



# Effects of food supplementation on behavioural decisions of hoopoe-larks in the Arabian Desert: balancing water, energy and thermoregulation

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Patterns of time allocation to different activities can help reveal how natural selection has solved optimality problems that involve simultaneous environmental constraints. To investigate how time budgets of desert birds are affected by ambient temperature, lack of drinking water and low food availability, we provided food and water to hoopoe-larks, *Alaemon alaudipes*, in the Arabian Desert during years in which no larks reared young. We followed birds continuously from sunrise to sunset on unsupplemented and supplemented days, and recorded their behaviour every 15 s. Taking into account the variation in temperature between days, hoopoe-larks decreased foraging time by 13–29% of total daytime, and increased resting and preening time by 7–16 and 8%, respectively, when they had access to supplemental food. When birds had access to extra food, they began and ended their midday resting period when shade temperature was on average 2.2°C lower, and operative temperature was on average 3.1°C lower, than on unsupplemented days, a significant effect of food supplementation. We concluded that birds optimized time spent on foraging and thermoregulating based on a combination of physiological state variables, including body temperature, hydration state and level of energy reserves. Our results do not support a previous hypothesis that activity budgets of desert birds are dictated by thermal constraints alone.

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Many studies on the allocation of time and energy resources have focused on how temperate zone birds maximize breeding success, and more specifically on the effects of timing of laying, clutch size and parental effort on current and future reproduction (e.g. Daan et al. 1990, 1996; Svensson 1995; Nager et al. 1997). In contrast, in deserts, where rainfall and concomitant food supply are scarce and unpredictable, birds encounter years during which the trade-off between current and future reproduction ostensibly leads to the decision not to breed at all. This decision may be based on a combination of resource availability, state of an animal's nutrient reserves and abiotic factors, such as temperature, that may constrain the time that can be allocated to caring for young. In these nonbreeding years, the only contribution to fitness is future reproductive success, which depends to a large extent on survival (Stearns 1992). Given the environ-

mental conditions that have led to the omission of breeding, survival may be a considerable challenge during such years.

Time budgets, patterns of time allocation to different activities, can help reveal how natural selection has solved optimality problems that involve simultaneous environmental constraints. Behavioural allocation patterns are influenced by a plethora of factors, including time of year (Bryant et al. 1985; Carmi-Winkler et al. 1987; Enoksson 1990), temperature (Askenmo et al. 1992), and water and food availability (Davies & Lundberg 1985; Enoksson 1990). Investigating time budgets in deserts may provide insights into the combined roles of temperature, water and food resources in determining these patterns of desert birds.

Environmental manipulations are frequently used to study environmental constraints, and the accompanying trade-offs that animals face when allocating time and energy resources. Food supplementation experiments have provided insights into how reproductive decisions, such as timing of breeding and clutch size, are affected by resource availability (e.g. Lack 1954; Högstedt 1981;

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Arcese & Smith 1988; Svensson & Nilsson 1995; Nager et al. 1997) and insights into the trade-off between current and future reproduction by changing the level of parental effort (Daan et al. 1990; Wiehn & Korpimäki 1997). Few studies have investigated the effect of food availability on time budgets outside the breeding season (Enoksson 1990). However, food supplementation studies could also increase our understanding of optimal resource allocation strategies and of the existence of potential environmental constraints in times when an individual's main concern is to maximize the chance of survival, in either non-breeding seasons or years.

Despite general avian characteristics such as high rates of metabolism and evaporative water loss, which do not seem to favour desert occupancy (Dawson 1984; Williams & Tieleman, 2001), several bird species are able to obtain adequate water and food while avoiding potentially lethal heat stress in desert environments. Studies on time budgets have shown that desert birds have bimodal activity patterns, with a period of rest during the middle part of the day when ambient temperatures ( $T_a$ ) are high (Goldstein 1984; Carmi-Winkler et al. 1987; Hinsley 1994; Williams 2001). Although the birds in these studies spent a significant part of their time in activities other than foraging or resting, they extended their foraging time on cooler days, a finding that led to the suggestion that the thermal environment constrains foraging time. This 'thermal constraint' hypothesis suggests that the risk of overheating increases in the course of the morning as  $T_a$  increases, and that body temperature ( $T_b$ ) potentially plays a role in determining the onset of thermoregulatory behaviours such as resting in shade or perching in the wind. This simplistic view does not consider that the cues used by birds to minimize the risk of overheating while meeting water and energy requirements might be a combination of several physiological state variables, including  $T_b$ , hydration state and level of energy reserves. The optimal pattern of time allocated to various behaviours, and the time at which to switch from one behaviour to another, for example from foraging to resting in shade, may shift when one of these state variables alters (Houston & McNamara 1999). In this study we focus on how environmental variables that influence the physiological state affect behaviour, although we recognize that other characteristics of the environment, particularly predation risk, may also influence behavioural decisions (McNamara & Houston 1986). Years or seasons in which birds do not breed lend themselves well to studying the influence of  $T_a$ , water and energy balance on behaviour, without the need to consider complicating effects of reproductive activities.

To investigate whether and how the time budgets of desert birds are constrained by  $T_a$ , water or food resources, we provided food and water to hoopoe-larks, *Alaemon alaudipes*, in the Arabian Desert during the late spring of 2 years in which no larks reared young. We predicted that if thermal constraints alone dictate the time spent active, supplemental food and water would not change the time allocated to thermoregulation. However, if birds optimize time spent foraging and thermoregulating based on a combination of  $T_b$ , hydration state

and level of energy reserves, an increase in food and water intake on supplemented days would decrease foraging time, increase time spent on thermoregulation, and decrease the  $T_a$  at which birds start thermoregulating. We point out that throughout this paper the term thermoregulation describes behavioural thermoregulation, that is, resting in shade and perching in the wind, as opposed to physiological thermoregulation, which includes panting or shivering. This is the first study to report the effects of manipulating food and water resources on the time budgets of a desert bird, established by following individuals continuously from sunrise to sunset.

