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RELATION OF GROWTH AND DEVELOPMENT TO TEMPERATURE REGULATION IN NESTLING VESPER SPARROWS

By WILLIAM R. DAWSON and FRANCIS C. EVANS

Simultaneous measurements of growth, metabolism, and body temperature of young altricial birds have as yet been reported for only a few species, and further data are necessary before an adequate analysis can be made of the factors involved in the establishment of homeothermy, or constant high temperature, in these animals. We have therefore extended our previous study of nestling Field and Chipping sparrows, *Spizella pusilla* and *S. passerina* (Dawson and Evans, 1957) to include an investigation of the Vesper Sparrow, *Pooecetes gramineus gramineus*. In addition to studying the general growth and temperature regulation of nestlings of this species, we have also analyzed the growth rates of certain of their visceral organs.

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MATERIALS AND METHODS

The field observations reported in this study were made on the Edwin S. George Reserve of The University of Michigan, approximately 4.5 miles west of Pinckney, Livingston County, Michigan, from 1949 to 1957. The 46 nestlings studied in the laboratory were obtained in the breeding seasons of 1955, 1956, and 1957; most of them were from the Reserve, but a few were obtained in adjacent areas. The procedures for nestling inspection were the same as those used previously (Dawson and Evans, 1957).

Observations were made of body weight, developmental state, condition of the plumage, and behavior. As in Field and Chipping sparrows, removal of Vesper Sparrows from the nest for the few minutes required for examination did not appear to disturb the younger nestlings, but those about to fledge sometimes left the nest at the approach of the observer. It was therefore difficult to obtain information for the last day or so of the nestling period. We have also followed our earlier procedure with regard to age designation: young examined on the day of hatching were recorded as 0 days old.

Nestling Vesper Sparrows to be studied under experimental conditions were generally taken into the laboratory in the afternoon, with approximately an hour elapsing between removal from the nest and arrival at the laboratory. Weight losses in transit were rarely more than 0.5 gm. Upon entering the laboratory, all nestlings were fed meal worms (*Tenebrio* larvae) and crickets until replete. They were then subjected to experimental procedures for determination of the relation of oxygen consumption and body temperature to environmental temperature. Subsequently the birds were fed every 2 hours between experiments. This feeding schedule kept them in good condition throughout the period in which they were studied. All measurements were made within 12 hours of the removal of the birds from the nest.

Our methods for determining the effects of environmental temperature on oxygen consumption and on body temperature were similar to those we had used previously. During the experimental periods, the nestlings were kept in chambers fitted with ports for connection to an air line and with a housing for a thermometer. In the chambers, the birds rested on packing material shaped to simulate a nest. They were housed singly, except for very small nestlings which were placed two in a chamber and prevented from huddling by means of a partition.

Metabolic rate was measured as oxygen consumption, with a Beckman paramagnetic oxygen analyzer. Rate of air flow through the chambers was maintained constant in

