ENERGETICS OF GROWTH AND MATURATION IN SYMPATRIC PASSERINES THAT FLEDGE AT DIFFERENT AGES

Patrick J. Mock,[1] Marina Khubesrian,
and Dee M. Larcheveque

*Department of Biology and Laboratory of Biomedical and Environmental Science, University of California,
Los Angeles, California 90024 USA*

Abstract.—We studied the energetics of growth and maturation of sympatric Western Bluebird (*Sialia mexicana*) and Ash-throated Flycatcher (*Myiarchus cinerascens*) nestlings in the San Jacinto Mountains, Riverside County, California. Both species fledge at a body mass of 27–28 g, but the flycatcher leaves the nest 4–5 days earlier than the bluebird. The growth curves of these two species become asymptotic by 14 days of age. Energy budgets, derived from estimates of CO_2 production and energy accumulation in tissues, demonstrate that the average daily total metabolizable energy requirement of the nestling flycatcher is approximately 22% (range: 16–32%) higher than the nestling bluebird. Most of this difference is due to a significantly higher field metabolic rate throughout the nestling period of the flycatcher. We attribute this higher energy expenditure to a greater daily allocation of energy to the metabolic processes and activity associated with maturation, which allows the flycatcher to fledge at a younger age than the bluebird. Because of the nestling flycatcher's higher daily energy requirements, adult flycatchers must gather up to 20 g more food each day than bluebird parents with the same number of young. Nestling mortality indicates that Ash-throated Flycatchers may be more susceptible to nest failure than Western Bluebirds during periods of poor food availability. *Received 7 October 1988, accepted 7 July 1990.*

The energy requirements of young in relation to the parents' ability to provide sufficient food to meet those requirements is an intrinsic relationship that affects the reproductive strategies of birds. Many factors influence the energy requirements of growing birds. Differences in body size, growth pattern, and the thermal environment of the nest site can affect the peak energy demands of a brood (Fiala and Congdon 1983, Ricklefs and White 1981, Mertens 1969, O'Connor 1975, Bryant and Gardiner 1979, Drent and Daan 1980).

Our purpose was to compare the energy expenditure of sympatric nestling Western Bluebirds (*Sialia mexicana*) and Ash-throated Flycatchers (*Myiarchus cinerascens*). The adult mass of both species is similar (range: 25–30 g), and nestlings fledge at a body mass ca. 27–28 g. The age at fledging differs by 4–5 days (bluebird: 20–21 days; flycatcher: 16–17 days). These two species have very similar breeding ecologies. The species share the same habitat, both are cavity nesters, and both are insectivorous during the breeding season. Because the breeding ecologies of these species were so similar, except for the age at fledging, this was an ideal situation to investigate energetic differences associated with the age difference at fledging.

We tested the hypothesis that the earlier fledging flycatcher would have greater daily energy requirements relative to the bluebird. Ricklefs (1973) proposed that biochemical and molecular constraints may limit the extent to which a tissue can both differentiate functionally and continue to proliferate and grow. This Precocity Hypothesis was proposed to explain differences in growth rates observed between precocial and altricial species. When tissue becomes functionally mature, energy needed for growth declines and a greater proportion of the energy budget is allocated to tissue maintenance and function. On a relative scale, the early-fledging flycatcher would be expected to be more precocious than the later-fledging bluebird. Energy allocated to tissue maintenance and activity associated with the process of fledging would occur at an earlier stage in the flycatcher, thereby incurring additional daily energy expenditures.

METHODS

Study area and species.—We worked at Garner Valley in the San Jacinto Mountains, Riverside County, Cal-

ifornia (33°47'N, 116°58'W; 1,375 m altitude), during the 1986 breeding season. The vegetation consisted of stands of Jeffrey Pine (*Pinus jeffreyi*) interspersed with wet and dry meadows dominated by native (*Stipa* sp.) and introduced (*Bromus* sp.) grasses and sagebrush (*Artemesia* sp.). Both bird species utilized artificial nest boxes placed on the northern side of pine tree trunks at a height of 1.5 m.

