DEVELOPMENT OF ENDOThERMY IN NESTLING BANK SWALLOWS (RIPARIA RIPARIA)\textsuperscript{1}

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Body temperature ($T_b$) measurements after exposure to air temperatures ($T_a$) of 20 C or 27 C for 2 h in conjunction with metabolism measurements were used to describe the timing of and basis for developing temperature regulation in nestling swallows. As growth proceeds from hatching to 10 g there is a gradual increase in the $T_b$ after exposure to low $T_a$. As growth continues beyond this point, the ability of nestlings to maintain $T_b$ above $T_a$ improves rapidly, such that nestlings weighing over 14 g are completely homeothermic when exposed to 20 C. Conductance ($C$, in cal [g·h·°C]\textsuperscript{−1}) decreases throughout growth following the equation: \[ \log C = -0.501 \log m + \log 6.902, \] where \( m \) = mass in grams. Conductance values and the relation of $T_b$ to metabolism were used to predict the $T_b$ after exposure to 20 C for 2 h, assuming the nestlings cooled passively. These calculations demonstrate that large changes in $T_b - T_a$ can occur with growth even in the absence of active metabolic regulation. The major conclusions of this study are: (1) in bank swallows, mass is a better predictor of thermoregulatory ability than age; (2) conductance values are influenced mostly by increasing mass, whereas the developing plumage during the nesting period does not significantly retard heat loss; (3) apparent improvement in thermoregulation with growth in nestlings weighing less than 10 g is due to changes in passive resistance to cooling, not improvement in active metabolic regulation; and (4) active metabolic regulation develops rapidly as nestlings increase in mass above 10 g.

INTRODUCTION

The limited thermoregulatory capacities of young altricial birds have been the subject of numerous investigations over the last several decades (see recent reviews by Dawson and Hudson 1970; Dunn 1975). However, the causal factors responsible for the development of temperature regulation in altricial nestlings have not been clearly elucidated. Previous authors have concluded that several factors—including increasing mass, increasing insulation, and increasing thermogenic capacities—are involved in this development (see Baldwin and Kendigh 1932) but have disagreed on the relative importance of these factors. Dawson and Evans (1957, 1960) implicated improving thermogenic capacities and a declining surface-to-volume ratio due to increasing mass as the most important factors. Ricklefs (1974), on the other hand, has emphasized the importance of insulation. Such judgments have been hampered by a lack of adequate quantification of the thermal characteristics of nestlings. Insulation has been assessed by examining feather growth, but the measurement of feather length gives little information regarding the quality of insulation provided by the developing feathers. It is

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difficult to determine from existing data whether the limited thermoregulatory capacities of young nestlings are a result of a lack of metabolic response or are simply due to high rates of heat loss.

The present investigation of development in nestling bank swallows (*Riparia riparia*) seeks to pinpoint both the timing of and basis for improving temperature regulation in this altricial passerine. Specifically, I have asked: (1) What are the relative roles of thermogenesis and decreasing conductance in the development of temperature regulation, and (2) is the development of the regulatory response to low temperatures a continuous process or are there critical periods during which improvement occurs?

**MATERIAL AND METHODS**

Bank swallows were studied during June and July, 1973 and 1974. Nestlings were obtained from two colonies located in sandpits near Ann Arbor, Washtenaw County, Michigan. Hatching was monitored using a 3-ft wooden dowel with a dental mirror mounted on the end. The burrow was illuminated with a bulb from a penlight flashlight mounted on the dowel approximately 1 inch from the mirror and wired to a 3-V dry cell. The small diameter of the nest holes made it necessary to enlarge the burrows with a trowel before removing or replacing the young. After removal or replacement of the young, the burrows were restored to approximately their original diameter by filling with packed, moist sand. Burrows which were not refilled were subject to higher rates of predation. The nestlings were transported to and from the laboratory in covered styrofoam bowls ("China-foam," Atlantic Richfield). Measurements in the laboratory commenced within 40 min after removal from the nest, and the young were returned to the nest within 4 h of the time of removal. At least 3 days elapsed between successive removals of nestlings from any single burrow. Nestlings from a given brood were used no more than three times during the nestling period and, in many cases, were employed only once. The nestlings were not individually marked. At least two nestlings were left in a burrow while laboratory measurements were performed on their siblings. The most common brood size encountered was 5, with a range of 4–7. In all, 161 individuals from 78 nests were used for the various measurements.

