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ENERGETICS OF GROWTH IN NESTLING SAVANNAH SPARROWS: A COMPARISON OF DOUBLY LABELED WATER AND LABORATORY ESTIMATES[1]

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Abstract. The energy expenditure of free-living nestlings has previously been estimated by any of several methods, each of which contains assumptions that may result in errors of uncertain magnitude. We evaluated the energy budget of nestling Savannah Sparrows (*Passerculus sandwichensis*) by analyzing their oxygen consumption and their accumulation of energy in tissues during growth. These results were compared with those obtained by means of the doubly labeled water (DLW) technique.

From data on oxygen consumption of individual nestlings in metabolism chambers at 35°C, we calculated that a neonate metabolized 110.4 kJ of energy during the eight days that it occupied a nest. Applying standard conversion factors, we determined that a nestling accumulated 20.0 and 61.6 kJ of energy in lipid and non-lipid dry matter, respectively, for a total production (*P*) of 81.6 kJ. Direct evaluation of the energy in tissues by means of bomb calorimetry indicated that nestlings actually accumulated 75.2 kJ of energy, a value 7.8% lower than we previously obtained by converting lipid and non-lipid dry matter to energy with accepted conversion factors. From our analysis using data obtained in the laboratory, total metabolized energy (*TME*) equaled 185.8 kJ.

Field metabolism, as estimated by DLW, summed to 171.5 kJ for the 8-day nestling period whereas estimates from oxygen consumption in the laboratory amounted to 110.4 kJ, a 35.6% difference. This disparity may have resulted from an increased energy expenditure for thermoregulation and activity during the latter stages of the nestling period, components which are not measured in laboratory experiments. Total metabolized energy (*TME*) as estimated by DLW (246.7 kJ) differed from laboratory estimates (182.9 kJ) by about 25%.

Production (*P*) to *TME* ratios for Savannah Sparrows on a daily basis were nearly as high as those for altricial embryos (*Agapornis*) with values declining from a maxima of 0.4–0.5 to 0.1 near the end of the nestling period.

Key words: Nestling energetics; doubly labeled water; Savannah Sparrow; field metabolic rate; daily energy expenditure; energy budget.

INTRODUCTION

The energy required by altricial nestlings during growth constitutes an integral part of the reproductive performance of parent birds (Ricklefs 1974). The additional amount of food that parents must procure above their own needs can be evaluated by constructing energy budgets for their young along with reasonable assumptions about their efficiency of assimilation (Williams and Nagy 1985). Additionally, compartmentalization of energy budgets for nestlings of different species allows comparison of their energy allocation patterns during their growth period, which presumably may clarify the mosaic of selective pressures that have impinged upon the species in the past (Dunn 1980).

Several approaches have been employed in estimating the economics of energy use by nestling birds. Ricklefs (1974), Ricklefs et al. (1980), and Bryant and Hails (1983) used measurements of oxygen consumption of chicks in laboratory metabolism chambers, coupled with information on the accumulation of tissues during growth. While these studies have physiological relevance, attempts to extrapolate their results to ecological questions are uncertain because of their frequent omission of important components of an overall energy budget, namely the heat increment of digestion (SDA) and/or the energy cost of locomotor activity (A; Kendeigh et al. 1977, Dunn 1980). The contribution of thermoregulation (TR) to the total energy budget of altricial nestlings may be difficult if not impossible to assess from laboratory studies on individual chicks within metabolism chambers (Clark 1982). Additionally, a single measurement of metabolism ignores the possibility that metabolic rates of nestlings may vary between day and night periods as shown by Brenner (1968) for nestling Red-winged Blackbirds (*Agelaius phoeniceus*).

A second method used to estimate the energetics of growth in free-living birds has been the estimation of rates of feeding and feces production of nestlings together with laboratory analysis of the energy content of their food, feces, and tissues accumulated during growth (Westerterp 1973, Hubbard 1978, Dunn 1980). However, results from these studies are problematical, owing to the difficulty in reliably measuring the quantity of food delivered or

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the actual amount of feces produced (e.g., Hubbard 1978, Bryant and Hails 1983).

A third method has been the measurement of energy utilization by laboratory-reared birds and analyses of carcass composition during growth (Blem 1975, Kendeigh et al. 1977, Montevecchi et al. 1984). These studies reflect the energy budget of free-living birds only to the degree to which the environment that they experience and the foods that they eat in the laboratory mirror their natural setting. In some studies, growth of captive chicks differed from those in the wild (Montevecchi et al. 1984).

Each of the above approaches makes assumptions that seem questionable or at best untested, rendering the results uncertain; thus generalizations drawn from such studies may be misleading. Indeed, Brafield and Llewellyn (1982) wrote that the reliability of energy budgets was difficult to determine and that present energy budgets may contain sufficient uncertainty as to prevent valid comparisons and generalization.

We constructed an energy budget for Savannah Sparrow (*Passerculus sandwichensis*) nestlings using data from laboratory metabolism experiments and from the energy accumulated in tissues during growth. We compared these results with those obtained by means of the doubly labeled water (DLW) technique in order to test the hypothesis that energy budgets constructed from laboratory data are comparable to energy budgets of nestlings in the field.

