TEMPERATURE REGULATION IN NESTLING CACTUS WRENS: 
THE DEVELOPMENT OF HOMEOTHERMY

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The development of the capacity to regulate 
body temperature at low ambient tempera-
tures has been well documented for the young 
of several species of altricial birds (Baldwin 
and Kendeigh 1932; Kendeigh 1939; Boni 
1942; Odum 1942; Dawson and Evans 1957, 
1960; Maher 1964). Altricial nestlings are 
essentially poikilothermic at hatching, but 
during the period of growth their capacity 
to produce heat (thermogenesis) increases, 
and before the young leave the nest they 
have attained a state of homeothermy ap-
proaching that of the adult.

The ability of altricial nestlings to regulate 
their body temperatures under heat stress has 
not been extensively investigated. Because 
the problems facing homeothermic organisms 
at low and high environmental temperatures 
differ in several basic respects, the develop-
ment of physiological and behavioral regula-
tory responses involved in the dissipation of 
heat (thermolysis) could be expected to differ 
from those involved in thermogenesis. This 
report presents an account of the thermo-
regulatory capabilities of nestling Cactus 
Wrens (Campylorhynchus brunneicapillus) 
over the temperature range encountered in 
their environment during the breeding sea-
son (approximately 5 to 45°C).

SUBJECT AND METHODS

The Cactus Wren is a permanent resident of 
semi-arid desert-scrub areas of the south-
western part of the United States and northern 
México. In the Sonoran Desert near 
Tucson, Arizona, its breeding season usually 
extends from March to August, during which 
two and occasionally three broods of three 
or four young are raised. The Cactus Wren is 
an ideal subject for developmental studies 
because of its long nestling period (20 days), 
convenient size, and accessibility. The de-
velopment of structural and behavioral fea-
tures of the Cactus Wren are described in 
detail by Anderson and Anderson (1961).

Nestlings were collected in the evening or 
the morning before measurements were made, 
and they were returned to their nests within 
24 hours. Individuals were not used more than 
time. The young were fed ground beef and 
meal worms (Tenebrio larvae) and were 
maintained in a replete condition during the 
experiments. The ages of nestlings were usu-
ally known from our observations at nests and 
were confirmed by comparing wing length 
with a standard wing length growth curve 
(Anderson and Anderson 1961).

Temperature regulation at ambient tem-
peratures below 35°C was studied by placing 
nestlings in 200-ml plastic jars with air-tight 
lids. Air was passed through these containers 
at a constant rate (one liter/min) after it was 
dried by passage through tubes of Drierite 
dessicant (anhydrous calcium sulfate). Tem-
peratures inside the containers were measured 
with indwelling mercury thermometers. The 
nestlings were isolated from the walls of the 
containers by nylon mesh so that a maximum 
amount of the body surface was exposed to the 
circulating air. A range of ambient tempera-
tures was obtained by taking measurements 
at various times during the day throughout 
the breeding season. After the nestlings had 
been in the chambers for 45 minutes their 
body temperatures were measured by insert-
ing a thermistor probe through the mouth 
deep into the proventriculus. Regulation at 
temperatures above 35°C was studied by 
placing nestlings in shallow paper cups in a 
constant temperature incubator (+ 0.5°C).

Body temperatures were measured over a 
three-hour interval at ambient temperatures 
of 36, 40, and 44°C. The relative humidity 
was not controlled but never exceeded 20 
per cent.

Temperatures of nestlings in the field were 
measured with orally inserted thermistors. 
Temperatures in the center of the nest cav-
ities and in the shade outside the nests were 
measured with permanently fixed mercury 
thermometers.

RESULTS

Thermogenesis. Thermostatic regulation first 

becomes evident at 9 days of age in the Cactus Wren (fig 1). Body temperatures of younger nestlings change with ambient temperature in a typically poikilothermic manner. An obvious, gradual transition toward thermogenic homeostasis occurred from 10 to 12 days, and regulatory capability is essentially complete by the 13th day after hatching.

The temporal aspects of the development of thermogenesis in the Cactus Wren differ from those of other altricial species. For comparative purposes the rate of development of homeothermy can be illustrated by graphing the difference between body and ambient temperature for nestlings as a percentage of the difference maintained by the adult. This index can be averaged over a wide range of ambient temperatures and gives a useful estimate of the percentage of adult regulatory capability that is achieved at a given stage of development. Data for the Cactus Wren at temperatures between 13 and 23°C were used to calculate the index presented in figure 2, with comparable data for the Vesper Sparrow (Poecetes gramineus) from Dawson and Evans (1960). Boni (1942) used an analogous method for comparing several Old World species graphically.