Thermoregulatory capacities were assessed by exposing the nestlings to $T_a$'s of 20 C or 27 C in constant-temperature cabinets. Birds were placed individually in open styrofoam bowls (approximately 0.3 cm thick) lined with a double layer of cheesecloth. Nestlings which had cooled during transport to the laboratory were rewarmed to 37 C before the tests. Body temperatures after 2 h were determined orally by inserting a thermistor probe (Yellow Springs Instruments, no. 402, connected to a YSI telethermometer) down the esophagus and into the proventriculus.

Measurements of oxygen consumption ($\dot{V}O_2$) involved an open flow system containing a Beckman G-2 paramagnetic oxygen analyzer. The animals were placed, individually, in metabolism chambers fashioned from half-gallon paint cans with the inner surfaces painted flat black. The tops of the chambers contained inlet and outlet ports. Air temperature within the cans was monitored with 30-gauge copper-constantan thermocouples extending approximately 1 cm inside the outlet port. The thermocouples were connected to a Honeywell 15 multipoint recording potentiometer. Temperature control was
achieved by maintaining the chambers in a constant-temperature cabinet. The animal rested on a double layer of cheesecloth which covered a styrofoam bowl placed in the bottom of the can. Flow rates were monitored upstream by a rotameter (Brook’s Instruments) and ranged from 96 to 400 ml/min among the various tests. (The lower flow rates were used with the smaller nestlings.) Calculations of \( \dot{V}_O_2 \) were made according to the method of Hill (1972) and results were converted to cal (g·h\(^{-1} \)) by using a conversion factor of 4.8 cal (cm\(^3 \) O\(_2 \))\(^{-1} \). Except in the cooling-curve measurements outlined below, the reported values are means of three measurements taken during the last 30 min of a 2-h run or the final rate at 2 h if the rate was declining during the last 30 min. The various measurements were obtained from 1100 to 1800 EST. The values designated at standard metabolic rates (SMR) met the following criteria: \( T_b \) upon removal from the test chamber was 35.9 to 40.5 C; no activity or panting was evident at the conclusion of the tests. To meet these criteria the smaller nestlings had to be exposed to warmer \( T_s \)’s than the larger nestlings. Air temperatures among all the tests measuring SMR ranged from 32 to 38 C. Although the definition of SMR in growing nestlings before the development of endothermy is ambiguous, my criteria are consistent with current usage (cf. Hudson, Dawson, and Hill 1974).

During some measurements of metabolic rate at a \( T_s \) of 20 C, body temperature was monitored continuously in order to generate a cooling curve. Thermocouples made from 0.1 mm copper and constantan wires and covered with 0.6 mm (outside diameter) polyethylene tubing were inserted 15 to 20 mm into the cloaca. They were held in place with a piece of adhesive tape placed in a semicircle around the cloaca and pinched tightly on the leads. Sufficient slack was allowed in the thin leads to allow the bird to move around in the chamber and assume a normal position. The position of the thermocouple was checked at the end of the run, and if it had been dislodged completely or partially the run was discounted.

The amount of lag and washout time in the system used for simultaneous \( T_b \) and metabolism measurements was determined by injecting aliquots of helium into a chamber at each of the flow rates used and measuring the time to the first response of the analyzer and the time to purge the system. In all cases, the rate of change of oxygen consumption measured in the runs with nestlings was slower than the washout rate. The lag was 1–3 min, depending on the flow rate used.

Body mass was determined by weighing nestlings to the nearest 0.1 g on a triple beam balance. Body masses used in construction of the growth curve were determined upon arrival in the laboratory; otherwise the mean of the masses at the beginning and end of the particular test was used in calculations and statistical correlations. Feather length was measured with a ruler to the nearest millimeter.

**RESULTS**

**BODY MASS**

Growth in body mass in bank swallows (fig. 1) occurs rapidly, reaching a peak body mass at approximately 13 days of age. The logistic growth constant (\( K_L \), calculated by the method of Ricklefs (1967), for the bank swallow is 0.46 with an estimated asymptote of 17.0. The asymptote of the bank swallow curve is considerably greater than the mean adult mass of 14.5 g (no. = 15; SE = .24; specimens in the University
Fig. 1.—Growth curve for nestling bank swallows; * = present study; vertical bars = ±95% confidence interval; ○ = data from Petersen (1955).