MATERIALS AND METHODS

STUDY AREAS AND SPECIES

One of our two study areas was in the middle of the upper littoral zone of a large salt marsh on the Pt. Mugu Naval Air Station, Pt. Mugu, California (34°07′N, 119°07′W). The vegetation consisted of *Salicornia virginica, Frankenia grandifolia, Batis maritima,* and *Monanthochloe littorolis.* Savannah Sparrows breed here from early April until July. Clutch size is 3.16 ± 0.46 eggs and the nestling period lasts 7 to 9 days (Williams and Nagy 1985). All DLW measurements were made on nestling Savannah Sparrows in this area during the month of June. Our second study area was situated in the northern end of a large, undisturbed salt marsh, Bahia de San Quintin, approximately 273 km south of the United States border on the Pacific side of Baja California, Mexico (116°00′W, 30°31′N). The flora was similar to that at Pt. Mugu. Neuenschwander et al. (1979) described completely the vegetation of this marsh. All measurements of oxygen consumption and carcass composition were made using birds from Bahia de San Quintin.

We knew the exact age (day of hatching is zero) for 13 of the 48 nestlings that we collected. Other nestlings were aged from a growth curve for nestlings from the Pt. Mugu population, for which sample size ranged from 111 on Day 0 down to 47 on Day 6.

The weather at Pt. Mugu is typical of areas adjacent to the southern California coast, with cool summers, mild winters, and a relatively small range of mean monthly temperatures throughout the year. From a 25-year summary of weather data at the Pt. Mugu weather station, De Violini (1975) reported mean monthly temperatures of 13.2, 15.9, and 17.5°C for May, June, and July, respectively. During May 1984 at Bahia de San Quintin, we recorded ambient temperature continuously with a thermograph wrapped in aluminum foil and placed in the shade. Mean temperature for the month averaged 18.3 ± 3.8°C.

OXYGEN CONSUMPTION

The rate of oxygen consumption ($\dot{V}O_2$) of nestlings was measured by means of a closed-circuit manometric system. Each of our four stainless steel chambers (1,000 ml) was wrapped with 3/8-inch copper tubing through which a mixture of water and methanol was circulated, with a refrigerated bath controlling the internal temperature of the chambers to within ±0.1°C. Each chamber was attached to a glass manometer with Tygon tubing; manometers were filled with a light gauge oil. Before each trial we placed into each chamber fresh Ascarite (CO_2 absorbent) and Drierite (water absorbent) in semicircular screen wire containers that were painted with flat black paint. Each nestling was placed on a wire platform covered with tissue paper. As nestlings depleted the O_2 within the system, we restored the pressure by injecting O_2 into the chamber with a glass syringe. We monitored the temperature inside each chamber with a 38-gauge thermocouple suspended about 3 cm above the nestling and a Bailey thermometer (Model 12). We weighed each nestling to 0.01 g on a Mettler balance before and after each trial and recorded initial and final body temperature (T_b) with a 38-gauge thermocouple inserted into the proventriculus. Most chicks were taken from their nests during midday and immediately placed within our system for equilibration. If more than 30 min lapsed before our trial began, we fed the nestlings canned tuna (packed in water) to assure that the heat increment of digestion would be included in our measurements of metabolism. After adjusting the total volume of our system for the volumes of the nestling, the Ascarite, and the Drierite, we corrected all our values of $\dot{V}O_2$ to STPD.

TABLE 1. Summary of validation studies of the doubly labeled water method on birds.

Species (*n*)	Mass (g)	Mean error (%)[a]	Range	Method[b]	Source
Rock Dove (10) (*Columba livia*)	380.0	+3.6	−12.2 to +16.8	GM	Le Febvre (1964)
House Martin (4) (*Delichon urbica*)	17.8	+3.4	···	IR	Hails and Bryant (1979)
Savannah Sparrow (6) (*Passerculus sandwichensis*)	16.6	+6.5	−0.2 to +11.0	GM	Williams and Nagy (1984)
European Starling (4) (*Sturnus vulgaris*)	69.8	+2.5	−14.7 to +16.3	GM	Williams (1985)
White-throated Sparrow (3) (*Zonotrichia albicollis*)	23.2	+6.1	−4.0 to +13.4	GM	Williams (1985)
Budgerigar (9) (*Melopsittacus undulatus*)	41.5	−0.04	−5.2 to +6.22	GM	Buttermer et al. (unpubl.)
Gambel's Quail (7) (*Callipepla gambelii*)	143.4	−4.9	−17.0 to +8.0	BAL	Goldstein and Nagy (1985)

[a] Calculated as (DLW − DM/DM) × 100 where DM is direct measurement.

[b] GM represents the gravimetric method, IR the infrared gas analysis method, and BAL the balance method.

