks (*Alaemon alaudipes* Desfontaines) during the breeding season in spring and during the postbreeding season in summer in the Arabian Desert. We quantified parental effort during chick rearing of females and males by measuring time spent brooding and feeding frequencies. We hypothesized that high T_a s limited activity time, which in turn constrained parental energy and water intake, resulting in relatively small investments in reproduction. Because spring and summer are both hot in the Arabian Desert, we expected that WIR and FMR during the nestling period exceeded water and energy requirements for survival in summer, when activity levels may be lower. To understand how seasonal variation in the desert environment influences the allocation of time, water and energy of Hoopoe Larks, we measured the thermal environment.

Methods

STUDY AREA AND SPECIES

This study took place in Mahazat as-Sayd during the breeding season in the springs of 1998 (June) and 2001 (April–June), and the summer of 1998 (July). Mahazat as-Sayd is a 2244-km² reserve in central-west Saudi Arabia (22° N, 41° E), an area that receives a mean \pm SD of 96 \pm 70 mm of rain per year (National Wildlife

Research Center, unpublished data). The flat gravel plains in this part of the Arabian Desert are intersected by wadis and dominated by sparse vegetation of perennial grasses, including *Stipagrostis* sp., *Panicum turgidum* and *Lasiurus scindicus*, and small acacia trees, *Acacia* sp. (Mandeville 1990).

Residents of Mahazat, Hoopoe Larks (35–45 g) are ground-foraging birds with a diet that consists mainly of adult and larval arthropods, although seeds and small lizards are eaten. Drinking water is not available in Mahazat, except for short periods after rains, but Hoopoe Larks have not been observed to drink even when water is available. Hoopoe Larks breed in Mahazat from February to June. After a winter with 127 mm of rain, a locust plague in spring of 1998 resulted in large numbers of successful breeding pairs and a breeding season that stretched until the end of June. During the following 2 years Mahazat received very little rain and the larks did not breed (Tieleman & Williams 2002). In 2001, after winter and spring rains equalling 148 mm, all individuals in our study population nested, although high rates of nest predation resulted in low fledging success.

MACRO- AND MICROCLIMATE

During our fieldwork in 1998 and 2001, we obtained daily temperature and wind records from a weather station that we established in our study area. We measured air temperature (T_a) 10 cm above the soil surface, using a thermocouple surrounded by a cone of aluminium foil to shield it from direct and reflected solar radiation. Soil surface temperature (T_s) was estimated with a thermocouple soldered to a 25-cm² piece of wire mesh, covered with a thin layer of sand (1 mm) to reflect the radiative properties of the soil. In 2001, we measured operative temperature (T_e) using two or three differently oriented, plumage-covered copper mounts (Bakken *et al.* 1981), placed on the ground and protected from shrikes (*Lanius* sp.) by a wire cage with 8-cm² mesh. Operative temperature is an integrated index of environmental temperature that reflects the external conductive, convective and radiative properties of an animal without heat production or evaporative water loss (Bakken 1976). To measure wind speed, two Thorntwaite cup anemometers (Thorntwaite Assoc., Pitts Grove, NJ, USA), previously calibrated in a wind tunnel, were placed at 12.5 cm and 1 m above the ground surface. The output of thermocouples and anemometers was recorded every minute and averaged over 15-min periods by a Campbell Scientific data logger, model 21X (Campbell Scientific, Logan, UT, USA).

DOUBLY LABELLED WATER

Measurements of WIR and FMR were obtained using the doubly labelled water (DLW) technique, in which the rate of decline of ²H in the body water pool provides a measure of WIR (Nagy & Costa 1980), and the loss

