

BEHAVIORAL ADAPTATIONS OF THE VERDIN TO THE DESERT

GEORGE T. AUSTIN

LITTLE or no free water and great seasonal and daily extremes of temperature are common features of deserts of the world. Maintenance of a homeostatic state under such conditions involves the opposing requirements of maintaining water balance and thermoregulation. The harshness of the desert is well documented. Any trait that lessens heat stress and reduces water loss is adaptive. How resident organisms have adapted to, or avoided, these features has been a field of fruitful research in recent years (see Brown 1968, Farner and King 1971, for reviews).

Certain desert mammals are strikingly specialized compared to nondesert forms in ways that can be correlated with environmental extremes (Dawson 1955; Schmidt-Nielsen et al. 1957, 1967; Schmidt-Nielsen 1958, 1964; Bartholomew and Hudson 1960, 1961; Hudson 1962; Carpenter 1966; and others). The general physiological similarity of desert and nondesert birds, however, has led to the conclusion that birds have no special adaptations to the desert (Miller 1963).

Yet subtle adaptations and preadaptations occurring in the class as a whole enable many species to inhabit these hot, arid regions. Preadaptive features of birds are discussed by Dawson and Bartholomew (1968). Several data are available that suggest small physiological refinements rather than striking adaptations are common among desert birds. These include lower basal metabolic rates, higher evaporative cooling efficiencies, and greater tolerances for high ambient temperatures in desert species (or populations) compared with closely related forms occurring in more mesic environments (Salt 1952, Dawson 1954, Hudson and Kimzey 1966, Rising 1969, Carey and Morton 1971, Henderson 1971). Breeding of the Abert's Towhee (*Pipilo aberti*) and Rufous-winged Sparrow (*Aimophila carpalis*) in response to rain rather than photoperiod (Marshall 1963, Ohmart 1969) is another adaptation of this type. Several recent studies indicated that some desert species are physiologically more efficient in conserving water than nondesert species (Smyth and Bartholomew 1966, Willoughby 1968, Ohmart and Smith 1970).

Preadaptive and physiological features alone appear insufficient to allow many species to adapt to the desert completely. Behavioral adjustments appear to be of major importance as adaptations to the desert judging from the few data available. For example, some species reduce

and shift their activity to cooler microhabitats during midday (Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969).

This study deals with behavioral features of the Verdin (*Auriparus flaviceps*), one of the smaller desert birds (6.5 to 7.5 g). Because of its size it is faced with the greater problems incurred by surface-volume relationships than larger species, and studies of its adaptations are desirable. The life history of the Verdin was studied by Moore (1965) and Taylor (1971). Goldstein (1974) made limited measurements of oxygen consumption of the Verdin at various ambient temperatures.

METHODS

I studied the ecology of the Verdin in southern Arizona (Pima County) and southern Nevada (Clark County). Data recorded on nest placement (Arizona and Nevada) included entrance orientation, side of tree, height from ground, relationship to branch structure (forks), and amount of shading at various times of the day. Entrance orientation and side of tree were measured with a compass and corrected to true direction. These circular data were treated statistically with the methods of Batschelet (1965).

Three types of nests were distinguished: breeding, small roost, and large roost. Breeding nests were identified primarily by the presence of eggs and/or young. Other characteristics of breeding nests are a cavity depressed below the level of the entrance, a larger cavity than roosts, and more lining. Large roosts are similar in size but are often unlined and have a smaller, shallower cavity. Large roosts are generally used during the winter, but if they remain in good repair the male uses them through the breeding season. Small roosts are not only reduced in size but are thin-walled structures with no lining and are generally built in summer by both adults and young. Nests are described in more detail by Taylor (1971). In order to detect changes in placement and success, the breeding season was divided into early and late periods with 1 May as the division date. Nests with the majority of activity before or after 1 May were designated early and late nests respectively. Eggs are laid from March through June (rarely July). The first of May is the approximate midpoint of the breeding season. About this time, first broods are fledging and nests for second broods are under construction.

A number of breeding nests were inspected periodically to determine success. Hatching success is the percentage of eggs laid that hatched, fledging success is the percentage of eggs laid that fledged, and nestling success is the percentage of young hatched that fledged. A successful nest is one that fledges at least one young. Success data were treated statistically by Chi-square.