We verified the measurements of $\dot{V}_{O_2}$ in the closed system by comparing them with those obtained with an open-flow system. Flow rates of the open-flow system were controlled with a Tylan mass flow controller, temperature was measured as in our closed system, and the percentage of O_2 in the air stream was determined by an Applied Electrochemistry oxygen analyzer. Values for $\dot{V}_{O_2}$ for a laboratory mouse (*Mus musculus*) did not differ between the systems [mean (ml O_2/hr) for O_2 analyzer = 47.1 ± 7.4, mean for manometric system = 51.4 ± 7.2, $t = 1.11$, $n = 14$, $p > 0.2$].

CARCASS ANALYSIS

We validated each method that we used in determining the constituents of a nestling's body (Prints and Williams, unpubl.). Nestlings and adults were oven-dried at 70°C to constant mass, then homogenized in a Wiley Mill or, for small nestlings, in a mortar and pestle. Subsamples were then used for carcass analysis.

For the determination of total lipids within the body, we followed Bligh and Dyer (1959). Energy content was determined with a Parr adiabatic bomb calorimeter calibrated with standard benzoic acid pellets. We determined nitrogen content with an ammonia electrode method following Bremner and Tabatabai (1972). Experimentation with this technique in the laboratory using known ammonium chloride solutions demonstrated a small error in our technique (±5%) (Prints and Williams unpubl.). Thus, for each analysis we simultaneously ran standard NH_4Cl solutions with our samples to assure accuracy. Crude protein was estimated by the relationship, crude protein (g protein/kg dry matter) = (g N/kg dry matter) × 6.25 (McDonald et al. 1981).

DOUBLY LABELED WATER

Our procedure using DLW has been described elsewhere (Williams and Nagy 1985). In brief, we injected tritiated water (0.3 microcuries tritium per microliter solution) mixed with 95 atom % oxygen-18 into the pectoral muscles of nestlings using a laboratory-calibrated glass syringe. An hour later we weighed the nestling to 0.1 g with a calibrated Pesola scale and took a blood sample (0.025–0.1 ml, depending on the size of the nestling) from a vein either in the neck region (small nestlings) or in the wing (larger nestlings). We injected nestlings between 1000 and 1200. Watching from a blind, we noted that parents resumed their feeding trips 15–30 min after our departure from a nest. We bled and weighed birds a second time, 22 to 24 hr after the initial blood sampling. Nestlings ranged in age from 0 to 7 days, which included most of the 7 to 9 days that they require to fledge. We did not inject older nestlings because they would likely have fledged before our return to the nest.

In the laboratory we micro-distilled (Wood et al. 1975) each blood sample to obtain pure water. We assayed the water for tritium activity with a Beckman LS 230 liquid scintillation counter using a toluene-Triton X 100-PPO scintillation cocktail, and for oxygen-18 content by cyclotron-generated proton activation of 0-18 to fluorine-18, with subsequent counting of the gamma-emitting F-18 with a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Rates of CO_2 production ($\dot{V}_{CO_2}$) were calculated using Equation (8) of Nagy (1975).

The DLW technique has been compared with direct measures of $\dot{V}_{CO_2}$ for seven species of adult birds ranging in size from 16 to 380 g

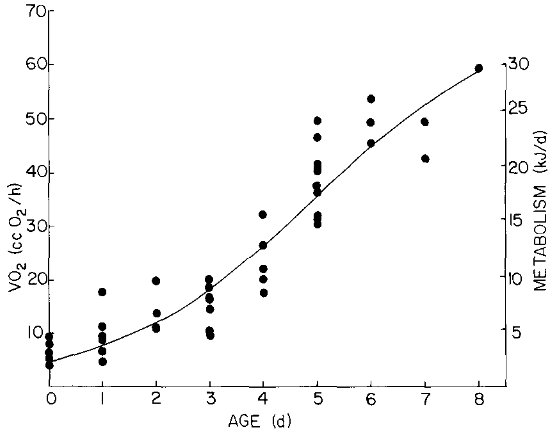

FIGURE 1. Relationship of oxygen consumption (cc O_2/hr) and energy metabolism (kJ/d) to age in nestling Savannah Sparrows.

with mean errors averaging between −4.9 and +6.5% (Table 1). Because rapidly growing birds can incorporate isotopes differentially into newly synthesized tissues, the possibility exists that errors larger than those found in previous validation studies on adults could occur. Williams and Nagy (1985) presented several lines of evidence suggesting that, in the measurement of CO_2 production, errors due to the incorporation of isotopes into newly synthesized tissue would be small.

STATISTICS

To fit logistic curves to our data, we used an iterative program (P3R) from the BMDP statistical package (Dixon et al. 1983). Means are presented ±1 SD.