In Garner Valley, bluebirds begin to nest approx. 3–4 weeks ahead of the flycatcher. The first bluebird clutches are completed in mid-April, whereas the flycatchers begin to lay eggs in mid-May (Mock unpubl. data). In 1986 mean temperature was 13.4°C in May, 17.8°C in June, and 18.0°C in July. The range of clutch sizes for the two species was 3–6 eggs, and the modal clutch size for both species was 5. We checked nest boxes at 2-day intervals during the breeding season and daily at the time of expected hatching. All laying and hatching dates were estimated to the nearest 0.5 day. Doubly labeled water measurements of CO_2 production were conducted between 6 May and 6 July. Bluebirds were measured mostly in May (6 May to 6 June); flycatchers were measured mostly in June (4 June to 6 July).

Doubly labeled water.—In the field we followed standard procedures for the doubly labeled water method to determine daily energy expenditure (Nagy 1983). Nestlings were weighed to the nearest 0.25 g, and tritiated water (1 μCi·g^{-1} body mass) that was mixed with 97 atom % oxygen-18 (3 μl·g^{-1} body mass) was injected into the pectoral muscles of nestlings with a calibrated glass syringe. After a 45–60 min equilibration period, a blood sample (25–100 μl, depending on the size of the nestling) was taken from a vein in the neck (young birds) or from a vein in the wing (older nestlings). The bird was color-marked with a felt-tipped pen and returned to the nest. Blood samples were flame-sealed in heparinized microhematocrit tubes and stored at 4°C pending isotope analyses. All birds were injected between 1600 and 2000. The nestlings were weighed and bled a second time 22–26 h after the initial blood sampling. After obtaining the second blood sample, we killed and froze the labeled nestlings for subsequent carcass analysis.

Blood samples were microdistilled to obtain pure water (Wood et al. 1975, Nagy 1983). The water was assayed for tritium activity with a Beckman LS 1801 liquid scintillation counter in a toluene-Triton X 100-PPO scintillation cocktail. Oxygen-18 content of the samples was determined by the proton activation of oxygen-18 to fluorine-18, with subsequent counting of the gamma emissions of fluorine-18 by a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Water efflux and influx were calculated using equations 5 and 6, respectively, of Nagy and Costa (1980), and rates of CO_2 production were calculated using equation 3 of Nagy (1980). Background levels of isotopes measured in uninjected nestlings were subtracted from all values before calculations. The total body

water (TBW) volume of growing animals changes constantly, and the TBW estimate used in the calculation of CO_2 production and water flux was derived by drying individuals.

Carcass analysis.—Nestlings and food samples (grasshoppers) were oven-dried at 60°C to constant mass, then homogenized in a Wiley Mill or, for small nestlings and insects, in a Spex Mixer-Mill. Subsamples were then used to determine energy and lipid content. To estimate body total lipids, we used the Folch method (Folch et al. 1957) with a 2:1 chloroform : methanol solvent. Energy content was determined with a Phillipson microbomb calorimeter using benzoic acid as a standard. For the analysis both of lipid content and total tissue energy, two subsamples were used. If the coefficient of variation (CV) between replicates was greater than 5%, additional subsamples were analyzed until the total CV was less than 5%. Energy conversion factors used to generate the energy budgets were 24.6 kJ·(l CO_2)$^{-1}$ (Williams and Prints 1986) and 39.4 kJ·(g lipid)$^{-1}$ (Schmidt-Nielsen 1979). Energy content of the nonlipid portion of tissue was calculated from the difference between lipid energy content and total tissue energy content.

Description of growth.—We used Richards equation: $W = A[1 + (M - 1)e^{-K(T-I)}]^{1/(1-M)}$ where W = body mass, T = age, A = asymptotic mass after growth is completed, K = growth constant, I = the time to reach the inflection point, M = curve shape constant. The equation was fitted to growth data of individual nestlings with the program described by Bradley et al. (1984). Each individual was measured every 2–3 days until fledged. All individual growth curves were fitted to data sets that had at least seven data points. Means are ±1 SE unless otherwise indicated.