## METHODS

### Study Area

Mahazat as-Sayd is a reserve 2244 km<sup>2</sup> 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 a sparse vegetation of perennial grasses, including *Stipagrostis* sp., *Panicum turgidum* and *Lasiurus scindicus* and small acacia trees *Acacia* sp. (Mandeville 1990).

### Macro- and Microclimate

During the field seasons of 1999 and 2000, we obtained daily temperature and wind records from a weather station that we established about 5 km from our study area. We measured  $T_a$  10 cm above the soil surface, using a thermocouple surrounded by a cone of aluminium foil to shield it from solar radiation and reradiation from the soil surface. Soil temperature ( $T_s$ ) was estimated with a thermocouple soldered to a 25-cm<sup>2</sup> piece of wire mesh, which was covered with a thin layer of sand (1 mm) to mimic the radiative properties of the soil. Operative temperature ( $T_e$ ) is an integrated index of environmental temperature that reflects the external conductive, convective and radiative properties of an animal without internal heat production or evaporative water loss (Bakken 1976). We measured  $T_e$  with thermocouples inside two or three differently oriented, plumage-covered copper mounts (Bakken et al. 1981), which were protected from shrikes (*Lanius* sp.) by a wire cage with 8-cm<sup>2</sup> mesh. Two Thornthwaite cup anemometers, previously calibrated in a wind tunnel, and placed at 12.5 cm and 1 m above the surface, measured wind speed. The output of thermocouples and anemometers was recorded every minute and averaged over 15-min periods by a Campbell Scientific data logger, model 21X. On 3 days when microclimate records were unreliable, for example sandstorms damaged the set-up or predators attacked the taxidermic mounts, we substituted records for a day earlier or later to correlate with behavioural observations.

### Natural History of Hoopoe-larks

The natural history of hoopoe-larks (35–45 g) has only partially been described and varies between populations

(Cramp 1988). Here, we describe some aspects that are relevant to the population in Mahazat as-Sayd. Hoopoe-larks are ground-foraging birds with a diet that consists mainly of adult and larval insects and spiders, although seeds and an occasional lizard are eaten. Drinking water is not available except for short periods after rains. Owing to a lack of banding studies, little is known about individual movement patterns. Although hoopoe-larks are known as resident birds (Cramp 1988), some individuals may leave their territories in extremely dry years. Hoopoe-larks ostensibly breed in Mahazat from February to June. After a wet winter with 127 mm of rain, a locust plague in spring and summer 1998 resulted in large numbers of successful breeding pairs. During the following 2 years, Mahazat had very little rain and, despite some nest-building activity of a few pairs that responded to a late local rain, none reared young. In 1999 and 2000, despite not breeding, pairs of larks in Mahazat defended territories with a mean  $\pm$  SD size of  $0.41 \pm 0.18$  km<sup>2</sup> ( $N=9$ ), at least during our presence from March to August. Pairs remain together throughout most of the day, mutually calling while foraging or resting in shade.

### 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 colour-banded individuals from sunrise (0600 hours) to sunset (1830 hours), so avoiding sampling bias. We attempted to obtain continuous observations throughout the day. On four occasions we lost sight of them and returned the following day to collect data for the time period without observations. Each bird was observed one complete day with supplemental food, and one complete day without supplemental food. Total observation time on supplemented days was a mean  $\pm$  SD of  $699 \pm 73$  min, and on unsupplemented days  $697 \pm 41$  min ( $N=9$  birds).

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 forage, rest, preen 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 at the base of vegetation, and short aerial chases of grasshoppers that jumped from the surface. Resting, or thermoregulatory behaviour, was a combination of standing, sitting or lying down in the shade, and perching on top of a bush or rock exposed to wind. The preen category was the sum of preening while standing or sitting and preening while perched on a bush. All other activities, including territorial interactions, pair bond interactions and vocalizations were included in the 'other' category. Our intention was to distinguish thermoregulatory behaviours (resting) from non-thermoregulatory behaviours (foraging, preening, other). However, birds sometimes combined preening and

thermoregulation when they preened while sitting in the shade, or while perching on a bush. Therefore, excluding these activities from our resting category provided a conservative estimate of the time allocated to thermoregulatory behaviour.

### Food Supplementation

We established feeding sites in nine territories with colour-banded birds, where we provided birds daily between 0530 hours and 0600 hours with 200 g of mealworms and 100 g of canary seeds, and with water in a drinking basin. Because the hoopoe-larks did not eat the seeds that we provided, we considered only mealworm intake in our analyses. The resident pair found the food usually within a few hours, and kept visiting the site during the rest of the day, and during the following days. We focused our observations on males, but did not succeed in capturing the male of the last pair. Therefore we made observations on eight males and one female from nine different pairs. Time budgets of males and females are very similar because pairs spend most of their time foraging together, and stay in contact by frequently calling to each other when they are in shade.

We supplied food and water in seven territories on a mean  $\pm$  SD of  $23 \pm 7.5$  days between 15 April and 7 June 1999, and in two territories between 27 April and 7 May 2000. To habituate the birds to the feeding sites, we provided food and water for at least 2 days before we made behavioural observations. After completion of the observations on these supplemented days we stopped providing food for at least 2 days before making observations on the same individuals on unsupplemented days. Observations on unsupplemented days were made a mean  $\pm$  SD of  $7.7 \pm 4.4$  days after observations on supplemented days ( $N=9$ ). Because we observed the same individuals on supplemented and unsupplemented days, we analysed the data in a pairwise manner. We realize that a balanced experimental design would have been more appropriate, and that time is a potentially confounding variable in the analysis of our data, because observations on unsupplemented days were always conducted after observations on supplemented days. However, we do not think that the results are significantly altered by our experimental design. A potential problem could have arisen if the natural food situation varied with season, but our insect sampling data for 1999 do not show a seasonal trend (unpublished data). Birds may be less motivated to forage on unsupplemented days if they have built up substantial reserves during previous supplemented days. This effect of a previous good meal would reduce the chance of finding a difference in foraging time between unsupplemented and supplemented days, and renders the size of the difference that we report in this study a conservative estimate.