rates of both ^2H and ^{18}O yield an estimate of CO_2 production (Lifson & McClintock 1966; Nagy 1980; Speakman 1997). We mist-netted birds, injected them with a 1 : 2 mixture of 99.9 atom percentage ^2H and 95.5 atom percentage ^{18}O using a 250- μl Hamilton syringe (Hamilton Co., Reno, NV, USA). The injection volume equalled 4.3 μl per gram mass. We weighed birds with a Pesola spring balance that had been calibrated against a Mettler analytical balance (Mettler-Toledo, Inc., Columbus, OH, USA). After a 1-h equilibration period (Williams & Nagy 1984), a 80–100 μl sample of blood (initial) was removed from the brachial vein, and birds were banded and released. After about 24 h (average 24.6 ± 0.26 h, $n = 3$, range 23.8–26.0 h) or 48 h (average 46.8 ± 0.43 h, $n = 18$, range 39.8–50.3 h), we recaptured birds, took a second blood sample (final), measured body mass and released them. Birds were caught during spring when feeding nestlings at the nest ($n = 1$ in 1998, $n = 12$ in 2001), and during summer ($n = 8$ during 1998) when shading in a limited number of shade spots. In each year we obtained blood samples of three uninjected individuals to determine background levels of isotopes.

Isotope ratios of $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ were determined in duplicate (initial) or triplicate (final) for each sample at the Center for Isotope Research, University of Groningen (Visser & Schekkerman 1999). The coefficient of variation of the duplicate or triplicate measurements was less than 2%. We calculated WIR with equation 3 of Nagy & Costa (1980), and corrected for isotope fractionation effects assuming an evaporative water loss of 25% and a fractionation factor of 0.941 (equation 7.6 in Speakman 1997; see also Visser *et al.* 2000). Total body water was estimated from isotope dilution using the equation $(N_o + N_D/1.037)/2$ (Speakman 1997). Average total body water equalled $63.2 \pm 1.57\%$ ($n = 6$) and this average was used for all birds. Rates of CO_2 production were calculated with equation 7.17 of Speakman (1997). CO_2 production can be converted to energy expenditure when the composition of the diet is known (Gessaman & Nagy 1988; Weathers & Sullivan 1989). We assumed that seeds contain 13.5% protein, 5.1% lipid and 81.4% carbohydrate (MacMillen 1990) and that insects contain 62.0% protein, 14.9% lipid and 15.0% carbohydrate (Williams & Prints 1986). We assumed that Hoopoe Larks consume a diet of 90% insects and 10% seeds, and calculated a conversion factor of $24.16 \text{ kJ l}^{-1} \text{ CO}_2$ based on conversion factors for protein, fat and carbohydrate metabolism (Gessaman & Nagy 1988). Hoopoe Larks carry insects and occasionally a small lizard in their bill to the nest and do not regurgitate food for their young. Water in food brought to nestlings therefore does not equilibrate with body water of adults.

BEHAVIOURAL OBSERVATIONS

Time budget observations can be biased when the visibility of the animal depends on its activities or on

time of day (Altmann 1974; Rugg & Buech 1990). Because Hoopoe Larks in Mahazat as-Sayd are ground-foraging birds that are reluctant to fly, in an area with low vegetation cover, we were able to follow individuals almost continuously for set time periods. We quantified time-activity budgets of birds by recording behaviour and position of the bird in the sun or shade every 15 s at the signal of an electronic metronome. For analyses, we placed behaviours in the categories of foraging, resting, feeding young, attending nest and other. Foraging included walking over gravel plains or along vegetation strips with intermittent stops to inspect bushes for insects, pecking at insects, digging for prey and short aerial chases of grasshoppers. Resting, or thermoregulatory behaviour, was a combination of standing, sitting or lying down in the shade, and perching on top of a bush or a rock exposed to wind. Care of the chicks was divided into the categories of feeding the chicks and attending the nest to brood or shade the young. All other activities, including territorial interactions, pair bond interactions, preening and vocalizations, were included in the 'other' category. Our intention was to distinguish thermoregulatory behaviours (resting) from non-thermoregulatory behaviours (foraging, care for chicks, other).

We made behavioural observations on ten individual larks during spring and summer and at nine different nests during spring. During the end of June 1998 we quantified time budgets of a pair of Hoopoe Larks feeding 5–6-day-old chicks at an unusually late nest on 2 consecutive days (observation periods 365 ± 123 min $\text{day}^{-1} \text{ bird}^{-1}$, $n = 4$). During July 1998 we made continuous observations on eight individuals during time periods of 86 ± 61 min (range 36–231 min) between 6.00 h and 18.30 h. From these observations we calculated the proportion of time spent on each behavioral category per hour. In the breeding season of 2001 we did not follow individual Hoopoe Larks but observed nine different nests from 6.00 h until 18.30 h between 26 April and 4 June and noted the times at which each parent fed or brooded the chicks.