RESULTS

Growth.—The growth curves of the Western Bluebird and Ash-throated Flycatcher are very similar with much overlapping variation among individuals (Table 1). Both species attain an asymptote of 27–28 g body mass and require 10–11 days to reach 90% of the asymptotic mass. Because the growth curves of the two species are similar, we used a common growth curve intermediate between the two species' growth curves to calculate energy budgets. This controlled for relatively minor species differences in growth rate and asymptote, and it allowed for comparison of energy allocation with a common growth curve (Table 1).

Tissue composition.—Tissue composition and energy metabolism are primarily dependent upon the mass of the nestling. Due to the complex logistic nature of the relationship between age and tissue accumulation or metabolism, age

TABLE 1. Mean (±SE) growth parameters of Richards equation for Western Bluebird and Ash-throated Flycatcher nestlings at Garner Valley, Riverside County, California.

	Species		Values used in energy budget model
Growth parameter	Western Bluebird (564)[a]	Ash-throated Flycatcher (12)[a]	
Asymptotic mass (g)	28.0 ± 0.08	27.3 ± 0.17	27.65
Growth constant (day^{-1})	0.44 ± 0.01	0.40 ± 0.03	0.42
Time to inflection (days)	5.31 ± 0.04	5.50 ± 0.31	5.4
Shape constant	2.05 ± 0.03	1.94 ± 0.13	2.0
T_{10-90}[b]	10.4 ± 0.06	11.1 ± 0.51	

[a] Number of individuals. Each individual was measured 7–10 times during the nestling period.
[b] T_{10-90} is the time to pass from 10% to 90% of asymptotic mass.

is not an accurate predictor of the energy expenditure for individuals. Variation in individual developmental history in relation to nutritional status and growth rates prevents age from being correlated closely to the energy requirements of a growing nestling (Ricklefs and White 1981, Williams and Prints 1986). To generate comparable energy budgets for flycatchers and bluebirds, we used regression of field metabolism and tissue components against either wet or dry body mass (Table 2).

For the relationship between wet and dry mass, most of the variation in wet mass was due to changes in total body water associated with the process of tissue maturation (Ricklefs 1983, Hughes et al. 1987; Table 2, Fig. 1). Western Bluebird and Ash-throated Flycatcher nestlings accumulate lipid at nearly identical rates throughout the nestling period (ANCOVA, P

TABLE 2. Least-squares regression equations used to generate the energy budget models for Western Bluebird and Ash-throated Flycatcher nestlings.

Western Bluebird	Ash-throated Flycatcher
1. Dry mass (g) on wet mass (g)	
$y = 0.0836x^{1.37}$	$y = 0.1007x^{1.31}$
($n = 40$; $r^2 = 0.99$)	($n = 19$; $r^2 = 0.99$)
2. Total lipid energy[a] (kJ) on dry mass (g)	
$y = 0.0642 + 7.26x$	$y = -0.707 + 7.16x$
($n = 33$; $r^2 = 0.85$)	($n = 19$; $r^2 = 0.94$)
3. Total tissue energy (kJ) on dry mass (g)	
$y = 17.69x^{1.09}$	$y = 17.39x^{1.06}$
($n = 40$; $r^2 = 0.97$)	($n = 18$; $r^2 = 0.98$)
4. Field metabolic rate[b] (kJ·day^{-1}) on mean wet mass (g)	
$y = 0.924x^{1.28}$	$y = 1.654x^{1.17}$
($n = 40$; $r^2 = 0.97$)	($n = 19$; $r^2 = 0.92$)

[a] Assumed 39.4 kJ·g^{-1} lipid (Schmidt-Nielsen 1979).
[b] Assumed 24.6 kJ·l^{-1} CO$_2$ (Williams and Prints 1986).

> 0.05). A large portion of the variance in total body lipids of nestlings occurred during the later stage of the nestling period, after asymptotic mass was attained. Total tissue energy (TTE) content of nestlings increases at similar rates in both species (ANCOVA, $P > 0.05$). A typical hatchling of either species with a dry body mass of 0.3 g had approx. 4.6 kJ stored in its tissues. Fledglings with about 8 g dry body mass leave the nest with approx. 171 kJ of accumulated tissue energy (Table 2).