Differential habitat utilization over a range of ambient temperatures was studied following the procedures of Ricklefs and Hainsworth (1968). Four microhabitats used by Verdins for foraging were distinguished: exposed portions of the vegetation above 1.5 m (high exposed), exposed portions of the vegetation below 1.5 m (low exposed), portions of the vegetation with a mosaic of exposed and shaded vegetation but predominantly shaded (shade), and those portions receiving little or no sun, generally near the trunks of trees (deep shade). In winter, only exposed and shaded microhabitats were distinguished. Microhabitats were simple to delineate on clear days; on cloudy days the delineation was more subjective. Accuracy on the latter days was enhanced by limiting my observations to familiar trees. Thus I could be

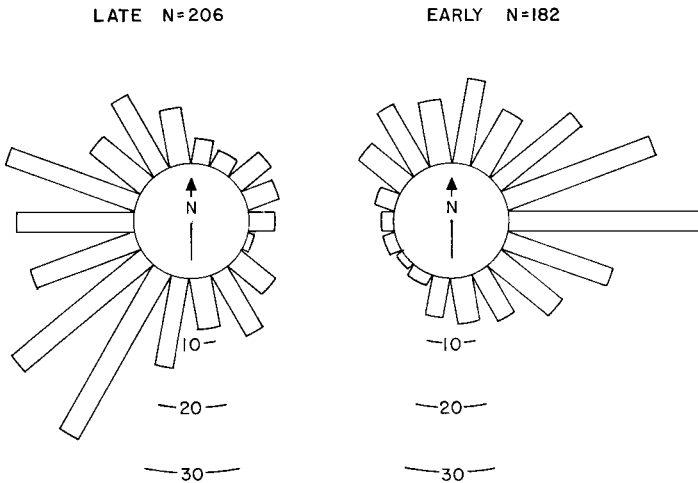


Fig. 1. Entrance orientations of Verdin brood nests.

reasonably sure of what portions of these trees would be exposed or shaded if it were not cloudy. Observations on cloudy days when temperatures were relatively cool and the four microhabitats were nearly isothermic serve as a control for comparison with clear, hot midday conditions.

Temperatures were obtained concurrently for each microhabitat. Foraging observations were obtained only on windless days to reduce the number of variables involved in foraging behavior.

Amount of time a foraging Verdin spent in each microhabitat was timed with a stopwatch. Data are for seven pairs of postbreeding (July–August) adult birds in southern Nevada and about six individuals during winter (December–February) in Arizona. Data on foraging intensity (expressed as number of perch changes per minute) were gathered in both Nevada (seven postbreeding pairs) and Arizona (five postbreeding pairs). When a foraging bird was encountered, the number of perch changes were counted over a stopwatch-timed interval. Observations less than 2 min in length were discarded. When a bird stopped foraging, was out of my sight for more than 10 sec, or made a flight of over 15 m, observations were ended. Concurrently deep shade temperatures were measured. Rates of nest visitation (to feed young) were counted visually.

Statistical significance is defined throughout at the 0.05 level.

RESULTS AND DISCUSSION

Nest placement and orientation.—Nest entrance orientations in Nevada and Arizona do not differ significantly and the data are lumped. Early nests are oriented predominantly in an easterly direction (mean = 84° , significantly different from uniform, Fig. 1). Late nests are oriented southwest (mean = 257° , significantly different from uniform, Fig. 1). Small roosts are similarly oriented (mean = 264° , significantly different

TABLE 1
ENTRANCE ORIENTATIONS OF VERDIN NESTS

| Entrance orientation (degrees) | Early brood (%) | Late brood (%) | Large roost (%) | Small roost (%) |
|--------------------------------|-----------------|----------------|-----------------|-----------------|
| 0-30 | 12.6 | 6.3 | 9.2 | 9.7 |
| 40-70 | 14.3 | 4.4 | 7.2 | 5.8 |
| 80-110 | 29.7 | 4.4 | 8.6 | 2.9 |
| 120-150 | 15.9 | 3.9 | 11.2 | 7.8 |
| 160-190 | 8.2 | 9.2 | 9.9 | 8.7 |
| 200-230 | 4.4 | 20.9 | 9.9 | 14.6 |
| 240-270 | 1.6 | 20.9 | 15.1 | 24.2 |
| 280-310 | 2.7 | 18.9 | 10.5 | 17.5 |
| 320-350 | 10.4 | 11.2 | 18.4 | 8.7 |
| N | 182 | 206 | 152 | 103 |
| Mean orientation | 84° ± 59° | 257° ± 61° | Uniform | 264° ± 66° |

from uniform, Table 1). Large roosts are uniformly oriented (Table 1). Early nests are oriented significantly different from late nests and small roosts. The orientation of late nests and small roosts do not differ significantly.

Early nests are placed on the east side of trees (mean = 86°, significantly different from uniform, Table 2). Late nests are placed on the southwest side of trees (mean = 234°, significantly different from uniform, Table 2). Roost placement is not significantly different from uniform (Table 2).

