

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 temperatures 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 approaching 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 development of physiological and behavioral regulatory 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 thermoregulatory capabilities of nestling Cactus Wrens (*Campylorhynchus brunneicapillus*) over the temperature range encountered in their environment during the breeding season (approximately 5 to 45°C).

SUBJECT AND METHODS

The Cactus Wren is a permanent resident of semi-arid desert-scrub areas of the southwestern 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 development of structural and behavioral features 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 once. 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 usually 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 temperatures 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 desiccant (anhydrous calcium sulfate). Temperatures 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 temperatures 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 inserting 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 ($\pm 0.5^\circ\text{C}$). 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 cavities and in the shade outside the nests were measured with permanently fixed mercury thermometers.

RESULTS

Thermogenesis. Thermostatic regulation first

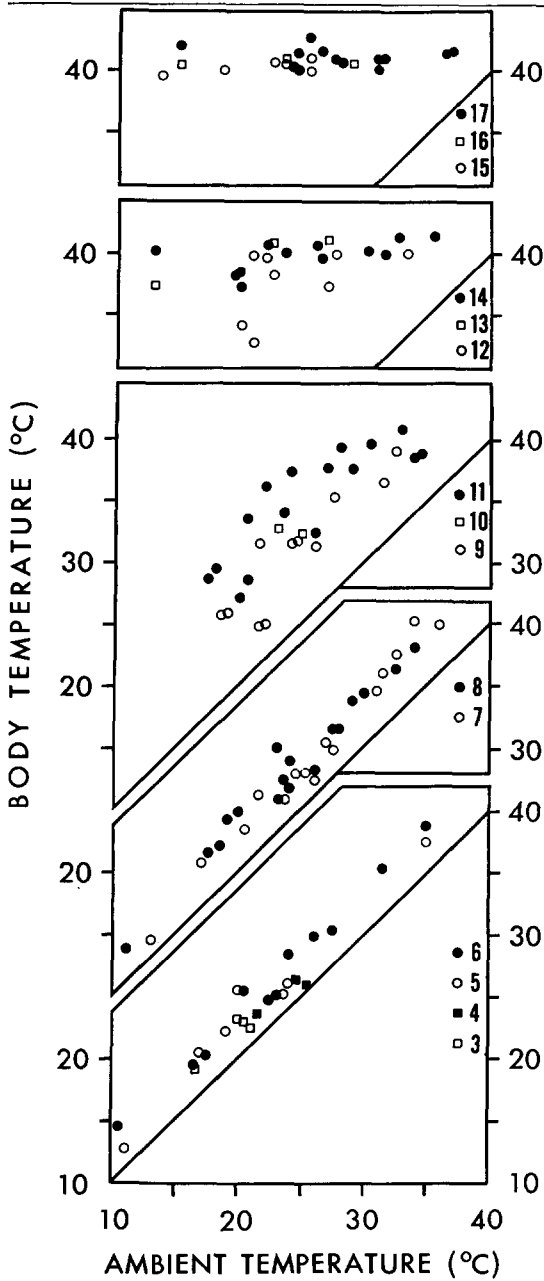


FIGURE 1. The relationship between body and ambient temperature in nestling Cactus Wrens as a function of age. Ages in days are shown at the lower right of each section. Each point represents a single measurement.

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 (*Pooecetes 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