Energy metabolism.—Rates of CO$_2$ production increased in relation to wet mass. Nestling Ash-throated Flycatchers had significantly higher field metabolic rate (FMR) than nestling Western Bluebirds of the same size (Fig. 2). Analysis of covariance of regressions of log$_{10}$ field metabolic rate on log$_{10}$ mean wet mass for both species showed that the slopes were significantly different ($F_{54} = 6.03$, $P < 0.025$). Field metabolism was not correlated significantly with
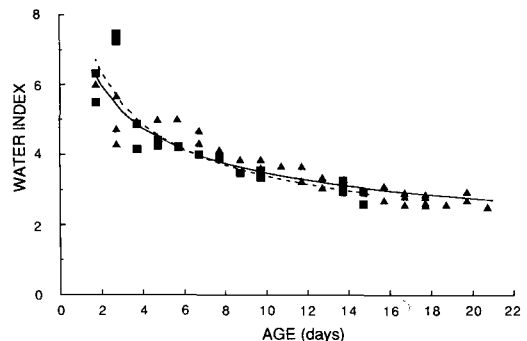

Fig. 1. The relationship between water index and age for nestling Western Bluebird (triangle, solid line) and Ash-throated Flycatcher (square, dashed line). Regression equations for water indices [g water/(g lean dry mass)] on age (days): $y = 7.55 + x^{-0.33}$, $n = 40$, $r^2 = 0.88$ (bluebird); $y = 8.34 + x^{-0.39}$, $n = 19$, $r^2 = 0.85$ (flycatcher).

TABLE 3. Energy budget of nestling Western Bluebird. Abbreviations: field metabolic rate (FMR), total tissue energy (TTE), total lipid energy (TLE), total nonlipid energy (TNL), and total metabolizable energy (TME).

Age interval (day)	Body mass (g)	Energy (kJ·day⁻¹)				
		FMR	TTE	TLE	TNL	TME
0–1	3.7	3.9	3.4	1.4	2.0	7.3
1–2	5.3	6.3	6.0	2.3	3.7	12.3
2–3	7.4	9.8	9.3	3.5	5.8	19.1
3–4	9.9	14.5	12.9	4.6	8.3	27.4
4–5	12.7	20.4	16.5	5.7	10.8	36.9
5–6	15.6	27.3	19.1	6.5	12.6	46.4
6–7	18.3	34.7	19.4	6.4	13.0	54.1
7–8	20.7	41.7	18.5	6.0	12.5	60.2
8–9	22.7	47.7	16.3	5.2	11.1	64.0
9–10	24.2	52.6	12.7	4.0	8.7	65.3
10–11	25.3	56.3	9.5	3.0	6.5	65.8
11–12	26.0	58.9	6.2	1.9	4.3	65.1
12–13	26.6	60.7	5.4	1.7	3.7	66.1
13–14	26.9	62.2	2.7	0.9	1.8	64.9
14–15	27.2	63.1	2.7	0.9	1.8	65.8
15–16	27.3	63.7	0.9	0.3	0.6	64.6
16–17	27.4	64.0	0.9	0.3	0.6	64.9
17–18	27.5	64.3	0.9	0.3	0.6	65.2
18–19	27.6	64.3	0.9	0.3	0.6	65.2
19–20	27.6	64.6	—	—	—	64.6
20–21	27.6	64.6	—	—	—	64.6
Total (entire period)		945.4	164.3	55.3	109.0	1,109.7
TME·(g tissue growth)⁻¹						46.4

either maximum or minimum ambient temperature measured during the injection interval. Ash-throated Flycatcher nestlings allocate, on average, approx. 33% (range: 24–59%) more energy to field metabolism during the first 17 days of the nestling period than Western Bluebird nestlings.