All nest types are placed at similar heights (early brood mean = 189 cm, late brood mean = 185 cm, large roost mean = 199 cm, small roost mean = 171 cm). Most late nests are shaded while early nests are

TABLE 2
SIDE OF TREE PLACEMENT OF VERDIN NESTS

| Side of tree (degrees) | Early brood (%) | Late brood (%) | Large roost (%) | Small roost (%) |
|------------------------|-----------------|----------------|-----------------|-----------------|
| 0-30 | 12.8 | 16.9 | 9.5 | 8.7 |
| 40-70 | 14.5 | 4.8 | 6.8 | 9.7 |
| 80-110 | 19.0 | 5.3 | 10.1 | 8.7 |
| 120-150 | 18.4 | 6.8 | 8.1 | 7.8 |
| 160-190 | 10.6 | 15.5 | 12.8 | 7.8 |
| 200-230 | 6.7 | 9.2 | 9.5 | 13.6 |
| 240-270 | 2.7 | 12.1 | 10.1 | 17.5 |
| 280-310 | 5.0 | 14.5 | 19.6 | 14.6 |
| 320-350 | 10.1 | 15.0 | 13.5 | 11.7 |
| N | 179 | 207 | 148 | 103 |
| Mean side of tree | 86° ± 67° | 234° ± 72° | Uniform | Uniform |

TABLE 3
PLACEMENT OF BREEDING NESTS WITH RESPECT TO SHADE

| Amount of shade | Early brood (%) | Late brood (%) |
|------------------------|-----------------|----------------|
| Deep shade (all day) | 1.8 | 24.0 |
| Deep shade (afternoon) | 4.2 | 50.4 |
| Not shaded | 94.0 | 25.6 |
| Number of nests | 167 | 121 |

exposed (Table 3). Roosts are predominantly (85.8%) placed in forks of branches greater than 0.5 cm in diameter; breeding nests are generally (79.2%) placed among twigs less than 0.5 cm in diameter.

The majority of Temperate Zone species of birds build nests open on top; some utilize cavities, which appear to afford more protection to eggs and nestlings (Nice 1957, Ricklefs 1969). A number of species construct enclosed nests that combine some of the advantages of open nests (relatively inaccessible placement near tips of branches) and cavity nests (energy conservation and protection from isolation and large predators). That enclosed nests conserve energy at low temperatures has been recognized (Kendeigh 1961, Ricklefs and Hainsworth 1969). For the same reason, the enclosure could prove disadvantageous at high environmental temperatures because of metabolic heat production. Mechanisms that prevent the nest from overheating must be present. Thus nest placement must take into account nest structure and supportive needs as well as protection and nest environment. Flexibility and variability are favored to allow for spatial and temporal environmental variations.

Adaptations of the nest in respect to placement and environmental variables have been studied little. Nest site selection of Calliope Hummingbirds (*Stellula calliope*) was suggested as a major factor in nesting success (Calder 1971). Cactus Wrens (*Campylorhynchus brunneicapillus*) build an enclosed nest, the entrance of which is oriented away from and into the prevailing winds during the cool and hot parts of the breeding season respectively (Ricklefs and Hainsworth 1969). Success of Cactus Wren nests oriented into the wind during the hot part of the breeding season is greater than those oriented otherwise (Austin 1974). This probably helps moderate the nest temperature. Relation of nesting success to nest placement is poorly known (Goddard and Board 1967, Tenaza 1971).

Season specific orientations were found among Verdin nests (Fig. 1).

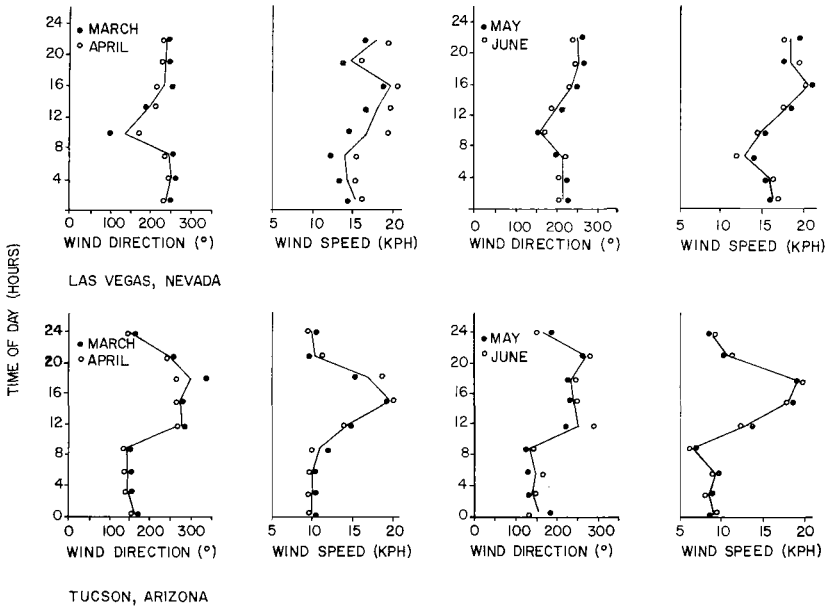


Fig. 2. Mean wind direction and speed in southern Nevada and southern Arizona in relation to time of day (Nevada data from U.S. Weather Bureau, McCarran Field, Las Vegas, Nevada; Arizona data from U.S. Weather Bureau, Tucson International Airport, Tucson, Arizona adapted from Ricklefs and Hainsworth 1969).

