

GROWTH AND ENERGETICS OF NESTLING YELLOW-EYED JUNCOS¹

WESLEY W. WEATHERS

Department of Avian Sciences, University of California, Davis, CA 95616

KIMBERLY A. SULLIVAN

Department of Biology, Utah State University, Logan, UT 84322-5305

Abstract. We calculated the energy budget of nestling Yellow-eyed Juncos (*Junco phaeonotus*) from measurements of their growth, field metabolic rate (FMR), and resting metabolic rate (RMR). We used the doubly labeled water technique to measure the FMR of 69 nestlings that ranged in mass from 4.1 to 15.3 g. We calculated RMR of fed nestlings during the day and fasted nestlings at night from measurements of their O₂ consumption. Nestling FMR (kJ/hr) increased linearly with mass (m , grams) according to the relation: $FMR = -0.44 + 0.14m$. RMR (kJ/hr) = $-0.11 + 0.08m$ for fed nestlings during the day, and $RMR = -0.10 + 0.06m$ for fasted nestlings at night. The growth of 75 nestling juncos was best described by the logistic equation $m = 18.53/(1 + (6.5e^{-0.471t}))$; where t is age in days and m is mass in grams. The growth constant ($k = 0.471$) is not significantly different from that predicted allometrically for an altricial species with an asymptotic mass of 18.5 g.

Total metabolized energy of nestlings averaged 322 to 483 kJ/bird over the 9 to 12 day nestling period (depending on age at fledging). Of the total energy metabolized, RMR comprised 46–48%, whereas activity and thermoregulation combined accounted for 30–33%. The energy accumulated in tissue was estimated to be 84–95 kJ, or 20–26% of the total metabolized energy.

Key words: *Yellow-eyed Junco; doubly labeled water; nestling; growth; energy metabolism; Junco phaeonotus.*

INTRODUCTION

Clutch size evolution in birds continues to fascinate evolutionary biologists and to stimulate vigorous debate (see Murray 1985, Murphy and Haukioja 1986). Although the roots of the debate go back as far as 1923 (Murray 1985), Lack (1947) is generally credited with proposing one of the two main theories; namely, that clutch size in altricial birds is determined by the parents' capacity to feed their young and that brood size and growth rate are adjusted accordingly. Evaluating Lack's hypothesis requires knowledge of the energy requirements of growing nestlings and their parents. Unfortunately, direct measurements of nestling energetics are so scarce that investigators of this topic have been forced to rely upon indirect methods and/or speculative reasoning. The two principal indirect methods for estimating nestling energy requirements are: 1) extrapolating laboratory measurements of nestling O₂ consumption to the field, and 2) estimating food consumption and feces production

of nestlings. Both methods have inherent limitations. The former typically ignores the energy costs of activity and thermoregulation (but see Westerterp 1973, Dunn 1980) and hence underestimates actual nestling energy requirements (Gettinger et al. 1985). The magnitude of the underestimation involved in this method undoubtedly varies with the species; in Savannah Sparrows (*Passerculus sandwichensis*) it was 25% (Williams and Prints 1986). The second method is unreliable because neither the quantity of food delivered nor the amount of feces produced can be accurately ascertained (Hubbard 1978, Bryant and Hails 1983). The doubly labeled water (DLW) method, in contrast, provides a direct measure of nestling CO₂ production and hence energy expenditure. Despite its advantage over the indirect methods, DLW has been used to determine nestling energetics in only a few species (Gettinger et al. 1985, Williams and Prints 1986, Klaassen et al. 1989, Weathers and Sullivan 1989, Weathers et al. 1990). Additional studies of nestling energetics based on the DLW method are needed before general patterns will become apparent. Accordingly, in this study we used DLW to evaluate the energetics of nestling Yellow-eyed

¹ Received 22 June 1990. Final acceptance 16 October 1990.

Juncos (*Junco phaeonotus*) throughout the nestling stage.

METHODS

We conducted this study on a population of marked Yellow-eyed Juncos that were nesting at an elevation of 2,560 m in the Chiricahua Mountains, Cochise County, Arizona (31°55'N, 109°17'W). The study site consists of coniferous forest with little understory, short-grass meadows, and areas of bracken fern (*Pteridium* sp.). The predominant tree species are *Pinus ponderosa*, *Pinus strobiformis*, and *Pseudotsuga menziesii* (see Balda 1967 for detailed site description). At this site, Yellow-eyed Juncos breed from late April through late August, and typically produce broods of 3–4 young with up to 3 broods/season. Incubation lasts 13 days, nestlings spend 9–12 days in the nest, and both parents feed the young. For details concerning the species' natural history, population biology, and energetics see: Moore (1972), Sullivan (1988, 1989), and Weathers and Sullivan (1989).