STATISTICAL ANALYSIS

We used General Linear Model procedures in SPSS version 11.0 (SPSS 2001) for analysis of covariance. We always tested the significance of the interaction term before removing it from the model, but do not report non-significant results. Means are presented ± 1 SD.

Results

MACRO- AND MICROCLIMATE

Characterized by long, hot and dry summers, the Arabian Desert is classified as an arid inland desert, similar to large parts of the Sahara (Meigs 1953). During our field seasons, average daily T_a s varied from 23 °C in the beginning of April to around 38 °C in July, while maximum T_a s increased from 31 °C to 53 °C (Fig. 1a).

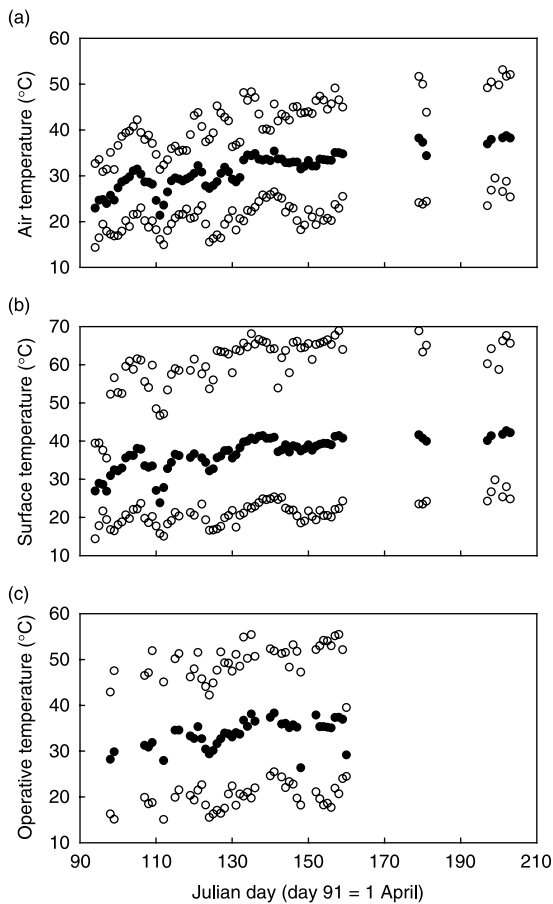


Fig. 1. Seasonal variation in (a) air temperature, (b) soil surface temperature and (c) operative temperature in Mahazat as-Sayd. Filled symbols are 24-h averages, open symbols represent daily minimum and maximum values.

When foraging on the ground, Hoopoe Larks were in contact with the soil surface, which reached daily maximum T_s s ranging from 37 °C on overcast days in the beginning of April up to 69 °C in July (Fig. 1b). Operative temperatures were intermediate between T_a and T_s (Fig. 1c).

Air temperatures showed a daily pattern with monthly average minimum T_a s of 21.7 °C and 24.2 °C early in the morning, and maximum T_a s of 41.5 °C and 49.3 °C during the middle part of the day for May and July, respectively (Fig. 2a). Average surface temperature varied from 21.3 °C to 61.9 °C in May and from 25.7 °C to 63.8 °C in July (Fig. 2b). Average T_e measured with copper models on the ground reached maxima of 49.0 °C during the breeding season (Fig. 2c). Wind speeds varied more between days than temperatures, and although there was generally little wind in the early morning, there was no clear daily trend (see also Tieleman & Williams 2002).