The change in orientation is rather abrupt, occurring in late April and early May (Table 4). As with the Cactus Wren (Ricklefs and Hainsworth 1969), wind appears to be the important factor governing orientation (Fig. 2). The nest of the Verdin is built with the entrance avoiding the wind during the cool part of the season, possibly to reduce heat loss by convection. Late nests are oriented into the prevailing winds (predominant wind direction not significantly different from nest entrance orientation, Fig. 2). As wind direction throughout the breeding season remains roughly the same (Fig. 2), early and late nests are oriented very differently. These orientations may be of importance in moderating the nest environment by taking advantage of prevailing wind conditions as suggested by Ricklefs and Hainsworth (1969). Orientation into the wind may increase convection, thus removing excess heat from the nest or enhance evaporative cooling of the young and evaporation from fecal sacs (see below). Although Taylor (1971) stated that Verdin brood nests were not oriented in any particular direction, he did not separate early and late nests. Reevaluation of some of his data according to season showed similar orientations to those I found.

TABLE 4
CHANGES IN ENTRANCE ORIENTATION OF VERDIN NESTS¹

| Entrance orientation (degrees) | March | Early April | Late April | Early May | Late May | Early June | Late June | July |
|--------------------------------|-------|-------------|------------|-----------|----------|------------|-----------|------|
| 0-30 | 4 | 8 | 15 | 1 | 2 | 4 | 1 | 0 |
| 40-70 | 7 | 9 | 10 | 1 | 2 | 3 | 1 | 1 |
| 80-110 | 1 | 30 | 22 | 5 | 3 | 1 | 0 | 0 |
| 120-150 | 5 | 16 | 9 | 4 | 3 | 0 | 1 | 0 |
| 160-190 | 5 | 6 | 7 | 4 | 6 | 5 | 0 | 2 |
| 200-230 | 0 | 4 | 9 | 12 | 17 | 9 | 0 | 1 |
| 240-270 | 0 | 1 | 3 | 17 | 18 | 5 | 3 | 0 |
| 280-310 | 0 | 2 | 5 | 14 | 18 | 4 | 2 | 0 |
| 320-350 | 2 | 7 | 12 | 8 | 8 | 3 | 1 | 1 |
| Number of nests | 24 | 83 | 92 | 66 | 77 | 34 | 9 | 5 |

¹ As number built during each time period.

The uniform orientation of large roosts is possibly related to lower wind speeds at night as with the Cactus Wren (Ricklefs and Hainsworth 1969). Small roost orientation may be related to the time of year they are built (late May through July). These nests are built and used at a time when temperatures reach their highest levels and little insulation is needed.

Other variables involved in nest placement are more difficult to interpret. Nests are generally oriented with the entrance facing outward from the center of the tree (Taylor 1971). Entrance orientation of early nests is eastwards and nests are placed on the east side of the tree (Tables 1, 2). Thus nests are exposed to the warming sun in the cool morning but are somewhat protected from the afternoon sun. Similar placement of late nests seems advantageous. Placement orientation is similar to entrance orientation (Tables 1, 2), which probably results from an engineering limitation imposed by branch structure that requires facing the nest away from the center of the tree. Late nests are generally well shaded, at least during the heat of the day (Table 3). Such shading reduces radiant heat load and thus reduces heat gain by the nest through conduction and convection. Late nests placed on the west side of the tree are somewhat lower (not statistically different) than those placed elsewhere. The strong tendency for a southwest entrance orientation (Fig. 1) in late nests along with success data (below) indicate that entrance orientation is the primary factor governing late nest placement.

Roost placement in larger forks is apparently related to support. Roosts (especially large roosts) are used for at least several months. Thus placement on a strong support is advantageous. On the other

TABLE 5
RELATION OF SUCCESS AND ENTRANCE ORIENTATION OF EARLY AND LATE
VERDIN NESTS¹

| | Early | | Late | |
|----------------------------|-------------------|--------|-------------------|---------|
| | 70-160 | 170-60 | 220-310 | 320-210 |
| % nests found | 54.9 | 45.1 | 53.9 | 46.1 |
| Hatching success (%) | 91.7 ² | 80.9 | 87.5 ² | 64.4 |
| No. eggs | 108 | 68 | 136 | 177 |
| No. nests | 28 | 17 | 46 | 55 |
| Fledging success (%) | 84.6 ² | 63.3 | 81.5 ² | 44.6 |
| No. eggs | 104 | 60 | 124 | 168 |
| No. nests | 27 | 15 | 42 | 53 |
| Nestling success (%) | 92.6 ² | 79.2 | 94.4 ² | 70.8 |
| No. hatch | 95 | 48 | 107 | 106 |
| No. nests | 27 | 15 | 34 | 39 |
| % successful nests | 100.0 | 86.7 | 76.2 | 58.5 |
| % totally successful nests | 66.7 ² | 33.0 | 66.7 ² | 26.4 |

¹ Preferred orientation given first = 100 continuous degrees containing the most nests.