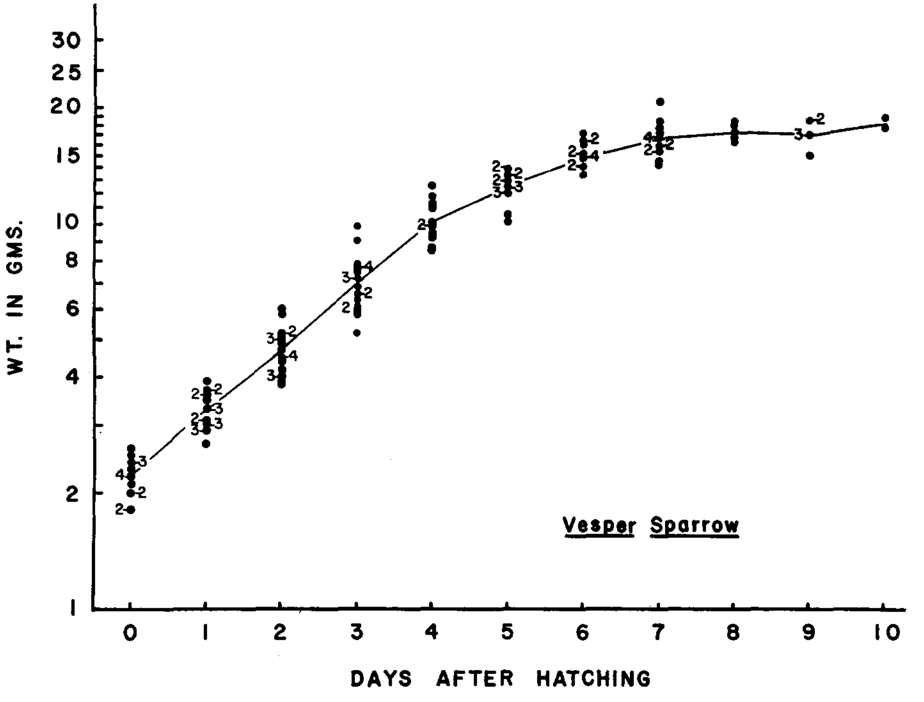

Fig. 1. Growth of nestling Vesper Sparrows plotted on a semi-logarithmic grid. The numerals indicate the number of individuals represented by the points which they accompany. The line connects the mean weights for successive ages.

each experiment but ranged from 100 to 350 cc/min. in the course of the investigation. All gas volumes specified in relation to metabolic rate have been corrected to 0°C. and 760 mm. Hg. Body temperatures were measured rectally, either with a quick-registering thermometer designed for small-animal work or with fine (30 gauge) wire copper-constantan thermocouples sheathed in vinyl tubing and used in conjunction with a suitably calibrated recording potentiometer. The values presented for body temperature and oxygen consumption at various environmental temperatures are those observed at the end of the 2-hour experimental periods. Handling of the birds between removal from the chamber and determination of body temperature was kept at a minimum to avoid transfer of heat.

Temperature was maintained within 0.5°C. of the desired level during the experiments by placing the chambers in a 17 cubic foot constant temperature cabinet. Prior to the initiation of each experiment, the birds were adjusted to room temperature (23° to 30°C.); in the experimental program they were exposed to constant temperatures between 10° and 40°C. When several experiments were run with the same bird, the initial one involved a warm environmental temperature (30° to 40°C.), the next a moderate temperature (20° to 30°C.), and the last a cool temperature (10° to 20°C.).

All young Vesper Sparrows studied in 1955 were sacrificed at the completion of the physiological measurements, and their thyroid glands were removed for histological study (see Dawson and Allen, 1960). Immediately after thyroid removal, the carcasses were tightly wrapped in aluminum foil and quick-frozen. They were later thawed and the liver and heart were carefully dissected out and weighed.

RESULTS

DURATION OF THE INCUBATION AND NESTLING PERIODS

The incubation period, defined as the interval between the date of laying of the last egg and the date of hatching of the last young when all eggs hatch (Nice, 1953), was observed throughout for 11 nests of the Vesper Sparrow; it was recorded as 12 days for 6 nests and as 13 days for 5 nests.

Table 1

Age at Fledging in the Vesper Sparrow

Age at leaving nest (days after hatching)	Number of individual records
7	3
8	4
9	32
10	46
11	10
12	1
Total records	96
Mean age on leaving nest	9.6 days

The length of the nestling period was recorded for 96 Vesper Sparows (table 1). The mean age on leaving the nest was 9.6 days, although some birds did not remain in the nest for more than 7 days and one stayed for 12 days. If the day of deposition of the last egg is taken as the beginning of development, the average age at fledging is approximately 22 days for the Vesper Sparrow. However, in this as well as in our previous study, we have followed the general practice of calculating the ages of nestlings from the day of hatching, as mentioned previously.

GROWTH DURING THE NESTLING PERIOD

Weights of 42 nestling Vesper Sparrows of known age were obtained; 34 birds were weighed on two or more days and two were weighed throughout the nestling period. Vesper Sparrows weigh about 2 gm. at hatching. They attain a weight of approximately 18 gm. before leaving the nest (fig. 1). However, despite this rapid growth, they achieve prior to fledging only about three-quarters of their mature weight—the mean weights of 15 adult female and of 28 male Vesper Sparrows taken in lower Michigan in spring and early summer (from the collections of The University of Michigan Museum of Zoology) were 24.9 and 26.5 gm., respectively.