DISCUSSION

Calculation of energy budgets.—We calculated energy budgets of Western Bluebird and Ash-throated Flycatcher nestlings after Ricklefs et al. (1980), except that energy expenditure and energy accumulation in tissues are derived from regression equations (Table 2). These equations are based on changes in wet and dry mass rather than age. The intermediate growth curve parameters (Table 1) were used to generate the appropriate wet mass for each age interval. The amount of dry mass associated with a given wet mass was calculated using Equation 1 (Table 2). These values were then used to calculate total lipid (Eq. 2) and tissue energy content (Eq. 3) (Table 2). Nonlipid tissue energy content was calculated as the difference between total tissue and lipid energy content for each age interval.

To derive the accumulated energy in each tissue component during each age interval, we subtracted the amount of accumulated energy at the start of the interval from the value at the end of the interval. We used Equation 4 (Table 2) to predict FMR at the mean body mass for each age interval.

The peak energy requirement for growth for both species occurs ca. 6–7 days of age, when approximately 50% of growth is completed and the growth rate is maximal (Tables 3 and 4). The rate of accumulation of lipid energy is approximately 50% of the accumulation of nonlipid energy throughout the growth period. Lipid indices did not vary with age and averaged approximately 0.22 ± 0.01 g lipid·(g lean dry mass)⁻¹. This amount of lipid accumulation is sufficient to provide 1–2 days of energy, assuming no energetic cost of growth during periods of food deprivation and minimal activity costs. Therefore, both species must rely on relatively predictable and abundant food resources during the nesting season to feed young. This seems to be the usual pattern for many passerine species that obtain their food at or near the ground, where insect prey abundance is less affected by variable weather conditions (Johnson 1969, Fi-

TABLE 4. Energy budget of nestling Ash-throated Flycatcher. Abbreviations as in Table 3.

Age interval (day)	Body mass (g)	Energy (kJ·day)$^{-1}$				
		FMR	TTE	TLE	TNL	TME
0–1	3.7	6.2	3.6	1.5	2.1	9.8
1–2	5.3	9.6	6.1	2.4	3.7	15.7
2–3	7.4	14.3	9.2	3.5	5.7	23.5
3–4	9.9	20.5	12.3	4.6	7.7	32.8
4–5	12.7	27.9	15.3	5.6	9.7	43.2
5–6	15.6	36.6	17.3	6.3	11.0	53.9
6–7	18.3	45.5	17.3	6.2	11.1	62.8
7–8	20.7	53.8	16.3	5.7	10.6	70.1
8–9	22.7	60.9	14.1	4.9	9.2	75.0
9–10	24.2	66.5	10.9	3.8	7.1	77.4
10–11	25.3	70.8	8.2	2.8	5.4	79.0
11–12	26.0	73.8	5.3	1.8	3.5	79.1
12–13	26.6	75.8	4.6	1.6	3.0	80.4
13–14	26.9	77.5	2.3	0.8	1.5	79.8
14–15	27.2	78.5	2.3	0.8	1.5	80.8
15–16	27.3	79.2	0.8	0.3	0.5	80.0
16–17	27.4	79.6	0.8	0.3	0.5	80.4
Total for entire period		877.0	146.8	53.0	93.8	1,023.7
TME·(g of tissue growth)$^{-1}$						43.2

ala and Congdon 1983, Austin and Ricklefs 1977, O'Connor 1978, Ricklefs 1983, Williams and Prints 1986).

The energy budgets of Western Bluebird and Ash-throated Flycatcher nestlings differed significantly in the field metabolism (FM) component (Tables 3 and 4). Ash-throated Flycatcher nestlings allocate approximately 33% more energy to field metabolism than do Western Bluebird nestlings during the first 17 days of the nestling period. Field metabolism can be partitioned into maintenance of existing mature tissue (M), cost of biosynthesis and maturation of new tissue (B), specific dynamic action of food assimilation (SDA), thermoregulatory costs (TR), and the cost of activity (A): FM = M + B + SDA + TR + A (Williams and Prints 1986). Although quantitative data are lacking, incidental observations indicate that both species are opportunistic ground foragers and are likely to have a substantial degree of dietary overlap during the breeding season. It seems unlikely that there would be substantial species differences in SDA because both species probably have similar diets.