### Body Mass

We captured birds with mist nets and weighed 13 members of the seven food-supplemented pairs of

hoopoe larks during the first week of our experiment in 1999. In week 5 of our experiment, we recaptured and reweighed eight individuals. We calculated the mass gain during food supplementation of each individual by dividing the difference between final and initial mass by the number of days that the bird had access to supplemental food. In 2000, we captured both pairs at the beginning of our food supplementation, before we carried out behavioural observations. The average mass  $\pm$  SD of hoopoe-larks in the field was  $42.2 \pm 5.3$  g ( $N=17$ ).

## Statistical Analysis

We used the general linear model procedures for analyses of variance in SPSS 10.0. For repeated measures analysis we specified the repeated factor as random factor in the analysis of variance. Proportions were arcsine-square-root transformed prior to analyses (Zar 1996). Means are reported  $\pm$  1 SD. Statistical tests are two tailed.

## 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). Weather records for Mahazat as-Sayd in January show night-time low  $T_{as}$  of about 5°C and daytime high  $T_{as}$  of 25°C, whereas in June/July minima around 28°C and maxima of 49°C are common (National Wildlife Research Center, unpublished data). During our field seasons, average daily  $T_{as}$  varied from below 30°C at the beginning of April, to around 35°C in the first week of June, while maximum  $T_{as}$  increased from about 40 to 48°C (Fig. 1). Operative temperature in the shade ( $T_{e\text{ shade}}$ ) is equal to  $T_{a'}$  and optimally describes the microclimate that larks experience in the shade (Bakken 1980). In the sun,  $T_e$  averaged around 38°C, and reached maxima between 54 and 61°C, well above the upper critical temperature of 37°C we measured for hoopoe-larks in the laboratory (unpublished data). Because hoopoe-larks foraged on the ground, they were in contact with the soil surface that reached  $T_s$  exceeding  $T_e$  by about 10°C (Fig. 1).

Temperatures showed a daily pattern during our observations, with average minimum  $T_a$ ,  $T_e$  and  $T_s$  of 23.0, 21.4 and 22.6°C, respectively, early in the morning, and average maximum values of 43.6, 52.6 and 62.8°C during the middle part of the day (Fig. 2a). Although  $T_a$  was fairly constant from 1000 to 1700 hours,  $T_e$  and  $T_s$  showed higher and narrower peaks between 1200 and 1500 hours, owing to the effect of solar radiation. 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 (Fig. 2c). On days with a strong breeze, birds perched on bushes during the middle part of the day, whereas on days with little wind, they lay down in the shade with their ventral apteria pressed to the ground (personal observation). Presumably the increased heat load from solar radiation when

perching can be offset by convective heat loss when wind speeds are high. Perching on bushes would not only decrease a bird's heat load caused by reradiation from the surface, but also increase the capacity for convective cooling by doubling the experienced wind speed compared to ground level.

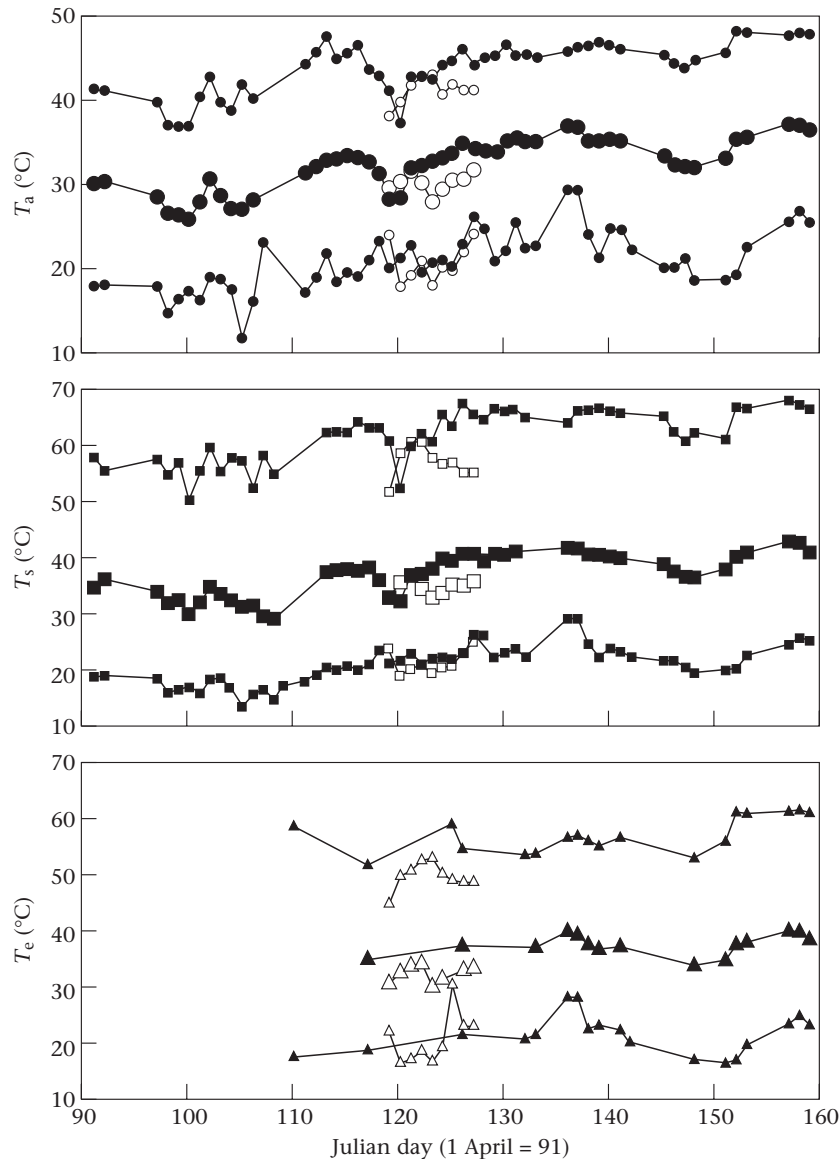
We calculated the average  $T_a$  and  $T_e$  per time block of 1 h experienced by each individual on unsupplemented and supplemented days (Fig. 2b). In a repeated measures ANOVA with  $T_a$  or  $T_e$  as the dependent variable, individual and time block as random factors, and food supplementation as a fixed factor, we tested whether temperatures were significantly different between supplemented and unsupplemented days. The significant interaction between food supplementation and individual (ANOVA:  $F_{8,204}=18.21$ ,  $P<0.001$ ), and the significant food supplementation effect (ANOVA:  $F_{1,8}=6.23$ ,  $P=0.037$ ), indicated that on some unsupplemented days  $T_a$  was higher than on supplemented days. Similarly,  $T_e$  was significantly different between unsupplemented and supplemented days as shown by the significant interaction between individual and food supplementation (ANOVA:  $F_{8,108}=15.32$ ,  $P<0.001$ ). Because one might expect birds to spend less time foraging on hotter days, and when they have access to supplemental food, the slightly lower temperatures on supplemented days lead to a conservative estimate of the effect of the food supplement on the thermoregulatory resting behaviour of hoopoe-larks. The significant effect of individual in our analyses (ANOVA:  $T_a$ :  $F_{8,8}=6.01$ ,  $P=0.01$ ;  $T_e$ :  $F_{8,8.5}=4.75$ ,  $P=0.018$ ) confirmed that temperatures varied between days or changed during the field season (Fig. 1). Although the temperature differences between unsupplemented and supplemented days averaged only 1–2°C (Fig. 2b), we were careful to incorporate temperature as a covariate in our analyses.