Body temperature

When exposed to a $T_a$ of 20 C for 2 h, young nestling bank swallows cool to within a few degrees of the $T_a$ (fig. 4A). Little improvement in thermoregulatory capacity occurs in the first 6 days, but thereafter improvement is rapid. Due to this sharp transition point, the data are fit well by the cubic regression equation:

$$ (T_b - 30.9)^3 = 118.43 a - 900.09 \quad (1) $$

(no. = 47, $r = .84$, $p < .001$), where $T_b$, is the body temperature in °C after 2 h at 20 C, $a$ is the age in days, $r =$ correlation coefficient, $p =$ probability that the slope = 0. (This equation was

![Graph](attachment:image.png)

Fig. 2.—Feather growth in nestling bank swallows during growth in body mass up to the asymptotic mass (see fig. 1); ● = total feather length; X = length of feather sheath. The shaded areas show the length free from the sheath. A, Dorsal contour feathers measured in the center of the tract. B, Primary no. 8. The curves were drawn by eye.

FEATHER LENGTH

Feather growth in the bank swallow becomes apparent as the birds attain a mass of 7–10 g at an age of 5–6 days (figs. 2, 3). Both primaries and dorsal contours erupt from their sheaths when the nestlings weigh about 11.5–12.0 g (7 days) and the proportion free from the sheath increases throughout the rest of the growth phase. By the time the nestlings weigh 16 g (10 days) they appear, when viewed from above, totally covered with a layer of unsheathed feathers (fig. 3), although the ventral apertia is still largely bare (see fig. 3, age 12 days). As can be seen by the 17-day-old nestling in figure 3, an important phase of feather growth occurs while the nestlings are losing body mass late in nestling life.
fitted by simple linear regression after transformation of the data on $T_b$. It and all subsequent regression equations are left in the form to which the regression statistics apply.) There is much less spread in the data when $T_b$ is plotted against mass rather than age (fig. 4B). The $T_b$ increases gradually as mass increases from 2 to 10 g. As mass increases above 10 g, thermoregulatory capacity increases dramatically such that nestlings weighing 14 g or more have $T_b$'s above 37 C after 2 h at 20 C. The relationship between $T_b$, and mass can be described by:

$$(T_b - 30.9)^3 = 90.023m - 1039.6 \quad (2)$$

(no. = 48, $r = .92$, $p < .001$), where $T_b$ is in °C and $m$ is the mass in grams. On the basis of correlation coefficients, mass is a better predictor of body temperature after exposure to 20 C than age is. (Using mass and age together in a multiple linear regression does not result in an increase in $r$).

The data on nestlings exposed to 27 C

![Fig. 3.—Bank swallows of various ages. The age in days is indicated beside each nestling. The top scale beneath the 0- and 1-day-old nestlings is in millimeters. The bottom scale beneath the 4-, 6-, and 12-day-old nestlings is in millimeters. Both scales with the 10- and 17-day-old nestlings are in millimeters.](image)
for 2 h confirm the pattern of development described above. Again there is much less scatter when body temperatures are plotted against mass (fig. 4B) rather than age (fig. 4A). Further, the transition point in development of thermoregulatory capacity can be seen to occur at approximately 10 g.

Visual observations of shivering correlate well with the transition point in development of temperature regulation; shivering was first noted in bank swallows weighing 9.5–10.5 g.

**Metabolic Rate**

The changes in rates of heat production in bank swallows parallel the changes in body temperature (fig. 5). As nestlings increase in mass from 2.5–10.0 g, the metabolic rate recorded after 2 h at 20 C ($M_2$) increases gradually from less than 4 cal (g·h)$^{-1}$ to approximately 10 cal (g·h)$^{-1}$. Metabolism increases rapidly after 10 g, and by 13 g almost all nestlings are able to sustain a metabolic rate greater than 30 cal (g·h)$^{-1}$. The overall relation can be described by the cubic equation:

$$ (M_2 - 18.0)^3 = 548.27 M - 6099.8 \quad (3) $$

(no. = 32, $r = .89$, $p < .001$), where $M_2$ is in cal (g·h)$^{-1}$ and $M$ is in grams. Despite the dramatic change in metabolic rate at 20 C, little change in the SMR
occurs during the nestling period. Data gathered at $T_a$'s of 32–38°C (see Material and Methods) where $T_b$ was always greater than 36°C show a weak correlation with nestling mass (Fig. 6). This relationship is described by the linear equation:

