



WHY GROW SLOWLY IN A DANGEROUS PLACE? POSTNATAL GROWTH, THERMOREGULATION, AND ENERGETICS OF NESTLING GREEN-RUMPED PARROTLETS (*FORPUS PASSERINUS*)

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ABSTRACT.—We studied growth in the Green-rumped Parrotlet (*Forpus passerinus*), a small Neotropical parrotlet that has an unusually long nestling period (28–35 days) and feeds nestlings nutritionally poor seeds. We asked why nestlings grow slowly even though nest predation is their main mortality factor. We examined nutrient accretion and the development of thermoregulation and computed an energy budget until fledging. We described three periods of growth: (1) days 1–13, when peak accretion for sodium, lipids, and energy occurred; (2) days 14–22, when nestlings became endothermic and accretion for proteins, calcium, and phosphorus peaked; and (3) days 23–30, when nestlings reached 90% of the asymptotic values of body components. The deposition rate of lipids (logistic constant $K = 0.33$) was higher than that of protein ($K = 0.19$), ash and calcium ($K = 0.20$), and, particularly, phosphorus ($K = 0.14$). In concordance with their slow growth, nestlings became endothermic only 10 days before fledging, considerably later than expected from asymptotic mass. Total metabolized energy during the nestling period was 1,133.3 kJ, of which 59.2% accounted for resting metabolic rate and 26.2% for activity. Growth efficiency, the proportion of total metabolized energy allocated to tissue deposition, was 14.5%, one of the lowest reported for altricial nestlings. We argue that nestling growth was not energy-limited and that limiting nutrients were deposited slowly as a result of restrictions imposed by low availability of protein and phosphorus in the diet. We propose that slow growth and poor diets are interrelated in Green-rumped Parrotlets and other Psittaciformes, but the direction of the causal relationship between them is unclear. Received 24 June 2009, accepted 12 December 2009.

Key words: body composition, *Forpus passerinus*, Green-rumped Parrotlet, growth efficiency, nutrient accretion, postnatal growth, thermoregulation, total metabolized energy.

¿Por qué Crecer Lentamente en un Lugar Peligroso? Crecimiento Postnatal, Termorregulación y Energética de los Pichones de *Forpus passerinus*

RESUMEN.—Estudiamos el crecimiento en *Forpus passerinus*, un periquito neotropical pequeño que presenta un período inusualmente largo de presencia de pichones en el nido (28–35 días) y que alimenta a sus pichones con semillas nutricionalmente pobres. Nos preguntamos por qué los pichones crecen tan lentamente a pesar de que la depredación de los nidos es su principal factor de mortalidad. Examinamos la acumulación de nutrientes y el desarrollo de la termorregulación y estimamos un presupuesto energético hasta el emplumamiento. Describimos tres períodos de crecimiento: (1) días 1–13, cuando ocurrieron los picos de acumulación de sodio, lípidos y energía; (2) días 14–22, cuando los pichones se volvieron endotérmicos y ocurrieron los picos de acumulación de proteína, calcio y fósforo; y (3) días 23–30, cuando los pichones alcanzaron el 90% de los valores asintóticos de los componentes corporales. La tasa de acumulación de lípidos (constante logística $K = 0.33$) fue mayor que la de proteína ($K = 0.19$), cenizas y calcio ($K = 0.20$) y, particularmente, que la de fósforo ($K = 0.14$). De acuerdo con su crecimiento lento, los pichones se volvieron endotérmicos sólo 10 días antes de abandonar el nido, considerablemente más tarde que lo esperado de acuerdo a su masa asintótica. La energía total metabolizada durante el período de crecimiento fue de 1133.3 kJ, de los cuales el 59.2% correspondió a la tasa metabólica de reposo y el 26.2% a la actividad. La eficiencia de crecimiento, estimada como la proporción del total de energía metabolizada asignada a acumulación en los tejidos, fue del 14.5%, uno de los valores más bajos reportados para pichones nidícolas.

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Argumentamos que el crecimiento de los pichones no estuvo limitado por la energía y que los nutrientes limitantes se depositaron lentamente como resultado de restricciones impuestas por una baja disponibilidad de proteína y fósforo en la dieta. Proponemos que el crecimiento lento y las dietas pobres están relacionados en *F. passerinus* y en otros Psittaciformes, pero la dirección de la relación causal entre estas variables no está clara.

AVIAN NESTLING GROWTH rates vary widely both within and among species, but the mechanisms that generate such variation remain unclear. Intrinsic factors related to variation in growth rate include body size, development mode, life history, and phylogenetic effects (Ricklefs 1979a, b; Starck and Ricklefs 1998). Extrinsic factors include the rate of nest predation, food availability and quality, clutch size, hatching asynchrony, and sibling competition (Lack 1968; Ricklefs 1982, 1984; Remeš and Martin 2002).

Altricial species typically grow more quickly than precocial species of similar body size (Ricklefs 1969), but some altricial species exhibit the slower growth rates typical of precocial species. Examples include pelagic seabirds, swifts, Coraciiformes, and many tropical birds, including parrots and some passerines (Bucher 1983, Ricklefs 1984, Starck and Ricklefs 1998). These altricial exceptions challenge our understanding of the factors that shape avian growth patterns. The slow growth of pelagic seabirds may be a response to variable environmental conditions that determine food quantity or quality (Ricklefs 1968, 1973; Perrins and Birkhead 1983; Langham 1984; Boersma and Parrish 1998; Dahdul and Horn 2003; Tobón and Osorno 2006). However, there is limited information on extrinsic factors that could help to explain the extremely slow growth in wild Psittaciformes (Bucher 1983; Bucher and Bartholomew 1984, 1986; Pearson 1998; Masello and Quillfeldt 2002).

The Green-rumped Parrotlet (*Forpus passerinus*; hereafter "parrotlet"), a small (24–36 g) granivorous Neotropical species, has an unusual reproductive strategy. Its clutch size (average of 7 and up to 12 eggs) is among the largest recorded for a tropical bird, including parrots (Beissinger and Waltman 1991, Masello and Quillfeldt 2002), and its incubation period (20 days) and nestling period (28–35 days) are unusually long for its size (Stoleson and Beissinger 1997, Grenier and Beissinger 1999). The nestling growth constant K of *F. passerinus* (0.23 ± 0.005 [SD]) is considerably lower than expected (0.4) for an altricial bird of its size (Ricklefs 1969) but corresponds well with the value expected for a parrot of similar mass (Masello and Quillfeldt 2002). Because faster development and growth reduce the risk of predation (Case 1978, Bosque and Bosque 1995), the major mortality factor for eggs and nestlings in this species (Stoleson and Beissinger 2001), we asked why nestlings do not grow more quickly, even at the expense of a reduction in the number of eggs laid.

To study the slow growth of parrotlets, we examined nestling development, nutrient accretion during growth, and development of thermoregulation and computed an energy budget for growing nestlings. We interpreted our findings in relation to the composition of the main food item fed to nestlings at our study site, the unripe seeds of *Croton hirtus* (Euphorbiaceae; Stoleson and Beissinger 1997, Pacheco 2000), and in relation to possible growth constraints shared by the common evolutionary origin of Psittaciformes. Wild seeds are nutritionally more complete than other plant products, such as nectar or fruit pulps, but are usually more difficult to digest and have low to moderate content of proteins, lipids, and some minerals, such as phosphorus and calcium (Hungerford et al. 1993, Klasing 1998). Because nutritionally

unbalanced diets can limit growth, we examined whether energy and nutrient deposition rates of parrotlet nestlings are related to the nutritional composition of the seeds of *C. hirtus*.

METHODS

Study area and nestlings.—Our study was conducted at Fundo Pecuario Masaguaral (8°34'N, 67°35'W), a cattle ranch located in the Venezuelan central llanos, 45 km south of Calabozo in Guárico State. The habitat is a seasonally flooded wooded savannah with small patches of gallery forest (Troth 1979) and yearly rainfall averages of 1400–1500 mm. The rainy season usually starts in April–May and ends in October–November, followed by a dry season. Temperature fluctuates only slightly throughout the year, with monthly averages of 22–29°C (Troth 1979, Pacheco 2000). Field work was done during the annual nesting period, from late June through September (rainy season) of 1994 to 1998 (Beissinger and Waltman 1991).