### Supplemental Food Intake

On supplemented days, birds frequently visited the feeding site to eat mealworms. We counted the number of mealworms consumed by five birds that allowed close approach. Combining these data with simultaneous time–activity observations at 15-s intervals, we calculated the regression of mealworm intake and number of pecks at the feeding site ( $r^2=0.89$ ,  $N=64$ ,  $P<0.001$ ) to estimate mealworm consumption of the remaining four birds from their time budgets. Mealworm intake averaged  $158 \pm 69$  mealworms ( $N=9$ ), or  $16.3 \pm 7.1$  g wet weight/bird per day. To determine water content, we dried 20 mealworms for 2 days in an oven at 68°C, and found that they contained 65% water. Only one of nine pairs of larks was observed to drink from the water that we provided.

### Time–Activity Budgets on Unsupplemented and Supplemented Days

On unsupplemented days, birds spent 95% of the day foraging or resting. The first 2 h after sunrise and the last hour before sunset were allocated almost exclusively to



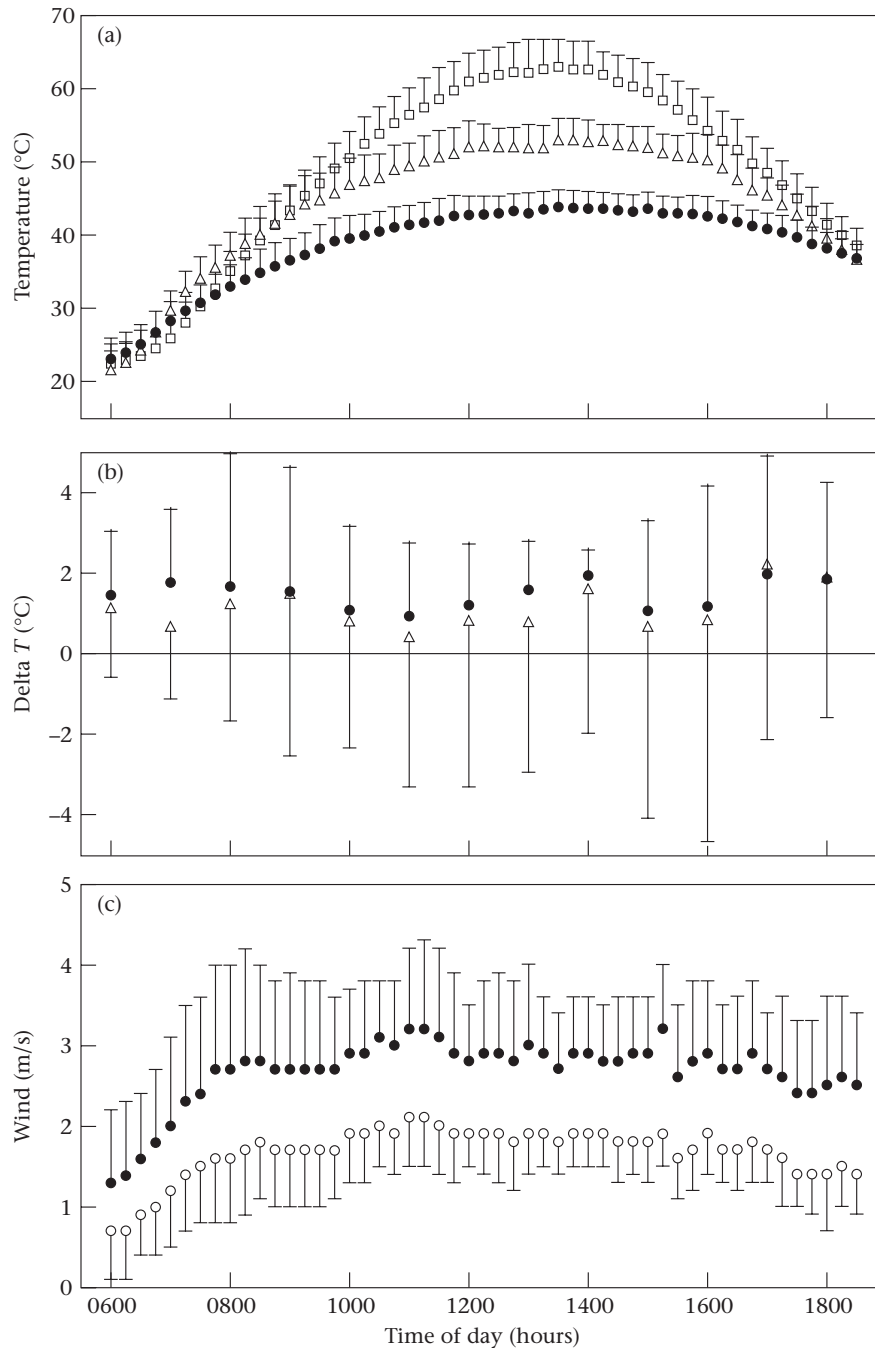
**Figure 1.** Minimum, maximum and daily 24-h averages of air temperature ( $T_a$ ), soil temperature ( $T_s$ ) and operative temperature ( $T_e$ ) in Mahazat as-Sayd in the late spring of 1999 (●, ■, ▲) and 2000 (○, □, △).  $T_e$  is an integrated index of environmental temperature that reflects the external conductive, convective and radiative properties of the animal without internal heat production or evaporative water loss.