BODY MASS, FIELD METABOLIC RATE AND WATER INFLUX RATE

Body mass of breeding birds during spring 2001 and 1998 (39.8 ± 6.40 g, $n = 13$) was not significantly dif-

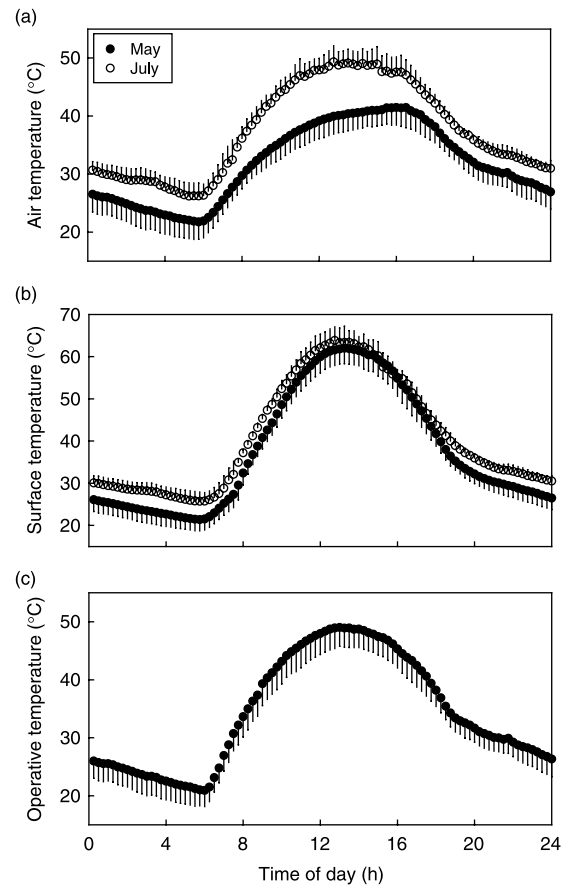


Fig. 2. Daily patterns of average (\pm SD) (a) air temperature, (b) soil surface temperature and (c) operative temperature in Mahazat as-Sayd during spring (May, filled symbols) and summer (July, open symbols).

ferent from body mass of non-breeding birds during summer 1998 (42.3 ± 6.30 g, $n = 8$) ($t = 0.88$, $df = 19$, $P = 0.39$). Average body mass of Hoopoe Larks during spring and summer was 40.7 ± 6.25 g ($n = 21$). Males (46.0 ± 3.61 g, $n = 10$) were significantly heavier than females (35.9 ± 3.74 g, $n = 11$; $t = 6.23$, $df = 19$, $P < 0.0001$).

Field metabolic rates varied between 47.3 and 89.3 kJ day⁻¹ in spring and between 44.1 and 71.1 kJ day⁻¹ in summer (Fig. 3a). Using body mass as a covariate, we found that FMR was higher in spring than in summer (season $F_{1,18} = 26.58$, $P < 0.0001$; mass $F_{1,18} = 34.69$, $P < 0.0001$). FMR of an average 40.7-g Hoopoe Lark was 72.0 kJ day⁻¹ in spring and 54.2 kJ day⁻¹ in summer, or 24.7% lower in summer than in spring.

Water intake rates varied from 8.4 to 18.2 g day⁻¹ for Hoopoe Larks feeding chicks in spring and from 7.7 to 15.1 g day⁻¹ in summer (Fig. 3b). Taking into account variation in body mass, WIR was higher in spring than in summer (season $F_{1,18} = 12.35$, $P = 0.002$; mass $F_{1,18} = 10.18$, $P = 0.005$). WIR of a 40.7-g bird equalled 13.0 g day⁻¹ in spring and 9.3 g day⁻¹ in summer, a 28.2% decrease in summer.