From figure 2 it can be seen that the initiation of homeothermic responses occurs later in the Cactus Wren (9 days) than in the Vesper Sparrow (5 days) and further that the period in which thermoregulatory capacity develops is somewhat prolonged in the former (9-12 days vs. 5-7 days). These differences are consistent with the comparative lengths of the nestling periods in the two species: young Vesper Sparrows leave the nest after about 10 days (Dawson and Evans 1960), whereas Cactus Wrens fledge at 20 days. It is interesting in this regard that there is also a considerable difference between the time homeothermy is attained and the time of fledging. This period amounts to 7-8 days for the Cactus Wren but only 2-3 days for the Vesper Sparrow.

**Thermolysis.** Ambient temperatures above 36°C induce a progressively greater state of hyperthermia in nestling Cactus Wrens of all ages (fig. 3). After one-half hour exposure at each temperature the nestlings achieve a body temperature that is maintained relatively constant for the remaining two and one-half hours of the observation. At 36°C body temperatures are typical of those observed in homeothermic nestlings at lower ambient temperatures, except for nestlings younger than 9 or 10 days whose body temperatures are slightly lower. At 40°C body temperature increases slightly, and at 44°C hyperthermia is pronounced with a body-temperature elevation of at least 2 degrees. Simultaneous with the increasing hyperthermia there is a reduction in the difference between body and ambient temperature until, at 44°C, nestlings maintain their temperatures an average of about one-half to a full degree below ambient. There is also some indication that the extent...
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FIGURE 2. The development of homeothermy at ambient temperatures between 13 and 23°C in the Vesper Sparrow, Pooecetes gramineus (open circles, from Dawson and Evans 1960), and the Cactus Wren (blackened circles). Each point represents a single measurement; the solid lines are drawn through the averages for each age. An adult body temperature of 42°C was used for the calculation of percentages.

Field observations. In order to relate the physiological responses observed in the laboratory to the behavior and ecology of the Cactus Wren, we made supplementary field measurements of body temperatures of nestlings. It was found that nonregulating young (less than 7 days old) are maintained at near homeothermic temperatures in the nest by parental brooding (fig. 5). Thus, the behavior of the adult birds effectively compensates for the absence of thermogenesis in very small nestlings.

During hot weather, when air temperatures in the field exceed 36°C, the nestlings exhibit diurnal patterns of hyperthermia in response to the daily temperature fluctuations (fig. 6). As their body temperatures increase they display all of the typical thermolytic responses that are seen during experimental heat stress in the laboratory. The field observations also indicate that older nestlings maintain higher body temperatures under heat stress in the nest than do younger nestlings.

DISCUSSION

The lack of thermogenic capabilities of altricial nestlings at early ages is probably linked to evolutionary advantages associated with rapid development (Dawson and Evans 1957).
The delayed maturation of the neuromuscular systems and the insulative integument necessary for thermogenesis and heat retention may result in the allocation of additional tissue to growth rather than maintenance functions. The fact that adult brooding can economically maintain nestling body temperatures within suitable limits for development may also be a factor in the retention of poikilothermy in altricial nestlings.

Thermoregulatory responses to cold are not initiated in the Cactus Wren until 9 days of age, several days later than the first evidences of thermogenesis in the Vesper Sparrow (fig. 2). Dawson and Evans (1957) noted a correlation among several species between the age at which homeothermy was achieved and the length of the nestling period. We may ask if these differences are a result merely of increases in overall growth rate that may be correlated with shorter nestling periods, or of a more precocious development of temperature regulation in species whose young fledge quickly. We have answered this question by comparing the development of homeothermy by means of the percentage index described above (fig. 2) plotted on a modified time scale, the growth index (Ricklefs 1967) that is adjusted for growth rate and causes the curves for body weight of the different species being considered to coincide. This is accomplished by fitting the "logistic" equation to the growth curve of each species and normalizing the time scale by a factor that is proportional to the rate constant of the fitted equation. Zero time is arbitrarily designated as the point at which half of the total growth is attained. In this manner we may compare the development of thermoregulation among species with respect to growth, rather
than time, but still retain the proper temporal relationships of each development curve.

If differences in the development of homo-
thermy are a result of differences in growth rate, all of the curves for thermogenic de-
velopment in different species should coincide when plotted as a function of the develop-
ment index. This does not occur (figs. 7 and 
8). It can be seen, for example, that the 
Vesper Sparrow and other finches show a 
much more rapid development of thermo-
genesis with respect to growth than do the 
Cactus Wren and the House Wren, even 
though growth rates have been normalized.

This finding indicates that the development 
of thermogenesis with respect to growth is 
evolutionarily flexible in its adjustment to 
short nesting periods.