Nestlings were sampled from artificial nest boxes made of polyvinyl chloride (PVC) tubes (Beissinger and Bucher 1992) that simulate natural nests without protection from predators. Nest contents were checked daily, or every other day, to determine the precise dates of egg laying, hatching, and fledging. Eggs were uniquely marked with indelible ink to identify nestlings individually, and nestlings were marked with nail polish on their toe nails with unique color combinations.

Postnatal growth and body composition.—A total of 59 parrotlet nestlings were sampled during the first 2 years of the study to describe their postnatal growth and development. To control for possible interannual differences, we selected only chicks that had body masses that fell within 1 SD of the expected mass for their age, according to the logistic growth curve reported by Waltman and Beissinger (1992) for this species at our study site. There were no significant differences in the energy and protein contents of the diet between those 2 years (Pacheco 2000), so we pooled the nestling data from both years for analysis. Growth parameters estimated in the present study (Table 1) were similar to those reported previously (Waltman and Beissinger 1992, Stoleson and Beissinger 1997).

The nestlings were randomly sampled from at least 30 nests (1–2 per nest) during early morning hours. To avoid pseudoreplication, no nestling was measured twice. The 59 nestlings included ages from hatching (day 0) to day 30 (1–2 days before fledging), with at least 2 individuals for each day class. We recorded mass with a Pesola spring balance (accuracy: ± 0.1 g), and measured the length of tarsus (± 0.01 mm), culmen (± 0.01 mm), and wing cord (± 0.5 mm). Relationships of these morphometric characters with age in days were fitted by nonlinear regression to a logistic model: variable = $A/(1 + e^{-K(\text{age} - I)})$, where A is the asymptotic size, K is the rate constant of the equation, and I is the inflection point of the curve. All analyses were conducted in SYSTAT, version 7.0 (Systat, Evanston, Illinois). We also described plumage development through the nestling period.

TABLE 1. Logistic growth function parameters in relation to age for morphometric characters and body components in nestling Green-rumped Parrotlets. The logistic curve is described by the following equation: variable = $A/(1 + e^{[-K(\text{age} - I)])}$, where A is the asymptotic size, K is the rate constant of the equation, and I is the inflection point of the curve.

Variable	A	K	I (days)	MDI ^a	r^2 (n)	Figure
Postnatal mass growth ^b (g)	23.73	0.23	10.49	—	— (1,128)	—
Postnatal mass growth ^c (g)	26.90	0.25	11.00	—	— (20)	—
Culmen length (mm)	11.02	0.12	8.15	0.33	0.93 (59)	1A
Tarsus length (mm)	13.54	0.35	2.16	1.16	0.92 (59)	1B
Wing length (mm)	71.61	0.18	15.51	3.25	0.97 (59)	1C
Energy content (kJ individual ⁻¹)	180.54	0.22	12.30	9.74	0.96 (14)	2A, B
Protein content (g individual ⁻¹)	4.81	0.19	15.51	0.23	0.99 (14)	2C, D
Lipid content (g individual ⁻¹)	1.26	0.33	8.13	0.11	0.56 (10)	2E, F
Ash content (mg individual ⁻¹)	1,040.34	0.20	14.22	52.19	0.97 (14)	3A, B
Phosphorus content (mg individual ⁻¹)	149.36	0.14	15.61	5.37	0.97 (9)	3C, D
Calcium content (mg individual ⁻¹)	176.60	0.20	15.21	8.90	0.98 (9)	3C, D
Sodium content (mg individual ⁻¹)	39.36	0.64	7.00	6.13	0.99 (7)	3C, D

^aMaximum daily increment (MDI).

^bWaltman and Beissinger 1992.

^cPresent study.

During the first year, body composition was determined on a sample of 14 nestlings that were 2–25 days old and had body masses appropriate for their age. Nestlings with empty crops were collected early in the morning before their parents fed them and were euthanized using Halothan (2-Bromo-2chloro-1,1,1-trifluoroethane; Roche S.A., Venezuela). Fresh carcasses were weighed (± 0.01 g) and frozen at -20°C until they were dried at 55°C to a constant weight for later analysis. We estimated the percentage of body water and determined the energy, ash (mineral), nitrogen, total lipid, calcium, phosphorus, and sodium contents of each sample. Specifically, the acid-corrected energy content was measured in a Parr adiabatic bomb calorimeter calibrated with benzoic acid. Ash (mineral) content was determined by mass change after combustion for 6 h in a muffle furnace at 500°C . Nitrogen was measured by micro-Kjeldahl with a Tecator model 1003, and the lipid fraction was extracted with anhydrous ether in a Labconco Goldfish apparatus. Chemical analysis was done using standard methods of the American Organization of Analytical Chemists (Horwitz 1984). All samples were analyzed in triplicate, and their coefficients of variation were always $<5\%$. Lipid, calcium, phosphorus, and sodium contents could not be determined in nestlings younger than 7 days because of their minute dry mass. The relationship between each body component and age in days was fitted to a logistic model by nonlinear regression. The daily increment for each body component was also estimated from the logistic curves.

Nestling body temperature and ontogeny of thermoregulation.—The ability of nestlings to maintain constant body temperature, independently of environmental fluctuations, was determined in a field experiment by estimating the thermoregulatory index (TI):

$$\text{TI} = 100 (T_{20} - T_a) / (T_{\text{ad}} - T_a)$$

where T_{20} and T_{ad} are the body temperatures of nestling and adults, respectively, after exposure to $19\text{--}20^\circ\text{C}$ (T_a) for 20 min (O'Connor 1984, Ricklefs 1987, Weathers et al. 1990). This index

should approach 0 when nestlings are fully poikilothermic and 100 when they are as competent as adults at maintaining their body temperature. If nestlings did not reach an equilibrium temperature at the end of the 20-min exposure period—the maximum duration that we felt it reasonable to expose young nestlings—their TIs would be slightly overestimated. Interspecific comparisons of TIs may be hindered by the lack of standardized conditions among studies (Ricklefs 1987). We sampled 2 or 3 nestlings with body masses expected for their ages from individual nest boxes and immediately recorded their cloacal temperatures (T_0) before placing each inside a small temperature-controlled chamber at $19\text{--}20^\circ\text{C}$ for 20 min. This temperature is the minimum recorded at night at the study site. After 20 min, we again recorded the nestlings' cloacal temperatures (T_{20}). A total of 273 measurements (T_{20}) was obtained during 5 years of the study, with 5–10 data points (nestlings) for each age in days. We sampled any given individual only once and pooled the data from all years for analysis. T_{ad} was the average for 8 mist-netted adults (4 males and 4 females). Temperatures were measured by inserting into the cloaca a thermocouple connected to a data logger OM-160. In addition to the TIs, we report the difference $\Delta T = T_0 - T_{20}$. The relationship of TI and ΔT with body mass was explored by using generalized linear models; simple linear regression produced a good model fit (e.g., Weathers et al. 1990), and an exponential relationship did not improve it.

Energetics of postnatal growth.—We determined resting metabolic rate (RMR) and thermoregulatory energy requirements by measuring oxygen consumption (VO_2 , $\text{mL g}^{-1} \text{h}^{-1}$) of 40 nestlings at night (2000–0200 hours). We collected nestlings aged 1–28 days in the late morning, after the parents had fed them. Before recording VO_2 , we held the nestlings in small PVC tubes at $34\text{--}36^\circ\text{C}$ (nest-box temperatures during midday hours) for at least 4 h to empty their guts. However, we later determined that this period was insufficient because the nestlings had an unusually long overall digesta retention time; it took them 18–20 h for complete evacuation of the crop after a full meal (Pacheco 2000); hence, the nestlings were not post-absorptive.

