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Published in:
 Condor

DOI:
[10.2307/1370208](https://doi.org/10.2307/1370208)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 1999

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Citation for published version (APA):

Williams, J. B., Tieleman, B. I., & Shobrak, M. (1999). Lizard burrows provide thermal refugia for larks in the Arabian desert. *Condor*, 101(3), 714 - 717. <https://doi.org/10.2307/1370208>

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Author(s): Joseph B. Williams, B. Irene Tieleman and Mohammed Shobrak
Source: *The Condor*, Vol. 101, No. 3 (Aug., 1999), pp. 714-717
Published by: American Ornithological Society
Stable URL: <https://www.jstor.org/stable/1370208>
Accessed: 31-10-2018 11:08 UTC

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LIZARD BURROWS PROVIDE THERMAL REFUGIA FOR LARKS IN THE ARABIAN DESERT¹

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Abstract. A common perception is that desert birds experience greater extremes of heat and aridity than their mammalian counterparts, in part, because birds do not use burrows as a refuge from the desert environment. We report observations of Dunn's Larks (*Eremalauda dunnii*), Bar-tailed Desert Larks (*Ammomanes cincturus*), Black-crowned Finch Larks (*Eremopterix nigriceps*), and Hoopoe Larks (*Alaemon alaudipes*) using burrows of the large herbivorous lizard *Uromastix aegypticus* as thermal refugia during hot summer days in the Arabian Desert. Continuous recordings of shade air temperature (T_a), soil surface temperature (T_{surface}), burrow air temperature ($T_{\text{a-burrow}}$), and burrow substrate temperature ($T_{\text{substrate}}$) showed that T_{surface} exceeded 60°C on most days. T_a typically exceeded 45°C, whereas $T_{\text{a-burrow}}$ was around 41°C during midday. Calculations of total evaporative water loss at different temperatures indicated that Hoopoe Larks can potentially reduce their water loss by as much as 81% by sheltering in *Uromastix* burrows during the hottest periods of the summer day.

Key words: *Alaemon alaudipes*, *Arabian Desert*, *desert birds*, *evaporative water loss*, *Hoopoe Lark*, *thermal refugia*, *water economy*.

Environments of hot deserts can include periods of high ambient air temperature (T_a), sometimes in excess of 50°C, intense solar radiation, desiccating winds, lack of surface water for drinking, and low primary production, conditions which in combination may pose a serious challenge to the survival and reproduction of inhabitants (Meigs 1953, Louw and Seely 1982). Studies on vertebrate animals that live in these habitats have often revealed both physiological and behavioral specializations which function in concert enabling species to maintain a positive water balance. For birds, behavioral strategies, such as selection of favorable

microenvironments, are often identified as the most effective means of water conservation (Dawson and Bartholomew 1968, Williams et al. 1995, Maclean 1996). Many small mammals that live in deserts evade the vicissitudes of their environment because they forage at night, and remain within a subterranean burrow during the day where T_a s are less thermally stressful (Schmidt-Nielsen 1964). Desert birds, which are mostly diurnal, usually seek shade during midday when solar radiation is most intense and T_a s are highest, but the physiological consequences of this microsite selection have been seldom explored (Walsberg 1985, Wolf and Walsberg 1996, Wolf et al. 1996). Knowledge about how birds perform under these conditions provide insights that are fundamental to the understanding of the ecology of species that live in deserts.

It is often stated that arid-zone birds do not use burrows as a shelter, and as a result, experience greater extremes of heat and aridity than many of their mammalian counterparts (Dawson and Bartholomew 1968, Wolf et al. 1996). Although birds do not dig underground tunnels to avert exposure to high T_a s of the desert, we observed Dunn's Larks (*Eremalauda dunnii*), Bar-tailed Desert Larks (*Ammomanes cincturus*), Black-crowned Finch Larks (*Eremopterix nigriceps*), and Hoopoe Larks (*Alaemon alaudipes*) using burrows of the large herbivorous lizard *Uromastix aegypticus* as thermal refugia during hot summer days in the Arabian Desert. We document this unusual behavior, describe the thermal environment of these burrows, and estimate the consequences of their use for the water economy of the Hoopoe Lark.

METHODS

Our study area consisted of the eastern portion of Mahazat as-Sayd, a 2,244 km² fenced reserve located in the west-central region of the Arabian Desert (22°15'N 41°50'E), among the hottest regions of the world (Meigs 1953). The terrain of this area consisted of flat gravel plains, known as regs, occasionally interdigitated by dry sandy wadis. Air temperatures (T_a) in Mahazat, as recorded in a standard weather shelter, often

¹ Received 14 October 1998. Accepted 19 March 1999.

exceed 43°C during the summer, and occasionally reached 50°C (Seddon 1996, Shobrak 1996). Rainfall averages ca. 100 mm year⁻¹.

