TEMPERATURE REGULATION IN NESTLING CACTUS WRENS: THE NEST ENVIRONMENT

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Thermogenesis and thermolysis require resources (energy and water, respectively) that may often be present in the environment in limiting quantities. Birds are usually thought of as being limited by food during the breeding season (Lack 1954) and we have indicated elsewhere (Ricklefs and Hainsworth 1968b) that the activities of the Cactus Wren may be restricted by lack of free water during the hot parts of the breeding season. Under these conditions, evolution of the reproductive strategy should proceed toward the most efficient utilization of food and water.

The insulative properties of the nest, huddling behavior of the nestlings, and brooding behavior of the adults all act to conserve heat. Conversely, these strategies would impede the dissipation of heat in a hot climate. Huddling and brooding are responsive to changes in ambient temperature and they create few problems when conditions requiring heat conservation and heat loss arise within short periods of time. Nest construction, however, is fixed and must represent a compromise strategy in the southwestern deserts where diurnal changes in ambient temperature may exceed 20°C and the hottest temperatures may be several degrees higher than normal nestling body temperatures (Ricklefs and Hainsworth 1968a). Under these conditions the location and construction of the nest may be critical to the efficiency of temperature regulation of the young. The role of the nest of the Cactus Wren in maintenance of homeothermy of nestlings is evaluated indirectly in this report through a study of the relationships between temperatures within occupied nest cavities and the surrounding air.

THE NEST AND THE BREEDING SEASON

Near Tucson, Arizona, the Cactus Wren prefers tree-like cholla cacti (*Opuntia* spp.) for nesting sites, but other trees and shrubs are used when cholla is unavailable. The nest is flask- or retort-shaped, with the entrance to one side and is placed three to ten feet above the ground, usually in the exposed periphery of the cholla. The bulky structure is constructed of grasses and is often well-lined with feathers. Adults and juveniles sleep in separate nests of similar construction (roosting nests). More detailed descriptions of the nest are given by Bailey (1922), Bent (1948), and Anderson and Anderson (1959, 1960).

Field observations were made in an area of Lower Sonoran desert at 2400 feet elevation 10 miles east of Tucson, Arizona, from April through mid-July 1966 and briefly in July 1967 (described in detail in Ricklefs and Hainsworth 1968b). The occupancy of breeding nests on the study area during the 1966 breeding season and environmental temperatures recorded one mile from the study area are shown in figure 1. The two peaks in nest occupancy are first and second broods of the 15 pairs of wrens on the study area. Breeding in this species often continues as late as August, and during exceptional years begins as early as February (Anderson and Anderson 1959); however, in 1966 the breeding season was curtailed. During the 1966 season there was no evidence of starvation among the nestlings and few nests were lost to natural causes.

The daily air-temperature range approximated 20°C and temperatures increased throughout the season (fig. 1). In March and April maximum temperatures were in the middle to high 20's. Minimum temperatures occurred shortly before dawn and were generally below 10°C during these months. In June and July temperatures often exceeded 35°C, at which point the foraging activity of adult wrens is depressed (Ricklefs and Hains-