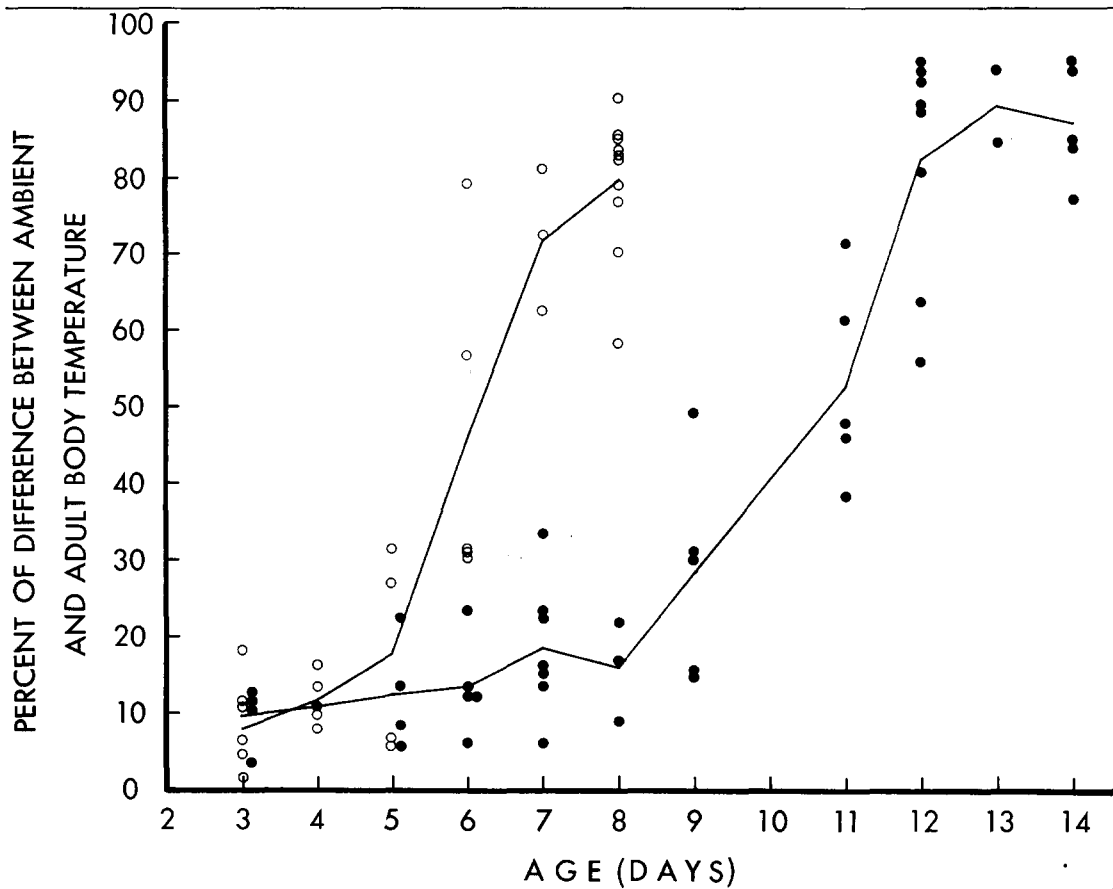


FIGURE 2. The development of homeothermy at ambient temperatures between 13 and 23°C in the Vesper Sparrow, *Pooecetes gramineus* (open circles, from Dawson and Evans 1960), and the Cactus Wren (blackened circles). Each point represents a single measurement; the solid lines are drawn through the averages for each age. An adult body temperature of 42°C was used for the calculation of percentages.

of hyperthermia maintained at a given temperature increases slightly with age.

Nestlings of all ages show homeostatic responses to increased temperatures that are similar to those shown by adults. Open-mouth breathing is obvious at temperatures of 40 and 44°C. In addition, the inside of the mouth is kept quite moist and provides a relatively large evaporative surface. Older nestlings hold their wings away from their bodies, thereby increasing the exposed surface and facilitating heat loss. Limited data also indicate that breathing rates of nestlings of all ages increase at temperatures above 36°C (fig. 4). All of these observations emphasize the presence of a well-developed thermolytic response in nestlings of all ages.

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).