The Egyptian spiny-tailed lizard, *Uromastyx aegypticus*, common throughout the Arabian Peninsula, feeds primarily on leaves and seeds (Al Sadoon et al. 1994). Weighing from 1.0–1.6 kg as adults, these large lizards excavate a single burrow which typically extends 3–4 m in length at a depth of >1 m. In Mahazat, densities of *Uromastyx* burrows averaged 28.5 ± 8.5 burrows km⁻² along two 15 km transects (Shobrak, unpubl. data).

Observations made in early June 1998 suggested that several species of larks were entering *Uromastyx* burrows during periods of extreme heat, a behavior that we hypothesized reduced water loss. Judging from the depth of bird feces in burrows, of circular depressions in burrows presumably fashioned by the birds, and of three Hoopoe Larks that we observed while they occupied a burrow, we estimated that birds were usually descending 20–30 cm into these tunnels. For the remainder of June and all of July 1998, we spent numerous hours driving off-road across the gravel plains of Mahazat. When the noise of our vehicle flushed a bird from a burrow, we recorded both the time and species, and on 25 occasions the shade air temperature (T_a) taken 10 cm above ground, soil temperature (T_{surface}) 1 mm below the surface, burrow air temperature ($T_{\text{a-burrow}}$), and burrow substrate temperature ($T_{\text{substrate}}$). The latter two temperatures were measured at a depth of 20 cm from the burrow entrance, a distance deemed to be a conservative estimate of the depth larks were descending into burrows. To measure temperatures, we used a 30 gauge copper-constantan thermocouple attached to an Omega 450 ATT thermometer. We compared temperatures given by this system against a mercury-in-glass thermometer that had a calibration traceable to the National Institutes of Standards and Technology. Additionally we measured the height and width of each burrow entrance and its orientation.

As the season progressed, we focused our attention on Hoopoe Larks because a large proportion of the population in Mahazat seemed to be utilizing *Uromastyx* burrows during midday. To determine the exact time that Hoopoe Larks entered burrows, we watched nine burrows from a vehicle beginning at 09:00 until birds entered burrows. We continued our vigil at least 1 hr after the birds arrived. To ascertain the daily pattern of burrow use, we watched burrows known to be used by Hoopoe Larks continuously from 06:00 to 18:00 on two different days. On five occasions when we found a bird using a burrow during midday, we watched until it left.

In three burrows, previously used by Hoopoe Larks, we continuously recorded 15 min averages of T_a , T_{surface} , $T_{\text{a-burrow}}$, and $T_{\text{substrate}}$ over a period of 2–3 days using a Campbell 21X data logger. Here, we measured T_a 10 cm from the ground with a 36-gauge thermocouple inside a cylindrical cone fashioned from aluminum foil, T_{surface} and $T_{\text{substrate}}$ were measured using a 30-gauge thermocouple soldered to a piece of fine-gauged wire mesh (4 × 5 cm) that was covered with 1 mm of sand, and $T_{\text{a-burrow}}$ was measured with a 36-gauge ther-

mocouple 20 cm into the burrow and attached to a stick 5 cm above the burrow floor. Although these methods provided a reliable measure of T_a , they only yielded approximations of surface temperatures.

To estimate the consequences of using a burrow for the water economy of Hoopoe Larks, we used data from laboratory measurements of their total evaporative water loss (Tieleman and Williams, unpubl. data), combined with our measurements of temperatures in the field. We recognize that measurements of T_a only provide a crude index of environmental temperatures experienced by animals (Gates 1980), but below ground where convection and solar radiation are minimal, measurements of T_a may closely approximate operative temperature (T_o) (Bakken 1976, Robinson et al. 1976).

Statistical analyses were performed following Zar (1984). Means are reported ± SD.

RESULTS

We recorded 70 Hoopoe Larks, 32 Dunn's Larks, 8 Bar-tailed Desert Larks, and 1 Black-crowned Finch Lark using *Uromastyx* burrows during June and July 1998 (Fig. 1A). Larks typically utilized burrows between 11:00 and 16:00. During this period T_a averaged 44.1 ± 1.2°C ($n = 25$), $T_{\text{surface}} = 57.9 ± 3.6°C$ ($n = 25$), $T_{\text{a-burrow}} = 41.5 ± 1.7°C$ ($n = 25$), and $T_{\text{substrate}}$ within the burrow averaged 38.6 ± 1.3°C ($n = 17$). Entrances of burrows used by larks averaged 20 ± 5 cm in width and 14 ± 5 cm in height. We found no evidence that larks selected burrows based on the compass orientation of the entrance ($\chi^2_3 = 0.8$, $P > 0.7$, $n = 23$).