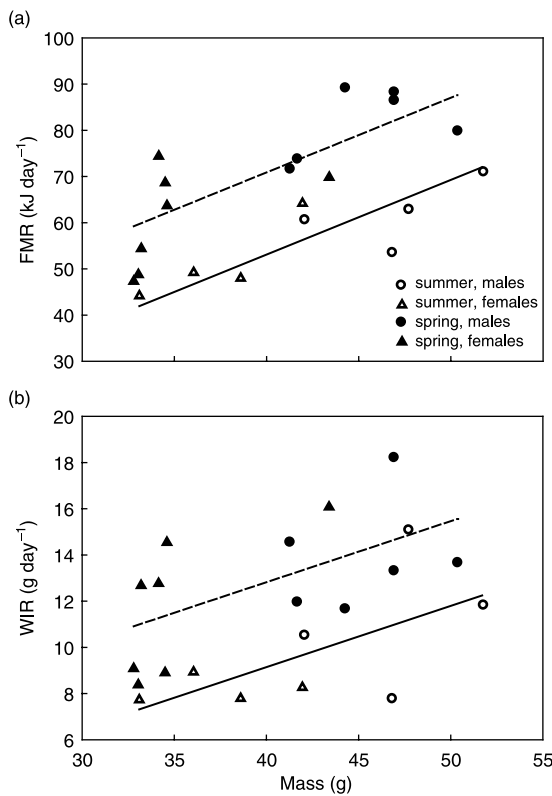


Fig. 3. (a) Field metabolic rate and (b) water influx rate of Hoopoe Larks in Mahazat as-Sayd during breeding in spring (filled symbols, dashed line) and during summer (open symbols, solid line).

TIME BUDGETS OF BREEDING AND NON-BREEDING LARKS

Hoopoe Larks feeding chicks at the nest in late June spent 32.0% of the daylight hours foraging, 29.4% brooding or shading chicks, 1.7% feeding chicks, 36.6% resting in the shade, and 0.3% doing other activities (Fig. 4a). Non-breeding Hoopoe Larks in July spent 33.6% of the daylight hours foraging, 64.8% resting in the shade, and 1.6% performing other activities including interactions with other birds and preening (Fig. 4b). A large proportion of the resting time in the latter group was spent in burrows of the herbivorous lizard *Uromastix aegypticus* (Williams *et al.* 1999).

BEHAVIOURAL OBSERVATIONS AT THE NEST

We made behavioural observations of parents feeding and brooding chicks at nine nests between 26 April and 4 June 2001. Chicks in six of these nests (observed between 26 April and 12 May) grew normally during our observations, although few fledged as a result of high nest predation rates. The chicks in the remaining three nests (observed between 13 May and 4 June) were not cared for sufficiently by the parents, and died from starvation because the parents did not bring enough food or from overheating because the parents did not provide shade during the middle part of the day. These three nests were omitted from the analyses.

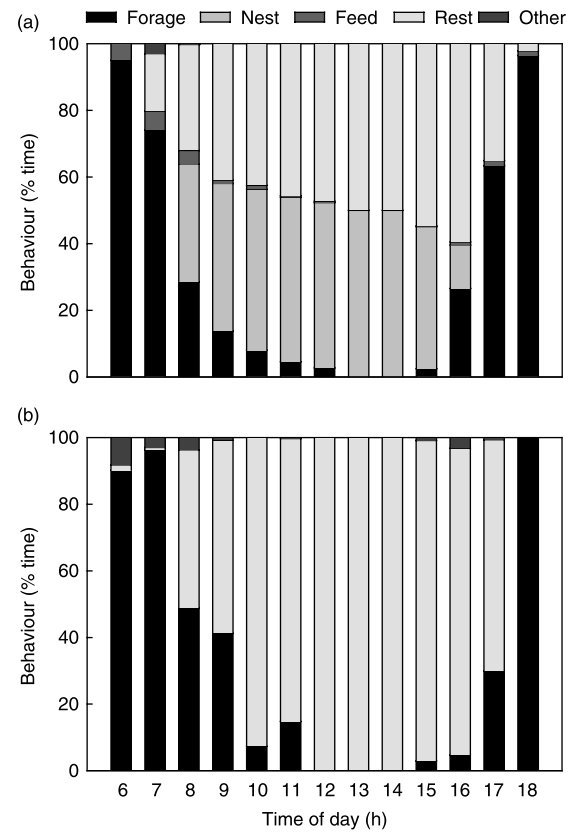


Fig. 4. Percentage of time allocated to various behaviours as a function of time of day for individual (a) breeding and (b) non-breeding Hoopoe larks.

Together, the parents brought food to the nest 55.3 ± 8.36 times ($n = 6$) per day between 6.00 h and 18.30 h (Fig. 5a). The total number of feedings per parent per day did not differ between females (26.5 ± 7.94 , $n = 6$) and males (23.8 ± 3.06 , $n = 6$) ($t = 0.767$, $df = 10$, $P = 0.46$) (Fig. 5a).