The general pattern of nestling growth in the Vesper Sparrow is in most respects similar to that found in the Field and Chipping sparrows. Growth is relatively rapid during the first four days after hatching and slows thereafter. The values for the instantaneous percentage growth rate *r* (Brody, 1945:508) range from approximately 40 per cent in the early part of the nestling period to 5 per cent between the seventh and eighth days after hatching (table 2).

Table 2

Instantaneous Percentage Growth Rates (r) in Nestling Vesper Sparrows

Interval in days after hatching	r (per cent/day)
0–1	40.4
1–2	35.4
2–3	41.2
3–4	34.5
4–5	20.1
5–6	18.1
6–7	10.1
7–8	5.2

Records of heart and liver weight were obtained for 34 nestling Vesper Sparrows (figs. 2, 3). The essentially straight-line relationship between the weights of these organs and total body weight on a double logarithmic grid is described by the familiar equation for heterogonic growth,

$$D = a\ W^k$$

where D is organ weight, W is body weight, and a and k are constants, the latter indicating the slope (Huxley, 1932; Brody, 1945). The values of k for the lines fitted free-hand to the data are 1.1 and 1.2 for heart and liver, respectively. The fact that the values exceed unity indicates that these organs grow relatively more rapidly during the nestling period than the body as a whole. This may well contribute to the increase of metabolism per unit of body weight evident during the nestling period (fig. 4). Com-

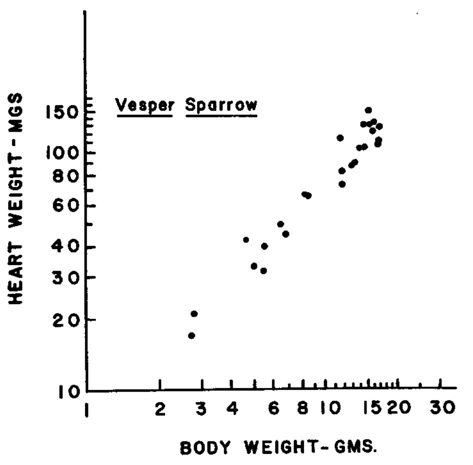

Fig. 2. The relation of heart weight of nestling Vesper Sparrows to body weight, plotted on a double logarithmic grid. The slope of the best line fitted free-hand to these points is 1.1.

parable data on nestlings of other altricial species are not available, except for those summarized in Brody (1945) for the Rock Dove (*Columba livia*). In this latter species, the value of *k* for the relationship between heart and body weight declines from 1.8 to 1.0 during the first 9 days of post-hatching growth. The value of *k* for the relation between liver weight and body weight decreases from 1.6 to 1.1 in the same period.

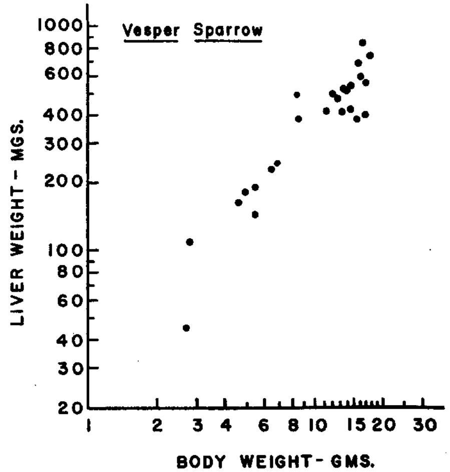

Fig. 3. The relation of liver weight of nestling Vesper Sparrows to body weight, plotted on double logarithmic grid. The slope of the best line fitted free-hand to these points is 1.2.