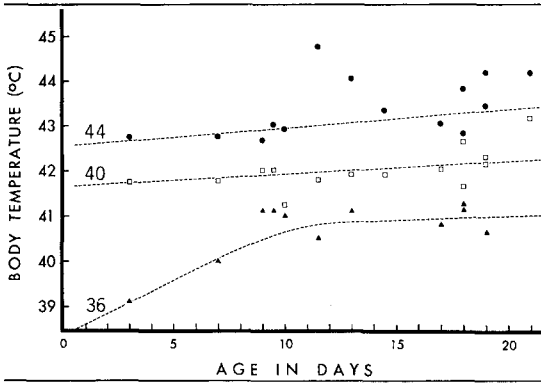


FIGURE 3. Body temperatures of nestling Cactus Wrens as a function of age at ambient temperatures of 36, 40, and 44°C. Each point represents the average of five measurements made with one individual during a two and one-half hour period. The curves for each ambient temperature (dashed lines) were fitted by eye with emphasis on the lower body temperatures.

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

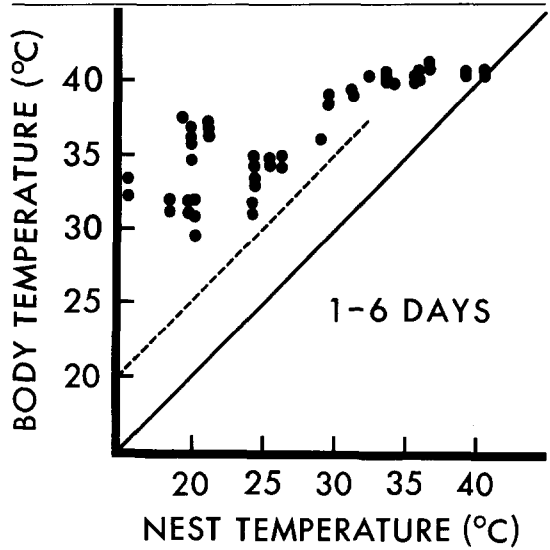


FIGURE 5. The relationship between temperatures of nestling Cactus Wrens and their nest-cavity temperature before the onset of thermogenesis. Each point represents a single measurement. The broken line indicates the upper limit of the relationship between body and ambient temperature observed in the laboratory.

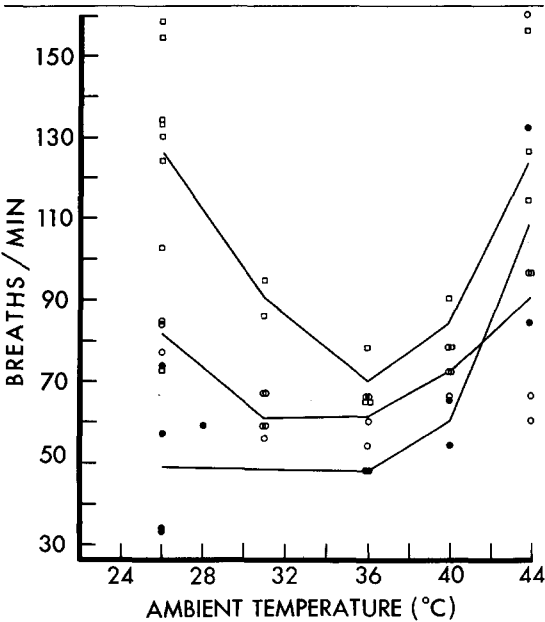


FIGURE 4. Breathing rate as a function of temperature in Cactus Wrens: (1) before the onset of thermogenesis (less than 8 days; blackened circles), (2) during the development of thermogenesis (8 to 12 days; open circles), and (3) fully homeothermic (greater than 12 days; open squares). Each point represents a single observation. Curves are drawn through the averages for each temperature.