We determined VO_2 with an open-circuit respirometry system (model S-3A, AEI Technologies, Pittsburgh, Pennsylvania) using a constant flow rate of oxygen between 0.140 and 0.594 L min^{-1} , depending on the nestling's body mass. Nestlings were weighed (± 0.01 g) and their body temperatures were recorded before and after we placed them in the metabolic chambers at 34–35°C for 90 min. This is the brooding temperature recorded in the nests in our study site (Stoleson and Beissinger 1999); it falls within the thermal neutral zone reported for large nestlings of several species (Visser 1998). Methods, apparatus, and calibration procedures were similar to those of Weathers et al. (1980).

Rates of oxygen consumption were calculated from equation 2 of Hill (1972) and converted to heat production by using an energy equivalent of 21.07 $\text{kJ L}^{-1} \text{O}_2$, based on the composition of the seeds of *C. hirtus* (84.26% carbohydrates and 1.15% lipids dry; Pacheco 2000), the most important seed of the nestlings' diet.

We used the doubly-labeled-water (DLW) technique to measure the field metabolic rate (FMR) of 23 nestlings aged 1–28 days from 12 nests. Each nestling was removed from its nest box between 0500 and 0700 hours and weighed with a Pesola scale (± 0.1 g), and a background blood sample of 75–150 μL was collected from a brachial vein. We then immediately gave it an intramuscular injection (2 μL per gram of body mass) containing 97 atoms-percent ^{18}O and 2.5 $\text{mCi/ml}^3\text{H}$. Following injection, the nestlings were returned to their nest for isotopic equilibration for 1 h, and then a second blood sample was taken. Two days after injection, the nestlings were reweighed and duplicate blood samples (75–150 μL) were collected. For smaller nestlings (<5 g), only the 48-h sample was collected, following the method of Webster and Weathers (1989). All nestlings within a given brood were given a dose of DLW to minimize errors due to their breathing of exogenous carbon dioxide from other nestlings that could have a different isotopic ratio from the test animals (Weathers et al. 1990), but blood samples were taken from only 2 nestlings from each nest (one sample was lost). All blood samples were stored at 4°C in flame-sealed glass microhematocrit tubes for later analysis. The reported error of this technique for rates of carbon dioxide production is <5% (Nagy and Costa 1980, Webster and Weathers 1989, Weathers and Sullivan 1991, Gessaman et al. 2004). Nestlings used in the DLW experiments were different from those used in the oxygen consumption and cooling experiments.

Blood samples were microdistilled to obtain pure water, which was assayed for tritium activity (liquid scintillation counter) and for oxygen-18 content in a mass spectrometer. These analyses were performed by Brian Green (Division of Ecology and Wildlife, CSIRO, Canberra, Australia), according to procedures described by Green et al. (1991). We calculated the rates of carbon dioxide production from isotope ratios by the equations of Lifson and McClintock (1966), as modified by Nagy (1980: equation 2). The production rates of carbon dioxide were transformed to heat production by using an energy equivalent of 21.27 $\text{kJ L}^{-1} \text{CO}_2$, based on the composition of the seeds of *C. hirtus*. The curves relating RMR and FMR to age were fitted to logistic equations by nonlinear regression methods.

We estimated the nestlings' energy budgets by using the following components of the daily metabolized energy (DME):

$$\text{DME} = \text{TE} + \text{FMR}$$

where TE is the daily energy accumulated in tissue (i.e., growth). FMR includes RMR and physical activity (*A*), whereas RMR includes the heat increment of feeding (HI) and the cost of thermoregulation (TR). We estimated *A* as $\text{FMR} - \text{RMR}$. The relationship of DME with age was fitted to a logistic equation. We also report total metabolized energy (TME) as the sum of the daily values (DME) during the 30-day nestling period. Results are presented as means \pm SD.

RESULTS

Postnatal growth, body composition, and nutrient accretion rates.—Parrotlet nestlings were extremely altricial according to the definition of Nice (1962). They exhibited no mobility, fused eyelids, and almost no yellow down at hatching and were fed by parents for almost 30 ± 1.17 days ($n = 20$). At hatching, nestlings weighed 1.9 ± 0.2 g ($n = 20$), and they grew slowly until they reached the asymptotic mass ($A = 25.4 \pm 1.8$ g, $n = 20$) around day 23, which was 7 days before fledging, as previously described (Waltman and Beissinger 1992, Stoleson and Beissinger 1997). The egg tooth disappeared 10 days after hatching ($n = 59$), and eyes opened 5–10 days after hatching. Primary and secondary feather shafts began to erupt between 7 and 10 days of age, and contour feathers and rectrices erupted between days 15 and 20. Male nestlings could be identified by the presence of a blue patch on the wing and forehead by day 18. Plumage is adult-like at fledging, when flight and tail feathers have reached 95% of adult length. Lipid deposits became visible around the crop and flanks around days 11–15 and increased until days 16–20. After days 24–25, lipid deposits were no longer apparent. Nestlings became active in the bottom of the nest around day 15. After day 20, they stood up by expanding their wings and by raising their head to maintain balance and began to climb to the nest opening to receive food from their parents.

All morphometric variables fitted logistic growth functions well (Table 1). The culmen was the slowest-growing body part, increasing rather constantly from hatching to 11 mm following a very shallow logistic curve (Table 1 and Fig. 1A). The tarsus was the fastest-growing body part; it grew rapidly from hatching until day 10, reaching an asymptote value (13.54 mm) rather early at around day 12 (Table 1 and Fig. 1B). The wings grew at an intermediate rate, increasing slowly during the first 10 days (from 4.7 to 19.1 mm; Fig. 1C) and then rapidly from day 11 to day 30, reaching 60% of total length by day 18.

The deposition of energy, nutrients, and minerals in relation to age also fitted well to logistic curves (Table 1). Only lipid content had a rather low coefficient of determination, likely because of variations in the extent of fat deposits among individuals (Table 1 and Fig. 2E, F). Lipids were deposited at a considerably faster rate than protein (compare *K* values in Table 1); the peak lipid accretion rate occurred around day 8, nearly twice as early as peak protein deposition, which occurred at days 15–16 (Table 1 and Fig. 2C, D). Lipids were also deposited at a considerably faster rate than energy or total minerals (ash) (Table 1 and Figs. 2A, B and 3A, B). Among minerals (Table 1 and Fig. 3C, D), sodium was deposited at the fastest rate, whereas phosphorus was deposited at the slowest rate. The deposition rate of calcium was also low, but higher than that of phosphorus.