GENERAL DEVELOPMENT

Feathers.—The newly hatched Vesper Sparrow has a flesh-pink skin with patches of gray down on the capital, dorsal, humeral, femoral, secondary, and caudal tracts (Saunders, 1956). The pattern of feather development is similar to that of Field and Chipping sparrows and the Tree Sparrow, *Spizella arborea* (Baumgartner, 1938). The rate of growth of the feathers (table 3) is slower than those of the first two species and more rapid than that of the last. Unpigmented at first, the feather tracts of the Vesper Sparrows are clearly marked at 2 days of age, when the primaries have just emerged from their papillae. Extension of the feather sheaths occurs gradually; the rectrices emerge about the sixth day, when the primary quills are 10–12 mm. long and there is evidence of bursting sheaths, first seen in the feathers of the ventral tracts. By the eighth day, the lack of pigment in the outer rectrix is evident, in contrast to the dark quills of the other tail feathers. At 9 days of age the primary barbs have emerged 8 to 9 mm., the tail is 8 to 10 mm. long, and the birds appear well feathered and ready to leave the nest, although traces of down are still present and no feather is fully out of its sheath. Sutton (1941) observed that new feathers were emerging at either side of the ventral apterium in 13-day-old fledglings and that the rectrices continued growing until 31 days; the first signs of postjuvenal molt were noted by the eighteenth day.

Eyes.—As in Field and Chipping sparrows, the eyes of nestling Vesper Sparrows remain closed for the first few days after hatching. In some individuals, eyes began to open on the third day; in most they did not do so until the fourth or fifth day. The ocular opening increased gradually and at 8 to 9 days of age was fully round. Like feather growth, eye development seems to take place a little more slowly in the Vesper Sparrow than in Field and Chipping sparrows.

Form and behavior.—Young Vesper Sparrows undergo a marked change in form while they are in the nest. At hatching the head is bent down, the legs are stretched forward, and the bird rests largely on its abdomen, which is conspicuously distended and remains so for the first few days. When upset a young bird rights itself only with

Table 3

Feather Development in Nestling Vesper Sparrows

Age (days) after hatching)	Sample size	Mean length of third primary sheath (mm.)	Mean length of exposed barbs of third primary (mm.)	Mean length of outer rectrix (mm.)
3	6	1.0	0	0
4	5	2.5	0	0
5	3	8.0	0	0
6	5	11.0	0	1.0
7	4	16.0	1.0	3.0
8	4	21.0	4.0	5.5
9	4	27.5	8.0	8.0
10	3	30.0	11.0	10.0

difficulty. At 6 days of age, the enlargement of pectoral and other muscles makes the abdomen less conspicuous. The legs now provide increased support, permitting the bird to stand. Movements are still awkward, however, and it is not until the eighth or ninth day that the nestling appears well coordinated.

Gaping was observed in Vesper Sparrows soon after they hatched, and it was the usual response to the presence of an observer at the nest as late as the sixth day. From the seventh day on, the birds typically assumed a crouching position and did not gape when the nest was disturbed. This change in reaction appears correlated with the completion of the opening of the eyes, as noted for the White-crowned Sparrow, *Zonotrichia leucophrys* (Banks, 1959).

OXYGEN CONSUMPTION

The relation of oxygen consumption to environmental temperature in Vesper Sparrows undergoes a pronounced change in the week following hatching (fig. 4). The oxygen consumption of birds 0 to 2 days old varied directly with temperature, with rates ranging in most cases from less than 0.5 cc/gm./hr. at 13° to 23°C. to 2–3 cc/gm./hr. at 35° to 38°C. A direct relation between temperature and metabolism was also evident in 3-day-old birds, but somewhat higher weight-relative rates of oxygen consumption than those observed in the younger individuals were maintained at all temperatures. The first suggestion of an inverse relation between oxygen consumption and environmental temperature was noted in 4-day-old Vesper Sparrows at temperatures between 20° and 35°C. In this range, metabolic rates were in excess of 3 cc/gm./hr. Below 20°C., oxygen consumption declined with decreasing temperature. Four-day-old Vesper Sparrows are apparently at a stage in the development of temperature regulation comparable to that achieved by Field Sparrows at 4 days, by Chipping Sparrows at 4 to 5 days, by House Wrens (*Troglodytes aedon*) at 6 days (Kendeigh, 1939), and by pigeons at 8 to 9 days (Pembrey, 1895) after hatching. On the fifth day, a few Vesper Sparrows increased their metabolism when exposed to environmental temperatures below 20°C., but this was not the characteristic response. A strictly inverse rela-