foraging, whereas the middle part of the day was devoted to resting (Fig. 3). From 0800 to 1000 hours and 1600 to 1700 hours birds foraged from shade spot to shade spot, interrupted by resting bouts during which they perched or were in shade, sometimes with intermittent short periods of preening (Fig. 3c). Of the total day, unsupplemented birds ( $N=9$ ) allocated  $5.5 \pm 1.4$  h to foraging,  $6.3 \pm 1.5$  h to resting,  $0.4 \pm 0.3$  h to preening and  $0.3 \pm 0.2$  h to other activities.

In contrast, when birds had access to supplemental food, they allocated only 81% of the daytime to resting and foraging. The 20–40% reduction in foraging time early in the morning and late in the afternoon (Fig. 3a) led for most birds to extra preening (Fig. 3c). On supplemented days ( $N=9$ ), birds allocated  $3.8 \pm 0.5$  h to foraging,  $6.9 \pm 0.7$  h to resting,  $1.3 \pm 0.3$  h to preening and

$0.5 \pm 0.5$  h to other activities. Even on days with unlimited access to mealworms and seeds, larks spent a significant amount of time digging for insect larvae at the base of plants and chasing an occasional grasshopper or lizard. If we define thermoregulatory resting behaviour less conservatively and include preening while birds were in the shade or perched in the wind, total resting time increased on unsupplemented days by 17 min to  $6.6 \pm 1.5$  h, and on supplemented days by 26 min to  $7.3 \pm 0.6$  h.

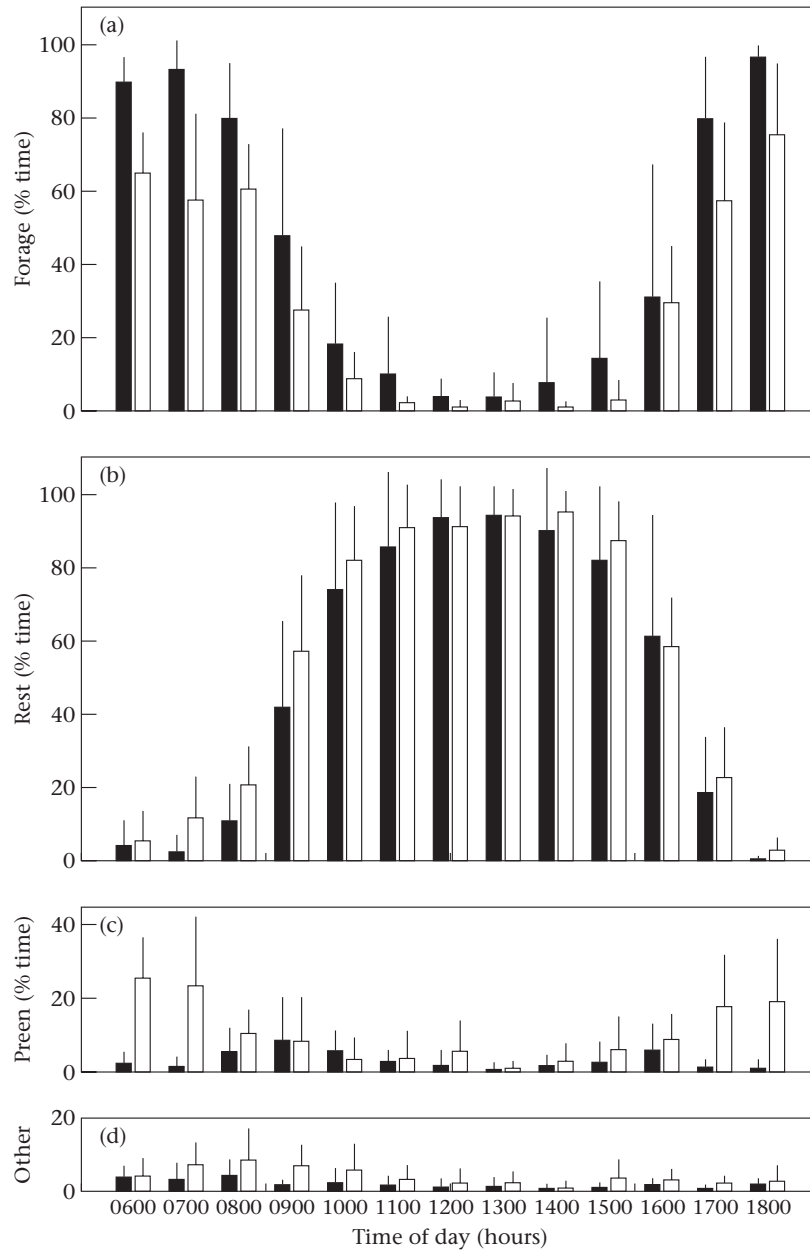
Taking into account the variation in temperature between days, hoopoe-larks decreased foraging time by 13–29% of total daytime (at  $T_a$ s ranging from 40 to 34°C), and increased resting and preening time by 7–16 and 8%, respectively, when they had access to supplemental food (Fig. 4). We used an ANOVA to compare the fraction



**Figure 2.** (a) Daily patterns of  $T_a$  (●)  $T_s$  (□) and  $T_e$  (△) on unsupplemented and food-supplemented days. (b) Average difference in  $T_a$  (●) and  $T_e$  (△) between unsupplemented and food-supplemented days, calculated for each bird, as a function of time of day. (c) Daily patterns of wind speed on observation days at 12.5 cm (○) and 100 cm (●) above ground level. Means are given  $\pm$ SD.