We monitored the mass of 75 nestlings from hatching until fledging or disappearance. Nestlings were weighed daily to the nearest 0.05 g, at approximately the same time of day, with a K-Tron model DS-10 electronic balance that was calibrated using a standard mass. Most nestlings (85%) were weighed between 08:30 and 12:00, but some were weighed as early as 06:15 or as late as 15:46 (Table 1). Prior to banding at 4–6 days of age, nestlings were identified using unique combinations of non-toxic paint applied to their toes.

OXYGEN CONSUMPTION

We measured the oxygen consumption ($\dot{V}O_2$) of nestlings with a closed-circuit respiratory system both during the day (13:00–17:00) and at night (20:00–01:00). For these measurements, nestlings were collected in the field, transported in an insulated carrying case (held at about 35°C) to the laboratory (located at the Southwestern Research Station about 18 km away), and placed in an incubator maintained at 36–37°C. After about 30 min in the incubator, nestlings were weighed, fed a semi-liquid diet by syringe until their esophagus was bulging (Gerber's baby food; 62.5% protein, 34.4% fat, 3.1% carbohydrate), and then immediately placed in individual darkened, 400-ml metabolism chambers that were submerged in a water bath maintained at 36–

TABLE 1. Time of day that nestlings were weighed.

Time interval	No. nestlings weighed
06:00–07:59	25
08:00–09:59	262
10:00–11:59	207
12:00–13:59	20
14:00–15:59	26

37°C. This temperature was chosen to prevent hypothermia in small chicks, but still provide a thermally neutral environment for larger chicks. Although the thermoneutral zone (TNZ) of chicks is unknown, the upper critical temperature of most adult birds is 38–40°C (Weathers 1981). Since larger chicks exhibited none of the signs of heat stress (e.g., panting, drooping wings) when removed from the metabolism chamber, they were undoubtedly within their TNZ. Although we can not rule out the possibility that chicks engaged in spontaneous physical activity while in the metabolism chambers, such activity seems highly unlikely. Warm, fed chicks maintained in the dark tend to be quiescent (daytime measurements), while fasted chicks under simulated nighttime conditions probably slept. The chamber contained an artificial, cotton-lined nest-cup suspended above a 10% KOH solution. The chamber was attached to a fluid-filled glass manometer. During a 30-min equilibration period, the metabolism chamber was open to the atmosphere. It was then flushed with O_2 , closed, and the time required to consume 2–5 ml of O_2 was determined. The process was repeated 3–5 times and the average time calculated. An identical chamber, adjusted for the volume occupied by the nestling, was used as a thermobarometer to correct for changes in atmospheric pressure or chamber temperature. We monitored the temperature within the chamber with a 36-gauge thermocouple that was suspended about 3 cm above the nestling and connected to a Bailey/Sensortek model Bat-12 thermocouple thermometer. The Bailey Bat was calibrated against a mercury thermometer traceable to the National Bureau of Standards. Atmospheric pressure was measured with a precision aneroid barometer (Tayama & Co., Ltd.). We corrected all $\dot{V}O_2$ values to STPD. Measurements of nighttime $\dot{V}O_2$ followed a similar protocol, except that nestlings were fasted for 3 hr before the measurements

began. The same individuals were measured at night and during the day.

FIELD METABOLIC RATE

Between June 2 and July 14, we determined the field metabolic rate (FMR) of 69 nestlings using either the single-sample ($n = 26$) or the double-sample ($n = 43$) doubly-labeled water (DLW) method (Webster and Weathers 1989). The single-sample method was used with all of the very small individuals (< 6 g). Nestlings were weighed to the nearest 0.05 g (K-Tron model DS-10 balance), given an intramuscular injection of water (2.5 μ l/g body mass) containing 97 atoms-percent ^{18}O and 12 kBq $^3\text{H}/\mu$ l, and returned to their nest. After allowing 1 hr for the labeled water to reach equilibrium with body water, we obtained a blood sample from a brachial vein (double-sample method). Approximately 24 hr later, injected nestlings were reweighed and final blood samples were obtained. The elapsed time between initial and final blood samples averaged 24.01 ± 0.13 hr. Blood samples were stored at 4°C in flame-sealed glass microhematocrit tubes for later analysis.

