

THE USE OF THERMAL REFUGIA BY TWO SMALL DESERT BIRDS¹

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Key words: *Verdin; Auriparus flaviceps; Black-tailed Gnatcatcher; Polioptila melanura; diurnal microsite selection; thermal ecology; evaporative water loss; operative temperature.*

The extent to which birds select specific microsites during their diurnal activity and the thermal consequences of microsite selection during the day has received scant attention (DeWoskin 1980; Walsberg 1985, 1993; Weathers and Sullivan 1989). Most research has focused on microsite selection and the physiological consequences of occupancy of specific sites such as nocturnal roosts or nest sites (Walsberg 1985). Diurnal microsite selection based on thermal constraints may have important effects on other daily activities such as foraging, social behavior, reproduction and the avoidance of predators. Observations of the curtailment of these activities due to thermally imposed physiological constraints is thus important to understanding the behavioral ecology of birds in desert environments.

The general problems presented by terrestrial environments are carried to an extreme in subtropical deserts. In such areas, surface water is rare, humidities are low, and intense solar radiation produces very high air temperatures during the four to five month-long summer. For example, air temperature—which is best regarded as a *minimum* index of environmental temperature—sometimes exceeds 50°C and commonly is above 35°C for over 12 hours each day in the Sonoran Desert. Most birds are diurnal and do not use burrows for refuge, thus they must directly confront the hottest periods of the summer day. Small passerine birds also have high mass-specific metabolic rates, resulting in high rates of internal heat production and frequent ventilation of respiratory surfaces with resultant high rates of pulmonary water loss (Dawson 1982). In addition, their small size confers a low thermal inertia and limited capacity for storage of vital resources such as water. Such species must balance water budgets over time periods of minutes to hours (Goudie and Piatt 1990) and may be under extreme pressures to optimize their use of water resources.

In this paper we report observations of diurnal microsite selection during the summer in the Sonoran Desert for two small (five to seven g) insectivorous birds, the Verdin (*Auriparus flaviceps*) and the Black-tailed Gnatcatcher (*Polioptila melanura*). We also evaluate the potential effects of occupancy of these sites on avian water economy and rates of evaporative water loss.

METHODS AND MATERIALS

Observations were made in a wash in the Goldfield Mountains, Pinal County, Arizona, at 473 m elevation. The wash is a normally dry watercourse passing through Bulldog Canyon and its edges are populated by foothill paloverde (*Cercidium floridum*), mesquite (*Prosopis velutina*), ironwood (*Olneya tesota*), catclaw acacia (*Acacia greggi*) and wolfberry (*Lycium sp.*) The surrounding hillsides and slopes are dominated by white bur-sage (*Franseria dumosa*), creosote bush (*Larrea tridentata*) and cactus (*Carnegia, Opuntia, Ferocactus* and *Mammalaria*).

During late July and early August of 1995, one Verdin and eight Black-tailed Gnatcatchers were observed persistently occupying three very distinctive microsites on several afternoons during our occasional visits to the area. The physical location of the sites and the persistence with which the birds reoccupied them even in our presence suggested that occupancy of these sites may confer important thermal advantages.

Air and substrate temperature measurements were made at each microsite using a Miller and Weber quick reading cloacal thermometer. These substrate temperatures represent a weighted value between the temperature of the surface and that of the surrounding air when the entire mercury bulb is not in contact with the surface being measured. As a consequence, our measurements of trunk surface temperature were somewhat higher than the actual temperatures of this substrate. Operative temperatures for Verdins were continuously measured in full and partial sun using five unheated taxidermic mounts in each microhabitat (Bakken et al. 1985). Operative temperatures for Verdins in deep shade were assumed to equal air temperature as measured by two 26 ga. copper-constantan thermocouples placed 1 m above the ground and 0.1 m from the trunk of an ironwood tree. Mount and thermocouple signals were measured five times a minute and averaged every 15 minutes by a Campbell 21X datalogger. The activities of the Verdin were also recorded on two consecutive afternoons using an event-timing program and a Hewlett-Packard 95LX palmtop computer mounted on a pair of binoculars.

