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## Development of temperature regulation in nestling tree swallows

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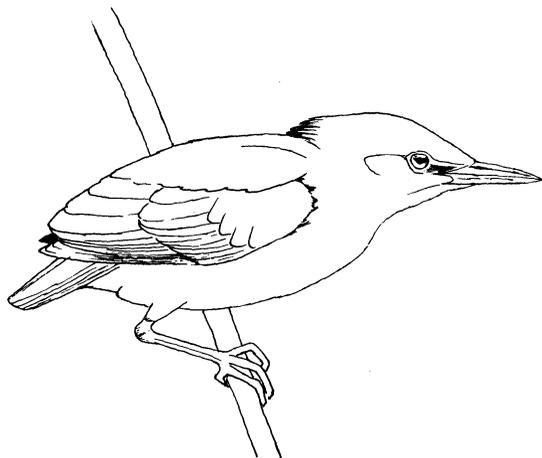


FIGURE 1. Zigzag Heron (*Zebriulus undulatus*), drawn from field sketch by Paul K. Donahue.

Nervous tail flicking also occurs in the Rufescent Tiger-Heron (*Tigrisoma lineatum*), a forest heron commonly observed at Explorer's Inn. One immature bird observed by Donahue continuously flicked its tail, bringing the tail down slowly and then flicking it up rapidly. Herons in the genus *Butorides* also flick their tails.

Although the Zigzag Heron allowed our close ob-

servation, it appeared nervous and at irregular intervals (every minute or so) performed 180° manakin-like jumping turns on its perch. Observation ended when the bird flew into the dense undergrowth.

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## DEVELOPMENT OF TEMPERATURE REGULATION IN NESTLING TREE SWALLOWS

RICHARD L. MARSH

The nestlings of several species of altricial passerines lack any thermogenic response to low ambient temperatures ( $T_a$ ) during approximately the first half of their growth (see discussion in Marsh 1979; also, Mertens 1977a). Apparent improvements in the thermoregulatory capacity during the early phase of growth, as reflected by body temperatures ( $T_b$ ) after a standardized cold exposure, are due to the relationship of cooling rate to size and are not due to active metabolic regulation (Marsh 1979). This pattern of development may influence the parental behavior and nesting ecology of passerines (see Dawson and Hudson 1970, Dunn 1975, for reviews). The present study examines the development of temperature regulation in individual nestling Tree Swallows (*Iridoprocne bicolor*) under laboratory conditions. These data extend the range of observations of thermoregulatory development in passerines and aid in interpreting the mechanisms underlying the maintenance of homeothermy under field conditions (cf. Dunn 1979).

I studied Tree Swallow nestlings during July 1971, at the University of Michigan Biological Station, Pellston, Cheboygan County, Michigan. Nestlings from

three nests (two clutches of five and one clutch of three) located in nest boxes were used. The nestlings were individually marked, and at least two days elapsed between the successive use of any individual in laboratory tests.

Nestlings were weighed in the field to the nearest 0.1 g and were taken to the laboratory in covered insulated containers. Laboratory tests began 5-30 min after removal of the birds from the nest box. Nestlings were placed individually in open, one-pint containers lined with paper packing material, 1 cm thick, and maintained for 2 h at a  $T_a$  between 19.3 and 21.0°C in a darkened basement room. Body temperatures at the beginning and end of the tests were measured orally with a Yellow Springs Instruments thermistor probe (no. 402). The initial body temperatures varied somewhat due to cooling of the smaller nestlings in transit. However, relatively warm air temperatures (mean 26.4°C) and the insulated transport containers minimized this effect. The lowest initial  $T_b$  was 32.6°C. Nestlings were examined for shivering at the beginning and end of the tests. Feather lengths were measured to the nearest millimeter with a ruler.