Both species nest in the same microhabitat (nest boxes in this study) at overlapping times of year. Bluebird field metabolism was measured mostly during May, while the field metabolism of the flycatcher was measured mostly in June. Mean ambient temperature during May

(13.3°C) was significantly lower than in June (17.8°C), thus potential differences in the thermal environment probably favor the flycatcher. Field metabolic rate was not correlated with either maximum or minimum ambient temperature during the doubly labeled water measurement interval. We suggest that brooding by the female and huddling of nestmates effectively ameliorate the effect of cool weather. Given the higher ambient temperature during June, the thermoregulatory component of the flycatcher energy budget would be expected to be less than that of the bluebird at a given body mass. Therefore, the higher FMR values for the flycatcher cannot be adequately explained by differences in the thermal environment.

There may be some species differences in the maintenance component of the energy budget. These presumptive differences may be reflected by adult basal metabolic rate (BMR), lower critical temperature (T_{lc}), or both. The BMR of the adult Western Bluebird is within 1% of that predicted allometrically (Mock 1990, Kendeigh et al. 1977). The T_{lc} of the bluebird is ca. 21°C (Mock, 1990), typical for a 25–30 g temperate zone passerine in the summer (Kendeigh et al. 1977). The BMR of the adult Ash-throated Flycatcher has not been measured. Yarbrough (1971) reports BMR and T_{lc} of four tyrannid flycatchers, including the Great Crested Flycatcher (M. crinitus; 33.9 g body mass). The BMR of M. crinitus

was ca. 22% less than the predicted value and T_{lc} was 24°C. The BMR of the four flycatcher species studied by Yarbrough (1971) were 3–27% below the predicted value for passerines in summer (Kendeigh et al. 1977). The T_{lc} for these flycatchers ranged from 22°C to 26°C (Yarbrough 1971), values similar to that of the bluebird.

As a group, tyrannid flycatchers may have moderately lower BMRs than other passerines. If adult maintenance requirements and thermoregulatory capacity are relevant to nestling energy expenditure, then it could be expected that nestling flycatchers would allocate less energy to the maintenance and thermoregulatory components of the energy budget than nestling bluebirds. The BMR of the flycatcher would have to be >40% above the allometrically predicted value in order for maintenance metabolism to account fully for the observed species differences in field metabolism. From this information, substantial differences in basal metabolism and thermoregulatory ability appear to be unlikely and probably do not contribute to observed species differences in field metabolism of bluebird and flycatcher nestlings.

The activity and biosynthesis components of field metabolism may be influenced greatly by the length of the nestling period and its effect on the rate of tissue maturation. Western Bluebirds normally fledge at 20–21 days of age, but Ash-throated Flycatchers leave the nest 16–17 days after hatch. The flycatcher may become functionally mature (i.e. capable of sustained flight) at an earlier age than the bluebird, even though their growth curves are similar. Activity costs associated with fledging could be expected to become a significant component of field metabolism at an earlier age for the flycatcher than the bluebird. Because the flycatcher breeds 3–4 weeks later than most of the bluebird population, differences in day length (<1 h between May and June) may allow for flycatchers to be more active each day than bluebirds. A longer daily activity period would increase the activity component of the flycatcher energy budget relative to the bluebird. Differences in activity may account for much of the difference in field metabolism during the later portion of the nestling period, but activity costs are probably low during the early part of nestling development (Williams and Prints 1986).