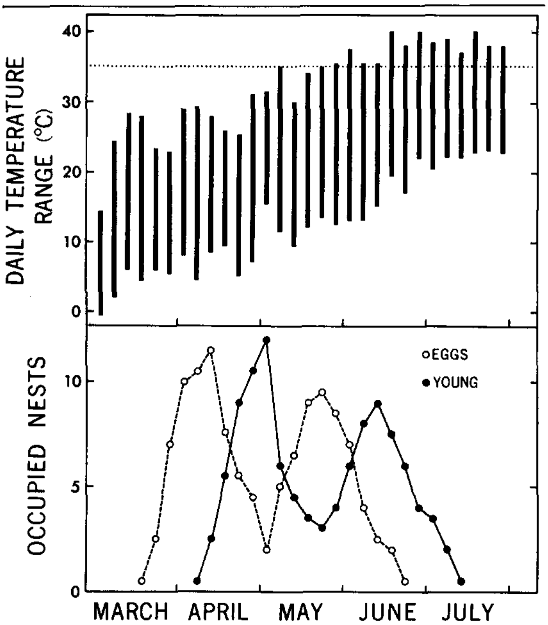

FIGURE 1. Daily air-temperature range and occupancy of breeding nests averaged over five-day periods during the 1966 breeding season. Dotted line in upper panel indicates temperatures at which feeding activity of the Cactus Wren begins to decrease (from Ricklefs and Hainsworth, 1968b).

worth 1968b). The extreme range of daily temperatures and the general increase in ambient temperature throughout the season create opposing problems in temperature regulation, especially in June when temperatures reach 40°C and morning lows are often below 15°C.

NEST TEMPERATURES

Ambient and nest temperatures were measured in occupied and unoccupied nests with mercury bulb thermometers placed in the shadow outside the nest and in the center of the nest cavity. Nest and ambient temperatures were taken systematically during a hot day in June at two empty nests which had recently fledged young. Temperatures within these nests varied between ambient and as much as 6°C warmer depending on the amount of sun striking the nest and the movement of air around it. Most of the measurements were less than 2°C above ambient temperature.

Temperatures within nests which contained young were modified in a homeostatic manner with respect to outside temperature (figs. 2 and 3). When outside air was cold the heat production in nests containing young capable of thermogenesis (older than 7 days, Ricklefs and Hainsworth 1968a) maintained the nest

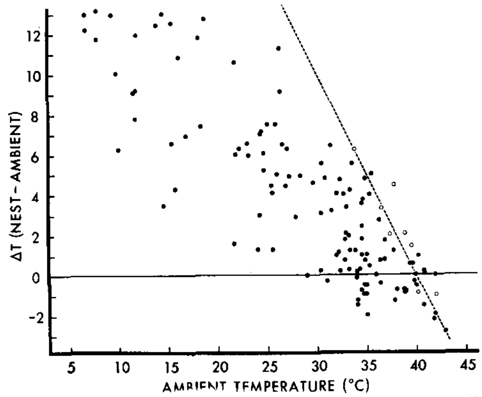

FIGURE 2. Difference between nest cavity and ambient temperatures as a function of ambient temperature for broods older than 8 days. Each point represents a single measurement; open circles indicate panting nestlings. The dashed line represents nest temperatures of 40°C.

environment as much as 13°C above ambient (fig. 2). Temperatures within nests containing young incapable of thermogenesis were elevated as much as 10°C (fig. 3). Most of this heat was probably contributed by the brooding adult.

Some nests were typically "hotter" than others, probably because of their location and construction. Wind conditions and the exposure of the nests as well as the number of young may also have contributed to the variations in the relationship between nest and outside temperature. The measurements in nests with small young may have depended partly on the time between our readings and the departure of the brooding parent from the nest.

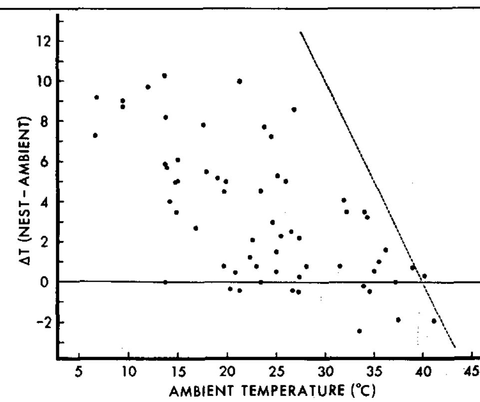

FIGURE 3. Difference between nest cavity and ambient temperatures for broods younger than 8 days. Each point represents a single measurement. The dashed line represents nest temperatures of 40°C.