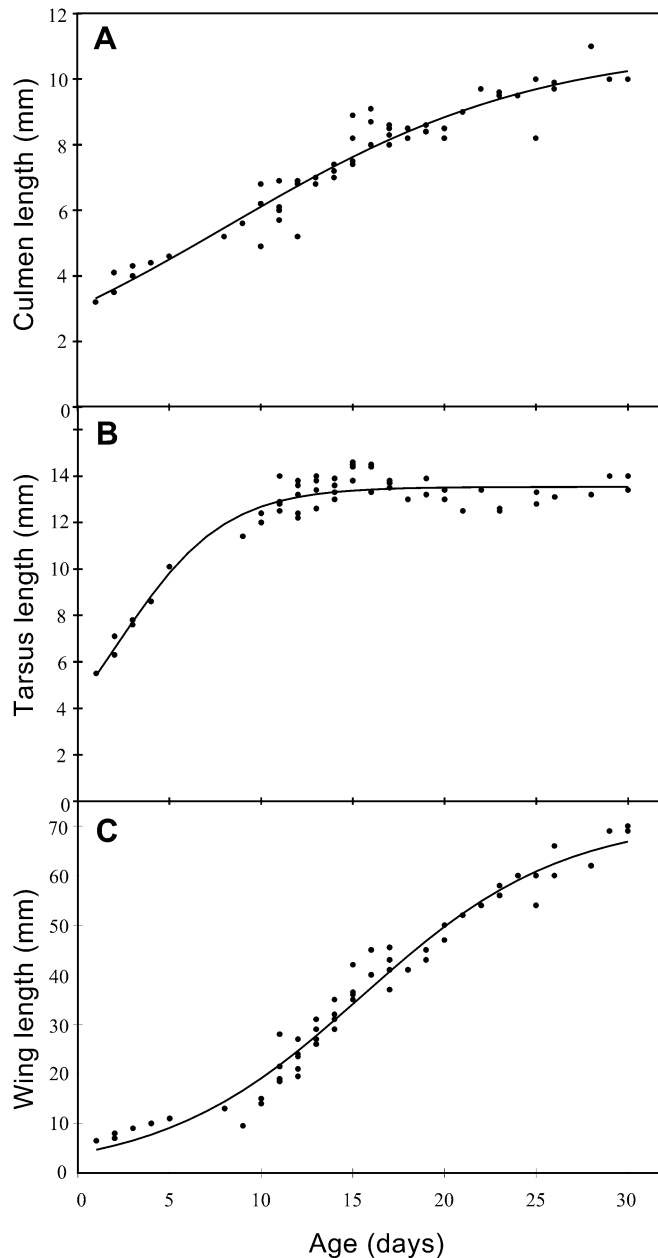


FIG. 1. (A) Culmen, (B) tarsus, and (C) wing lengths in relation to age (days) in nestling Green-rumped Parrotlets. Parameters of the logistic equations fitted to each data set are presented in Table 1.

Energy, protein, ash, and phosphorus content per gram of dry tissue (density) were linearly independent of nestling age in days ($P > 0.05$ in all cases). Averages were $23.36 \pm 1.35 \text{ kJ g}^{-1}$ ash-free ($n = 14$), $0.48 \pm 0.05 \text{ g protein g}^{-1}$ ($n = 14$), $121.1 \pm 0.02 \text{ mg ash g}^{-1}$ ($n = 14$), and $15.44 \pm 0.43 \text{ mg P g}^{-1}$. By contrast, sodium density decreased significantly with tissue maturation ($\text{mg Na g}^{-1} = 12.48 - 0.32 \times \text{age}$; $P = 0.001$, $n = 7$), whereas calcium increased significantly with age of nestlings ($\text{mg Ca g}^{-1} = 11.83 + 0.38 \times \text{age}$; $P = 0.011$, $n = 9$). Density of tissue lipids also decreased as nestlings aged ($\text{g lipids g}^{-1} = 0.324 - 0.006 \times \text{age}$; $P = 0.045$, $n = 10$). Total body water

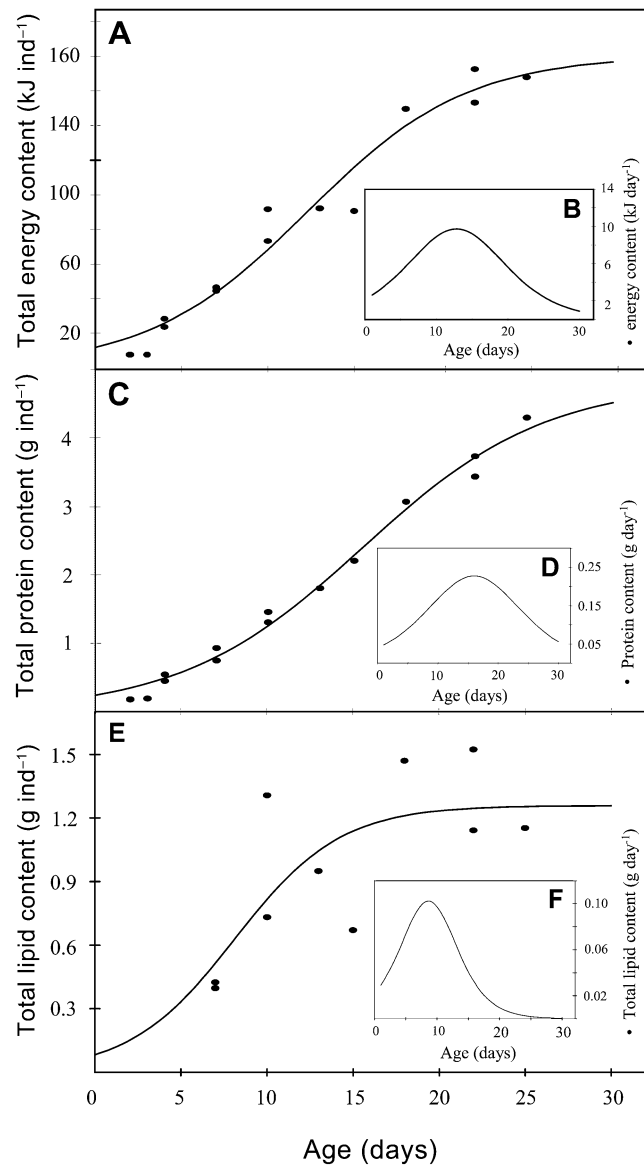


FIG. 2. (A) Total energy content of tissue ($\text{kJ individual}^{-1}$) and (B) daily increment (kJ day^{-1}), (C) total protein content of tissue (g individual^{-1}) and (D) daily increment (g day^{-1}), and (E) total lipid content of tissue (g individual^{-1}) and (F) daily increment (g day^{-1}), in relation to age in nestling Green-rumped Parrotlets. Parameters of the logistic equations fitted to each data set are presented in Table 1.

(TBW) decreased linearly with body mass from 84.1% at hatching to 66.5% before fledging. The relationship was described by the equation

$$\text{TBW (\%)} = 84.1 - 0.75 \times \text{mass}$$

$$(r^2 = 0.86, P < 0.001, n = 19)$$

Nestling body temperature and ontogeny of thermoregulation.—Parrotlet nestlings were ectothermic at hatching. Average body temperature in the nest on day 0 (T_0) was $36.6 \pm 0.44^\circ\text{C}$ ($n = 5$),

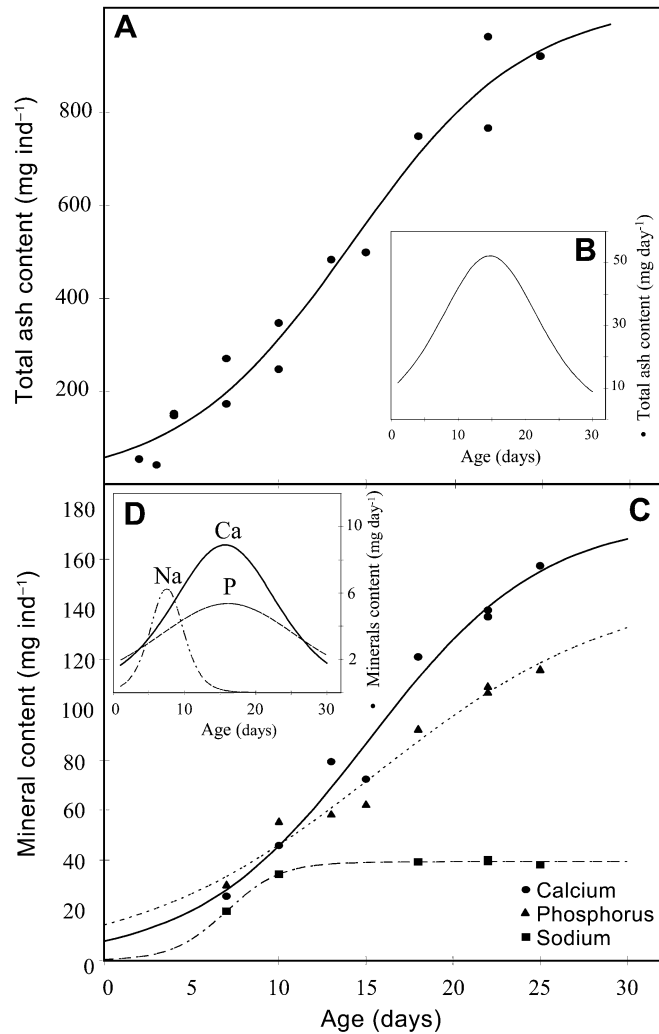


FIG. 3. (A) Total ash content of tissue (mg individual⁻¹) and (B) daily increment (mg day⁻¹), and (C) total phosphorus, calcium, and sodium in content of tissue (mg individual⁻¹) and (D) daily increment (mg day⁻¹), in relation to age in nestling Green-rumped Parrotlets. Parameters of the logistic equations fitted to each data set are presented in Table 1.