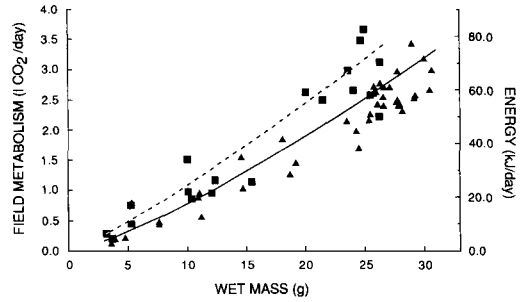There appears to be a systematic difference in field metabolism between bluebirds and fly-

Fig. 2. The relationship between field metabolism and body mass for nestling Western Bluebird (triangle, solid line) and Ash-throated Flycatcher (square, dashed line). Regression equations for field metabolism (kJ·day^{-1}) on body mass (g): $y = 0.924x^{1.28}$, $n = 40$, $r^2 = 0.97$ (bluebird); $y = 1.654x^{1.17}$, $n = 19$, $r^2 = 0.92$ (flycatcher).

catchers throughout the nestling period (Fig. 2) that may not be accounted for by differences in the activity component of the energy budget. The biosynthesis component of nestling energy budgets has been assumed to be 75% efficient (Ricklefs 1974). If the energy cost of biosynthesis *on a per gram basis* were constant, then the rate at which growth and maturation proceeded would determine the actual daily energy costs (Drent and Daan 1980). For the growth curve used in the energy budget calculations, Ash-throated Flycatchers have an average approximately 33% higher FMR than Western Bluebirds during the first 17 days of the nestling period. This translates into a daily total metabolizable energy (TME) requirement that is approximately 22% higher for the flycatcher, but its nestling period is approximately 20–24% shorter than that of the bluebird. This supports the idea that the cost of growth and maturation on a per gram basis is approximately the same for these two species when averaged over the entire nestling period (Drent and Daan 1980).

Differences in the rate of maturation and activity associated with fledging may account for most of the difference in the field metabolism component of Western Bluebird and Ash-throated Flycatcher energy budgets. If the species mature at different rates, there may be differences in the age at which enzymes critical for mature tissue function are induced or differences in the neuromuscular development necessary for the complex coordinated locomotor function required for flight (Marsh and Wickler 1982, T. L. Bucher pers. comm.). We did not demonstrate such differences at the cellular

level, but the difference in FMR suggests that such an explanation is reasonable (Ricklefs 1973). Comparative data on the ontological development of tissue maturation of species pairs similar to the flycatcher and bluebird are needed to evaluate this hypothesis.

Energetic and ecological consequences of differing length of the nestling period.—We found an energetic cost to shortening the nestling period (Ricklefs 1973, Drent and Daan 1980). Although the total amount of energy necessary to produce a 27–28 g juvenile flycatcher or bluebird was approximately the same, the daily energy requirements of the flycatcher were ca. 22% higher than the bluebird when total metabolizable energy stabilized at 12–14 days of age. This implies that a pair of Ash-throated Flycatchers feeding a brood of five 14-day-old nestlings would have to gather 80 kJ more metabolizable energy per day than would a Western Bluebird pair with a brood of the same size and age. Assuming the energy density [grasshoppers: 5.6 kJ·(g wet mass)$^{-1}$] and assimilation efficiency (70%; Dol'nik et al. 1982) of insect food fed to nestlings are similar, this additional TME would be equivalent to approximately 20 g of insects per day.

Under similar feeding conditions, Ash-throated Flycatchers may be more susceptible to nest failure than Western Bluebirds during periods of poor food availability. This appeared to be true at Garner Valley. The incidence of brood abandonment late in the nestling period was greater for flycatchers than for bluebirds over 4 yr (Mock pers. obs.). Perhaps Ash-throated Flycatchers evolved under conditions with greater predator-induced mortality compared with the Western Bluebird. Because the flycatcher nests slightly later than other secondary cavity nesters such as the bluebird, many nest sites available to the flycatcher may be more vulnerable to predators. Others have noted the importance of nest predation and competition for safe nest sites (Dunn 1977, Nilsson 1984, Lundberg 1985). Therefore, selection to minimize the length of the nestling period may have been relatively greater for the flycatcher.

ACKNOWLEDGMENTS

LITERATURE CITED

AUSTIN, G. T., & R. E. RICKLEFS. 1977. Growth and development of the Rufous-winged Sparrow (*Aimophila carpalis*). Condor 79: 37–50.