Blood samples were micro-distilled (Wood et al. 1975) to obtain pure water, which was assayed for tritium activity (Searle model Mark III liquid scintillation counter, toluene-Triton X100-PPO scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of ^{18}O to fluorine-18 with subsequent counting of the positron-emitting ^{18}F in a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Using the equations of Lifson and McClintock (1966) as modified by Nagy (1975), we calculated rates of water flux and CO_2 production from the isotope measurements. In a recent validation of our single-sample DLW method (Webster and Weathers 1989), errors in measured rates of CO_2 production averaged $< 0.5\%$ (range -8.3 to 11.2% , $n = 9$). Errors are slightly smaller than this with the double-sample technique (Buttemer et al. 1986). For discussions of the accuracy and assumptions involved in our DLW technique, see Weathers and Sullivan (1989), Webster and Weathers (1989), Weathers et al. (1990).

Errors may attend DLW measurements of rapidly growing animals owing to irreversible and disproportional incorporation of isotopes into body tissue (Nagy 1980, Williams and Nagy 1985). Although the extent of the error remains uncertain for junco nestlings, Klaassen et al.

(1989) validated the use of DLW for rapidly growing Arctic Tern nestlings (*Sterna paradisaea*). They found that DLW underestimated CO_2 production of three chicks (as estimated from O_2 consumption) by 2–4% during a first 24 hr measurement period. The underestimation increased to 8–16% during a second 24 hr period. Because all of our DLW measurements of junco nestlings were based on one-day samples, the error attributable to incorporation of isotopes into tissue is probably small (i.e., $< 7\%$).

METEOROLOGY

Concurrent with the DLW measurements, we monitored the bird's thermal environment with a meteorological station placed centrally at the study site. The meteorological parameters measured at 0.1 m above ground level were air temperature (T_a) (shaded 36-gauge Cu-Cn thermocouples) and wind speed (1.27 cm dia. hot-ball anemometers; Roer and Kjölsvik 1973, Buttemer 1981). The output of the sensors was measured at 10-sec intervals and averaged every 15 min. The meteorological data were recorded with a Campbell Scientific 21X microdata logger. The hot-ball anemometers were calibrated in a laminar flow wind tunnel against a Pitot tube and a calibrated Campbell model CA-27 sonic anemometer. Thermocouples were calibrated against a National Bureau of Standards certified mercury thermometer.

RESULTS

WEATHER

The weather was mild and rainless during the period that we determined nestling FMR (2 June to 14 July 1988). Figure 1 depicts T_a and wind speed (both measured 0.1 m above ground) at the study site for the 4-day period 2–6 June 1988. During this period, the FMR of 20 of the 68 nestlings (29%) was determined. During the entire study, nighttime low T_a 's ranged from 9.7 to 15.5°C, while daytime high T_a 's reached 18.1 to 28.5°C. Mean daily T_a ranged from 13.3 to 19.7°C and the grand mean T_a was 16.3°C. Maximum wind speed 0.1 m above ground ranged from 0.52 to 1.30 m/sec. Average daily wind speed ranged from 0.26 to 0.85 m/sec. Because junco nests are often located within dense vegetation or under logs, nestlings probably experienced lower wind speeds than those which we measured in the open.

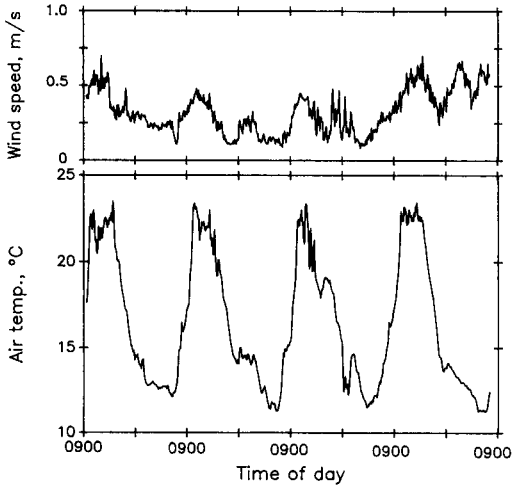


FIGURE 1. Relation of wind speed and air temperature measured 0.1 m above ground to time of day for the period 2-6 June 1988.