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

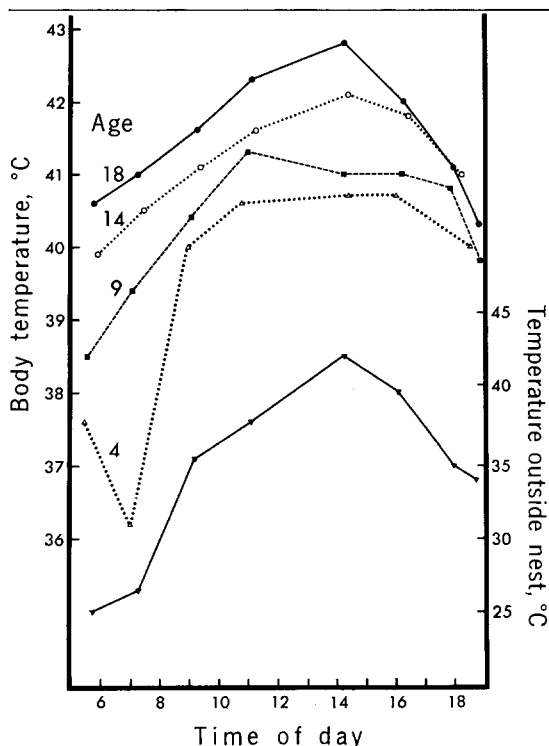


FIGURE 6. Diurnal pattern of body temperatures in the nest of four broods of different ages (days). Each point is the average of two measurements for each brood. The temperature measurements outside the nest are averages for all four nests.

than time, but still retain the proper temporal relationships of each development curve.

If differences in the development of homeothermy are a result of differences in growth rate, all of the curves for thermogenic development in different species should coincide when plotted as a function of the development 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 thermogenesis 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 nestling periods.

Because the Cactus Wren and the House Wren develop homeothermy long before fledging, one can assume that they are not under pressure to develop thermogenesis at an early age and, therefore, that the pattern of acquisition of homeothermy is optimal with respect to growth in these species. This would suggest 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. Temperature 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 continue to brood the young after homeothermy is achieved, and a full assessment of efficiencies of energy expenditure in different species would necessarily include examination of such factors. However, on the basis of the development of thermogenesis it appears that wrens are more efficient in energy allocation during growth.

Although small nestlings do not show regulatory 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 breathing rate in the heat, and (3) young nestlings maintain their body temperatures below ambient 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 important thermolytic response in very small nestlings, 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 respiratory gas exchange. These responses involve 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 integument 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