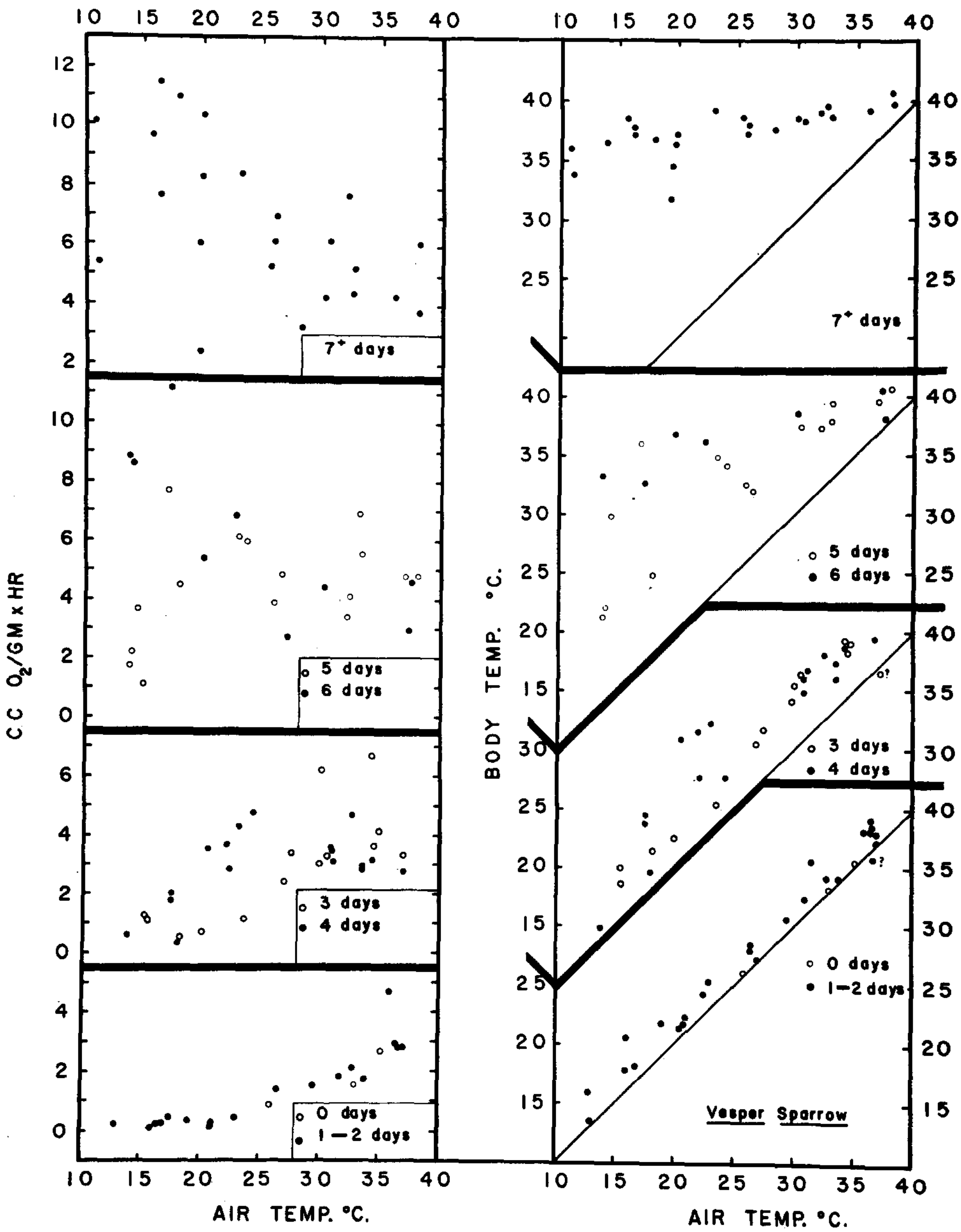

Fig. 4. The relation of oxygen consumption (left) and of body temperature (right) to environmental temperature. Oxygen consumption measured in cc/gm./hr.; temperature in degrees centigrade. All data obtained at the end of 2-hour experiments. Ages given as days after hatching. The uppermost graphs ("7+ days") summarize data for birds 7 to 9 days of age.

tion of metabolic rate to temperature was first evident on the sixth day. In the results for birds of 6 days or older, considerable scatter is evident, due most likely to variability in the activity of the birds in the course of the experiments. However, this does not obscure the basic relation between metabolism and temperature.