² Significantly different from nonpreferred orientation.

hand, breeding nests are used for a little more than a month and protection rather than long-term support is the prime requisite, although these nests may be used for roosting after the young fledge.

A few other species of birds have been shown to orient their nests in relation to environmental variables. A predominant east and south orientation of woodpecker nest entrances was attributed to problems of nest climate and lighting (Lawrence 1967). Summer nests of larks (Alaudidae) in Africa are strongly oriented on shaded sides of bushes while winter nests are less clearly oriented (Maclean 1970). Horned Lark (*Eremophila alpestris*), Water Pipit (*Anthus spinoletta*), and meadowlark (*Sturnella* spp.) nests tend to face away from prevailing winds (Lanyon 1957; Verbeek 1967, 1970). Such orientations were attributed to protection from cooling winds and rain. Desert Lark (*Ammodramus desertii*) nests are placed in such a way that they are warmed by the sun in the early morning but are shaded and cooled by winds later in the day (Orr 1970).

Although these orientations are suggestive, the question remains as to their biological significance. Success data for southern Nevada (2 years) and southern Arizona (2 years) demonstrate the importance of orientation to success (Table 5). Nearly all criteria of success were higher for nests oriented in the predominant directions. This is one of the few documentations of a relationship between breeding success and nest placement (see Goddard and Board 1967, Austin 1974).

Nest climate.—Temperatures of nests containing eggs and nonthermogenic nestlings tend to be correlated with ambient temperature but average

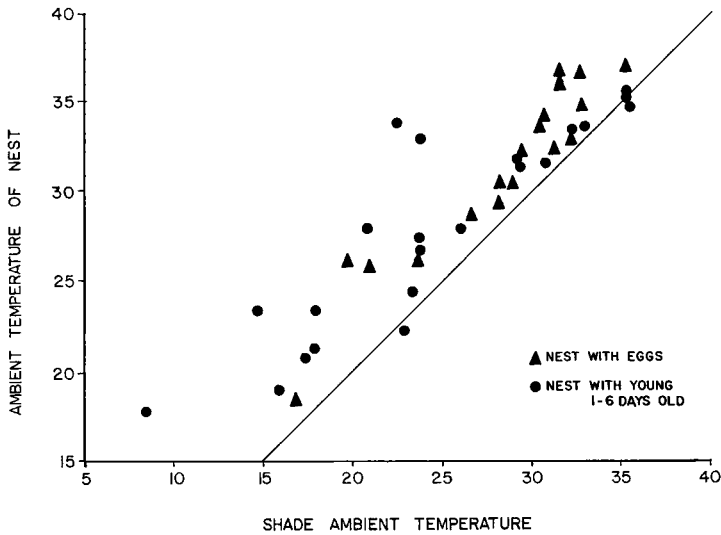


Fig. 3. Relation of ambient temperature and nest temperature of Verdin nests containing eggs and nonthermogenic nestlings.

a few degrees warmer; nests containing thermogenic young are considerably warmer than ambient at low temperatures but are little above ambient at higher temperatures (Figs. 3, 4). At shade temperatures below 20°C nest temperature averages 8 to 10°C greater than ambient, at temperatures 20 to 30°C nest temperature averages 3 to 5°C greater, and above 30°C nest temperature averages less than 1°C above ambient. At low ambient temperatures, nest temperature can be maintained by the sun, brooding by the female, and by metabolic heat. By brooding at low ambient temperatures, the female can maintain nestling body temperatures (Table 6). Brooding ceases by the 9th or 10th day (Taylor 1971, this study Table 6), at which time body temperature control has been attained (Austin MS).

Maintenance of near homeothermic body temperatures by nestlings allows them to be normally active. Young in the laboratory with body temperatures below 20°C had difficulty raising their heads to gape for food and swallowing. Also the lack of well-developed homeothermy of young less than 10 days of age reduces energy requirements needed for active maintenance of high body temperatures at low ambient temperatures. Thus energy intake can be channeled into growth.

At high ambient temperatures, nest temperatures can be moderated by shade, wind convection, and from evaporation of water from the young or from fecal sacs retained in the nest cavity. Taylor (1971)

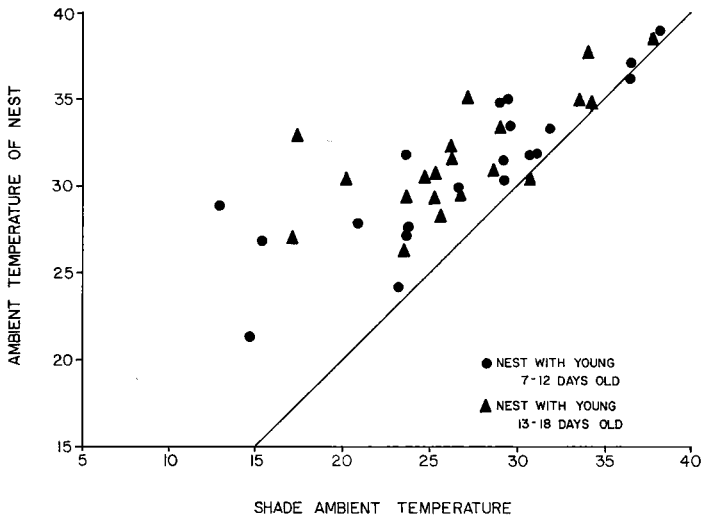


Fig. 4. Relation of ambient temperature and nest temperature in Verdin nests containing partially thermogenic and thermogenic nestlings.