From daylong watches using our vehicle as a blind, we noted that Hoopoe Larks began foraging in the shade of vegetation, often *Panicum turgidum*, between 08:00 and 09:00 (see also Shobrak 1998). As the sun reached its zenith, making shade less available, and as T_a increased, Hoopoe Larks sought lizard burrows for refuge. During these observations, birds entered burrows at 10:54 ± 0.8 ($n = 9$) and exited them at 16:36 ± 0.2 ($n = 5$). If birds remained in burrows continuously, they would spend 5 hr 42 min in them. In practice, birds came to the burrow entrance several times each hour, and occasionally foraged near the burrow for a few minutes, and thereafter returned below ground. On two days of continuous observation from 06:00 to 18:00, birds did not leave their burrow for more than 5 min between 11:00 and 16:00. For four days, from July 19–22, data recorded by our logger indicated that at the times that birds entered burrows, T_a , T_{surface} , $T_{\text{a-burrow}}$, and $T_{\text{substrate}}$ averaged 46.4 ± 2.2°C, 57.7 ± 4.8°C, 39.5 ± 1.7°C, and 37.1 ± 0.1°C, respectively, and when they exited them, these same values averaged 48.5 ± 1.6°C, 54.5 ± 1.7°C, 41.8 ± 0.8°C, and 38.1 ± 0.3°C, respectively.

On three occasions we watched a Hoopoe Lark while it was inside of a burrow. After entering the burrow, birds shuffled their feet, as if to remove the surface layer of soil, and then lay prostrate on the floor of the burrow pressing their chest and neck on the substratum. By using this behavior, the birds likely conduct heat away from their body that otherwise would require water for evaporation. Much of the ven-

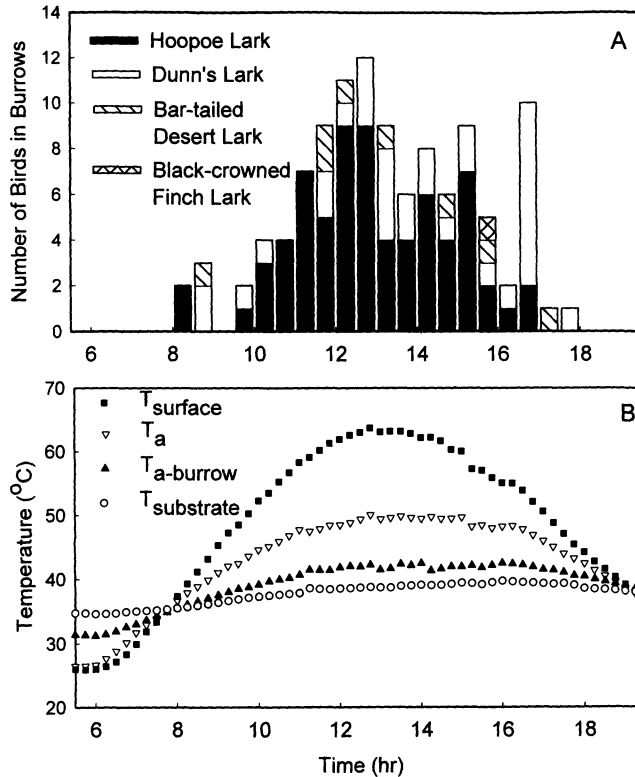


FIGURE 1. (A). The relationship between the number of birds observed in *Uromastix* burrows and time of day. (B). The relationship between ambient temperature T_a , the temperature of the soil surface T_{surface} , the air temperature in the burrow $T_{\text{a-burrow}}$, and the burrow substrate temperature $T_{\text{substrate}}$ vs. the time of day.

tral region of the body of Hoopoe Larks is devoid of feathers which would enhance dry heat loss to the soil.

When we purposefully flushed Hoopoe Larks from lizard burrows during the hottest part of the day, forcing them to find other shade, without exception, birds flew to another burrow and disappeared from our view ($n = 10$). If we evicted them from this second burrow, birds would either return to the first, or find another one. On 17 July, after we forced a bird from its burrow, it flew to one nearby, and was vigorously attacked by the Hoopoe Lark that was the occupant. On several days we observed an adult sharing a burrow with a second bird, presumably one of its offspring. The large proportion of the Hoopoe Lark population employing burrows as refuge, their unwillingness to use alternative sites, and their vigorous defense of burrows, together suggest that this microsite is important to their survival.