BODY TEMPERATURE

As suggested by the modification of metabolic response to temperature in the first few days after hatching, the nestling period is a time of rapid improvement in capacity for regulation of body temperature (fig. 4). Vesper Sparrows from 0 to 2 days old generally could not maintain body temperature more than 3°C. above environmental temperatures between 13° and 37°C. Some improvement was evident in 3-day-old birds, particularly at environmental temperatures from 28° to 35°C., and 4-day-old individuals successfully maintained body temperature as much as 10°C. above environmental temperatures between 20° and 25°C. Thermoregulatory capacity continued to improve on the fifth and sixth days after hatching, and at 7 to 9 days of age the birds were in most cases able to maintain body temperatures above 35° between environmental temperatures of 10° and 38°C.

The absence of effective temperature regulation in the younger nestlings resulted in their being chilled to relatively low body temperatures in the course of the experimental program, yet none of the birds tested appeared to suffer any ill effects, even when cooled to 13° to 20°C. for a period exceeding one hour. Additional observations were made to assess more fully the extent of the tolerance of 2-day-old Vesper Sparrows to chilling. Full recovery was made even when the birds were left at body temperatures of 18° to 20°C. for 8 hours. Tolerance of relatively low body temperatures by altricial nestlings has been noted previously in Field and Chipping sparrows, Horned Larks, *Eremophila alpestris* (Kelso, 1931), House Sparrows, *Passer domesticus* (Leichtentritt, 1919), and House Wrens (Baldwin and Kendeigh, 1932). Such tolerance is probably rarely required in nature, because of the effectiveness of parental brooding in maintaining body temperatures of the young at near-homeothermic levels.

DISCUSSION

In the Vesper Sparrow, as in other passerines for which information is available (see Dawson and Evans, 1957), the onset of homeothermy is not the culmination of any single aspect of development. It is linked with a complex array of processes which lead on the one hand to the establishment of functional neural mechanisms—sensory, integrative, and motor—controlling the various activities on which regulation of body temperature depends, and on the other hand to the development of capacities for heat conservation and to the improvement of abilities for heat production.

In the absence of direct information, we can say very little about the development in the Vesper Sparrow of the neural mechanisms on which homeothermy depends, except that they have started to function by the fourth day after hatching, when the first suggestion of an inverse relation between metabolism and oxygen consumption was noted (fig. 4). Similar observations were reported for Field and Chipping sparrows. Odum's (1942) report that the frequency of muscle tremors of 6-day-old House Wrens varied inversely with environmental temperature indicates at least partial function at this age of neural mechanisms responsible for regulation of heat production.

Newly hatched Vesper Sparrows possess little capacity for conserving heat, because of the relatively high proportion of their body surface to weight and because of their essentially naked condition. In the days following hatching, there is a progressive decline of the surface-weight relationship concomitant with increasing size; the values for this relationship (estimated by the formula $\text{cm}^2/\text{gm.} = 10\ \text{gm.}^{-0.33}$) for 6-day-old nestlings and for adult birds are, respectively, only 57 and 49 per cent of that for newly hatched young. The decline in the surface-weight relationship reduces heat loss of older nestlings per gm. of tissue and so assists in bringing it in line with the capacity for heat production.

The contribution of plumage development to the establishment of homeothermy in Vesper Sparrows is less clear cut, for effective regulation of body temperature at moderate (20° to 25°C.) environmental temperatures is evident when the contour feathers have just begun to erupt from their sheaths. A similar situation has been noted in the House Wren (Kendeigh, 1939), Rock Dove (Ginglinger and Kayser, 1929), and Field and Chipping sparrows (Dawson and Evans, 1957). These observations suggest that the development of an insulating plumage, although undoubtedly of importance in resistance to cold, is not requisite for the establishment of homeothermy at moderate environmental temperatures.

The capacities of newly hatched Vesper Sparrows for producing heat seem relatively restricted, probably owing primarily to the limited development of the muscular system and the rudimentary motor coordination at this age. These hatchlings are relatively passive creatures, whose awkward attempts at activity occur principally during feeding periods. In the first week after hatching, capacity for heat production increases concomitantly with the development of the musculature and increased motor activity. The relatively rapid growth of such organs as the heart and liver (figs. 2, 3) and the relatively high level of thyroid activity which seems to exist in nestlings from 2 to 6 days of age (see Dawson and Allen, 1960) may also serve to intensify heat production, which apparently reaches a level commensurate with homeothermy only during the latter portion of the nestling period (see fig. 4 in Dawson and Evans, 1957).