$$M = 0.077 \, m + 16.18 \quad (4)$$

In nestlings which cool when exposed to a $T_a$ of 20°C, the metabolic rate decreases with decreasing $T_b$. In most cases the relation between $T_b$ and $M$ during cooling can be satisfactorily described by a linear relation over the temperature range studied. The results from seven individuals ranging in mass from 2.4 to 11.3 g are plotted in figure 7. Only one individual tested (mass = 8.7 g) had a slope of $M$ versus $T_b$ which differed significantly from the overall slope of 1.19. The pooled data are described by the regression equation:

$$M = 1.19 \, T_b - 20.4 \quad (5)$$

(no. = 65, $r = .92$, $p < .001$).

**DISCUSSION**

**GROWTH**

The growth of the bank swallows measured in this study differs from that
recorded by Petersen (1955) (fig. 1). Petersen’s growth curve shows an unexplained slowing of growth from day 2 to day 4. The growth rate observed for the bank swallow is in accord with other swallow species studied to date (see summary in Ricklefs [1968]). Thus it may be concluded that my activities at the bank swallow colonies did not interfere substantially with the normal growth pattern in this species.

**Conductance**

In assessing the developmental patterns noted thus far it is important to have some estimates of the rates of heat loss by the nestlings under the conditions of this study. Conductances (heat transfer coefficients) were calculated in two ways. For nestlings capable of maintaining a steady state after 2 h such that \( T_b \) was considerably above \( T_s \), the usual steady state formula for calculating conductance was used:

\[
C = M(T_b - T_s)^{-1}, \tag{6}
\]

where \( C \) is conductance, \( M \) is metabolic heat production (not corrected for evaporative water loss). This formula cannot be used for young nestlings which cool appreciably during the course of the experiment for two reasons: (1) if the nestlings are still cooling after 2 h the use of this formula will underestimate the rate of heat loss, and (2) if the nestlings have reached steady state body temperature (\( T_{bec} \)) after 2 h which is close to the \( T_s \), then estimates of \( C \) are likely to be subject to large errors due to the very low metabolic rates measured and the small value of \( T_b - T_s \). (The designation \( T_{bec} \) is adopted from Bakken [1976], although this author realizes that the \( T_b \) reached is more precisely a steady state and not an equilibrium.) To determine the values of \( C \) for these young nestlings, I followed the procedures outlined by Bakken and Gates (1975) and Bakken (1976). The formula for conductance, in this case, is:

\[
C = C' + P, \tag{7}
\]

where \( C' \) is the apparent conductance calculated from the time constant of the cooling curve, and \( P \) is the slope of \( T_b \) versus \( M \) measured while the nestling cools. The \( C' \) was calculated using the program (Newton II) developed by Bakken (1976) for cooling-curve analysis. The program determines the time constant (from which \( C' \) can be calculated) from a plot of \( \ln (T_b - T_{beq}) \) versus time. The \( T_{beq} \) is determined by an iterative procedure which maximizes the correlation between \( \ln (T_b - T_{beq}) \) and time. The \( C' \) was determined for the section of the cooling curve for which simultaneous metabolic measurements were available, unless this value did not differ significantly from the value for the entire curve. In practice, the cooling curves for the nestlings weighing less than 10 g were smooth and the whole curve was used. Metabolic rate varied linearly over the range of body temperatures used in the cooling-curve analysis (fig. 7), and thus satisfied a necessary requirement for using equation (10) (see Bakken 1976).

Conductance values decrease with increasing body mass over the range studied (fig. 8). This decrease is linear when plotted on a double logarithmic plot following the equation:

\[
\log C = -0.501 \log m + \log 6.902 \tag{8}
\]

(no. = 21, \( r = .946, p < .001 \)), where \( m \) is in grams and \( C \) is in cal (g·h·°C)\(^{-1}\). The slope of this relation is almost identical to the value of -0.508 calculated for adult birds based on similar measurements (Lasiewski, Weathers, and Bernstein 1967), but the intercept is 1.7 times the value for adult birds.
Fig. 8.—Conductance values for nestling bank swallows as a function of body mass. $\Delta$, $\bigcirc$ = conductance calculated from the steady state formula; $\bigcirc$ = conductance calculated from cooling curve and metabolism data (see Discussion for the method). The two nestlings indicated by $\Delta$ are the oldest nestlings, but weigh less than the peak body mass due to the mass recession which occurs late in nestling development (see fig. 1). $\square$ = value for an adult bank swallow from Herreid and Kessel (1967). Line $a$ is the regression equation from Herreid and Kessel (1967) for dead, defeathered, adult birds. Line $b$ is a regression line through the data in the present study (eq. [8] in text). Line $c$ is the regression equation from Lasiewski, Weathers, and Bernstein (1967) for live adult birds.