RESULTS

OXYGEN CONSUMPTION

In metabolism chambers at 35°C, nestling Savannah Sparrows consumed O_2 at an average rate of 6.6 ± 2.2 ($n = 5$) ml O_2/hr on the day of hatch increasing to 58.2 ($n = 1$) ml O_2/hr on day 8 (Fig. 1). The relationship between $\dot{V}O_2$ (ml O_2/hr) and age (days) is described by the logistic equation;

$$\dot{V}O_2 = \frac{69.1}{1 + 13.6e^{(-0.55)(\text{age})}} \qquad (1)$$
$$(S^2\text{YX} = \pm 5.6,\ n = 42)$$

Assuming the relationship 20.08 J/cc O_2 (Schmidt-Nielsen 1979), nestlings metabolized an average of 3.2 ± 1.1 and 28.0 kJ/d on Day 0 and 8, respectively.

$$\text{kJ/d} = \frac{32.4}{1 + 13.6e^{(-0.55)(\text{age})}} \qquad (2)$$
$$(S^2\text{YX} = \pm 2.7,\ n = 42)$$

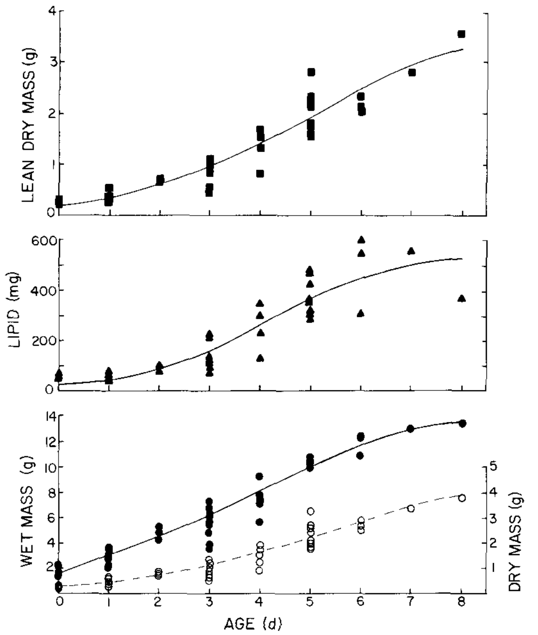

FIGURE 2. The relationship between the accumulation of materials and age for nestling Savannah Sparrows. Closed circles represent wet mass; open circles, dry mass; closed triangles, lipid; and closed squares, lean dry mass.

COMPOSITION OF CARCASSES

NESTLINGS

Nestlings ranged in wet mass (WM) from 2.05 ± 0.32 g ($n = 7$) on Day 0 to a mass of 12.78 g on Day 8 (Fig. 2).

$$\text{WM} = \frac{15.4}{1 + 7.6e^{(-0.53)(\text{age})}} \qquad (3)$$
$$(S^2\text{YX} = 0.84,\ n = 48)$$

Dry mass (DM) content of nestlings increased from 3.1 ± 0.04 g ($n = 7$) on Day 0 to a maximum of 3.89 g on Day 8.

$$\text{DM} = \frac{4.5}{1 + 18.4e^{(-0.59)(\text{age})}} \qquad (4)$$
$$(S^2\text{YX} = 0.29,\ n = 48)$$

Chicks at hatch contained 61.3 ± 5.5 mg of lipid which increased to a value of 578.0 mg by Day 7; a single nestling 8 days old contained 366 mg of lipid.

$$\text{lipid (g)} = \frac{0.55}{1 + 47.7e^{(-0.95)(\text{age})}} \qquad (5)$$
$$(S^2\text{YX} = 0.09,\ n = 33)$$

Lean dry mass (LDM), which is the dry mass with the lipid fraction removed, varied from 0.26 ± 0.05 g on Day 0 to a value of 3.52 on Day 8.

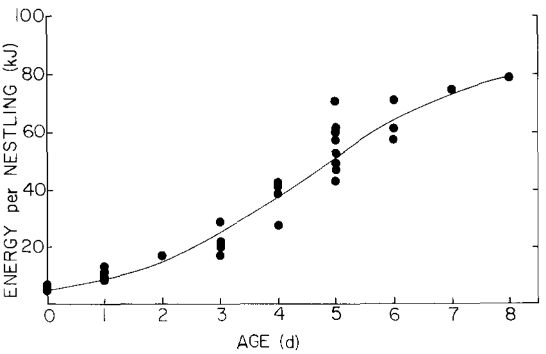

FIGURE 3. The accumulation of energy (kJ per nestling) during the nestling period for Savannah Sparrows.

$$\mathrm{LDM} = \frac{3.81}{1 + 18.2e^{(-0.59)(\mathrm{age})}} \quad (S^2\mathrm{YX} = 0.31,\ n = 33) \tag{6}$$

Nestlings hatched containing an average of 5.52 ± 1.1 kJ ($n = 3$); by day 8 this value had reached 78.40 kJ (Fig. 3).

$$\begin{array}{c}\text{Total Energy}\\ \text{of Nestling}\end{array} = \frac{86.59}{1 + 19.1e^{(-0.67)(\mathrm{age})}} \quad (S^2\mathrm{YX} = \pm 6.4,\ n = 32) \tag{7}$$

ADULTS

Our analysis of four adult carcasses (3 females and 1 male) showed an average wet mass of 17.54 ± 0.7 g, a dry mass of 5.97 ± 0.3 g, 596.1 mg of lipid per bird, a lean dry mass value of 5.37 ± 0.2 g, and 123.9 kJ of energy per bird.