The various processes contributing to the establishment of homeothermy seem to proceed more rapidly in the Vesper Sparrow than in any other altricial bird thus far studied, with the exception of Field and Chipping sparrows. These three fringillids show effective temperature regulation at moderate environmental temperatures, that is, the maintenance of body temperature above 37°C. in an environment at 20° to 25°C., by 6 to 7 days after hatching. This compares with 8 days for the House Wren (Baldwin and Kendeigh, 1932), 7 to 8 days for the Red-backed Shrike (*Lanius collurio*), 10 days for parakeets (*Melopsittacus undulatus*) and 11 days for the Wryneck, *Jynx torquilla* (Boni, 1942), and 11 days for the Rock Dove (Ginglinger and Kayser, 1929). The three species of sparrows fledge in 10 days or less, whereas the House Wren does not do so until it is 15 days old. The speed with which homeothermy is established thus appears to correlate with the general pattern of development.

There is general agreement that the altricial condition is of particular biological significance from the standpoint of energetics (Kendeigh, 1952; Witschi, 1956; Dawson and Evans, 1957). The immature state of newly hatched altricial young and the relatively short period between fertilization and hatching do not require an egg so large or with an energy content as great as that needed in the precocial mode of development. Reduction in egg size and energy content may have been key developments in the evolution of very small birds (Witschi, 1956).

Another reason for the energetic significance of the altricial condition is that it minimizes the maintenance costs of the young during a major part of their development. The extensive brooding of the young by the parents during the early part of the nestling period maintains them in a relatively constant environment, even in quite cool surroundings (Irving and Krog, 1956). This is apparently accomplished at a trifling energetic cost to the parent birds, for they would have expended much of the heat which they impart to the young in their own temperature regulation even if they were not brooding. During the later stages of the nestling period, when brooding is less frequent, the young can still be well protected from excessive heat loss by huddling with their siblings and by the insulation afforded by the nest. Their maintenance costs are further reduced by parental feeding during the nestling period and for some time after fledging. It is of particular interest that the metabolic rates (per unit of weight) of passerine nestlings that have been studied to date, including the Vesper Sparrow, do not, under conditions approximating those in the nest, rise to levels expected of homeotherms of comparable size until the approach of fledging (Dawson and Evans, 1957: fig. 4).

From the considerations outlined above, we conclude that the low maintenance costs of the sedentary and well-protected young of altricial birds should contribute to rapid and efficient growth. The extremely rapid growth of altricial nestlings is attested to by the statistics on instantaneous percentage growth rates provided in this and earlier studies (Dawson and Evans, 1957; Banks, 1959). A provisional consideration of growth efficiency can be made from an estimate based on data for the Vesper Sparrow. In this estimate, which is concerned with the early part of the nestling period when the young are generally inactive, the following assumptions are made: body temperature of young is 35°C.; 1 gm. of sparrow is equivalent to 2000 cal., based on data for the domestic fowl, *Gallus gallus* (Brody, 1945:53); and the caloric equivalent for oxygen is 4.8 cal. per cc consumed. The following data are used: metabolic rate of 0-, 1-, and 2-day-old Vesper Sparrows in a post-absorptive state at 35°C. is 2.5 cc O_2/gm./hr. (fig. 4), or 288 cal./gm./day; weight increments between 0 and 1 and between 1 and 2 days are 1.1 and 1.4 gm., respectively (fig. 1); and the geometric means of weight between 0 and 1 and between 1 and 2 days are 2.7 and 3.9 gm., respectively. Efficiency (E) can be calculated from the following equation:

$$E = \frac{(a)(100)}{(a+b)}$$

where a represents the calories accumulated in growth during the period considered and b represents the calories expended in metabolism (equivalent to the product of the geometric mean of weight and the cal./gm./day) during the same period. The denominator $(a+b)$ of this equation corresponds to the *net energy* expression of Brody (1945:34), that is, the difference between the gross (combustible) energy of the food ingested and the energy lost in the feces and excretory products plus the energy represented in specific dynamic action (SDA). In other words, the net energy equals the metabolizable energy increment of the food less the energy represented in SDA. Since b includes the energetic cost of maintenance, E represents a gross efficiency of growth. These specifications, although tedious, are necessary, since expressions of efficiency are ambiguous without them (Brody, 1945:54).