and it increased slowly with age to $38.8 \pm 0.52^\circ\text{C}$ ($n = 7$) at fledging (Fig. 4A). The average body temperature of adults was $40.45 \pm 0.44^\circ\text{C}$ ($n = 8$). The thermoregulatory index (TI) increased linearly with body mass (g) (Fig. 4B). We considered a TI value of 75% of adult level as the age of onset of endothermy (Dunn 1975, Weathers et al. 1990). According to this criterion, parrotlet nestlings became endothermic at ~20 days, when their mass reached 24.2 g, ~10 days before fledging. The difference between body temperature before and after exposure (20 min at 19°C) was inversely linearly related to body mass (Fig. 4C), dropped to $<2^\circ\text{C}$ by day 25, and became nearly zero on days 29–30 at fledging. Both TI and $\Delta T_0 - T_{20}$ indicated that nestlings improved their thermoregulatory capacities progressively until they became endothermic at about age 20 days.

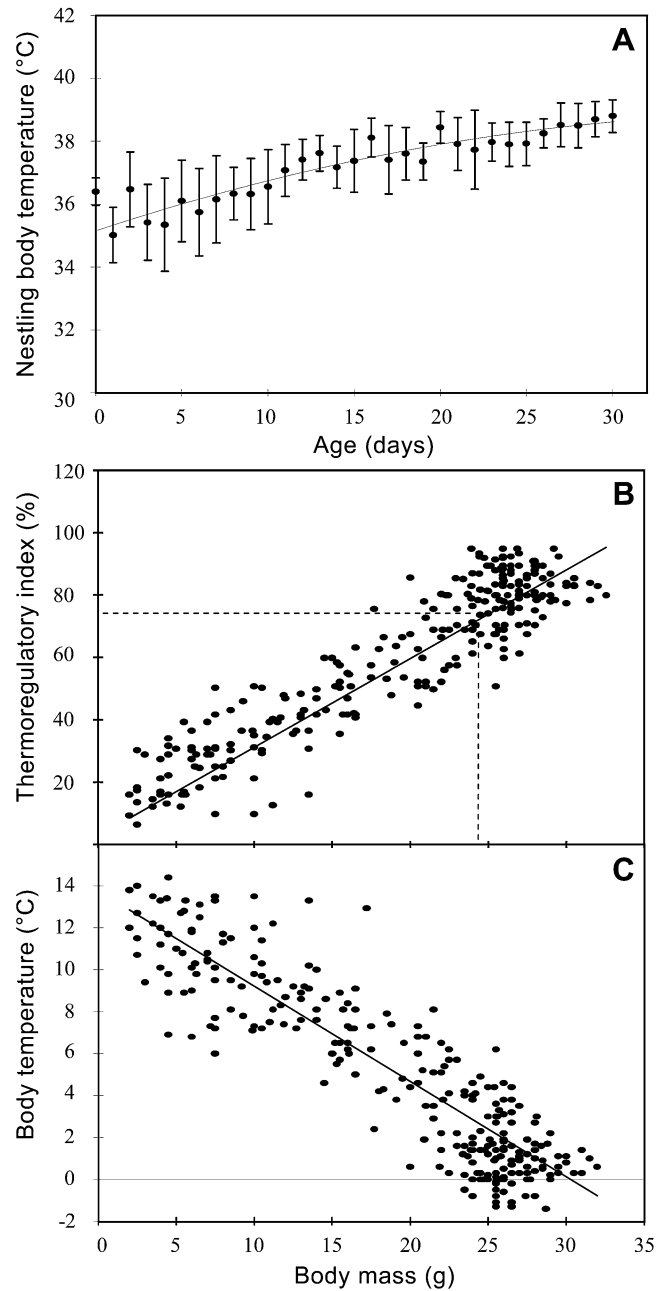


FIG. 4. (A) Average body temperature ($T_0 \pm 1$ SD) of nestling Green-rumped Parrotlets in relation to age. The equation estimated from the data is as follows: body temperature ($^\circ\text{C}$) = $-0.0022 \times \text{age}^2 + 0.18 \times \text{age} + 35.11$; $r^2 = 0.51$, $n = 270$. (B) Thermoregulatory index (TI) in relation to body mass. The equation estimated from the data is as follows: TI (%) = $8.47 + 2.75 \times \text{mass}$; $r^2 = 0.84$, $P < 0.001$, $n = 270$. (C) Difference in body temperature ($T_0 - T_{20}$) measured in nestlings, before (at the nest) and after exposure to 20 min at 19°C , in relation to body mass. The equation estimated from the data is as follows: $\Delta \text{body temperature } (^\circ\text{C}) = 13.92 - 0.47 \times \text{mass}$; $r^2 = 0.83$, $P < 0.001$, $n = 270$.

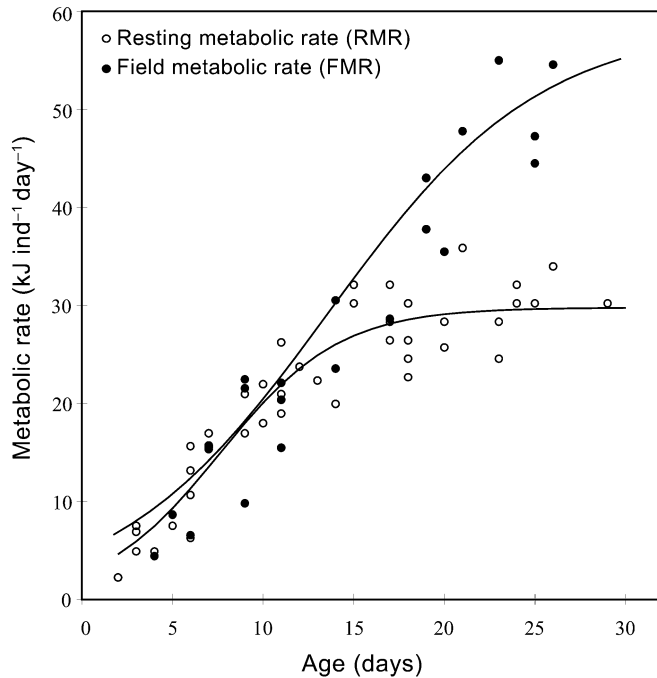


FIG. 5. Resting metabolic rate at night (RMR, open circles) and field metabolic rate (FMR, filled circles) for nestling Green-rumped Parrotlets in relation to age. The equations estimated from the data are as follows: $RMR_{(kJ/day)} = 29.80 / \{1 + \text{Exp}[-0.30(\text{age} - 7.61)]\}$, $r^2 = 0.89$, $n = 41$; and $FMR_{(kJ/day)} = 58.94 / \{1 + \text{Exp}[-0.17(\text{age} - 13.83)]\}$, $r^2 = 0.95$, $n = 24$.

Energetics of postnatal growth.—Resting metabolic rate (RMR; $\text{kJ individual}^{-1} \text{ day}^{-1}$) at night scaled with nestling body mass (g) to the 1.007 power (95% confidence interval [CI]: 1.001–1.013) and followed the equation

$$RMR_{\text{night}} = 0.134 \times \text{mass}^{1.007} \\ (r^2 = 0.96, P < 0.001, n = 41)$$

Field metabolic rate (FMR; $\text{kJ individual}^{-1} \text{ day}^{-1}$) scaled with nestling body mass (g) to the 1.137 power (95% CI: 1.05–1.21) as described by the equation

$$FMR = 1.135 \times \text{mass}^{1.137} \\ (r^2 = 0.97, P < 0.001, n = 24)$$

Both RMR and FMR increased with age and fitted well to logistic curves (Fig. 5). RMR reached 90% (26.8 kJ) of its asymptotic value at day 15, whereas FMR increased continuously, reaching 90% (53.1 kJ) of its asymptotic value at the end of the nestling period (Fig. 5).