The similarity in slope suggests that the decreases in conductance are predictable simply on the basis of increasing body mass. The plot of the equation for nestling bank swallows falls below the line for dead, defeathered birds (fig. 8) measured by Herreid and Kessel (1967). Somewhat surprisingly, the values of $C$ for two older nestlings (age 18 and 20 days) after the mass recession indicate no reduction in heat loss (fig. 8) despite the fact that they were fully feathered and capable of flight.

Based on conductance, the rapid development of thermoregulatory abilities after attaining a mass of 10 g in nestling bank swallows does not appear to be related to a reduction in heat loss. Feather growth is just beginning when the change takes place, and based on the conductance measurements on older nestlings, the feathers do not retard heat loss greatly even at these stages. The relatively high conductances in nestlings which are apparently well feathered deserves further comment since numerous investigators have used plumage development as an index of the development of insulation (Kendeigh and Baldwin 1928; Dawson and Evans 1957, 1960; Ricklefs and Hainsworth 1968; Yarbrough 1970; Morton and Carey 1971). Methodological and theoretical considerations complicate the interpretation of the conductance measurements. The higher air flow rates used in metabolism tests with older nestlings may tend to obscure the contribution of the developing plumage. On the other hand, the flow rates are lower than those typically used for adult birds of similar size. Also, if increases in evaporative water loss occur with age, then the contribution of the plumage would be obscured. It seems likely, however, that the developing plumage would retard cutaneous water loss (Bernstein 1971). It is important to bear in mind, however, that conductance values represent a measure of heat loss from several avenues (see Bakken and Gates 1975). Thus changes in conductance cannot be simply related to insulation provided by the plumage.

Unfortunately, there is very little information on nestling conductances with which the present data can be compared. Based on the original data (provided by W. R. Dawson) on which the reports of Dawson and Evans (1957, 1960) were based, I have calculated conductance values for nestlings which remained homeothermic during metabolic tests (conducted under conditions similar to those used in the present study). It is evident (table 1) that the values of $C$ for these nestling sparrows are high, compared with adult values, throughout the latter
part of nestling period, only showing
significant reductions after the normal
date of fledging in vesper sparrows
(*Poecetes gramineus*) and chipping sparrows (*Spizella passerina*). Measurements
of conductance for live adult swallows are not available, but the single value
for a bank swallow (fig. 8) obtained by
Herreid and Kessel (1967) by cooling-
curve analysis is relatively high compared
with the other species studied by them. It is, however, lower than the
values measured for nestling swallows. Based on the limited data available, cur-
tailment of heat loss, as measured by conductance, is not of major importance in
the development of temperature regulation at moderate ambient tempera-
tures by nestling swallows (or sparrows). Conductance values evidently remain
high relative to adult values until the time of fledging or after. Since over-
heating is a significant problem to a
number of passerine nestlings (Ricklefs
and Hainsworth 1968; Morton and Carev
Hainsworth 1971; Mertens 1977), it is possible
that low conductances would be mal-
adaptive under the crowded conditions
of the nest.

### BODY TEMPERATURE

I have relied heavily on a single type
of measurement in describing the pattern
of thermoregulatory development in
nestling bank swallows, namely, the
body temperature after 2 h at 20 C.
Since all nestlings were placed at 20 C
with approximately the same initial
body temperature (*T*<sub>b</sub>), any factors
which influence the cooling rate over 2 h
should influence the final body tem-
perature. The measurements on bank
swallows at a *T*<sub>a</sub> of 27 C (fig. 4) confirm
that the developmental pattern demon-
strated at 20 C is not an artifact of the
particular *T*<sub>a</sub> chosen. The measurement