CO_2 PRODUCTION AND FIELD METABOLISM

Rates of CO_2 production as determined by DLW for a sample of 35 nestling Savannah Sparrows have been reported previously (Williams and Nagy 1985). To convert units of CO_2 production into units of energy metabolism requires knowledge of the composition of the diet that an animal has eaten (Weathers and Nagy 1984). As an approximation of the insect foods that nestlings consumed, we analyzed individuals from three species of insects, obtained from Carolina Biological Supply, for protein, fat, carbohydrate, and ash content; we found mean values of 62.0, 14.9, 15.0, and 8.1% respectively (Table 2). Lepidopteran larvae and adult dipterans and orthopterans constitute a large percentage of the diet of nestling Savannah Sparrows (>70%) (Williams, unpubl. data). Removing ash content from these values and assuming that nestlings catabolized food stuffs in the same proportions as in their food, then they metabolized materials containing 67.5% protein, 16.2% fat, and 16.3% carbohydrate. For this diet we calculated a weighted conversion factor of 24.6 J/ml CO_2 by means of standard conversion factors for protein, fat, and carbohydrate metabolism (Schmidt-Nielsen 1979).

We recognize that our assumption that nestlings assimilated dietary protein, fat, and carbohydrate, in the same proportions as in the diet is questionable. We know of no data on the assimilation efficiencies of these nutrients by altricial nestlings. Our conversion factor of 24.6 J/ml CO_2 is within 5% of the value 25.75 J/ml CO_2 experimentally determined for an insectivorous lizard (*Uta stansburiana*) eating early instar mealworms (Nagy 1983), and thus our derived conversion factor seems reasonable.

Expenditure of energy by nestlings as given by DLW increased with age (Fig. 4).

$$\mathrm{kJ/d} = \frac{63.7}{1 + 16.2e^{(-0.48)(\mathrm{age})}}, \quad (S^2\mathrm{YX} = \pm 6.3,\ n = 35) \tag{8}$$

Integrating the two curves in Figure 4 (Equations 2 and 8) and subtracting the resulting values (171.5 − 110.4) yielded 61.1 kJ or a 35.6% increase in metabolism measured in the field compared with metabolism as determined by oxygen consumption in the laboratory. Analysis of covariance showed that field metabolism as given by DLW significantly dif-

TABLE 2. A comparison of the percentage of nitrogen, protein, fat, carbohydrate, and ash found in three species of insects. Blow flies and crickets were adults, hornworms were late instar larvae. All values are percent per gram dry mass. Data from Prints and Williams (unpubl.).

Species	% N[a]	% Protein[b]	% Fat	% Carbohydrate[c]	% Ash
Blow Fly (*Sarcophaga bullata*)	11.52 (0.10)	72.0	8.7 (0.3)	10.1	9.2 (0.6)
Tobacco Hornworm (*Manduca sexta*)	8.41 (0.10)	52.6	14.8 (3.7)	23.9	8.7
House Cricket (*Acheta domestica*)	9.82 (0.01)	61.4	21.1 (0.9)	11.0	6.5 (0.9)
Mean	9.92	62.0	14.9	15.0	8.1

[a] Values in parentheses represent ±1 SD. Each sample has $n = 2$ except for % ash for *Manduca sexta* where $n = 1$.
[b] Grams of nitrogen converted to grams of protein using the factor 6.25 (McDonald et al. 1981).
[c] Carbohydrate was determined by difference.

fered from our laboratory estimate of metabolism ($t = 6.37$, $p < 0.001$).

DISCUSSION

MODEL OF ENERGY FLOW

Because of the lack of uniformity in the terminology describing energy flow in growing animals, we describe here a simple model that compartmentalizes energy flow through a nestling. The amount of energy ingested (I) per unit time minus the energy excreted (EX) equals the total metabolizable energy (TME) (Kleiber 1961).

$$I = TME + EX \qquad (9)$$

We have partitioned TME into (1) maintenance metabolism, which is minimal metabolism minus biosynthesis, (2) biosynthesis (B), the energy cost of synthesizing complex polymers from simpler subunits, (3) SDA, the incremental increase in metabolism associated with digesting and assimilating food above that of fasted animals (Kendeigh et al. 1977), (4) energy cost of thermoregulation (TR), (5) energy cost of activity (A), and (6) production (P), the amount of energy accumulated in tissues. Thus,

$$TME = M + B + SDA + TR + A + P \qquad (10)$$

When $\dot{V}O_2$ of nestlings held at 35°C in metabolism chambers is used as a measure of field metabolism, M, B, and sometimes SDA are the components of metabolism measured; A and TR are generally assumed to be small or are ignored. Field metabolism (FM) estimated by DLW consists of:

$$FM = M + B + SDA + TR + A \qquad (11)$$

FM from DLW estimates should be a larger value than estimates based on $\dot{V}O_2$ from laboratory studies when TR and A are important components of the overall energy budget. Presumably small during the early stages of growth, the contribution of TR and A to the total energy budget of altricial nestlings is likely to increase toward the end of the nestling period.

For altricial nestlings, TR and A are at best complex parameters difficult to assess from laboratory studies. The age at which nestlings control their T_b, the internal thermostatic set point and how it varies between ages, feather development, the time spent brooding by parents, the number of nest mates, and the location and construction of the nest, all influence TR for a growing altricial bird. In some species, nest temperatures remain near normothermic levels (Diehl and Myrcha 1973) but in other species TR becomes increasingly important during the later stages of the nestling period (Westerterp 1973). Activity is usually ignored but may be an important component of the energy budget (Dunn 1980).