Nestling energy budgets.—Daily metabolized energy (DME; $\text{kJ individual}^{-1} \text{ day}^{-1}$) increased with age following the logistic equation

$$DME_{(kJ/ind. \text{ day})} = 56.81 / \{1 + \text{Exp}[-0.9(\text{age} - 9.85)]\}, (r^2 = 0.99)$$

DME reached 90% (51.13 kJ day^{-1}) of its asymptotic value at 21 to 22 days at approximately two-thirds of the growth period (Fig. 6).

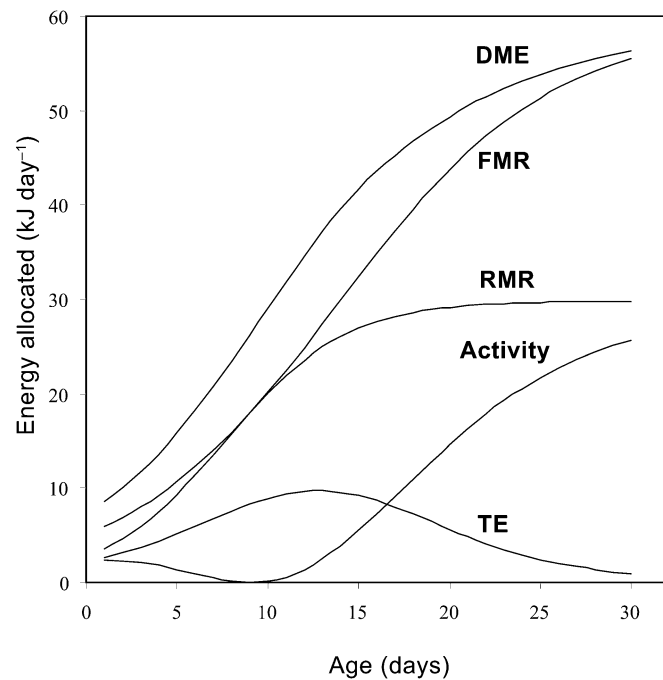


FIG. 6. Daily energy expenditure of nestling Green-rumped Parrotlets in relation to age. DME = daily metabolized energy, FMR = field metabolic rate (measured with doubly labeled water), RMR = resting metabolic rate, activity = FMR – RMR, and TE = energy accumulated in new tissue (i.e., growth).

The total energy requirement of a parrotlet chick during the 30-day nestling period was estimated as 1,133.3 kJ. Of this expenditure, 59.2% (671.3 kJ) was allocated to RMR, which includes the heat increment of feeding and thermoregulatory costs, 26.2% (297.2 kJ) to activity, and only 14.5% (164.8 kJ) to tissue deposition (TE).

DISCUSSION

Despite inhabiting a tropical environment in which nest predation is prevalent (Robinson et al. 2000) and is their main mortality factor (Stoleson and Beissinger 2001), nestling Green-rumped Parrotlets grew very slowly in the present study. Below, we discuss the patterns of growth, body composition, and nutrient accumulation in parrotlets, compare our results with patterns in psittacids and faster-growing species, and compare them with expectations from allometric relationships. We then examine the role of nestling body temperature and the ontogeny of thermoregulation as factors that affect dietary demands and discuss how these factors affect postnatal growth and nestling energy budgets. We conclude by revisiting the factors that result in slow growth in a hazardous environment.

Postnatal growth, body composition, and nutrient accretion rates.—Parrotlet nestlings are extremely altricial at hatching and have slow postnatal growth. Indeed, the parameter K of the logistic equation (0.23 ± 0.005 ; Waltman and Beissinger 1992) is only 61% of the expected value for an altricial species of similar size (Ricklefs 1969). Nonetheless, the slow growth patterns of parrotlets

were similar to those of other psittacids (Caccamise and Alexandro 1976, Bucher 1983, Navarro and Bucher 1990, Pearson 1998, Masello and Quillfeldt 2002) and comparable to those of precocial species of similar body size (Ricklefs 1969).

Growth rates of different body parts and accretion rates of nutrients occurred in three periods, similar to the timing in other altricial birds. The early period, from hatching through approximately day 13, was characterized by rapid growth of the tarsus (Fig. 1B), slow growth of the wings (Fig. 1C), and nearly constant culmen growth (Fig. 1A), a pattern observed in other psittacids (Masello and Quillfeldt 2002) and precocial species (O'Connor 1977; Ricklefs and White 1981; Bryant and Hails 1983; Klaassen et al. 1989a, b; Fournier et al. 2007). The fast growth of the tarsus is likely related to the development of the functional capacity of the legs, which is associated with an increase in activity within the nest, and resulted in the progressive increase of FMR with respect to RMR toward the end of this period (Fig. 6). In addition, the maximum daily increment for sodium, lipids, and energy stored was reached during this early stage (Table 1). Sodium was the mineral that first reached its maximum daily increment at day 7 (Fig. 3D). During an intermediate period, from day 14 to day 22, growth was maximum, nestlings were partially feathered, and peak accretion for protein, ash, and minerals (Ca and P) occurred. Total lipid content per individual reached its maximum around day 15 (Fig. 2E), whereas energy (Fig. 2A), protein (Fig. 2C), and total ash (Fig. 3A) increased continuously until the end of growth. During the third period, from day 22 to day 30, nestlings reached 90% of the asymptotic values of each body component, and their plumage was similar to that of the adult by day 28, two days before they left the nest.

Accretion of mass and energy occurred more quickly than deposition of protein and minerals (P and Ca). K values (Table 1) for total protein (0.19), phosphorus (0.14), calcium (0.20), and ash (0.20) were lower than K values of the logistic growth curve (0.23), energy (0.22), and lipids (0.33). Accordingly, inflection points occurred 4 to 6 days later for total protein, phosphorus, calcium, and ash than for growth, energy, and lipids (Table 1). These observations suggest that slow growth and low availability of certain nutrients in the diet are interrelated; however, our data do not allow us to discern cause from effect. It is not clear whether nestlings grow slowly in order to match requirements to low availability of protein or minerals in the diet or whether, by growing slowly—for reasons other than diet quality—they ultimately became able to use nutritionally poor foods. Unfortunately, there are few studies on nutrient accretions during growth in wild birds to allow for a proper comparison between fast- and slow-growing species.

Slow protein, phosphorus, and calcium deposition may be related to limited availability in the diet, to a limited capacity of the nestlings to metabolize nutrients, or both. Developing birds are often less efficient than adults at extracting energy and nutrients (Karasov 1990). However, among psittacids, younger Blue-fronted Amazons (*Amazona aestiva*) are as efficient as adults at extracting crude protein (Vendramin-Gallo et al. 2001), and nestling Cockatiels (*Nymphicus hollandicus*) can have more efficient digestion than adults (Brice et al. 1989). In addition, protein and mineral assimilation efficiency of granivorous birds is normally high (Klasing 1998). Therefore, we suggest that limitations in the capacity of nestlings to digest and absorb nutrients are less important than

nutrient availability in the diet. Unripe seeds of *C. hirtus*, the main food of nestlings, are carbohydrate rich (84.3% dry) but have low protein content (9.18% dry) and a low ratio of nitrogen to energy (0.79 mg N kJ⁻¹; Pacheco 2000). Protein requirements for growing psittacines have been determined only for Budgerigars (*Melopsittacus undulatus*), which are comparable in size (30–50 g) to parrotlets and have a similar nestling period (30 days), and the larger Cockatiel (80–120 g) (Koutsos et al. 2001). Maximum growth of Budgerigars was supported by a diet containing 13.2% protein, whereas the requirement for maximum growth of Cockatiel chicks was 20% crude protein (Koutsos et al. 2001). These values refer to high-quality protein sources; if amino acid composition of the diet was not optimal, a higher level of protein would be required.