Because the Cactus Wren and the House 
Wren develop homeothermy long before fledg-
ing, one can assume that they are not under 
pressure to develop thermogenesis at an early age and, therefore, that the pattern of acquisi-
tion of homeothermy is optimal with respect to growth in these species. This would sug-
gest that the more precocious development of homeothermy in the finches, which is related 
to their early fledging, may result in less-
efficient growth and energy utilization. For example, it can be seen in figures 7 and 8 that finches are able to regulate their body temperatures at a point in development where wrens are not capable of thermogenesis and must still be brooded by the adult. Tempera-
ture regulation at these early developmental stages is probably more costly owing to a less 
well-developed plumage and higher surface-
volume ratios. The energy expenditure of nestling finches may be reduced if adults con-
tinue to brood the young after homeothermy is achieved, and a full assessment of efficien-
cies of energy expenditure in different species would necessarily include examination of such factors. However, on the basis of the develop-
ment of thermogenesis it appears that wrens are more efficient in energy allocation during 
growth.

Although small nestlings do not show regu-
latory responses to cold temperatures, three observations of young Cactus Wrens indicate that they respond to heat stress in a manner similar to older birds: (1) nestlings of all ages show open-mouth breathing at high ambient temperatures, (2) they increase their breath-
ing rate in the heat, and (3) young nestlings maintain their body temperatures below am-
bitent temperature at 44°C. Kendeigh (1939) has also observed these responses in young nestling House Wrens (*Troglodytes aedon*) exposed to heat stress.

Panting, which is probably the most impor-
tant thermolytic response in very small nest-
lings, appears to involve an elaboration of 
two behavioral features that are normally 
present and have functions other than those 
associated with heat dissipation: (1) the 
gaping or begging response to obtain food 
from the parents, and (2) breathing for res-
piratory gas exchange. These responses in-
volve motor patterns that are well developed 
at hatching, and only an increase in the rate of respiration is necessary to accomplish the thermolytic function. This condition, plus the 
fact that the adults probably could not cool 
the nestlings as effectively as they can heat 
them, may explain the lack of a developmental 
dependence of thermolytic responses in young 
altricial nestlings.

Heat loss in small nestlings must also be 
facilitated by features that are not responsive 
in nature, such as the high surface-volume 
ratio, lack of plumage, and poorly keratinized 
tegument of the small nestlings. In addition, the 
area of the mouth, which is used as an 
evaporative surface, is large in comparison to 
body size in small nestlings. Dawson and
FIGURE 7. The development of temperature regulation between 13 and 23°C with respect to growth in four species: Snow Bunting, *Ectethops nivosus* (open circles, heavy dotted line; from Maher 1964), Field Sparrow, *Spizella pusilla* (open triangles, light dotted line; from Dawson and Evans 1957), Chipping Sparrow, *Spizella passerina* (open squares, dashed line; from Dawson and Evans 1957), and the Cactus Wren (solid circles, solid line). The growth index is -0.5 at 25 per cent, 0 at half growth, +0.5 at 75 per cent growth, 1.0 at 90 per cent growth and 1.5 at 96.5 per cent growth (for details see text).

FIGURE 8. The development of temperature regulation between 13 and 23°C with respect to growth in four species: Lapland Longspur, *Calcarius lapponicus* (open circles, heavy dotted line; from Maher 1964), Vesper Sparrow, *Pooecetes gramineus* (open triangles, light dotted line; from Dawson and Evans 1960), House Wren, *Troglodytes aedon* (open squares, dashed line; from Kendeigh 1939), and the Cactus Wren (solid circles, solid line).
Evans (1957) have further pointed out that the weight-relative production of heat may be lower in early stages of development of passerines. Thus it is not surprising that heat stress does not pose a serious challenge to the capacity of small nestlings to regulate their body temperature.

The observation that nestlings are able to maintain their body temperatures below ambient temperature at 44°C indicates that metabolic heat can be dissipated entirely by evaporative means. However, tolerance of hyperthermia until lethal body temperatures are approached further indicates that the amount of water necessary to maintain even lower body temperatures may be prohibitive. Controlled hyperthermia allows nestlings to take advantage of nonevaporative means of heat loss and thus to conserve water.

SUMMARY

The development of homeothermy in nestling Cactus Wrens was investigated over the range of ambient temperatures prevailing in their habitat during the nesting season. Thermogenic responses develop later and more slowly than in other species that have shorter nestling periods. This is at least partly a result of a more precocious development of homeothermy with respect to growth in species with shorter nestling periods. Very young nestlings do not demonstrate regulatory responses to cold temperatures, but they respond to heat stress by open-mouth breathing and increased respiration as do older nestlings. The problems of thermolysis are further alleviated in very young nestlings by their high surface-volume ratio and general lack of insulating plumage, features that render homeothermy at low temperatures very inefficient.

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LITERATURE CITED


MAHER, W. J. 1964. Growth rate and development of endothermy in the Snow Bunting (Plectrophenax nivalis) and Lapland Longspur (Calcarius lapponicus) at Barrow, Alaska. Ecology 45:520-528.


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