Total brooding/shading time of both parents together varied among nests from 118 to 421 min day^{-1} and averaged 293 ± 98.6 min day^{-1} ($n = 6$) (Fig. 5b). Brooding consisted mainly of shading the chicks during the middle part of the day, rather than warming the chicks early in the morning and late in the afternoon. The contribution of the male parent varied between 7.8% and 61.8% of total brooding time, but the average time spent brooding did not differ significantly between females (171 ± 79.2 min, $n = 6$) and males (122 ± 87.4 min, $n = 6$) ($t = 1.01$, $df = 10$, $P = 0.34$) (Fig. 5b).

Discussion

Energy and water requirements of Hoopoe Larks in the Arabian Desert were remarkably low during the breeding season and during the hot summer. When compared with an allometric equation for all birds, FMR of Hoopoe Larks was 45% below predictions for parents feeding nestlings in spring and 58% below predictions for larks in summer (Tieleman & Williams 2000). When expressed as multiples of basal metabolic

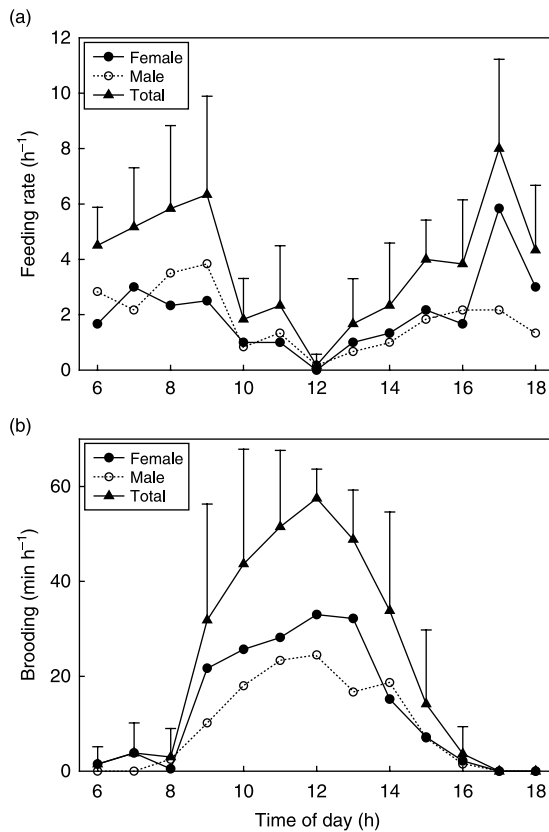


Fig. 5. (a) Feeding frequencies (average \pm SD) and (b) brooding times (average \pm SD) of Hoopoe Larks attending 5–7-day-old-chicks at the nest ($n = 6$ nests; three broods that died of starvation were excluded).

rate (BMR), measured during July in a separate study (Tieleman *et al.* 2002), FMR equalled 1.83 times BMR in spring and 1.37 times BMR in summer. The low FMR/BMR ratio of 1.37 in summer, when larks spent large parts of the day in the shade of vegetation or in the holes of the lizard *Uromastix aegypticus* (Williams *et al.* 1999), suggests that larks minimize or even eliminate energetic costs for thermoregulation by microclimate selection, and only add the costs of activity to their basal metabolism. Compared with an allometric equation for all birds, WIR was 37% below predictions for parents during the nestling period and 55% lower than predictions for birds during summer (Tieleman & Williams 2000). Analogous to the ratio FMR/BMR we calculated the ratio of WIR and total evaporative water loss (TEWL) measured in the laboratory at 25 °C (Tieleman *et al.* 2002); this ratio equalled 4.74 during spring and 3.39 during summer. Assuming that birds were in water and energy balance, the amount of water ingested per kJ energy provides an indication of the diet. The near identical ratios of WIR/FMR in spring (0.181) and summer (0.172) suggest that food items were similar in both periods.