Phosphorus availability is of particular interest because its deposition rate was the slowest ($K = 0.14$) of all variables considered, except for the growth constant of the culmen. Total phosphorus content in unripe seeds, the main food of nestling parrotlets, was 0.41% dry weight (Pacheco 2000). Required levels of phosphorus for maintenance and growth are unknown for psittacids (Koutsos et al. 2001). Dietary phosphorus may be present in inorganic or organic forms (Soares 1995); inorganic phosphorus is readily absorbed by birds, but not all organic phosphorus can be utilized because >50% of the phosphorus in seeds is in poorly digestible complexes with phytic acid (Klasing 1998, Koutsos et al. 2001). For this reason, phosphorus requirements for birds are expressed on a nonphytate basis. Nonphytate phosphorus requirements of growing precocial birds range from 0.3% to 0.6% (Murphy 1996, Klasing 1998). Altricial nestlings have higher phosphorus requirements because their rate of skeletal growth is considerably greater than that of precocial species and because calcification of their skeleton is lower at hatching (Klasing 1998). Unripe *Croton* seeds should be a poor source of available phosphorus because phytate levels in seeds are typically 60–70%. In addition, phytic acid reduces the bioavailability of cations such as calcium, magnesium, potassium, and other minerals (Klasing 1998).

Calcium content of ripe *Croton* seeds was 0.74% dry weight (Pacheco 2000), within the range of dietary calcium requirements for growing precocial nestlings (0.5–1.2%; Klasing 1998). The ratio of calcium to phosphorus in *Croton* seeds was 1.8:1 (Pacheco 2000), well within the optimal range for poultry (2:1; Klasing 1998); however, the appropriate ratio of calcium to phosphorus is not known for any psittacine (Koutsos et al. 2001). In addition to calcium from seeds, parents could easily provide supplemental calcium-rich snail shells or grit to nestlings, although we know of no supplementation behavior for inorganic phosphorus. Consequently, it is unlikely that dietary calcium may be a limiting nutrient for growing parrotlets. Peak accretion rates for calcium and phosphorus required for bone mineralization and homeostasis (Klasing 1998) occur around day 15, which coincides with peak bone growth at day 14 (Table 1).

Energy, protein, and phosphorus content per gram of tissue were constant during growth in parrotlets. Calcium increased, as in other altricial birds (Hungerford et al. 1993, Tilgar et al. 2005), whereas sodium and lipid density decreased with age. Rapid decrease in sodium concentration with age has also been noted in Eurasian Blackbirds (*Turdus merula*; Bilby and Widdowson 1971), in pectoral and leg muscles of altricial European Starlings (*Sturnus vulgaris*), and precocial Japanese Quail (*Coturnix c. japonica*)

and Northern Bobwhites (*Colinus virginianus*; Choi and Ricklefs 1997). In altricial Eastern Bluebirds (*Sialia sialis*), sodium concentration dropped markedly between embryos and nestlings but remained constant during the nestling stage (Hungerford et al. 1993). The rapid decrease in sodium concentration in tissues from eggs to fledging could be a general phenomenon in birds, but a paucity of information precludes a firm assertion. The decrease in bodily water content, from 84.1% at hatching to 66.5% at fledging, is typical of altricial and semiprecocial birds (Blem 1975, O'Connor 1977, Ricklefs and White 1981, Bryant and Hails 1983, Klaassen et al. 1989b, Weathers et al. 1990) and is related to the maturation and growth of tissues, particularly muscles (Ricklefs 1979b).

Nestling body temperature and ontogeny of thermoregulation.— The ability of nestlings to maintain body temperature, independent of their environment, is determined by their capacity to generate metabolic heat and to develop resistance to heat loss. Altricial nestlings have limited metabolic generation of heat, so they depend on their parents to maintain their body temperature (O'Connor 1975). Thus, nestlings just after hatching have a body temperature close to the incubation temperature of eggs (O'Connor 1975). We observed this pattern in parrotlets; mean hatching temperature (36.4°C) was similar to incubation temperature (34–35°C). As nestlings grew, their body temperature increased to 38.8°C (Fig. 4A), which reflects a better capacity for balancing heat loss with age (Bucher 1986, Pearson 1998).

Endothermy, defined as the ability to maintain 75% of the body temperature of adults (Dunn 1975), was reached at a mass of 24.2 g (Fig. 4B), when nestlings were 18–20 days old. On the basis of allometric relationships in Visser (1998), parrotlet nestlings should have developed endothermy at 17.8 g, or about day 15. The age at which effective endothermy is reached is inversely related to the growth constant; using the inverse function in Dunn (1975), parrotlet nestlings should have reached endothermy at day 12. Endothermy in parrotlets was reached considerably later (18–20 days) than both models predicted, a finding consistent with the slow growth in this species. This conclusion may be conservative given that TI values of younger nestlings may have been slightly overestimated, as mentioned above. It is of significance that at that age (18–20 days), wing and tail feathers had erupted and contour feathers already covered the nestlings' bodies, increasing their ability to resist heat loss.

Three factors could contribute to the late onset of endothermy in parrotlets. First, endothermy requires the functional development of skeletal muscles (Visser 1998). In species with slow rates of protein accumulation, such as the parrotlet, the development of endothermy should be delayed. This phenomenon has also been reported in other psittacids (Bucher 1986, Kattan and Gómez 1992, Pearson 1998). Second, young nestlings in large, asynchronous clutches can benefit from exogenous heat production by older siblings (Ovadia et al. 2002, Forbes 2007). In parrotlets, clutch size ranges from 4 to 12 eggs, hatching is very asynchronous, and the female finishes incubation when the oldest nestling is around 12–14 days old, which is just before or shortly after all eggs in a large clutch have hatched (Beissinger and Waltman 1991). In this situation, young, featherless nestlings can easily gain heat from older siblings. Third, at our study site, natural nests and artificial nest boxes typically reach temperatures up to 34–35°C at midday and occasionally may reach 44°C (Stoleson and Beissinger

1999), which favors high body temperatures while minimizing the need to increase endogenous heat production. In general, cavity-nesting species reach endothermy later than open-nesting species of similar mass (Visser 1998).

Energetics of postnatal growth and nestling energy budgets.— In growing altricial birds, the relationship between log RMR and log body mass is linear (Olson 1992, Weathers and Siegel 1995), as was the case in parrotlet nestlings. The slope of the relationship (1.007) was considerably lower than expected (1.27) for a nestling of a mature mass of 23.7 g, as predicted from Weathers and Siegel's (1995) equation, but was within the range of altricial species (0.25–1.5). In our study, RMR scaled nearly proportionally to the untransformed body mass of the chick, which indicates that it increased nearly constantly per unit of mass gain, irrespective of changes in body composition and mature function of tissues that concomitantly accompany growth. As chicks grow, a number of ontogenetic changes occur that potentially affect mass-specific metabolic rate (e.g., decrease in water density of tissues, changes in fat:protein ratio, onset of thermoregulation, and increase in mineral density). In the parrotlet, these effects balanced each other in such a way that mass-specific metabolic rate ($\text{kJ g}^{-1} \text{day}^{-1}$) remained constant, irrespective of size (but not necessarily of age). Field metabolic rate scaled with nestling mass with an exponent significantly greater than 1 (1.14), which likely reflects the mounting cost of activity as nestlings grow larger (see below).

Resting metabolic rate and FMR ($\text{kJ individual}^{-1} \text{day}^{-1}$) increased rapidly in parallel with age through day 10 (Fig. 5); subsequently, FMR continued to increase until fledging, as activity increased during the second part of the nestling period (Fig. 6). On the other hand, RMR plateaued around 29.5 $\text{kJ individual}^{-1} \text{day}^{-1}$ before reaching the end of the fledging period. As in other altricial species, body mass of parrotlet nestlings explained more of the variation in RMR ($r^2 = 0.96$) than chick age ($r^2 = 0.89$; Weathers 1996 and references therein). Our estimate of nestling RMR value is ~10% higher than the basal metabolic rate of adults (26.88 $\text{kJ individual}^{-1} \text{day}^{-1}$; Rodney B. Siegel pers. comm.), likely because it includes the metabolic cost associated with food processing (see above).