With respect to the net energy increment of the food ingested in the 24 hours after hatching, the gross efficiency of growth of Vesper Sparrows equals

$$\frac{(1.1)(2000)(100)}{(288)(2.7)+(1.1)(2000)}$$

or 74 per cent between 0 and 1 day after hatching. It equals 71 per cent for the interval between 1 and 2 days after hatching. These values seem quite high even though they are calculated with respect to the net energy increment of food. They may profitably be compared with estimates of gross efficiency for a precocial species, the domestic fowl, as summarized in Brody (1945:53). When the latter efficiencies are converted to a *net energy* increment basis (a conservative estimate is that net energy = 70 per cent of metabolizable energy) they are at least 10 per cent less than those calculated for the Vesper Sparrow. This provides further support for the conclusion that the altricial mode of development favors efficient growth.

SUMMARY

Observations on the growth and development of nestling Vesper Sparrows (*Pooecetes gramineus gramineus*) were made at the Edwin S. George Reserve, Pinckney, Michigan. Forty-six nestlings of various ages were used in the laboratory to establish the relations of oxygen consumption and body temperature to environmental temperatures. Growth rates of the heart and of the liver were also determined.

The incubation period, observed completely for 11 nests, was 12 to 13 days, and the mean length of the nestling stage for 96 young was 9.6 days. All ages subsequently specified indicate days after hatching. The young weighed about 2 gm. at hatching and attained a weight of approximately 18 gm. before leaving the nest. Growth was comparatively rapid during the first four days after hatching but slowed thereafter; liver and heart increased in weight relatively more rapidly than the body as a whole during the nestling period.

Feather tracts were clearly marked at 2 days of age when the primaries had just emerged. Rupture of feather sheaths and emergence of the rectrices occurred at 6 to 7 days, and the birds appeared well feathered at age 9 days. The eyes began to open at 3 to 5 days and the ocular opening was fully round at 8 to 9 days. Gradual muscular development permitted the young to stand when they were 6 days old, but well coordinated movement was not achieved until the eighth day after hatching. On approach of an observer the nestlings would gape during the first six days after hatching. Crouching replaced this response in older nestlings.

The oxygen consumption of birds 0 to 2 days old varied directly with environmental temperatures from 13° to 38°C. The first indication of an inverse relationship between oxygen consumption and environmental temperature was observed in 4-day-old birds at temperatures between 20° and 35°C. and was clearly evident at 6 days of age.

Nestlings from 0 to 2 days old were generally unable to maintain body temperature more than 3°C. above environmental temperatures between 13° and 37°C. Four-day-old individuals maintained body temperatures as much as 10°C. above environmental temperatures between 20° and 25°C. At 7 to 9 days of age most birds were able to keep their body temperature above 35°C. in environments between 10° and 38°C. Young nestlings showed considerable tolerance to chilling: 2-day-old birds recovered fully after being kept at body temperature of 18° to 20°C. for 8 hours.

The onset of homeothermy is linked with a complex array of processes leading to the establishment of functional neural control of body temperature regulation and to the development of capacities for heat production and conservation. Heat loss is reduced during the nestling period by a decline in the proportion of body surface to weight and probably also by feather development, although body temperatures were effectively regulated at moderate environmental temperatures even when the contour feathers had just begun to erupt from their sheaths.

The immature state of newly hatched young and the relatively short period between oviposition and hatching in altricial species do not require an egg as large or with as great an energy content as that needed in precocial species. The altricial condition also minimizes the maintenance costs of the young during a major part of their development, through parental brooding and feeding.

Based on the net energy increment of food ingested in the 24 hours after hatching, the gross efficiency of growth was estimated to be 74 per cent for the interval between 0 and 1 day after hatching, and 71 per cent for the succeeding 24-hour period. These high values support the conclusion that the altricial mode of development favors highly efficient growth.

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