Activity patterns in spring and summer were bimodal, with birds foraging in the early morning and late afternoon, and resting during the middle part of the day (Fig. 4). Time spent foraging was similar in spring

(32.0% of total daytime) and in summer (33.6% of total daytime), suggesting that food availability during the breeding season was higher because FMR and WIR were higher. An index of food availability, foraging efficiency, can be calculated as metabolizable energy intake divided by foraging time. During the breeding season parent birds not only have higher energy and water requirements to sustain their own elevated FMR and WIR, but also have to provide food for their offspring. Metabolizable energy intake during spring therefore is the sum of parental FMR and the energy requirements of the brood. Energy requirements of Hoopoe Lark offspring at age day 5–7, comprising FMR of the brood (2.7 chicks on average) and energy accumulated in new tissue, have been estimated previously at 120.5 kJ day⁻¹ (Tieleman *et al.* 2004). Assuming that each parent provides an equal share, foraging efficiency during the breeding season can be calculated as $(72.0 + 0.5 \times 120.5)$ kJ/240 min or 0.55 kJ min⁻¹. During summer, foraging efficiency is 54.2 kJ/252 min, or 0.22 kJ min⁻¹, indicating lower food availability during this time.

The higher FMR and WIR during breeding than during summer are largely attributable to feeding chicks and shading them during midday, because foraging times during spring and summer are equal. Whereas larks during summer spent all the non-foraging time resting in the shade, parent birds devoted about half of the non-foraging time to resting in the shade and the other half to caring for their chicks at the nest. Hoopoe Larks build open cup nests with usually limited cover from vegetation. Eggs and chicks therefore depend on the parents for protection from solar radiation. While shading chicks at the nest during the midday, parents experience T_c s exceeding 50 °C, temperatures at which evaporative water loss and metabolism are elevated (Tieleman *et al.* 2002).

Variation in allocation of resources at different times of the year has been studied in only a few desert birds, but these kinds of studies may improve our understanding of the role of environmental factors in reproduction and survival of species in hot, dry environments. FMR during the breeding season has been compared with FMR at other times of the annual cycle in only two other desert birds with altricial young. Arabian Babblers (*Turdoides squamiceps*) had a FMR 18% higher in individuals feeding nestlings than in non-breeding individuals during the breeding season, and showed no difference in FMR between summer and winter (Anava *et al.* 2002). FMR of Dune Larks (*Certhilauda erythrochlamys*) in the Namib Desert did not differ among the incubation period, the nestling period and winter (Williams 2001). In general, FMR of both these species during the nestling period was relatively low when compared with allometric predictions (Williams 2001; Anava *et al.* 2002; Tieleman *et al.* 2004). Owing to a diet shift from insects to fruit between summer and winter, WIR of Arabian Babblers was higher in winter than in summer, while

summer values were higher in breeding birds than in non-breeding individuals (Anava *et al.* 2002). Dune Larks had a low and constant WIR throughout the year, far below allometric predictions (Williams 2001). Most desert species increase time spent inactive during summer when high T_a s constrain time for foraging and other activities (Goldstein 1984; Carmi-Winkler *et al.* 1987; Nagy 1988). In general, desert birds allocate less time, energy and water to reproduction than temperate zone birds.

The level of effort parents employ to raise young has been a major topic of debate in evolutionary ecology (Drent & Daan 1980; Weathers & Sullivan 1989; Daan *et al.* 1990b; Stearns 1992). Even though Hoopoe Larks worked only at a level of 1.83 times BMR, parents appeared unable to work harder or unwilling to compromise their own survival (Daan *et al.* 1996), and instead let their offspring die from starvation or overheating towards the end of the season when thermal constraints became more severe and food availability was presumably dwindling. Compared with temperate zone counterparts within the same family, such as Skylarks and Woodlarks, which feed their nestlings 432 and 144 times per day, respectively (Delius 1963; Mackowicz 1970), Hoopoe Larks, with 55 feeds per day, provide food less frequently to their young. These temperate zone species can feed their offspring more often because Skylarks and Woodlarks do not brood chicks older than 5–6 days during the day, in contrast to Hoopoe Larks, which shade their chicks for almost 5 h per day. In addition, temperate zones provide a longer daylight period during which the parents can bring food to their offspring. We suggest that high T_a s combined with low and unpredictable food availability of desert environments constrain reproduction by limiting the amount of time, water and energy that parents can devote to rearing offspring. As a result, desert birds have been selected for a slow pace of living with small clutch sizes, low parental investments in reproduction and high survival of adult birds (Tieleman *et al.* 2004).

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