RESULTS AND DISCUSSION

All three microsites were near the base of two large (approximately 50–70 cm DBH) paloverde trees situated near the center of the wash. Microsite 1 was located on the basal trunk of a paloverde, 10 to 40 cm from the ground, where two large subsidiary trunks joined (Fig. 1). The tree's dense canopy was approximately 10 m in diameter and hung to within 1 m of the ground. The tree was surrounded by catclaw and

¹ Received 2 October 1995. Accepted 14 February 1996.



FIGURE 1. Black-tailed Gnatcatchers sitting at the base of a large paloverde tree (site 1) during the hottest part of the afternoon on 1 August 1995. Data showing the thermal advantages of this specific site are presented in Table 1.

bur-sage (*Franseria deltoidea*), producing deep shade beneath the tree. This site was occupied by from two to eight Black-tailed Gnatcatchers on two the consecutive afternoons, as well as when we visited the site the following week. On 1 August, between 16:00 and 17:00, two to six adult and juvenile Black-tailed Gnatcatchers were observed occupying the site 1 at different times (Fig. 1). These birds arrayed themselves in a line along the crevice created by the intersection of the two subsidiary trunks. The gnatcatchers sat with their wings held away from their axillary region and rested against the trunk surface. None of the birds were observed panting. Activity included occasional movements to other nearby sites, including the sand at the tree's base, and infrequent postural adjustments. During these observations, we were often within 2 m of the site and although our movements initially flushed the birds from the site they immediately returned to the crevice when we stopped moving. This behavior occurred at least six times during one of our visits. These birds may or may not have represented a family group, but the be-

havior of the juveniles indicated that they were independent. Walsberg's (1990) observations of 15 Black-tailed Gnatcatchers roosting in a single Verdin nest during the winter indicates that unrelated individuals of this species may aggregate in thermally advantageous sites.

The area beneath and surrounding the tree where Microsites 2 and 3 were situated was sandy and devoid of vegetation. The tree's dense canopy had a diameter of approximately 12 m and hung within 1.6 m of the ground. Consequently, the base of the tree and the surrounding sand were in full shade throughout most of the day. Microsite 2 was a knothole on the north side of the tree and approximately 1 meter above the ground. The knothole was approximately 8 cm high, 6 cm wide and 4 cm deep and was occupied on three consecutive afternoons by a juvenile Verdin (Fig. 2). This bird's activities were quantified on 1 and 3 August for three intervals ranging in length from 15 to 69 minutes, between 14:00 and 17:30 hours. The Verdin sat quietly in the knothole with its right side pressed



FIGURE 2. Juvenile Verdin resting in a knothole 1 m above the ground on the north side of a large paloverde tree (site 2) during the hottest part of the afternoon on 1 August 1995. The air and substrate temperatures of the microsite and nearby shade air temperatures are presented in Table 1.

against the trunk of the tree for 96% of the total time it was under observation (Fig. 2). The bird panted intermittently and occasionally closed its eyes, but otherwise sat motionless. The remaining time was characterized by an occasional brief foray into the canopy or to an adjacent tree where foraging or flying occupied 3% and 1%, respectively of the total observation time.

Microsite 3 was a slight depression in the sand at the base of the tree on its northwest side and was occupied by adult male Black-tailed Gnatcatcher between 15:25 and 15:45, on 1 August. During this period, the bird leaned against the trunk and frequently rested with its eyes closed. The juvenile Verdin sitting in Microsite 2 also rested quietly during the same interval. These birds also repeatedly returned to the microsite after our movements had disturbed them.

At 12:00 on 1 August 1995, 15°C range of thermal environments was available to a free-ranging animal (Fig. 3). For a Verdin sitting in full shade at mid-day, evaporative water loss (EWL) would be approximately

16 mg g⁻¹ hr⁻¹ or 1.6% of body mass per hour at an operative temperature of 40°C. Movement into the sun (operative temperature of 55°C) would result in greater than a five-fold increase in EWL to more than 70 mg g⁻¹ hr⁻¹ or 7% of body mass per hour (Wolf and Walsberg, in press). We would expect similar increases in EWL over the same range of operative temperatures for Black-tailed Gnatcatchers because of their equally small size.