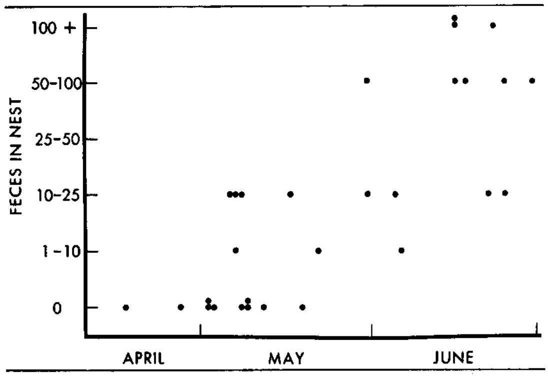

FIGURE 4. Approximate number of feces found in the floor of nest cavities after the young had fledged as a function of the fledging date.

TABLE 1. Results of nest cooling experiments.

	No treatment	Treatment a[a]	Treatment b[a]
Number of measurements	22	19	19
Average temperature difference from ambient, °C	0.78	0.66	–0.51[b]
Standard deviation	1.63	1.61	1.10

[a] See text.
[b] Significantly different from treatment a and from no treatment ($P < 0.05$).

NEST COOLING

Inspection of figures 2 and 3 reveals that above ambient temperatures of 33°C the nests were often cooler than the surrounding air, and that as the ambient temperature increased the difference between nest and outside temperature tended to decrease. A possible cause for this cooling could be evaporation from feces left in the nest. In early parts of the breeding season the fecal sacs of the young were usually removed by the parents immediately after being voided, but during the hotter parts of the nesting season they were often retained in the nest. Inspection of nests after young had fledged revealed that the number of feces had increased during the breeding season as the temperature increased (fig. 4).

Retention of fecal sacs in the nest may be an adaptation of the Cactus Wren to desert conditions, or it could result from physiological stress on the nestlings. Normally the young defecate only immediately after being fed (Ricklefs 1966). The act of defecation is made conspicuous to the attending adult which takes the fecal sac and discards it. In handling numerous nestlings we found that when they were subjected to high ambient temperatures they would defecate at times other than when they were fed. Presumably adults cannot find fecal sacs when they are not voided in their presence since they would be quickly worked into the mat of material on the floor of the nest by the movements of the nestlings.

Fecal sacs were collected from five well-grown nestlings (12 to 18 days) for a 12-hour period at an ambient temperature of 35° C to estimate fecal water loss involved in this behavior. Fecal sacs were collected in tared vessels, weighed, and dried to a constant weight at 70°C. The feces were found to contain an average of 66.3 per cent water. Approximately 1.4 ml of fecal water (5.6 per cent of body weight) was lost by each nestling during 12 hours. Since there are normally three or four nestlings to a brood, as much as 4–6 ml of water could be excreted with the feces during 12 hours in a single nest.

Experiments were performed to determine if water placed in the nest would lower the nest temperature. First, temperatures inside and outside five recently used nests were recorded as controls with no treatment. Second, a small vessel with a 4.5 cm^2 surface area of water was placed at the bottom of each nest cavity (treatment a). Third, 3 ml of water was spread onto the material at the bottom of the nest (treatment b). All of the measurements were taken between 14:00 and 16:00 during one hot July afternoon. There was very little wind and ambient temperatures ranged from 38° to 43°C.

The results are presented in table 1. Temperatures in the untreated nests averaged 0.8°C above ambient temperature. The first treatment with water (a) had no significant effect on the temperatures of the nests but the second treatment (b) lowered the temperatures of the nests an average of 1.3°C.

NEST ORIENTATION

The orientation of the nest entrance with respect to the prevailing winds may be of considerable importance in controlling the nest environment. If the nest entrance faces the wind one might expect air to circulate rapidly through the nest and reduce the difference between inside and outside temperatures. Thus, during cold weather it would seem advantageous to face away from the prevalent winds, but during hot weather circulating air might prevent heat produced by the young from overheating the nest.