GROWTH RATE

A total of 596 measurements of body mass was obtained on 75 nestlings of known age. These data (Fig. 2) were fit by both Gompertz and logistic equations (SAS). The logistic equation provided a better fit as judged by its lower residual mean square. The relation between nestling mass (*m*, g) and age (*t*, days), as described by the logistic equation, is;

$$m = \frac{18.53}{1 + 6.5e^{-0.471t}} \quad (1)$$

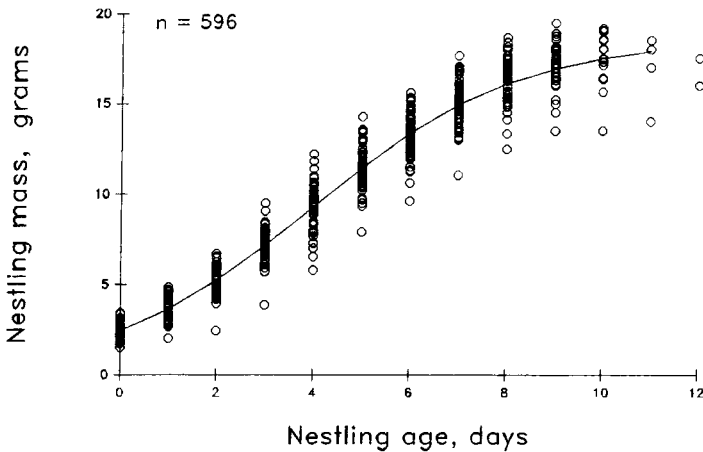


FIGURE 2. Nestling mass in relation to age. Solid line is the logistic fit described by Eq. 1.

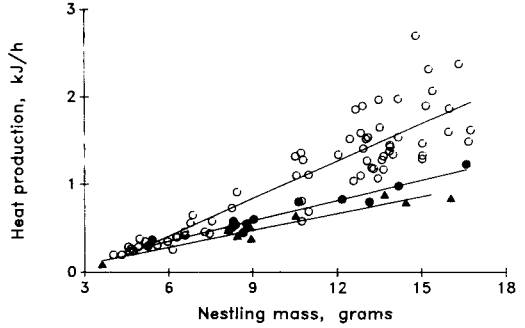


FIGURE 3. Field metabolic rate (unshaded circles) and resting metabolic rate (triangles = rest phase, fasted; shaded circles = active phase, fed) of nestlings in relation to mass. Lines are least-squares regressions described, respectively, by Eqs. 7, 3, and 2.

where *e* is the base of natural logarithms. Hatching day nestlings weighed an average of 2.42 ± 0.43 g (range, 1.53-3.45 g), and brood size ranged from 1-5 (mean = 3.96).

RESTING METABOLIC RATE (RMR)

The metabolic rate of nestling juncos resting in darkened metabolism chambers at 36-37°C was calculated from oxygen consumption based on an energy equivalency of 20.1 kJ/l O₂ for fasted nestlings and 19.8 kJ/l O₂ for fed nestlings (based on diet composition). RMR increased linearly with body mass (Fig. 3), and was higher for fed nestlings measured during the day than for fasted nestlings measured at night. Daytime RMR (kJ/

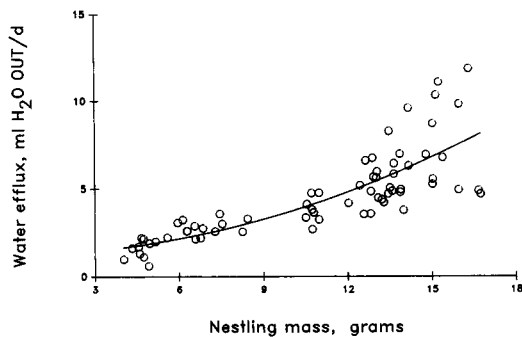


FIGURE 4. Total water efflux of nestlings in relation to mass. Line is least-squares regression described by Eq. 6.

hr) is described by:

$$\text{RMR}_{\text{day}} = -0.105 + 0.076m \quad (2)$$

$$(r^2 = 0.949, \quad s_{yx} = 0.059, \\ s_b = 0.005, \quad n = 14)$$

where m = mass in grams. Nighttime fasted RMR is:

$$\text{RMR}_{\text{night}} = -0.095 + 0.063m \quad (3)$$

$$(r^2 = 0.925, \quad s_{yx} = 0.070, \\ s_b = 0.006, \quad n = 10).$$

Daytime RMR predicted from the above equation is, on average, 23% greater than nighttime RMR.