of the day spent foraging on unsupplemented and supplemented days, with the average  $T_a$  during the observation period (0600–1830 hours) as covariate. The interaction between food supplementation and  $T_a$  was not significant (ANOVA:  $F_{1,6}=3.26$ ,  $P=0.12$ ), indicating no difference between slopes, but the effect of food supplementation was highly significant (ANOVA:  $F_{1,7}=6.41$ ,  $P=0.003$ ), showing that birds on supplemented days spent less time foraging. To investigate how birds allocated the remaining time on supplemented days, we

performed a similar analysis on the fraction of resting time, and found that access to supplemental food significantly increased resting time (ANOVA:  $F_{1,7}=10.01$ ,  $P=0.016$ ; interaction  $F_{1,6}=2.81$ ,  $P=0.15$ ). Similarly, food supplementation increased time spent preening (ANOVA:  $F_{1,7}=43.93$ ,  $P<0.001$ ; interaction:  $F_{1,6}=0.37$ ,  $P=0.57$ ). Other activities, including interactions with mates or neighbours, and vocalizing, were not affected by the extra food (ANOVA:  $F_{1,7}=2.13$ ,  $P=0.19$ ; interaction:  $F_{1,6}=1.82$ ,  $P=0.23$ ).

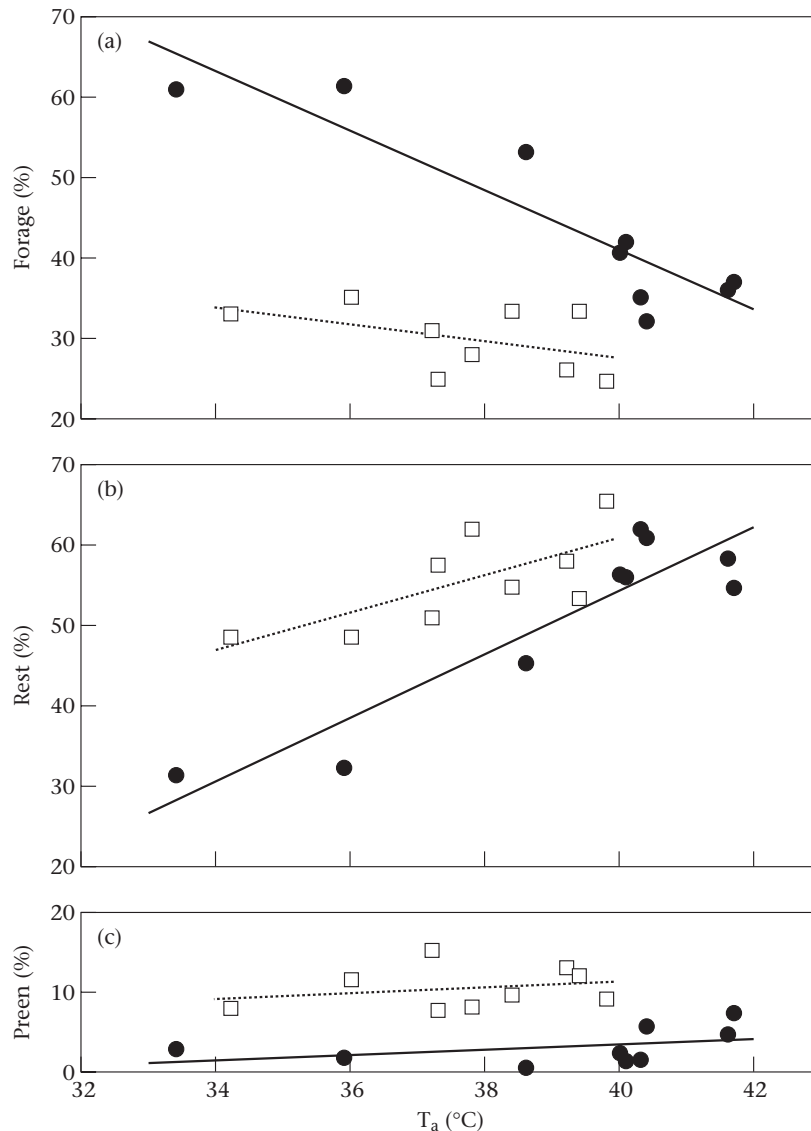


**Figure 3.** Percentage of time allocated to (a) foraging, (b) resting, (c) preening and (d) other activities on unsupplemented (■) and food-supplemented (□) days, as a function of time of day. Means are given  $\pm$ SD.

### Temperatures at Onset and End of Rest Period

The optimal temperature at which an individual stopped foraging and began resting in the morning, and ended resting and resumed foraging in the afternoon, could have depended on food and water intake of the bird earlier in the day. We defined the onset of resting as the first continuous bout of the day that lasted 5 min or longer during which the bird either rested in the shade or perched. The end of resting was defined as the last bout of the day with at least 5 min of inactivity. When birds foraged during the warmer parts of the day, they moved between patches of shade where they experienced  $T_{e \text{ shade}}$  (equal to  $T_a$ ), crossing sunny territory where they experi-

enced  $T_e$ . Birds might base their decision to start or stop resting on  $T_{e \text{ shade}}$  or  $T_e$ , depending on the proportion of time spent in the shade or the sun. On unsupplemented days, birds ( $N=9$ ) started resting at  $T_{e \text{ shade}}=40.0 \pm 2.1^\circ\text{C}$  and  $T_e=47.1 \pm 2.6^\circ\text{C}$ , and stopped resting at  $T_{e \text{ shade}}=41.9 \pm 2.1^\circ\text{C}$  and  $T_e=47.3 \pm 2.7^\circ\text{C}$ . With access to supplemental food, birds began resting when  $T_{e \text{ shade}}=38.1 \pm 2.0^\circ\text{C}$  and  $T_e=44.2 \pm 2.0^\circ\text{C}$ , and ended resting at  $T_{e \text{ shade}}=39.4 \pm 1.6^\circ\text{C}$  and  $T_e=44.0 \pm 3.0^\circ\text{C}$ . To see whether there was a difference in temperature between the onset and end of resting, and between supplemented and unsupplemented birds, we performed an ANOVA with  $T_{e \text{ shade}}$  or  $T_e$  as dependent variable, food supplementation and start/stop of resting as fixed factors,