Height and direction of nest entrances were measured for all nests on the study area and many in surrounding areas. The orienta-

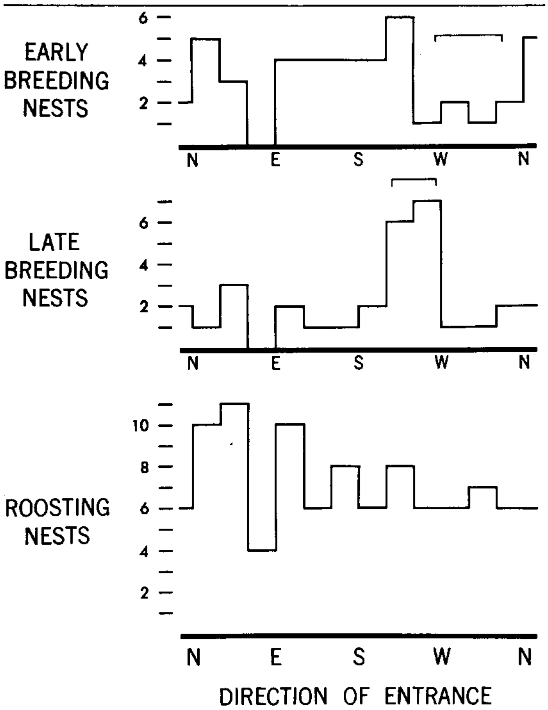

FIGURE 5. The orientation of the entrances of Cactus Wren nests with respect to true compass directions. Brackets indicate directions which are significantly avoided or favored (see text).

tion of early breeding nests (March and April), late breeding nests (May and June) and roosting nests are compared in figure 5. The distribution of entrance directions among roosting nests was not significantly different from random. Among the early breeding nests compass directions between west-southwest and north were significantly avoided ($P < 0.025$ by chi-square test), and among later breeding nests southwesterly directions were significantly favored ($P < 0.01$).

Wind directions were obtained from the U.S. Weather Bureau at the Tucson International Airport for comparison with nest entrance directions. Although these readings were taken several miles from our study area, there were no obstructions between the two locations to alter the wind direction, and casual observations of wind direction in our study area were consistent with the airport data. Wind and temperature data are summarized for early and late portions of the breeding season in figure 6. Early nests avoided the afternoon winds, which were not as cold as morning winds but were stronger. During the latter part of the breeding season most nests were constructed in such a way that they faced the wind during the hottest

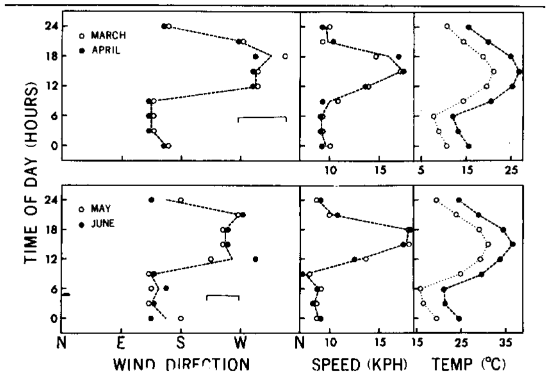

FIGURE 6. Average wind direction, speed, and temperature at different hours of the day during the early and late parts of the breeding season. Data are averaged over 8 years. Brackets indicate compass directions which are significantly avoided or favored for facing the nest entrance (see figure 5 and text).

part of the day. The random orientation among roosting nests may be related to the low wind speeds at night.

Nest height also shifted slightly with season and nest use (table 2). Roosting nests were generally placed lower than breeding nests, and during the hot part of the breeding season nests were built somewhat higher in the chollas. Suitable high nesting sites appeared to be available in all of the territories.

DISCUSSION

Measurements of nest and ambient temperatures demonstrate that the enclosed nest of the Cactus Wren in conjunction with certain behavioral patterns of the adults and nestlings provides a moderated environment for the nestlings. From these observations we can postulate economic benefits of the nest with respect to temperature regulation.