DOUBLY LABELED WATER—WATER CONTENT AND FLUX

The total body water content of nestlings (TBW, ml), as determined by oxygen-18 dilution, increased with mass (m , grams) according to:

$$\text{TBW} = 0.700 + 0.75m \quad (4)$$

$$(r^2 = 0.97, \quad s_{yx} = 0.386, \\ s_b = 0.019, \quad n = 40).$$

The fraction of nestling mass consisting of water (W_f) decreased with increasing mass (m , grams) from 0.91 in 2.5-g hatchlings to 0.78 in 16-g fledglings, and can be described by the relation:

$$W_f = 0.936 - 0.01m \quad (5)$$

$$(r^2 = 0.45, \quad s_{yx} = 0.037, \\ s_b = 0.002, \quad n = 40).$$

Total water efflux (TWE, ml/d) of nestlings measured in the field increased exponentially with mass (m , grams) (Fig. 4). Following logarithmic

transformation, the relation between water efflux and mass can be described as:

$$\log \text{TWE} = -0.590 + 1.181 \log m \quad (6)$$

$$(r^2 = 0.769, \quad \log s_{yx} = 0.122, \\ s_b = 0.079, \quad n = 69).$$

FIELD METABOLIC RATE (FMR)

Nestling FMR was calculated from CO_2 production measured by doubly labeled water assuming 26.2 kJ/l CO_2 (Weathers and Sullivan 1989). The FMR (kJ/hr) of 69 nestling juncos (Fig. 3) increased linearly with mass according to the relation:

$$\text{FMR} = -0.443 + 0.142m \quad (7)$$

$$(r^2 = 0.804, \quad s_{yx} = 0.279, \\ s_b = 0.0006, \quad n = 69).$$

DISCUSSION

GROWTH RATE

Yellow-eyed Juncos nest on the ground and experience relatively high rates of nest predation (Sullivan 1989). Accordingly, one might expect selection to have favored rapid growth and that this would be reflected in the growth rate constant. However, the growth rate constant of junco nestlings ($k = 0.471$; 95% C.I. = 0.451–0.492) is not significantly different from the value predicted ($k = 0.493$) for an altricial species of its size (Ricklefs 1968). Although hole-nesting altricial species grow slowly (Ricklefs 1968), cup-nesting species seem to grow as rapidly as possible, regardless of nest site—ground vs. tree. It may be that ground-nesting species compensate for higher predation rates by fledging at an earlier age than do species that nest in trees (Harrison 1978).

Plotting nestling mass versus age (Fig. 2) reveals substantial variation in the mass of same-age nestlings throughout the nestling period, with the largest nestlings weighing 2–3 times as much as the smallest (different broods). The coefficient of variation for mass averaged 12.6% throughout the nestling period and ranged from about 17% between age 0–4 days to 8% by 10-days age.

NESTLING ENERGETICS—FIELD METABOLIC RATE

Four independent estimates of nestling passerine FMR, as determined by the DLW method, are available (Table 2). Selecting data from these studies for near-fledging sized nestlings and ad-

TABLE 2. Field metabolic rate of nestling passerines determined by doubly labeled water.

Species	Mass g	Field metabolic rate		Source
		kJ/d	kJ g ^{0.75} d ⁻¹	
<i>Carpodacus mexicanus</i>	15.0	39.0	5.12	Gettinger et al. 1985
<i>Passerculus sandwichensis</i>	12.8	27.8	4.11	Williams and Prints 1986
<i>Junco phaeonotus</i>	14.8	36.3	4.81	Weathers and Sullivan 1989
<i>Junco phaeonotus</i>	15.0	39.8	5.22	Present study

justing for differences in mass (by expressing FMR on a mass to the $\frac{3}{4}$ power basis) reveals general agreement between the species. This is perhaps to be expected, since the species are rather similar. Additional studies of dissimilar species are needed if adaptive patterns are to be identified.

Although the field metabolic rate of nestling juncos is a linear function of body mass (Fig. 3), considerable variation is apparent in the data. Among the factors that might contribute to this variation are brood size and air temperature (T_a). We examined the contribution of both factors using stepwise multiple regression analysis with FMR as the dependent variable and with body mass, T_a , and brood size as independent variables. Colinearity between the independent variables was insignificant, hence the stepwise model is an appropriate one. Two of the variables, body size and T_a , contributed significantly to the overall relation ($t = 16.517$ and -2.891 , respectively). Brood size was very nearly significant ($t = -1.995$, $P = 0.0503$) and we have retained it in the regression equation. FMR varied directly with nestling mass and inversely with both T_a and brood size according to:

$$\text{FMR (kJ/day)} = 30.0 + 3.43m - 2.16T_a - 1.07B \quad (10)$$

where m is nestling mass (g), T_a is the mean air temperature ($^{\circ}\text{C}$) measured 0.1 m above ground, and B is brood size. The coefficient of multiple determination (r^2 adj. = 0.825) is slightly higher than the r^2 for mass alone (Eq. 7, above) and indicates that 83% of the variation in nestling FMR is accounted for by mass, T_a , and brood size. Body mass is by far the most important determinant of nestling FMR, however, as the partial correlation coefficients for mass, T_a , and brood size are, respectively 0.897, 0.327, and 0.184.