BRADLEY, D. W., R. E. LANDRY, & C. T. COLLINS. 1984. The use of jacknife confidence intervals with the Richards curve for describing avian growth patterns. Bull. Southern California Acad. Sci. 83: 133–147.

BRYANT, D. M., & A. GARDINER. 1979. Energetics of growth in House-Martins (*Delichon urbica*). J. Zool. London 189: 275–304.

DOL'NIK, V. R., T. V. DOL'NIK, & S. N. POSTNIKOV. 1982. Caloric densities and metabolic efficiency coefficients of objects eaten by birds. Akad. Nauk SSSR Trudy Zool. Inst. 113: 143–152.

DRENT, R. H., & S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225–252.

DUNN, E. 1977. Predation by weasels (*Mustela nivialis*) on breeding tits (*Parus* spp.) in relation to density of tits and rodents. J. Anim. Ecol. 46: 633–652.

FIALA, K. L., & J. D. CONGDON. 1983. Energetic consequences of sexual size dimorphism in nestling Red-winged Blackbirds. Ecology 64: 642–647.

FOLCH, J., M. LEES, & G. H. SLOANE STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497–409.

HUGHES, M. R., J. R. ROBERTS, & B. R. THOMAS. 1987. Total body water and its turnover in free-living nestling Glaucous-winged Gulls with a comparison of body water and water flux in avian species with and without salt glands. Physiol. Zool. 60: 481–491.

JOHNSON, C. G. 1969. Migration and dispersal of insects by flight. London, Methuen.

KENDEIGH, S. C., V. R. DOL'NIK, & V. M. GAVRILOV. 1977. Avian Energetics. Pp. 127–204 *in* Graniv-

orous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). London, Cambridge Univ. Press.

LUNDBERG, S. 1985. The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. Oikos 45: 110–117.

MARSH, R. L., & S. J. WICKLER. 1982. The role of muscle development in the transition to endothermy in nestling Bank Swallows, *Riparia riparia*. J. Comp. Physiol. 149: 99–105.

MERTENS, J. A. L. 1969. The influence of brood size on the energy metabolism and water loss of nestling Great Tits (*Parus major major*). Ibis 111: 11–17.

MOCK, P. J. 1990. Energetics of growth and reproduction of the Western Bluebird *Sialia mexicana*. Ph.D. dissertation, Univ. California, Los Angeles.

NAGY, K. A. 1980. CO_2 production in animals: analysis of potential errors in the doubly labeled water method. Am. J. Physiol. 238: R466–R473.

———. 1983. The doubly labeled water method: a guide to its use. Univ. California, Los Angeles Publ. No. 12-1417.

———, & D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. Am. J. Physiol. 238: R454–R465.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scandinavica 15: 167–175.

O'CONNOR, R. J. 1975. The influence of brood size upon metabolic rate and body temperature in nestling Blue Tits (*Parus caeruleus*) and House Sparrows (*Passer domesticus*). J. Zool. London 175: 391–440.

———. 1978. Growth strategies of nestling passerines. Living Bird 16: 209–238.

RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177–201.

———. 1974. Energetics of reproduction in birds. Pp. 152–292 *in* Avian energetics (R. Paynter, Ed.). Nuttall Ornithol. Club No. 15.

———. 1983. Avian postnatal development. Pp. 1–83 *in* Avian biology, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

———, & S. C. WHITE. 1981. Growth and energetics of chicks of the Sooty Tern (*Sterna fuscata*) and Common Tern (*S. hirundo*). Auk 98: 361–378.

———, ———, & J. CULLEN. 1980. Energetics of postnatal growth in Leach's Storm-Petrel. Auk 97: 566–575.

SCHMIDT-NIELSEN, K. 1979. Animal Physiology. New York, Cambridge Univ. Press.

WILLIAMS, J. B., & A. PRINTS. 1986. Energetics of growth in nestling Savannah Sparrows: a comparison of doubly labeled water and laboratory estimates. Condor 88: 74–83.

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

YARBROUGH, C. G. 1971. The influence of distribution and ecology on the thermoregulation of small birds. Comp. Biochem. Physiol. 39(2A): 235–266.