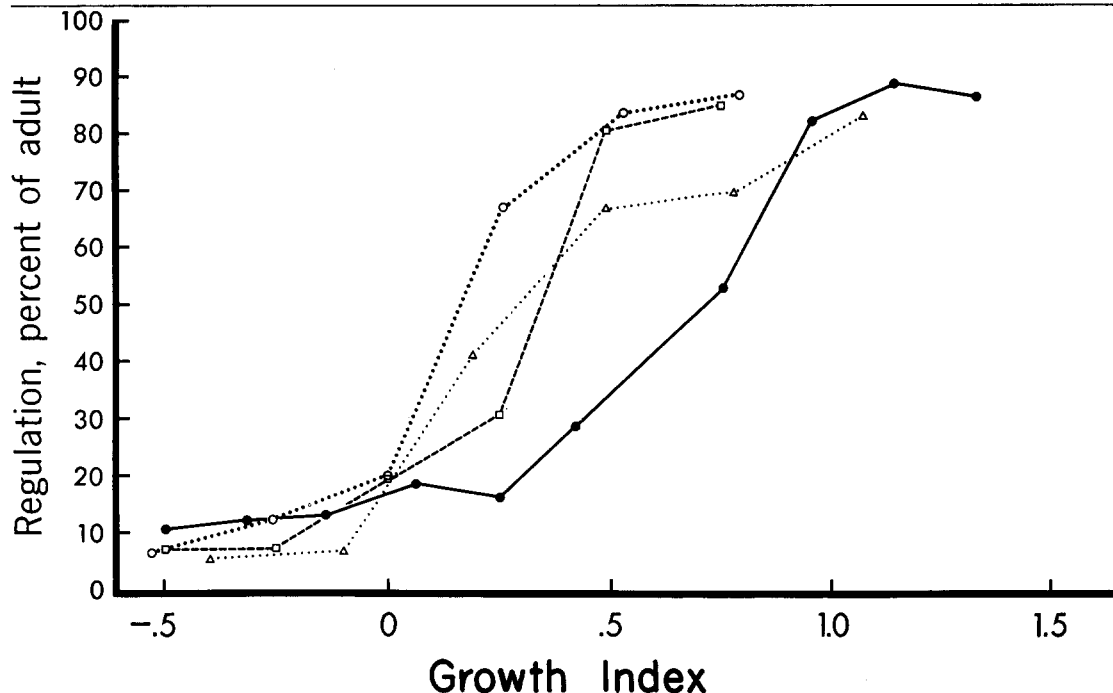


FIGURE 7. The development of temperature regulation between 13 and 23°C with respect to growth in four species: Snow Bunting, *Plectrophenax nivalis* (open circles, heavy dotted line; from Maher 1964), Field Sparrow, *Spizella pusilla* (open triangles, light dotted line; from Dawson and Evans 1957), 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).

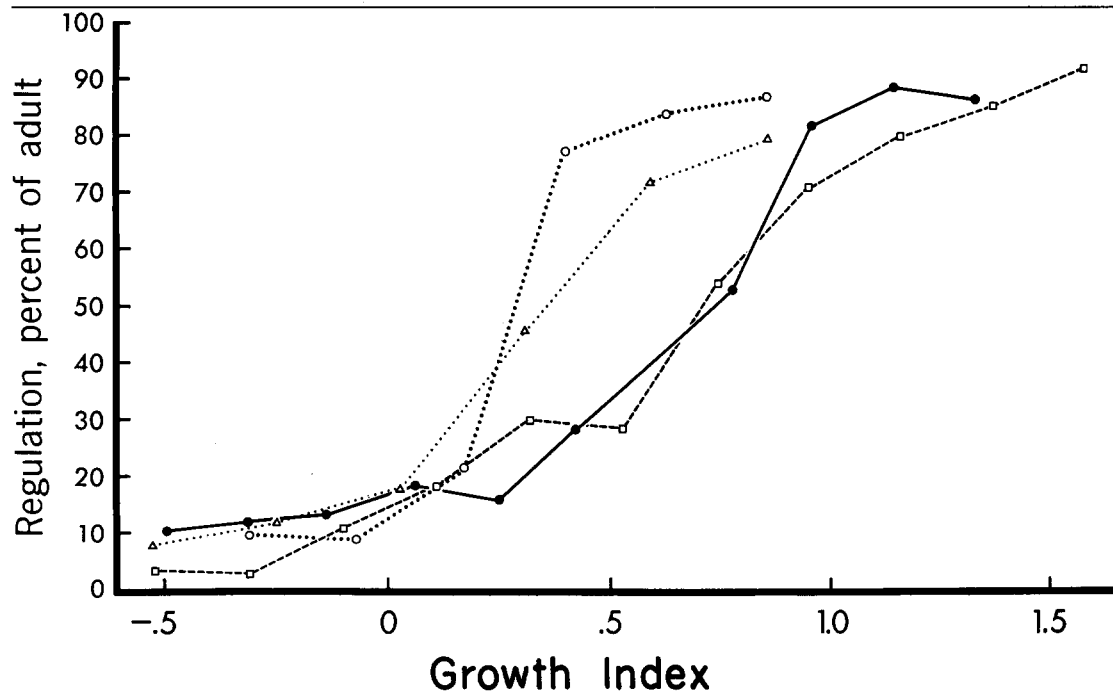


FIGURE 8. The development of temperature regulation between 13 and 23°C with respect to growth in four species: Lapland Longspur, *Calcarius lapponicus* (open circles, heavy dotted line; from Maher 1964), Vesper Sparrow, *Poocetes gramineus* (open triangles, light dotted line; from Dawson and Evans 1960), 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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