Nestlings reached peak body masses in approximately 12 days (Fig. 1). The growth curve can be described by the logistic equation with a growth constant (Ricklefs 1967) of 0.391 and an estimated asymptote of 23.0 g. The asymptotic value slightly exceeds the mean adult mass of Tree Swallows in Michigan (mean = 21.2 g,  $n = 18$ , S.E. = 0.37; specimens in the University of Michigan Museum of Zoology). Dorsal contour feathers appeared at six to seven days (10-15 g) and primary

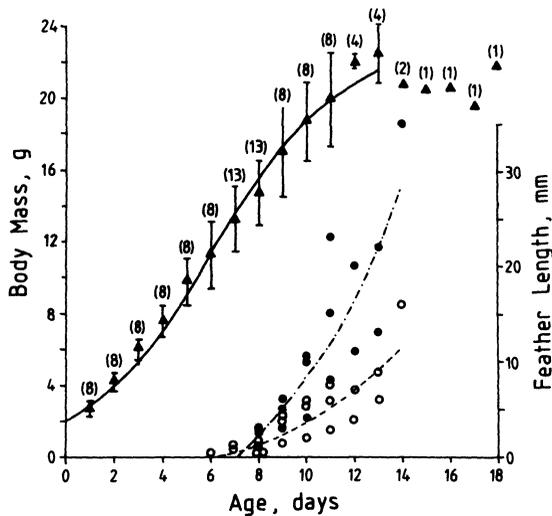


FIGURE 1. Body mass (triangles), length of the eighth primary (closed circles), and length of dorsal contour feathers (open circles) as a function of age in nestling Tree Swallows.

no. 8 at seven to eight days (15–17 g) (Fig. 1). The growth of the nestlings used in this study closely resembled that observed by Paynter (1954). Apparently, nestling growth was not slowed appreciably by the testing.

When exposed to a  $T_a$  of 20°C for 2 h, young nestlings cooled to within a few degrees of their surroundings (Fig. 2A). Thermoregulatory capacity improved little during the first seven to eight days, but rapidly thereafter. By 10 days of age, most nestlings maintained body temperatures above 35°C over 2 h at a  $T_a$  of 20°C. The data show less spread when  $T_b$  is plotted against mass rather than age (Fig. 2B). The  $T_b$  increases slight-

ly from 3 g to approximately 12–13 g and markedly thereafter. By 17 g most nestlings have a  $T_b$  of above 35°C. This pattern of development of thermoregulation closely resembles that found in Bank Swallows (*Riparia riparia*; Marsh 1979): it is probably related to the absence of a thermogenic response to cold during early post-hatching development and the subsequent rapid maturation of this response. This conclusion is supported by my observations of shivering in the nestling Tree Swallows. I never saw shivering in nestlings weighing less than 11 g during these tests. Nestlings weighing between 11.0–17.0 g shivered upon exposure to 20°C. Shivering was not evident in the two heaviest nestlings tested (17.8 and 18.4 g).

Numerous studies show that homeothermy is maintained under field conditions throughout the development of nestling passerines (see Irving and Krogh 1956). During the phase of growth in which an endothermic response to low  $T_a$ 's is absent,  $T_b$  must be maintained by mechanisms that retard the rate of cooling or by parental brooding. Thus, the dependence of nestlings on brooding during this stage will depend on brood size (Dunn 1976a, 1979), huddling behavior, and/or nest insulation (Mertens 1977b).

In contrast to the absence of a thermogenic response in young altricial passerines (Mertens 1977a, Marsh 1979), a metabolic response to low  $T_a$ 's has been found early in the growth phase ( $\leq 25\%$  adult mass) of several altricial nonpasserines (Ginglinger and Kayser 1929, Hudson et al. 1974, Hamas 1975, Dunn 1976b). This difference in thermoregulatory response reveals an underlying diversity in the development of species classified as having altricial development. Because of the importance of shivering thermogenesis in thermoregulatory development, such diversity may reside at least partially in the development of the skeletal muscles (see Ricklefs 1979).

I conducted this project while I was a student at the University of Michigan Biological Station. W. R. Dawson provided suggestions throughout the study, O. S. Pettingill provided access to the Tree Swallow nest