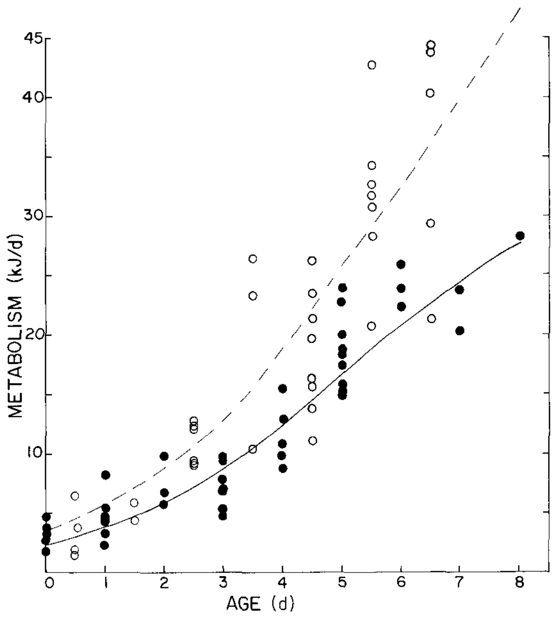

FIGURE 4. Metabolism (kJ/d) of nestling Savannah Sparrows vs. age. Closed circles and solid line represent metabolism in a laboratory metabolism chamber at 35°C; open circles and dashed line represent field metabolism as estimated by DLW.

In order to make interspecific comparisons of patterns of energy allocation, efficiencies are used. A frequently calculated value is growth efficiency:

$$GE = \frac{P}{TME} \qquad (12)$$

ENERGY BUDGET BASED ON DATA FROM THE LABORATORY

We calculated the energy budget of a Savannah Sparrow nestling from our data on $\dot{V}O_2$ and from the accumulation of energy in tissues (Table 3). From our equation relating $\dot{V}O_2$ to age, we calculated the O_2 consumption of a nestling at each age and converted these values to energy metabolism (kJ/d) (Column 1). Totaling values from Column 1 yielded 110.4 kJ for the 8-day nestling period, a figure which includes $M + B + SDA$. To derive the mg of lipid accumulated by nestlings (Column 2), we evaluated Equation (5) for each age, subtracted the value from the value for the previous age, and multiplied by 1,000. Quantities of lipid were translated into units of energy by means of the relationship 38 kJ/g lipid (Column 3). The accumulation of non-lipid dry matter was estimated from Equation 10 (Column 4), and energy units were obtained using 20 kJ/g lipid (Column 5). The energy equivalent of tissue accumulation (P) was evaluated by summing

TABLE 3. Calculation of the energy budget of a nestling Savannah Sparrow using data taken during laboratory experiments and from carcass analyses. Our procedure was patterned after Ricklefs et al. (1980).[a]

Age (days)	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]
0–1	2.9	17	0.65	0.15	3.0	3.65	3.72	4.96	1.67	6.63
1–2	4.3	39	1.48	0.23	4.6	6.08	6.40	8.53	2.19	10.72
2–3	7.8	79	3.00	0.35	7.0	10.00	9.89	13.19	4.54	17.73
3–4	10.9	120	4.56	0.47	9.4	13.96	13.17	17.56	6.55	24.11
4–5	15.1	123	4.67	0.55	11.0	15.67	14.36	19.15	10.36	29.51
5–6	19.5	85	3.23	0.54	10.8	14.03	12.63	16.84	15.33	32.17
6–7	23.4	44	1.67	0.46	9.2	10.87	9.18	12.24	20.37	32.61
7–8	26.5	19	0.72	0.33	6.6	7.32	5.80	7.73	24.59	32.32
Total	110.4	526	20.0	3.08	61.6	81.6	75.2	100.2	85.6	185.8

[a] Explanation of columns

[1] Energetic equivalent of oxygen consumption (kJ/d) obtained by integration of Equation (2) for each age interval.

[2] Values for the rate of accumulation of lipid (mg/d) obtained by evaluating Equation (5) at each age, multiplying by 1,000, and subtracting values for a given age from those for the previous age.

[3] Energy equivalent of lipid accumulation, (kJ/d) = [2] × (38 kJ/g lipid; Ricklefs 1974).

[4] Values for the rate of accumulation of non-lipid dry matter (g/d) obtained by evaluating Equation (6) for each age and subtracting values from those for the previous age.

[5] Energy equivalent of accumulation of non-lipid dry matter (kJ/d) = [4] × 20 kJ/g (Rickefs 1974).

[6] Energy equivalent of tissue accumulation (kJ/d) = [3] + [5].

[7] Energy equivalent of tissue accumulation (kJ/d) obtained by means of bomb calorimetry. We evaluated Equation (7) for each age and subtracted values from those of the previous age.

[8] Total energy requirement for growth (kJ/d), assuming a production efficiency of 75% = [7] ÷ 0.75.