**Figure 4.** Percentage of total daytime allocated to (a) foraging, (b) resting and (c) preening on unsupplemented (●) and food-supplemented (□) days, as a function of the average  $T_a$  between 0600 and 1830 hours.

and individual as random factor. On both unsupplemented and supplemented days, birds started resting in the morning at significantly lower  $T_{e\text{ shade}}$ s, but not  $T_{e\text{ s}}$ , than when they stopped resting in the afternoon (ANOVA:  $T_{e\text{ shade}}$ :  $F_{1,17}=16.69$ ,  $P=0.001$ ;  $T_{e\text{ s}}$ :  $F_{1,25}=0.00$ ,  $P=1.0$ ). When birds had access to additional food, they began and ended resting when  $T_{e\text{ shade}}$  was on average  $2.2 \pm 2.4^\circ\text{C}$  lower ( $N=18$ ), and  $T_{e\text{ s}}$  was on average  $3.1 \pm 3.5^\circ\text{C}$  lower, a significant effect of food supplementation (ANOVA:  $T_{e\text{ shade}}$ :  $F_{1,8}=9.51$ ,  $P=0.02$ ;  $T_{e\text{ s}}$ :  $F_{1,8}=11.08$ ,  $P=0.01$ ). The difference in  $T_{e\text{ shade}}$  between the start and the end of the resting period was not affected by supplying extra food as indicated by the nonsignificant interaction between food supplementation and start/stop of resting (ANOVA:  $F_{1,8}=0.55$ ,  $P=0.48$ ).

## DISCUSSION

When supplemented with food and water during a nonbreeding year, hoopoe-larks in the Arabian Desert decreased foraging time, increased time allocated to thermoregulation during the middle of the day, and started resting in the morning or resumed foraging in the afternoon at lower temperatures. In addition, food-supplemented birds allocated more time to preening than unsupplemented birds. These results suggest that hoopoe-larks face a trade-off between foraging, thermoregulation and, potentially, feather maintenance. They support the hypothesis that birds optimize time allocated to these behaviours based on a combination of physiological state variables, including hydration state, level of energy reserves and  $T_b$ , rather than the idea that the thermal

**Table 1.** Costs in terms of energy and evaporation of water of the behavioural allocation patterns of hoopoe-larks on unsupplemented and food-supplemented days

	Unsupplemented			Supplemented		
	Time* (h)	Energy (kJ)	Water (g)	Time* (h)	Energy (kJ)	Water (g)
Forage	6.5	42.12	7.28	3.9	25.27	4.37
Rest	5.3	9.33	2.17	6.7	11.79	2.75
Preen	0.3	0.95	0.03	1.3	4.12	0.14
Other	0.4	4.22	0.17	0.6	6.34	0.25
Night	11.5	20.24	1.27	11.5	20.24	1.27
Total		76.86	10.92		67.76	8.78

Energy and water costs for each behaviour are calculated from Table 2.

\*Based on Fig. 4, at  $T_a=37^\circ\text{C}$ .

environment alone dictates activity patterns of desert birds. The natural low availability of water and food resources during some years or seasons forces larks to expose themselves to higher temperatures while foraging, and to invest little time in feather maintenance. This riskier lifestyle of larks when energy and water intake are constrained is analogous to the decision of starlings, *Sturnus vulgaris*, that choose a more dangerous flight path when deprived of food (Cuthill & Guilford 1990), and consistent with theoretical work that predicts changes in patterns of behaviour as physiological state alters (McNamara & Houston 1986; Houston & McNamara 1999).

Although this study was done before the hottest months of the year, hoopoe-larks spent little time on activities other than foraging and resting compared with other desert birds: these together accounted for 95% of daylight time on unsupplemented days.  $T_{es}$  during the middle part of the day in the Arabian Desert were so high that larks were forced to be inactive to avoid overheating. Chukars, *Alectoris chukar*, during the summer in the Negev Desert allocated 76% of their time to foraging and resting, which left 3 h per day for other activities (Carmi-Winkler et al. 1987). Similarly, black-bellied, *Pterocles orientalis*, and spotted sandgrouse, *P. senegallus*, in the same area in April and May spent about 75% of the day foraging or inactive (Hinsley 1994). The sandgrouse had access to drinking water, which left only energy requirements to be met by foraging. In a study on another lark species, Williams (2001) reported differences in time budgets between female and male dune larks, *Mirafra erythroclamys*, in the Namib Desert during the breeding season, before nests were built. Although males spent only about 80% of the day foraging and resting in the shade, females allocated 95% of their time to these activities, presumably building up reserves for egg laying.

Hoopoe-larks increased preening time on supplemented days, especially when  $T_{es}$  were moderate early or late in the day, when there was no need for staying in the shade or perching, and the birds' mealworm intake had possibly reached the limits of their digestive systems. Hoopoe-larks allocated only 2.4% of the day to preening on unsupplemented days, a small amount compared with

the average of 9.2% reported for 62 species of birds (Cotgreave & Clayton 1994). The increase in preening time to 10.4% on supplemented days suggested that this behaviour was subordinate to foraging, despite the significant fitness consequences that lack of preening could entail. Functions of preening include the removal of ectoparasites and feather maintenance (Cotgreave & Clayton 1994). Since we did not find any ectoparasites on the birds that we handled during this study, we propose that the benefit of preening for hoopoe-larks comes mainly from feather maintenance. Feather maintenance could not only improve flight ability to escape from predators, but, perhaps more importantly, also augment thermoregulatory properties of the feather layer, which contributes to the regulation of dry heat transfer and of the water vapour gradient for transcutaneous water loss.