reported that fecal sacs were removed from the nest by adult Verdins, but Moore (1965) stated that nests are not kept clean. I found that early nests are generally free of fecal material but it tends to build up in late nests and forms a matted mass with the lining in the floor of the nest. It is not uncommon to find a considerable buildup of fecal material at the entrance of late nests even while eggs are being incubated. A similar situation was found for the Cactus Wren (Ricklefs and Hainsworth 1969). The latter further demonstrated that experi-

TABLE 6

PERCENT OF TIME FEMALE VERDIN FOUND INCUBATING OR BROODING IN RELATION TO STAGE OF NESTING CYCLE AND AMBIENT TEMPERATURE¹

| Age (days) | Ambient temperature | | |
|--------------------|---------------------|---------|---------|
| | 10-20 | 20-30 | 30-35 |
| Eggs | 100 (2) | 67 (6) | 30 (10) |
| 0-1 | 100 (2) | 71 (7) | 25 (4) |
| 2-3 | 100 (4) | 100 (4) | 14 (7) |
| 4-5 | 100 (5) | 50 (4) | 0 (6) |
| 6-7 | 100 (2) | 18 (11) | 0 (2) |
| 8-9 | 75 (4) | 11 (9) | 0 (4) |
| 10-19 | 0 (9) | 0 (27) | 0 (15) |
| Total eggs, 9 days | 95 (19) | 44 (41) | 15 (33) |

¹ Number of observations in parentheses, all observations between sunrise and sunset, males do not incubate.

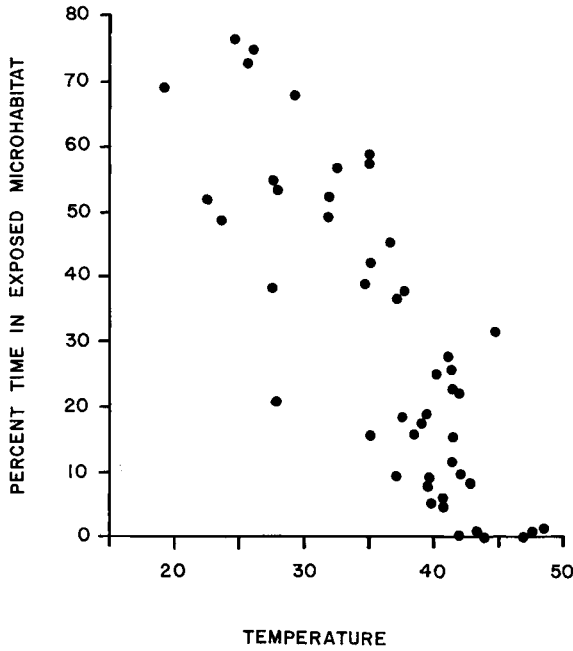


Fig. 5. Percent of time spent by foraging Verdins in exposed microhabitats as a function of temperature.

mental addition of a small amount of water to wren nests significantly lowered nest temperature. Evaporation from fecal sacs thus may contribute to nest cooling.

Temperature related behavior.—Time spent foraging in various micro-

TABLE 7

TIME SPENT FORAGING BY THE VERDIN IN VARIOUS MICROHABITATS AS A FUNCTION OF AMBIENT TEMPERATURE

| T _a (°C) | Total time (sec) | Low exposed (%) | High exposed (%) | Shade (%) | Deep shade (%) | Diversity of microhabitat use (H') ¹ |
|------------------------|---------------------|-----------------------|------------------------|--------------|----------------------|---|
| 20-25 | 911 | 20.2 | 28.6 | 42.8 | 8.3 | 1.02 |
| 25-30 | 6667 | 22.4 | 26.0 | 35.6 | 16.1 | 1.03 |
| 30-35 | 5963 | 16.4 | 35.6 | 40.4 | 7.5 | 1.02 |
| 35-40 | 2640 | 10.6 | 27.9 | 48.1 | 13.4 | 0.89 |
| 40-45 | 15271 | 5.2 | 14.5 | 51.4 | 28.9 | 0.61 |
| 45-50 | 7343 | 0.0 | 4.1 | 26.6 | 69.4 | 0.17 |
| Winter | 7032 | 52.9 | — ² | 47.1 | — ² | — |

¹ H' = -Σp_ilog_ep_i (see Lloyd et al. 1968) maximum H' = 1.10 if all three microhabitats (low exposed, high exposed, shaded) used equally.

² Only exposed and shaded microhabitats were distinguished in winter.