[9] Total energy requirement for maintenance (kJ/d) = [1] − (0.33 × [7]).

[10] Total energy expenditure for growth and maintenance (kJ/d) = [8] + [9].

Columns 3 and 5 (Column 6) which totals 81.6 kJ. The same information is ascertainable directly from our data on the accumulation of energy on a daily basis measured by bomb calorimetry (Column 7) which gives a total of 75.2 kJ accumulated energy, a 7.8% difference. Our data support the idea that quantities of lipid and lean dry mass can be converted into units of energy.

When data for the total energy content of a nestling are unavailable, authors sometimes apply the equation for the energy density of Rufous-winged Sparrow (*Aimophila carpalis*) nestlings presented by Ricklefs (1974). This equation predicts an energy content of 6.3 kJ and 99.9 kJ for a hatchling and an 8-day old nestling Savannah Sparrow, respectively, but our equation predicts values of 4.3 kJ and 79.5 kJ, a 46.5 and 25.7% difference. Apparently Ricklefs' equation should be used with caution when applied to other species.

The total energy requirement for growth ($P + B$) can be evaluated if the assumption is made that the production efficiency is 75% (Ricklefs 1974); thus (P, Column 7) ÷ 0.75 yields the energy requirement for growth (Column 8). By subtracting the values for biosynthesis [0.33 × (7); Ricklefs et al. 1980] from those in Column 1, an approximation for maintenance can be obtained (Column 9), a procedure that assumes SDA to be negligible. The total energy expenditure for growth and maintenance (TME) is given by the sum of Columns 8 and 9. Our estimate of the TME based on laboratory measurements is 185.8 kJ (Column 10).

The total energy requirement of a Savannah Sparrow nestling rises sharply until Days 5 to 6 when it reaches a maximum of around 35 kJ/d (Fig. 5). The cost of growth peaks about Days 4 to 6 and declines steadily thereafter. Lipid deposition is greatest midway through the nestling period and is markedly reduced by Day 8, when total accumulation, around 526 mg, is nearly equal to adult levels (596.1 mg).

COMPARISON OF *FM* AS DETERMINED BY DLW AND METABOLISM IN THE LABORATORY

The total field metabolism as given by DLW for a Savannah Sparrow nestling during Days 0 to 8 was 171.5 kJ (Fig. 5). This value represents $M + B + SDA + TR + A$ and is 35.6% higher than our estimate of metabolism from laboratory data (110.4 kJ) obtained by integration of Equation (2), a value which is comprised of $M + B + SDA$. Visual inspection of these curves suggests that values of field metabolism diverged from laboratory estimates midway through the nestling period, perhaps when TR and A became more important components of the overall energy budget. Dunn (1980) indirectly evaluated the energy costs of A and TR in the Double-crested Cormorant (*Phalacrocorax auritus*) and reported that these components amounted to 180% of the nestlings' thermoneutral maintenance requirement after the age at which brooding ceases. If sparrow nestlings used the same percentage of energy for A and TR, they would expend 198.7 kJ, a much higher value than we found. This difference may be attributable to the fact that cormorants stay in the nest until growth is completed and are active during the latter part of the nestling period (Dunn, pers. comm.). Westerterp (1973) indicated that for the European Starling (*Sturnus vulgaris*) TR and A

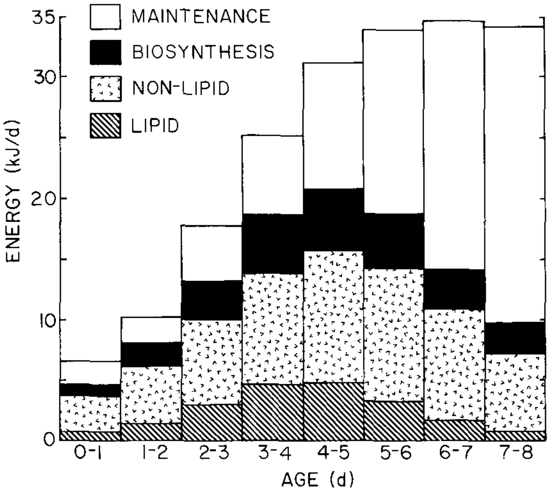

FIGURE 5. The energy budget of nestling Savannah Sparrows based on oxygen consumption and the accumulation of materials during growth.

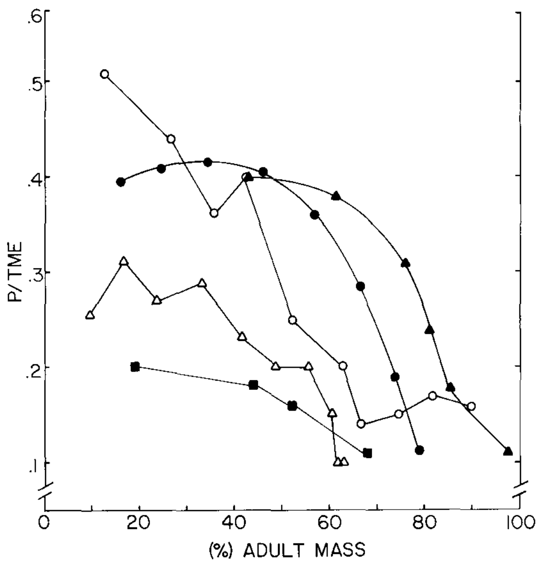

FIGURE 6. The relationship between the ratio *P/TME* and % adult mass for several altricial nestlings and one species of lizard. Closed circles represent data from this study; closed triangles, data from Westerterp (1973) on starlings; open circles, data from Blem (1975) on House Sparrows; open triangles, data from Fiala and Congdon (1983) on male Red-winged Blackbirds; closed squares, data from Nagy (1983) on *Uta stansburiana.*