NESTLING ENERGY BUDGET

In its simplest form, a nestling's energy budget consists of the following components of its total

metabolized energy (TME):

$$\text{TME} = \text{RMR} + \text{TR} + \text{A} + \text{TE} \quad (11)$$

where RMR is the resting metabolic rate of nestlings at nonstimulatory temperatures, TR is the cost of thermoregulation, A is cost of physical activity, and TE is energy accumulated in tissue (growth). RMR, which includes the cost of biosynthesis and the heat increment of feeding (HI), varies according to phase of the circadian cycle.

We used our metabolism and growth data to calculate the mean nestling energy budget (see Appendix). The increase in TME with age was sigmoidal (Fig. 5), with TME reaching 96% of its maximum value (ca. 54 kJ/day) by 7-days age (Table 3).

Total metabolized energy per nestling depends upon fledging age. For nestlings that fledge in 12 days, it is 483 kJ (Table 3). Of the total, RMR comprises about 47.9%, whereas activity and thermoregulation combined account for about 33.5% (calculated as $\text{FMR} - \text{RMR}$). The proportion of TME attributable to thermoregulation and activity increases throughout the nestling period. This is apparent from the divergence with age of the lines for RMR and FMR in Figure 5.

Although twelve previous studies have derived nestling energy budgets (see Wijnandts 1984, Klaassen et al. 1989), comparing them with our data is somewhat problematic owing to differences in methodology. Three of the 12 studies measured nestling FMR using the doubly labeled water (DLW) method and are thus directly comparable with the present study. The other seven studies estimated nestling FMR and TME indirectly, using methods involving numerous assumptions, some of which are rather tenuous. Williams and Prints' (1989) study is the only one that estimates nestling energy budgets by both direct (i.e., based on DLW) and indirect methods involving extrapolation of laboratory measurements of VO_2 to the field. In their study, the indirect method underestimated FMR as measured by DLW by 36%: TME measured with

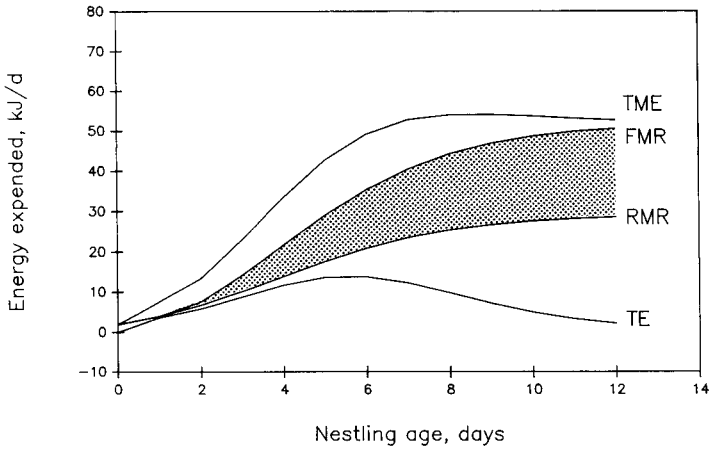


FIGURE 5. Energy expenditure of nestling Yellow-eyed Juncos as a function of age. TE = energy accumulated in new tissue (i.e., growth), RMR = resting metabolic rate, FMR = field metabolic rate (measured with doubly labeled water), and TME = total metabolized energy (i.e., field metabolic rate + growth). Shaded area represents the energy cost of thermoregulation plus physical activity. See Appendix for calculation methods.

DLW was about 25% higher than the indirect estimates. They attributed the higher values as measured by DLW to the energy cost of thermoregulation and activity during the later stages of the nestling period. A similar pattern of increasing amounts of energy being devoted to TR and A in older nestlings is evident in the Yellow-eyed Junco (Fig. 5), Arctic Tern (*Sterna paradisaea*) (Klaassen et al. 1989), and Acorn Woodpecker (*Melanerpes formicivorus*) (Weathers et

al. 1990). TR and A combined account for 25% of TME in Savannah Sparrow nestlings, 34% in the Yellow-eyed Junco, and 27% in the Arctic Tern. For Acorn Woodpecker nestlings, TR, A, and the heat increment of feeding combined represent 40% of TME. Thus in nestlings of four bird species that differ widely in growth rate, nest site, and body size, activity and thermoregulation combined comprise about 25–35% of TME. Gross growth efficiency for the entire nestling

TABLE 3. Parameters of the nestling Yellow-eyed Junco's energy budget.