T_{surface} often exceeded 60°C during the middle part of the day (Fig. 1B). At these extreme environmental temperatures larks must find microsites of lower temperature or suffer fatal consequences (Tieleman and Williams, unpubl. data). Larks that remain above ground experience T_a s in excess of 45°C , a temperature above their upper critical temperature (Tieleman and Williams, unpubl. data). At these high T_a s, we noted that birds were usually resting in the shade with the

ventral parts of their bodies pressed tightly to the ground, a behavior that would dissipate heat by conductance instead of by evaporative cooling and may result in significant water savings. However, we also noted that birds sometimes panted, an indication that metabolic heat could not be totally dissipated by conduction to the soil.

DISCUSSION

Our data show that occupancy of lizard burrows is a common behavior among larks in the Arabian Desert, and that Hoopoe Larks, the largest of the species (40–50 g), select this microsite more frequently than do smaller species, even though Hoopoe Larks were less common than either Dunn's Larks or Black-crowned Finch Larks (Newton and Newton 1997; Shobrak, unpubl. data). Although two earlier reports have mentioned that desert birds may seek shelter in underground burrows, Spike-heeled Larks *Cherosomanes albofasciata* in the Kalahari (Maclean 1974), and Ant-eating Chats *Myrmecocichla formicivora* in Bushman land, South Africa (Watkeys 1987), neither presented data describing the frequency that these microsites were selected, the environmental circumstances accompanying such behavior, or the physiological consequences of such behavior. Our data represent the first detailed assessment of this behavior among desert-

TABLE 1. Estimates of total evaporative water loss for Hoopoe Larks exposed to different environmental temperatures.

Temperature (°C)	Water loss		% body mass hr ⁻¹ a
	g H ₂ O hr ⁻¹	g H ₂ O 5 hr ⁻¹	
60.7	3.99	19.96	8.9
48.9	1.35	6.74	3.0
41.9	0.47	2.34	1.0
39.0	0.25	1.27	0.6

^a Based on a body mass of 45 g.

dwelling birds, and the first observations of this behavior for birds in the Arabian Desert.

From our recordings of temperatures, from 17–22 July, T_a , T_{surface} , $T_{\text{a-burrow}}$, and $T_{\text{substrate}}$ averaged 48.9°C, 60.7°C, 41.9°C, and 39.0°C, respectively, between 11:00 and 16:00. In the laboratory, over a temperature range of 35–50°C, total evaporative water loss (TEWL) of Hoopoe Larks increases curvilinearly: $\text{TEWL (g day}^{-1}\text{)} = 142.6 - 8.41T_a + 0.126 T_a^2$ ($r^2 = 0.96$) (Tieleman and Williams, unpubl. data). Based on the relationship between measurements of TEWL and T_a for Hoopoe Larks, we have estimated TEWL for this species at the average temperatures given above (Table 1). If T_e of a Hoopoe Lark in full sun on the ground approaches T_{surface} (Williams et al. 1995), then water loss would be nearly 9% of its body mass hr⁻¹, a rate that could be sustained for only short periods (Table 1). Wolf et al. (1996) calculated that Verdins *Auriparus flaviceps* (7 g) in the full sun in the Sonoran Desert would lose 7% of their body mass hr⁻¹.

If Hoopoe Larks (40–45 g) remained above ground, but sought shade, at a T_e of 48.9°C, they would evaporatively lose 1.35 g H₂O hr⁻¹, or 3.0% of their body mass (Table 1). By seeking underground shade, larks could reduce their TEWL to 0.47 g H₂O hr⁻¹, or 2.34 g H₂O over 5 hr, a 65% reduction. By pressing their ventral apertures to the burrow substrate, Hoopoe Larks can further reduce their TEWL, perhaps as low as 0.25 g H₂O hr⁻¹, a value 81% lower than for water loss in above ground shade. These calculations emphasize that the use of burrows can provide a significant savings to the water economy of Hoopoe Larks, and indicate that this behavior is potentially important to their survival.

We thank the entire staff of the National Wildlife Research Center, Taif, Saudi Arabia, for their support and encouragement, especially P. Paillat and Phil Seddon. A. H. Abuzinada kindly granted us permission to work in Mahazat as-Sayd. J. Williams was supported, in part, from funds provided by NSF grant no. OPP-9696134, and I. Tieleman received monies from the Doctor Catharine van Tussenbroek Foundation.

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