### TABLE 1

<table>
<thead>
<tr>
<th>Species and Age (Days)</th>
<th>Mean Mass (g)</th>
<th>Mean <em>C</em> (cal [g·h·°C]&lt;sup&gt;-1&lt;/sup&gt;)</th>
<th>No.</th>
<th>Predicted&lt;sup&gt;a&lt;/sup&gt; Adult <em>C</em> (cal [g·h·°C]&lt;sup&gt;-1&lt;/sup&gt;)</th>
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<sup>a</sup> Calculated from Lasiewski, Weathers, and Bernstein (1967).
<sup>b</sup> Indicates the time of normal fledging.
of $T_b$ at a specified time is important in that initial attempts to regulate $T_b$, by increasing metabolic rate, for example, may be missed if the nestlings remain exposed long enough for a steady state to be reached. A problem arises in the use of body temperatures to assess the degree of active regulation at any stage of development. What reference temperature does one choose to distinguish between active regulation and passive resistance to cooling? The $T_b$ at any time after exposure will be influenced by the rate of heat loss which changes during development simply due to increasing mass (fig. 8). The increasing mass also influences the steady state body temperature after cooling due to an increasing mass of metabolizing tissue.

Given the measurements of conductance and metabolism for bank swallows presented here, it is possible to calculate the $T_b$ expected if the nestlings made no attempts to regulate by increasing their metabolic rate. This calculation is facilitated since the mass specific metabolic rate during cooling is similar for all nestlings studied (fig. 7). The procedure uses relations pointed out by Bakken and Gates (1975) and Bakken (1976). The conductance $C$ for a nestling of given mass was obtained from figure 8. This value of $C$ was used to calculate the $T_{beq}$ according to:

$$T_{beq} = T_s + (M \cdot C^{-1}). \quad (9)$$

This equation differs from that of Bakken (1976) in using $T_s$ in place of $T_a$, the operative environmental temperature, and $M$, the total metabolic rate at steady state, in place of $M^*$, the "dry" metabolic heat production. In my experiments in a darkened chamber or room, $T_s \approx T_a$. Due to technical difficulties, $M^*$ was not measured. To use equation (9) it is necessary to know $M$ at steady state, but since $M$ changes with $T_b$ (fig. 7), an iterative procedure was followed. An initial estimate of $T_{beq}$ was used in equation (5) to determine $M$. This estimate of $M$ was used in equation (9) to calculate $T_{beq}$. The procedure was repeated until estimated $T_{beq}$ equalled calculated $T_{beq}$. Once $T_{beq}$ is known, then the $T_b$ at any time during cooling can be calculated since the rate of cooling can be estimated by subtracting the value $P$ (slope of $T_b$ versus $M$, fig. 7) from the value of $C$ (fig. 8) for a nestling of given mass. The formula for calculating the $T_b$ is therefore:

$$\ln (T_b - T_{beq}) = \ln (T_{b_1} - T_{beq}) - \frac{4C'}{\epsilon p}, \quad (10)$$

where $T_{beq}$ is estimated as above, $T_{b_1}$ is the initial body temperature (37°C), $C' = C - P$ with units of cal (g·h·°C)$^{-1}$, $t$ is the time in hours, and $\epsilon_p$ is the specific heat capacity, taken to be 0.82 cal (g·°C)$^{-1}$.

The results of these calculations for bank swallows are presented in figure 4B. Recall that these calculated $T_b$'s assume that the nestlings have passively cooled at 20°C for 2 h. The dramatic changes in the calculated $T_b$ with mass serve to illustrate the irrelevance of $T_s$ as a reference temperature in the type of measurements undertaken in this study. In marked contrast to the large increase in the calculated $T_b$ for live nestlings with increasing mass, a 17-g nestling with no metabolic heat production would be expected to reach a $T_b$ of 20.3°C after 2 h at 20°C. It can be seen from these calculations that the reduced cooling with increasing mass up to 10 g in bank swallow nestlings is to be expected, simply due to a more favorable relationship between the rate of heat loss and the mass of metabolizing tissue. Nestlings weighing greater than 10 g, on the other hand, have body temperatures
much greater than expected for passively cooling individuals. Thus we can identify rather precisely that the increase in measured \( T_b \) after 10 g is due to active metabolic regulation. It is gratifying to note the degree of correspondence between the calculated line and the measured \( T_b \)'s of bank swallows weighing less than 10 g. \( T_b \)'s reported in fig. 4 are independent of the cooling curve and metabolism measurements used in figs. 7 and 8 on which the calculations are based.