Age, days	Mass, ^a g	EC, ^b kJ	FMR, ^c kJ/d	RMR, ^d kJ/d	TE, ^e kJ/d	TME, ^f kJ/d
0	2.47	4.7	1.8	1.8	0.00	1.8
1	3.66	7.9	3.8	3.8	3.18	7.0
2	5.24	13.0	7.2	6.5	5.15	12.4
3	7.18	20.8	13.8	9.8	7.75	21.6
4	9.32	31.2	21.1	13.5	10.46	31.6
5	11.46	43.6	28.4	17.1	12.39	40.8
6	13.38	56.4	35.0	20.4	12.76	47.7
7	14.94	67.9	40.3	23.1	11.54	51.8
8	16.11	77.3	44.3	25.1	9.36	53.6
9	16.94	84.2	47.1	26.5	6.98	54.1
10	17.51	89.1	49.0	27.5	4.90	53.9
11	17.88	92.4	50.3	28.1	3.30	53.6
12	18.12	94.6	51.1	28.5	2.17	53.3
Sum			393.3	231.6	89.9	483.2

^a Calculated as: grams = 18.53/(1 + 6.5e^{-0.47t}), where t = days age.
^b Nestling energy content (EC) calculated as: kJ = (1 - (0.936 - 0.01 · m)) · 21.3 · m, where m = mass in grams.
^c Field metabolic rate calculated as: kJ/d = -0.443 + 0.142m, except for days 0 and 1, for which FMR was assumed to equal RMR.
^d Resting metabolic rate (RMR) of nestling calculated as: kJ/d = 24 · (0.375 · (-0.095 + 0.063m)) + (0.625 · (-0.105 + 0.076m)).
^e Daily increment in tissue energy (TE) calculated by subtracting the previous day's EC from the current day's EC.
^f Total metabolized energy calculated as the sum of FMR and TE.

period (expressed as TE/TME) averages 0.24 (range: 0.17–0.29) in 13 altricial species (data summarized by Wijnandts 1984, Klaassen et al. 1989), but is only 13% in the Acorn Woodpecker (Weathers et al. 1990). Growth efficiencies should be compared with caution, however, because many species continue to grow after they fledge (Williams and Nagy 1985). Furthermore in those species that exhibit a range of fledging ages, apparent growth efficiency will differ for early versus late fledging nestlings. For example, Yellow-eyed Juncos that fledge at nine days of age would have a growth efficiency of 0.26, whereas growth efficiency of those that fledge at 12 days is only 0.20 (calculated from data in Table 3).

ACKNOWLEDGMENTS

The Southwestern Research Station and the Douglas Ranger District Office provided logistic support and other assistance. Financial support was provided by NSF grants DEB-8022765, BSR-8505490, BSR-8718195, and by the California Agricultural Experiment Station. T. Gumbart, S. Zwicker, C. Frazier, S. Stoleson, and B. Lance provided field assistance and Lisa Beres helped with the RMR determinations. W. A. Buttemer provided useful comments on the manuscript.