Microsites occupied by the Black-tailed Gnatcatchers and the Verdin are significantly cooler than shade air temperatures and may enable these small birds to reduce their water loss rates to minimum levels (Table 1). Data from Table 1 and Wolf and Walsberg (in press) suggest that selection of these specific sites could reduce EWL by one-half to two-thirds when compared to EWL rates at the prevailing shade air temperature. Body size may also play an important role in determining the importance of microsite selection for animals in general; Figure 1 and 2 graphically illustrate how body size

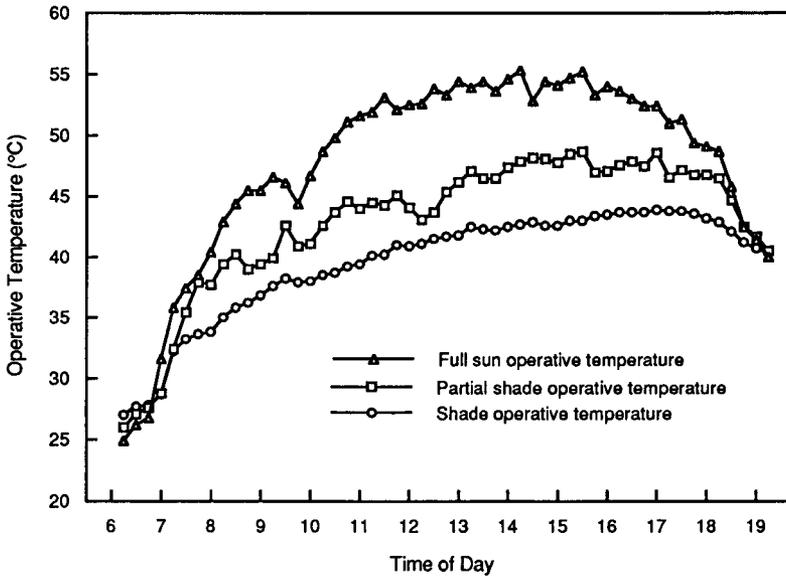


FIGURE 3. Mean operative environmental temperatures for Verdins in three contrasting microhabitats as a function of time of day on 1 August 1995.

may affect the number of available microsites. Increasing body size would clearly result in a decrease in the potential microsites available for occupancy.

Our observations suggest that small birds may be *very* specific in their selection of diurnal microsites and that site selection can have a large effect on rates of total evaporation. In addition, these observations also suggest that under moderately high heat stress small birds may almost totally forgo locomotor and foraging activity, presumably to minimize evaporative losses. This finding implies that continued foraging activity would further increase the bird's water deficit and have greater adverse effects on their water balance. The water savings accrued due to this suppression of activity are difficult to quantify, but even small savings may have important cumulative effects over periods of prolonged heat stress.

We emphasize that air temperatures experienced during this period were not abnormal for the Sonoran

Desert. These observations were made during a 17-day period in which air temperature daily exceeded 43°C and once reached 50°C. For birds living in this desert, these hot periods may represent a selective bottleneck and the ability to minimize evaporative water loss may mean the difference between life and death.

We thank Ty C. M. Hoffman and Todd Weaver for their skillful assistance. John Alcock and Michael C. Moore provided helpful comments on the manuscript. This research was supported by NSF grants BSR 91-07470 and IBN 92-24130 and a grant to BOW from the Chapman Memorial Fund of the American Museum of Natural History.

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TABLE 1. Air and substrate temperatures in microsites occupied by Black-tailed Gnatcatchers and a Verdin on 1 August 1995. See text for site description and time of occupancy. Sand surface temperatures were measured within 5 cm of the tree trunk.