accounted for 5.3% and 16.9% respectively, of *TME* (data from table). The difference between the integrated values of Equations 2 and 8 which presumably equals the energetic cost of $A + TR$, 61.1 kJ, amounts to 25.0% of *TME* as given by DLW, in close agreement with Westerterp's data (22.2%).

ENERGY BUDGET FROM DLW AND *P*

Combining Equations (10) and (11) results in the expression, $TME = FM + P$. Our estimate of *FM* by integration of Equation (8) is 171.5 kJ; our estimate of *P* is 75.2 kJ (Column 7, Table 3); thus *TME* equals 246.7 kJ. With our analysis of data from oxygen consumption and tissue accumulation, we arrived at a figure of 185.8 kJ for *TME,* a 24.7% difference.

If *TME* equals 246.7 kJ and the assimilation efficiency is 75%, then parents supplied 328.9 kJ of energy per nestling or 986.8 kJ for a brood of three. With a basal metabolic rate (BMR) of 1.48 kJ/($g \times d$) (Williams and Hansell 1981) or 26.6 kJ/d for an 18-g bird, then for eight days, adult BMR equals 213.1 kJ. If each parent supplies one-half of the energy requirements for a brood of three, then individually they provide energy amounting to 2.3 times their BMR (Williams and Nagy 1985).

ALLOCATION OF ENERGY DURING GROWTH

Assessment of the selective processes involved in the growth energetics of nestlings requires comparisons of the allocation of energy between species, based on some relative measure of allocation to the components of the energy budget. We disagree with Dunn (1980) that the appropriate common denominator for this comparison is BMR; according to Dunn, this is the minimum level of metabolism of a resting nestling under little or no thermal stress. The term "BMR" should not be applied to growing endotherms involved in biosynthetic functions, but rather should be reserved for the minimum level of metabolism of adults under a restricted set of conditions, namely, at temperatures in their thermoneutral zone, in their nocturnal phase, and during their post-absorptive period (Kendeigh et al. 1977). Dunn further suggested that "BMR" for nestlings equals adult BMR, but the evidence seems to indicate otherwise (Ricklefs 1974, Bryant and Hails 1983, Eppley 1984). For Savannah Sparrows, the assumption is certainly not true; "BMR" for nestlings exceeds adult BMR by as much as 35% during the 8-day growth period (Williams and Hansell 1981). Moreover, to extrapolate from nestling existence energy (EE; sensu Kendeigh et al. 1977) to "BMR" and assume that EE equals "BMR" × 1.3 as suggested by Dunn seems dubious. Existence energy for similar sized adults and nestlings differs in a number of species (Kendeigh et al. 1977). We believe it more useful to compare the proportion of *TME* allocated to *P* and other components of the energy budget.

Growth efficiencies (*P/TME*) for the entire nestling period (e.g., Drent and Daan 1980) should be compared with caution because these time periods vary, with many species continuing to grow after they have fledged (Williams and Nagy 1985). To address questions about energy allocation during growth, we have chosen *P/TME* ratios calculated at intervals during the nestling period. These efficiencies for avian embryos are poorly known. According to Brody (1945), chicken (*Gallus gallus*) embryos converted 62% of *TME* to *P* over the entire incubation period, but efficiencies for parrot embryos (*Agapornis roseicollis*), an altricial species, ranged from 0.22 to 0.58 through the incubation period and averaged 0.45 (Bucher and Bartholomew 1984). Values for nestling Savannah Sparrows, European Starlings (Westerterp 1973, calculated from fig. 10 and fig. 5), and House Sparrows (*Passer domesticus*) are nearly as high as those for *Agapornis* embryos when nestlings are young, but decline sharply beginning around the time that they attain 40 to 50% of adult mass (Fig. 6). Fiala and Congdon's (1983) data for male Red-winged Blackbird nestlings fall below those of other altricial species, suggesting either something unique in the allocation patterns for this species or perhaps an error in the measurement of *TME*. The ratios from Nagy (1983) for a small lizard, *Uta stansburiana,* lie below those calculated for rapidly growing altricial nestlings.

In summary, we have tested the notion that energy budgets constructed from laboratory data are comparable to those of nestlings in the field. We found that budgets constructed from laboratory data underestimated energy budgets of nestling Savannah Sparrows in the field by about 25%. The two measures of metabolism, $\dot{V}O_2$ and DLW, corresponded closely for the first few days of nestling life, but diverged as nestlings aged when activity and thermoregulation became a large component of their energy budget.

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