LITERATURE CITED

- BALDA, R. P. 1967. Ecological relationships of the breeding birds of the Chiricahua Mountains, Arizona. Ph.D. diss., Univ. of Illinois, Urbana.
- BRYANT, D. M., AND C. J. HAILS. 1983. Energetics and growth patterns of three tropical bird species. *Auk* 100:425–439.
- BUTTEMER, W. A. 1981. The thermal significance of winter roost-site selection by American Goldfinches (*Carduelis tristis*). Ph.D. diss., Univ. of Michigan, Ann Arbor.
- BUTTEMER, W. A., A. M. HAYWORTH, W. W. WEATHERS, AND K. A. NAGY. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* 59:131–149.
- DUNN, E. H. 1980. On the variability in energy allocation of nestling birds. *Auk* 97:19–27.
- GETTINGER, R. D., W. W. WEATHERS, AND K. A. NAGY. 1985. Energetics of free-living nestling house finches: measurements with doubly-labeled water. *Auk* 102:643–644.
- HARRISON, C. 1978. A field guide to the nests, eggs, and nestlings of North American birds. Collins: Glasgow.
- HUBBARD, J. D. 1978. Breeding biology and reproductive energetics of mountain white-crowned sparrows in Colorado. Ph.D. diss., Univ. of Colorado, Boulder.
- KLAASSEN, M., C. BECH, D. MASMAN, AND G. SLAGSVOLD. 1989. Growth and energetics of arctic tern chicks (*Sterna paradisaea*). *Auk* 106:240–248.
- LACK, D. 1947. The significance of clutch size. *Ibis* 89:302–352.
- LIFSON, N., AND R. MCCLINTOCK. 1966. Theory and use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* 12:46–74.
- MOORE, N. J. 1972. Ethology of the Mexican Junco (*Junco phaeonotus palliatus*). Ph.D. diss., Univ. of Arizona, Tucson.
- MURPHY, E. C., AND E. HAUKIOJA. 1986. Clutch size in nidicolous birds, p. 141–180. *In* R. F. Johnston [ed.], *Current ornithology*, Vol. 4. Plenum Press, New York.
- MURRAY, B. G., JR. 1985. Evolution of clutch size in tropical species of birds. *Ornithol. Monogr.* 36: 505–519.
- NAGY, K. A. 1975. Water and energy budgets of free-living animals: measurement using isotopically labeled water, p. 227–245. *In* N. F. Hadley [ed.], *Environmental physiology of desert organisms*. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- NAGY, K. A. 1980. CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Amer. J. Physiol.* 238:R466–R473.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- ROER, P., AND M. KJÖLSVIK. 1973. Equipment for measuring low air velocity. *Agric. Meteorol.* 12: 281–296.
- SULLIVAN, K. A. 1988. Ontogeny of time-budgets in yellow-eyed juncos: adaptation to ecological constraints. *Ecology* 69:118–124.
- SULLIVAN, K. A. 1989. Starvation and predation: age-specific mortality in juvenile juncos (*Junco phaeonotus*). *Journal of Anim. Ecol.* 58:275–286.
- WEATHERS, W. W. 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiol. Zool.* 54:345–361.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.* 59:223–246.
- WEATHERS, W. W., M. T. STANBACK, AND W. D. KOENIG. 1990. Breeding energetics and thermal ecology of the acorn woodpecker in central coastal California. *Condor* 92:341–359.
- WEBSTER, M. D., AND W. W. WEATHERS. 1989. Validation of single-sample doubly labeled water method. *Amer. J. Physiol.* 256 (Regulatory, Integrative Comp. Physiol. 25):R572–R576.
- WESTERTERP, K. 1973. The energy budget of the nestling starling (*Sturnus vulgaris*): a field study. *Ardea* 61:137–158.
- WIJNANDTS, H. 1984. Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* 72:1–92.
- WILLIAMS, J. B., AND K. A. NAGY. 1985. Water flux and energetics of nestling Savannah Sparrows in the field. *Physiol. Zool.* 58:515–525.
- WILLIAMS, J. B., AND A. PRINTS. 1986. Energetics of growth in nestling Savannah Sparrows: a compar-

ison of doubly labeled water and laboratory estimates. *Condor* 88:74-83.

WOOD, R. A., K. A. NAGY, S. MACDONALD, S. T. WAKAKUWA, R. J. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Anal. Chem.* 47:646-650.

APPENDIX

We based our nestling energy budget calculations (Fig. 5; Table 3) on nestling mass predicted by the logistic equation (Eq. 1). Total metabolized energy (TME) was calculated as the sum of the field metabolic rate (FMR), as measured with doubly labeled water, and the energy accumulated as new tissue (TE). We estimated resting metabolic rate (RMR, kJ/day) as the weighted average of Eqs. 2 and 3, based on a 15:9 L:D photoperiod for

nestlings in the field. As such, RMR includes the heat increment of feeding during the active phase of the daily cycle and the energy cost of biosynthesis. FMR was estimated from Eq. 7 and the mean nestling mass predicted for each day. For nestlings 0 to 1-day old, FMR was assumed to equal RMR, since Eq. 7 predicts $FMR < RMR$ for these ages. The energy content of nestlings (EC; kJ) was calculated by multiplying the dry mass calculated from Eq. 5 for each age by the assumed energy density of nestling tissue (21.3 kJ/g dry mass; mean value calculated from data of Williams and Prints 1986). The daily increment in TE (kJ/day) was obtained by subtracting the previous day's EC (kJ) from the current day's value. Because TE is a small fraction of TME, errors in our estimate of the energy density of dry nestling tissue will have relatively little effect on the nestling's overall energy budget.