Our emphasis on thermoregulatory benefits from resting, including resting in the shade and perching in the wind, does not exclude reduction of predation risk as a benefit from the increased resting time of larks on supplemented days. However, we think that predation risk may be less important than thermal environment in shaping the behavioural patterns of hoopoe-larks. Although we spent many hours in the field, we have never observed predators attacking hoopoe-larks. The majority of potential predators in Mahazat, including foxes and snakes, are nocturnal and unlikely to influence lark behaviour during the day. Diurnal predators could include birds of prey, such as harriers (*Circus* sp.), which migrate through the area in spring. If predation risk were a primary factor, food-supplemented birds should be indifferent to  $T_a$ , that is, they should be motionless as much as possible regardless of  $T_a$ . This prediction is not supported by our data, which show a significant relationship between time spent resting and  $T_a$  in food-supplemented birds ( $r^2=0.49$ ,  $N=9$ ,  $P_{\text{slope}}=0.04$ ; Fig. 4).

We estimated energy and water expenditure of a 42-g hoopoe-lark on unsupplemented and supplemented days based on the time budgets of a day when  $T_a$  averaged  $37^\circ\text{C}$  (Table 1). We estimated the metabolic rate and total evaporative water loss for each behavioural category from measurements of field metabolic rate and water influx rate of hoopoe-larks made with doubly labelled water

**Table 2.** Calculations of costs in terms of energy and evaporation of water of the various behaviours of hoopoe-larks, based on laboratory data of resting metabolic rate (RMR) and total evaporative water loss (TEWL) during the day and at night, and on a combination of time budgets and measurements of field metabolic rate (FMR) and water influx rate (WIR) in July 1998

	Time (h)	$T_a$ (°C)	Energy* (×RMR)	Energy (kJ)	Water (×TEWL)	Water (g)	Energy <sub>cost</sub> (kJ/h)	Water <sub>cost</sub> (g/h)
Forage	4.20		3.7†	27.2†	1.1‡	4.70‡	6.48	1.12
Rest	8.10	40	1	14.3	1	3.28	1.76	0.41
Preen	0.16	35	1.8	0.52	1	0.02	3.17	0.11
Other	0.04	35	6	0.40	4	0.02	10.56	0.42
Night	11.5	35	1	20.2	1	1.21	1.76	0.11
				FMR=62.6		WIR=11.1		

We assumed that 83.3% of WIR was used for evaporation (Bartholomew 1972) and that  $RMR_{\text{night}}=RMR_{\text{day}}=1.76$  kJ/h,  $TEWL_{35^\circ\text{C}}=0.11$  g/h, and  $TEWL_{40^\circ\text{C}}=0.41$  g/h (unpublished data).

\*Based on Williams & Nagy (1984).

†Calculated as  $FMR - RMR_{\text{night}} - RMR_{\text{rest}} - MR_{\text{preen}} - MR_{\text{other}}$ .

‡Calculated as  $0.83 \times WIR - TEWL_{\text{night}} - TEWL_{\text{rest}} - TEWL_{\text{preen}} - TEWL_{\text{other}}$ .

(Nagy 1980; Speakman 1997) in July 1998, in combination with time budgets during the same period (unpublished data), and our own laboratory data on metabolism and evaporation as a function of  $T_a$  during the day and night (Table 2; unpublished data). A comparison of the time–energy budgets of larks showed that access to supplemental food reduced energy expenditure by 12%, and evaporative water loss by 20% (Table 1).

Our experiment could not determine the separate effects of energy intake or water intake on the behavioural decisions of hoopoe-larks, because larks generally do not drink, excluding the possibility of supplementing water only, and because food manipulations simultaneously affect water and energy availability. However, we emphasize that water is a critical resource in desert ecosystems, especially because water availability limits the capacity for evaporative cooling, an important mechanism to avoid overheating during the hot hours of the day. The preference of hoopoe-larks for mealworms, which contained 65% water, compared with seeds, with a water content of 10% (Bartholomew 1972), indicates that water might be a major consideration in the selection of food items. Additional support for the idea that foraging time may be determined by the amount of water ingested with the food comes from a comparison of the amount of food required on unsupplemented days to meet either energy needs (76.9 kJ) or water needs (10.9 g for evaporation (Table 1) and 2.2 g for excretion, assuming birds excrete one-sixth of their total water efflux, Bartholomew 1972). To meet their daily energy requirements, larks have to eat 13.0 g of insects, assuming a water content of 65%, an energy content of 22.5 kJ/g dry weight (Golley 1961) and an assimilation efficiency of 75.1% (Williams & Hansell 1981). In contrast, to match water needs, larks have to take in 16.9 g of insects, if each kJ of energy expended yields 27.2 mg of metabolic water (Williams 2001), and the water content of the food is 65%.

The average mealworm intake on supplemented days, 16.3 g, yielded 10.6 g water and 5.7 g dry mass, which converted into 128 kJ of metabolizable energy, if energy content of dry mealworms was 30.0 kJ/g and the birds' assimilation efficiency 75.1% (Williams & Hansell 1981).

Metabolizable energy intake exceeded daily energy expenditure on supplemented days (Table 1), suggesting that larks were in a positive energy balance, a result confirmed by the average gain in body mass of  $0.48 \pm 0.44$  g/week ( $t_7=3.05$ ,  $P=0.02$ ) during the period of food supplementation. Water influx rate on supplemented days, the sum of water intake from food (10.6 g) and metabolic water production (1.8 g), exceeded total evaporative water loss (Table 1) by 3.6 g, a potential excretory water loss of 29%, which suggests larks were in positive water balance.

This study suggests that hoopoe-larks maintain a precarious balance between food intake and thermoregulation. On the one hand foraging time is restricted by high temperatures during the middle part of the day; on the other food intake is restricted by foraging time. We suggest that in years that larks do not breed, food availability may be too low to meet the requirements of growing young, in addition to self-maintenance. The window of breeding opportunity might be the result of an interaction between food availability and temperature. Early in the season, thermal constraints are mild, and food intake will be less affected by availability, as long as the latter exceeds a threshold. Reproduction late in the season, when the thermal environment severely restricts foraging time, can be successful only in years of food abundance, like the locust plague of 1998, when food requirements of young and adults can be met with little foraging time. When food availability in desert ecosystems decreases as a result of overgrazing or other human impact, or when climate changes increase daily temperatures, the balance between food and thermoregulatory requirements of desert birds can be compromised, with potential effects for their reproduction and survival.

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