Choice of nesting site is made with little regard to the problems of temperature regula-

TABLE 2. Distribution of nest heights above ground.

	Roosting nests	Early breeding nests	Late breeding nests
Number	88	27	36
Height above ground, feet			
3–4½	45%	28%	12%
5–5½	31%	31%	35%
6–6½	9%	25%	15%
7–7½	7%	11%	23%
8	8%	6%	16%
Average height, feet	5.0	5.4	5.8

tion. In our study area nests were invariably located in tree-like cholla cacti, whereas paloverde trees (*Cercidium* sp.) offering more shade were abundant. The differences in ambient temperature between actual nest sites and the potentially cooler sites in paloverde trees generally were between 2 and 4°C (Ricklefs and Hainsworth 1968b). Although of little consequence at low temperatures, this difference may become important when environmental temperatures approach body temperature. The protection from radiation offered by the paloverde tree also enhances its desirability as a nesting site. However, the bulky nest of the Cactus Wren is very conspicuous and it would seem that a premium is placed on the formidable spiny protection of the cholla cactus. When sites other than *Opuntia* are used the nests are often located in thorny clumps of mistletoe (Bailey 1922).

Kendeigh (1960) has pointed out the energetic advantages of roosting in cavities during cold weather. From the standpoint of insulation the breeding and roosting nests of the Cactus Wren are essentially cavities. Heat lost by nestlings and adults is held in the nest cavity, thus raising the temperature and reducing the amount of energy required for homeothermy. Nest temperature equilibrates with outside air temperature when the rate of heat loss from the nest balances the rate of heat production by its occupants. As ambient temperatures decrease, heat production increases and maintains the difference between nest and outside temperature at a higher level (figs. 2 and 3).

One of the most conspicuous advantages of an enclosed nest in hot weather is the protection which it provides the nestlings from direct exposure to the sun. We frequently noted that nestlings rapidly became overheated and began to pant when they were placed in the sun. The shading of the young by the nest also frees both adults for foraging activities or to seek shade during hot weather (Ricklefs and Hainsworth 1968b). Open-nesting species in our study area either nested in more shaded parts of the cactus (Curve-billed Thrasher, *Toxostoma curvirostre*), or nested in exposed locations but remained on their nests during the day and shielded their young from intense radiation (Mourning Dove, *Zenaidura macroura*, and House Finch, *Carpodacus mexicanus*).

During hot weather the enclosed nest of the Cactus Wren impedes heat dissipation just as in cold weather, but nest temperature measurements indicate that the Cactus Wren has successfully overcome this problem. Nestling birds probably produce as much heat at ambient temperatures of 40–45°C as they do between 30–35°C (Dawson and Evans 1957, 1960). However, from figure 2 it is clear that at the higher temperatures this heat is effectively dissipated from the enclosed nest whereas at lower temperatures it is retained. At high ambient temperatures dissipation of heat from the nest can be accomplished solely by convection or the evaporation of water. The orientation of the nests during the hot part of the breeding season to face the afternoon winds demonstrates that the Cactus Wren takes advantage of convectional cooling. The retention of fecal water within the nest also appears to play a role in lowering nest temperatures. However, in our experiments with water placed in the nest cavity, we could not produce temperature differences as large as those observed in occupied nests.

SUMMARY

The enclosed nest of the Cactus Wren aids temperature regulation during cold weather by retaining heat within the insulated nest cavity. During hot weather the nest protects the young from the direct rays of the sun but also impedes dissipation of heat produced by the nestlings. This may be partially compensated by the evaporation of water from fecal sacs retained within the nest cavity. Nest entrances are oriented to avoid winds during the early, cooler, parts of the breeding season and to face them during the hot part of the season. Thus, the construction and orientation of the nest and the behavior of the adults and young effectively moderate the nest environment under widely varying environmental conditions.

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