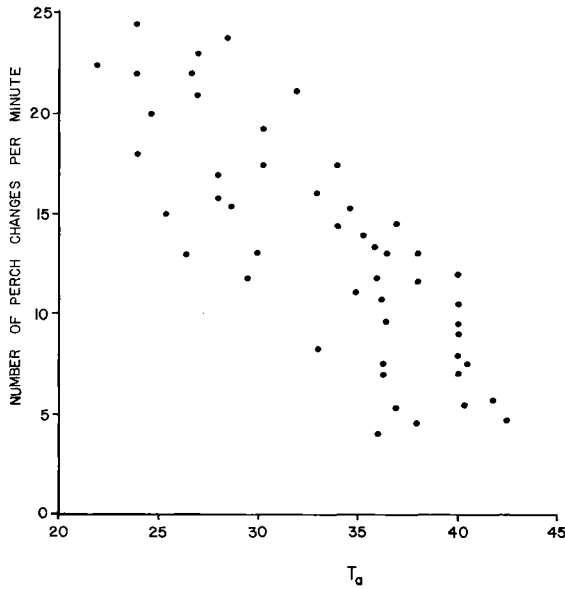


Fig. 6. Relation of foraging intensity of the Verdin and ambient temperature.

habitats as a function of ambient temperature is presented in Table 7. As ambient temperature increases, the percent of time spent in exposed microhabitats (low and high exposed) decreases (Fig. 5). Deep shade is the principal microhabitat utilized at temperatures greater than 45°C. Two indices of foraging intensity demonstrate a marked decrease at higher temperatures (Figs. 6, 7). The rate of feeding nonthermogenic young remains constant over a wide temperature range apparently a response to their lower energy requirements. Older young are fed more rapidly at low ambient temperatures than at high (Fig. 7) reflecting a reduction in the intensity of adult foraging behavior (Fig. 6). The proportion of time spent in various activities varies considerably with ambient temperature (Austin MS). Foraging is the principal activity at temperatures below 35°C, taking more than 80% of the time. Above 35°C foraging is greatly reduced and long periods of inactivity are predominant.

By foraging in the shade, the Verdin can continue to forage at high ambient temperatures and keep heat stress to a minimum. Average temperature encountered by the Verdin while foraging was calculated from microhabitat temperatures and the proportion of time spent in each (Fig. 8). These data indicate that, if possible, the Verdin restricts

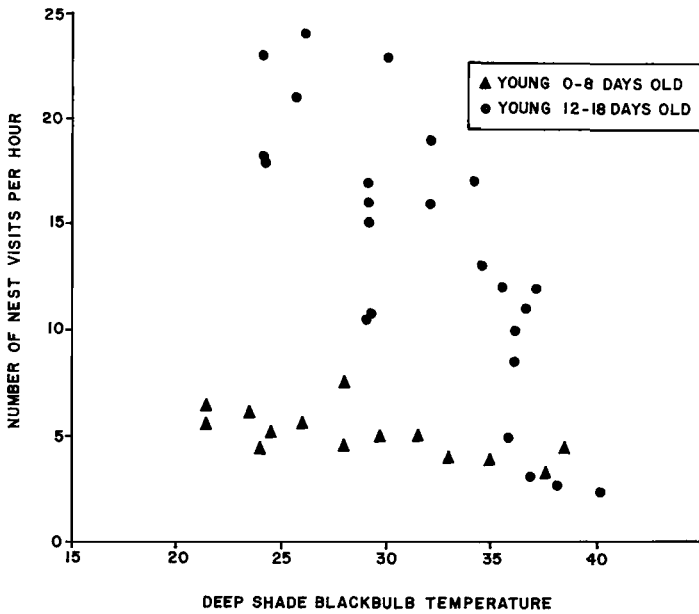


Fig. 7. Relation of number of feeding visits to nests by Verdins and ambient temperature ($N = 8$ nests).

its foraging activities to a mean temperature below 38°C . Otherwise the coolest microhabitat is used almost exclusively. Of interest, and possible significance, is that panting is initiated by nestlings (in the laboratory) at ambient temperatures of 38°C and above (Austin MS). The diversity of microhabitats used at different temperatures decreases as temperature increases (Table 7) similar to that reported for the Cactus Wren (Ricklefs and Hainsworth 1969). At temperatures above 40°C , shaded microhabitats are used almost exclusively. A shift to cooler microhabitats concurrently with a decrease in foraging intensity (Fig. 6) reduces heat gain from the environment and metabolic means respectively. The reduction in intensity of activity at higher temperatures is even more striking than indicated by foraging intensity in Fig. 6. Foraging activity is greatly reduced and frequently interrupted at higher temperatures by intervals of no activity, often several minutes in length.

In winter shaded and exposed microhabitats are used nearly equally (Table 7). Intensity of foraging at this season appeared to be at the summer maximum ($\bar{x} = 21.7$ perch changes per minute, $N = 51$).

A few data for cloudy periods during midday indicate that changes in behavior are responses to temperature rather than time of day (Fig. 9).