Site number	Air temperature @ 1 m	Air temperature in microsite	Tree surface temperature in microsite	Sand surface temperature
1	42°C	39°C	33°C	not recorded
2	42.5°C	39.8°C	38.5°C	37°C
3	42.5°C	41.0°C	37.5°C	37°C

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The Condor 98:428-430
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EGG LAYING IN DUSKY FLYCATCHERS AND WHITE-CROWNED SPARROWS¹

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Key words: *Dusky Flycatcher*; *Empidonax oberholseri*; *White-crowned Sparrow*; *Zonotrichia leucophrys oriantha*; *laying times*; *laying intervals*.

Many birds lay one egg per day, often in the early morning. The time interval between eggs is usually close to 24 hrs, although longer and more irregular periodicities have been noted in a number of species (Skutch 1952, Schifferli 1979, Astheimer 1985). Despite the interspecific variation in laying times and intervals, most of the speculation regarding adaptive significance has centered on the hour of laying (Schifferli 1979, Feare et al. 1982, Weatherhead et al. 1991, Watson et al. 1993).

The purpose of this note is twofold: first, to present data on the laying patterns observed in two passerine species inhabiting roughly the same environment and second, to stimulate new discussion of some of the factors that might influence laying patterns in general.

METHODS

This study was conducted between 1984 and 1995, inclusive, in the Sierra Nevada near Tioga Pass, Mono Co., California. The two species studied, Dusky Flycatcher (*Empidonax oberholseri*) and Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*) nested on subalpine meadows (both species) and the vegetated talus slopes immediately above (primarily *E. oberholseri*).

Laying times (noted in Pacific Standard Time) were determined by repeated visits to nests at approximately 1-hr intervals. If a new egg appeared between visits, the laying time was assumed to be midway between the visits. All eggs were numbered on the blunt end with waterproof ink according to laying order. Sitting females were usually left undisturbed and, to minimize error, an attempt was made to check the nest again soon after they had departed on their own accord. Lay-

ing times for *E. oberholseri* could sometimes be estimated very closely because as the egg's surface dries within a few minutes after laying, an air sac about 3 mm in diameter forms at the blunt end. The air sac, readily visible through the white shell, grows to about 4.5 mm over the next hour. Thus air sac measurements of recently laid eggs (air sac width smaller than 4.5 mm) allowed us to assign laying times even when nest visits were as much as three hours apart.

For *Z. l. oriantha*, 21 of the laying times were obtained by the multiple nest-visit technique, the other 11 from nest temperatures recorded with thermocouples during laying and attentive periods. When the female came onto the nest in the early morning, nest temperatures typically increased and then decreased sharply upon her departure after laying. Mean (\pm SD) laying attentive periods were 56.2 ± 10.2 min (range = 36-69 min), and their midpoints were taken to be the time of laying (see Fig. 1 in Zerba and Morton 1983). Modal clutch size for both species was four.

RESULTS

The mean hour of laying was 12:06 for the 117 cases measured in *E. oberholseri* and 05:44 for the 32 cases measured in *Z. l. oriantha* (Table 1). In *Z. l. oriantha* laying times did not vary with laying order (ANOVA: $F_{3,28} = 1.5, P = 0.24$), but in *E. oberholseri* the third egg was laid later than any of the others (ANOVA: $F_{3,113} = 5.8, P = 0.001$ and Student-Newman-Keuls multiple range test: $P < 0.05$).

Variation in laying time was greater in *E. oberholseri*. The eggs produced by a given female on consecutive days were laid nearly 27 hrs apart, whereas those of *Z. l. oriantha* were almost exactly 24 hrs apart (Table 2). On occasion, *E. oberholseri* skipped laying days and the interval between successively laid eggs became more than 42 hrs (Table 2). In two cases, the penultimate egg was laid before noon and the last egg followed the next afternoon between 13:30 and 15:00. In another two nests, the female laid the penultimate egg after 15:00, skipped the next day, and laid the final egg the following morning before 10:00. In two nests the female laid around 12:00; one laid the final egg the next

¹ Received 12 October 1995. Accepted 14 December 1995.