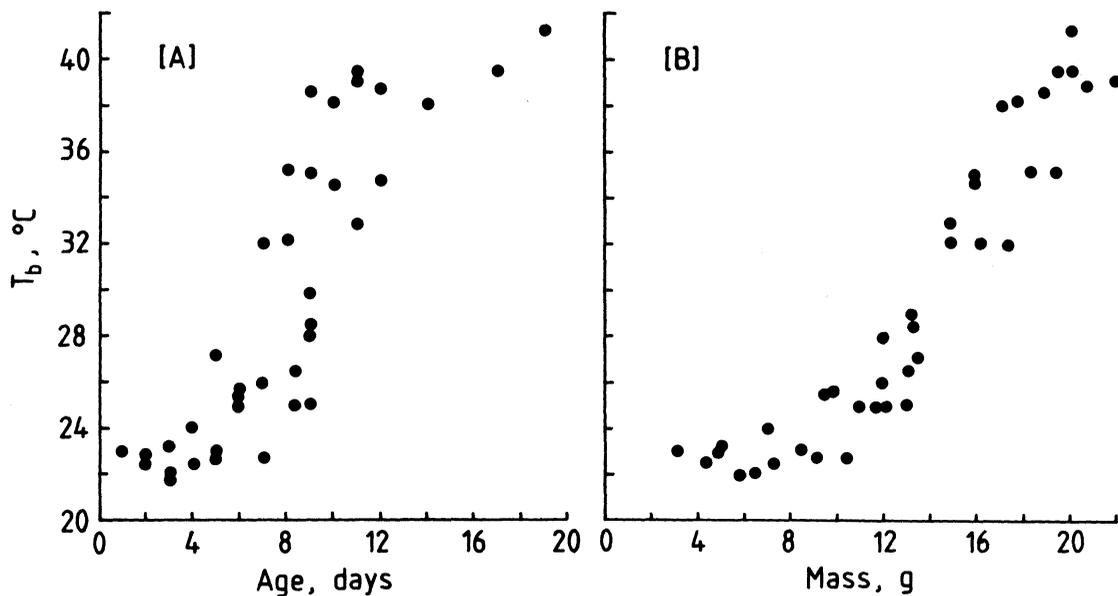


FIGURE 2. Body temperatures of nestling Tree Swallows after 2 h at  $\approx 20^\circ\text{C}$ . A, body temperature versus age. B, body temperature versus body mass.

boxes, and J. B. Odenheimer helped edit the manuscript. Financial support during the writing of this report was obtained from NSF grant DEB 77-25487 to W. R. Dawson.

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## A NESTING HUMMINGBIRD FEEDING SOLELY ON ARTHROPODS

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AND

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Hummingbirds usually forage on floral nectar and other sugar sources, apparently feeding on insects and other arthropods only incidentally (Feinsinger and Colwell 1978). Although Wagner (1946) and others have suggested that some species feed largely on insects at certain times of the year, detailed time budget studies of various hummingbirds have shown that less than 15% (and usually less than 5%) of their foraging time is spent catching arthropods (for summary, see Gass and Montgomerie 1980). Even during the nesting period, when animal food may be nutritionally important for egg production and nestling growth (Ricklefs 1974), female hummingbirds seem to rely on nectar as their primary energy source (Hainsworth 1977). Here we present evidence that a nesting hummingbird can subsist, at least for a few days, on a diet of arthropods.

During the last two weeks of May 1978, we observed a nesting female Broad-tailed Hummingbird (*Selasphorus platycercus*) in Rose Canyon, Santa Catalina Mountains, Arizona (elev. 2,200 m). The nest was 3.9 m up in a silverleaf oak (*Quercus hypoleucoides*) in an open woods of oak and ponderosa pine (*Pinus ponder-*

*osa*), and contained two eggs on both 21 and 31 May. We recorded time budgets of the female on 19, 20, and 21 May by sampling for a randomly chosen 10-min period during each daylight hour (06:00 to 20:00). Time spent by the bird in each activity was recorded to the nearest 2 s. We were able to keep the bird in sight for 91% of the 520 min of observation. We always began an observation from a location about 15 m from the nest, far enough away that the incubating female did not appear to be disturbed by our presence.

We began this study because the extensive woodland habitat around the nest lacked the nectar-producing flowers that hummingbirds usually visit. To measure this, we surveyed a transect 500 m long by 30 m wide along each of the eight cardinal compass directions away from the nest. These covered about 15% of the 1-km diameter circle centered on the nest. During 19-22 May we found only a few *Viola*, *Helianthus*, and *Potentilla* flowers within this area, and none of these produced measurable quantities of nectar. On 31 May, however, Indian paintbrush (*Castilleja miniata*) was common. Three inflorescences were blooming less than 50 m from the nest and all contained nectar.

During the 19 foraging bouts (totaling 1,150 s) that we observed, the hummingbird spent all of her time either flycatching, gleaning from leaves, probing among lichens on tree trunks, or flying between foraging sites. Most of these observations were made within 100 m of the nest, but twice we followed her about 400 m up a small stream where she caught flies above a pool. Although we were able to follow this bird only 22% of the time that she was off her nest, most of these bouts were brief ( $\bar{x} = 113$  s, SE = 18.7, n = 62), and the bird was often audible as she foraged