**METABOLIC RATE**

That active regulation begins at approximately 10 g is supported by the data on metabolic rate after 2 h at 20 C \( (M_2) \) (see fig. 5). Nestlings weighing less than 10 g have metabolic rates which appear to reflect the \( T_b \) to which they have cooled (cf. figs. 4, 5, 6). In contrast, the \( M_2 \) of nestlings weighing 14 g or more is approximately double the SMR and reflects their homeothermic condition (fig. 4). These metabolic data in conjunction with the body temperature measurements suggest a total lack of metabolic response to cold in young nestling bank swallows; however, there is the possibility that a relatively weak metabolic response would be missed under the conditions employed. Hill (1976) has shown that when tested in groups with an artificial nest, deer mice \( (\text{Peromyscus leucopus}) \) show a homeothermic response at an early age, whereas mice of the same age tested individually cool rapidly. On the other hand, Mertens (1977) found that nestling great tits \( (\text{Parus major}) \) tested as whole broods in nest boxes had no detectable metabolic response before the individual had attained a mass of approximately 8 g (5–6 days of age). Similarly, young bank swallows provided with cotton insulation and tested in groups of four to five individuals show no response to low \( T_a \) (Marsh, unpublished observations). The apparent difference between the mice and these altricial passerines may depend on the presence of brown fat and thus nonshivering thermogenesis in the neonatal mammals (Smith and Horwitz 1969) and its lack in young birds (Johnston 1971).

Metabolic intensity under standard conditions has been used as a comparative index of physiological development in several altricial and precocial species of birds (Koskimies and Lahti 1964; Dawson and Evans 1957). In bank swallows the transition to an endothermic condition is not marked by any substantial increase in SMR (fig. 6). In this respect bank swallows are similar to other altricial passerine species which show either no change in SMR during development (Westerterp 1973) or modest increases in SMR (Dawson and Evans 1957, 1960; Mertens 1977). Of course, although the absolute level of SMR does not change much, the relative level as judged by comparison with adult birds of similar size increases throughout development.

**COMPARATIVE OBSERVATIONS**

Available data suggest that other altricial passerines may show a biphasic pattern of development similar to bank swallows, with an initial phase of growth (until they reach 50%-70% of adult mass) during which there is little or no metabolic response to low \( T_a \)’s. Tree swallows are apparently identical to bank swallows in their pattern of development (Marsh, unpublished manuscript). Numerous other species show sharp transitions during development in the ability to maintain \( T_b \) above ambient (see Morton and Carey 1971; Johnson and Cowan 1974; Austin and Ricklefs 1977). On the other hand, several nonpasserine altricial species...
show some metabolic response very early in development (see Ginglinger and Kayser 1929; Hudson et al. 1974; Hamas 1975). Among the altricial mammals, several species may show a pattern similar to the passerines except for the presence of nonshivering thermogenesis in the mammals (see above) (see Morrison, Ryser, and Streeker 1954; Hill 1976). I consider it likely that the sudden onset and rapid improvement of the endothermic response seen in the bank swallow and certain other altricial birds is due to the development of shivering heat production. A similar suggestion has been made for mammals (Hill 1976). Visual observations of shivering in response to low $T_a$ show a correlation between the stage of development at which shivering is noted and the stage of rapid improvement in thermoregulation (this study; Morton and Carey 1971). Odum's (1941, 1942) measurements of shivering in nestling house wrens (Troglodytes aedon) also confirm this correlation.

Field observations of brooding behavior in passerine birds suggest that the biphasic pattern of development of thermoregulation described here influences parental behavior. A commonly observed pattern of brooding in passerines is a constant or gradually decreasing frequency of brooding during the first several days of nestling life followed by a rapid diminishment of brooding. Beyer (1938) indicates a diminution of brooding by adult bank swallows on day 5 and cessation on day 6 or 7, which coincides with my observations on the initiation of endothermy in this species. Similar correlations can be noted in white-crowned sparrows (Zonotrichia leucophrys; Morton and Carey [1971]) and rufous-winged sparrows (Aimophila carpalis; Austin and Ricklesfs [1977]).

**LITERATURE CITED**


HUDSON, J. W., W. R. DAWSON, and R. W. HILL. 1974. Growth and development of temperature...