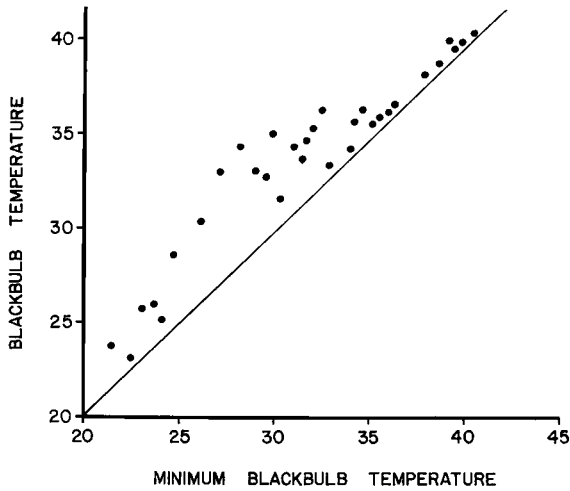


Fig. 8. Temperature microhabitat of the foraging Verdin as a function of temperature (line represents minimum temperature).

A similar pattern was found in the behavior of Black-tailed Gnatcatchers (*Polioptila melanura*) and Cactus Wrens (Smith 1967, Ricklefs and Hainsworth 1968). Captive Roadrunners (*Geococcyx californianus*) at temperatures below stress levels were highly active during midday, indicating that temperature is a factor in the midday activity depression in this species (Calder 1968, Kavanau and Ramos 1970). Thermoregulatory problems were suggested for the midday reduction in activity of Mangrove Swallows (*Iridoprocne albilinea*) in Panama (Ricklefs 1971). Amount of time spent foraging by Yellow-billed Magpies (*Pica nuttalli*) was depressed at high temperature except during the breeding season (Verbeek 1972). Changes of distribution or activity of insects and other prey may also be a factor, but it has been shown that, other factors being equal, temperature is the factor regulating Cactus Wren foraging activity (Ricklefs and Hainsworth 1968).

Little information is available on comparative behavior of birds in more moderate environments. Several have suggested environmental factors may be of importance in nest placement and nest entrance orientation (Lanyon 1957; Verbeek 1967, 1970; Lawrence 1967; Ricklefs and Hainsworth 1969). A relationship has been demonstrated between frequency of activity and microhabitat usage and temperature among desert birds (Smith 1967, Calder 1968, Ricklefs and Hainsworth 1968, Ohmart 1969). Many birds decrease their activity at midday during much of the year but this does not appear to be temperature related (e.g. see

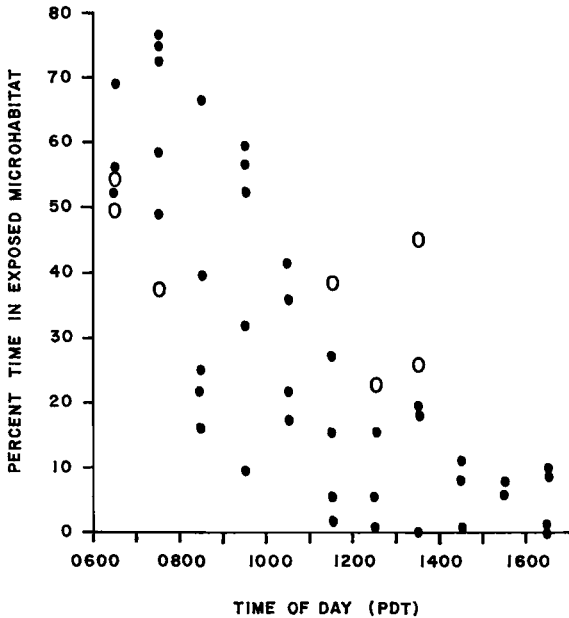


Fig. 9. Percent of time spent by foraging Verdins in exposed microhabitats as a function of time of day (circled points indicate data taken during cloudy periods, data replotted from Fig. 5).

Morton 1967, Coutlee 1968, Smith et al. 1969). Temperature related behavior of desert birds may be a refinement of this midday depression, but more of a response to temperature than to time of day. Data available for the Roadrunner, Cactus Wren, and Verdin seem to indicate this (Calder 1968, Ricklefs and Hainsworth 1968, Kavanau and Ramos 1970, present study). This reasoning is in agreement with physiological data for desert and nondesert birds.

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SUMMARY

Verdin breeding nest orientation is season specific with the entrances of early and late nests oriented to avoid and face respectively the prevailing winds. Nesting success is greater in nests oriented in the pre-

dominant directions. Verdins forage at all ambient temperatures they encounter but greatly reduce the intensity of and amount of time spent foraging at temperatures above 35°C. There is a concurrent shift of activity from exposed to shaded microhabitats. It is suggested that temperature related behavior is a refinement of the general midday depression of activity but in response to temperature rather than to time of day.

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Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, Nevada 89154. Accepted 2 December 1974.