Daily metabolized energy is expected to reach a maximum around the middle of the nestling period, when growth is faster, and then to decline or reach a plateau (Drent and Daan 1980, Weathers 1992). In parrotlets, DME increased progressively until fledging (Fig. 6), a pattern rarely recorded in altricial nestlings (Weathers 1992) but observed in semiprecocial species (Ricklefs and White 1981, Klaassen et al. 1989a). In parrotlet nestlings, tissue deposition accounted for only a minor fraction of DME, particularly toward the end of the nestling period (Fig. 6). The other component of DME, FMR, continued to increase because of the mounting cost of chick activity within the nest. During the 4 days before fledging, the approximate energy cost of activity (FMR – RMR) ranged from 22.72 to 25.69 kJ day^{-1} ; that accounted for 43.0–45.6% of DME. As in parrotlet chicks, energy needed for activity in Arctic Tern (*Sterna paradisaea*) chicks increased up to ~50% of the total energy requirement just before fledging (Klaassen et al. 1989a). The substantial cost of activity in parrotlet nestlings is likely attributable to intense competition for food between siblings (Budden and Beissinger 2009) as a result of a large clutch size and hatching asynchrony (Stoleson and Beissinger 1997).

Male parrotlets exhibit a feeding preference for larger offspring that may result from the outcome of sibling competition, whereas females practice more equitable food allocation, particularly in larger broods (Budden and Beissinger 2009). Adult Budgerigars also bias their feeding efforts in relation to the sex ratio of the brood (Stamps et al. 1987), and Crimson Rosella (*Platycercus elegans*) parents provision chicks at different rates depending on their hatching order (Krebs et al. 1999). Such feeding preferences by parents could also help to explain the large variation in fat deposits observed around the fitted lipid accumulation curve in relation to age in parrotlet nestlings (Fig. 4E).

Body mass and the length of the nestling period explain 99% of the observed variance in TME across species (Weathers 1992, 1996). Weathers' (1992) equation predicts a TME of 1,098.2 kJ for the parrotlet, only 3% lower than our estimated value (1,133.3 kJ). Maximum DME is also related to asymptotic body mass and the length of the nestling period (Weathers 1992). It is predicted to reach a maximum of 48.4 kJ, which is lower than the maximum DME that we recorded (56 kJ) before fledging but still within the $\pm 20\%$ range observed by Weathers (1992). Thus, DME and TME in the parrotlet are accurately predicted on the basis of size and the length of the nestling period.

Our results show that the extended length of the nestling period, linked to slow growth, concomitantly raised the total energy cost of maintenance and decreased the fraction of the energy budget allocated to tissue growth. The gross growth efficiency, expressed as TE/TME, was 0.15 in the parrotlet, which is one of the lowest values among altricial species (average, 0.23 ± 0.063 ; see Klaassen et al. 1989b; Weathers et al. 1990, 2003; Williams et al. 1991; Fournier et al. 2007).

Why grow slowly in a hazardous environment?—We asked why parrotlet nestlings grow so slowly, given that nest predation and infanticide, their main mortality factors, account for the loss of up to 30% of nests during the nestling and fledging stages (Stoleson and Beissinger 2001), as is quite typical in tropical environments (Robinson et al. 2000). It seems unlikely that nestling growth is energy-limited. The large number of eggs laid, the ability to raise large numbers of young (Beissinger and Waltman 1991), the apparent absence of a tradeoff between faster growth and smaller clutch size, and the low growth efficiency of nestlings suggest that factors other than energy limit growth in this species. Experiments and models of the effect of clutch size and hatching asynchrony on the peak metabolic demands of nestlings support the contention that reproductive output is not energy-limited in parrotlets (Stoleson and Beissinger 1997, Siegel et al. 1999).

Slow growth and a plant diet are common to species of Psittaciformes. Parrots and allies, with few exceptions, feed and raise their nestlings on some combination of fruit pulp, seeds, and nectar (Koutsos et al. 2001). These foods are unbalanced and nutritionally poor (Klasing 1998) in relation to the demands associated with fast growth. We have shown that, in accordance with restrictions imposed by poor foods, limiting nutrients are deposited at slow rates. Moreover, we suggest that slow growth and nutritionally poor diets are interrelated in parrotlets and, likely, in other Psittaciformes. However, the direction of the causal relationship between the two is unclear. Parrotlets have incubation and nesting periods that fall within the limits of allometric relationships for psittacids (see Masello and Quillfeldt 2002), which suggests that

evolutionary origin constrains developmental patterns, including growth rate, in this species. Slow growth, so constrained, would lessen the instantaneous demands for limiting nutrients by nestlings and would allow parents to raise large numbers of offspring on an abundant but nutritionally poor food.

Psittaciformes is a distinct, ancient, and uniform lineage with a consistent life-history pattern of slow growth coupled with delayed maturity and long life spans (Collar 1997, de Kloet and de Kloet 2005). This set of traits must be deeply rooted within this broad and wide-ranging group of >350 species (Collar 1997). Thus, factors other than diet likely restrict developmental patterns. Growth could be restricted by physiological limits of nestlings in utilizing resources or by basic constraints between growth and mature function of tissues and organs (e.g., Ricklefs 1979b, Ricklefs et al. 1998) linked to their common ancestry. If so, accumulation rates of nutrients would not necessarily reflect nutrient availability in the diet; they would mirror growth rates of body compartments as determined by physiological or phylogenetic constraints on the growing young. It is possible, then, to hypothesize that by growing slowly, for reasons other than diet quality, parrotlets (and possible other psittacines) ultimately became able to use nutritionally poor food sources to raise nestlings. Although growth rates of psittacines are flexible and are affected by food supply (Stoleson and Beissinger 1997, Renton 2002), food supplementation experiments in parrotlets (Stoleson and Beissinger 1997, Pacheco 2000) did not substantially increase growth rate or decrease the fledging period, which suggests that upper, possibly physiological, limits had been reached.

Ricklefs et al. (1998) pointed out three ways to circumvent limitations associated with raising chicks on a nutrient-poor diet. One is the selective uptake of limiting nutrients when energy-rich compounds are passed through the digestive tract. This mechanism does not seem to be used by parrotlet nestlings, because their metabolizable energy coefficient (0.8–0.9) is quite high (Pacheco 2000). A second alternative would be to decrease the required ratio of nitrogen (or any nutrient) to energy by increasing allocation of energy to thermogenesis, activity, or accumulation of fat. The late development of endothermy in parrotlet chicks (days 18–20) and the negligible amount of energy allocated to activity when at peak daily mass and energy gains (days 10–11; Table 1 and Fig. 6) argue against this alternative. In addition, the absence of notable mass recession before fledging in parrotlet nestlings (Waltman and Beissinger 1992, Pacheco 2000) does not support the accumulation of lipids as an energy sink. Nonetheless, this “solution” may be important in other psittacines that show considerable mass recession (Masello and Quillfeldt 2002, Renton 2002 and references therein). The third way to match nutrient requirements for growth to a nutrient-deficient diet is to grow more slowly to reduce the demands for nutrients in relation to energy (Ricklefs et al. 1998). This scenario seems to match our results in nestling parrotlets. Perhaps a fourth way to alleviate restrictions on growth imposed by a nutrient-poor diet is to supplement the diet of nestlings with endogenous, nutrient-rich secretions derived from the sloughing of epithelial cells that line the upper digestive tract of parents (e.g., Prévost and Vilter 1963, Desmeth and Vandeputte-Poma 1980, Blockstein 1989), with “crop milk” (e.g., Forshaw 1989), or with bacterial protein. The crop of parrotlet nestlings hosts a rich bacterial community comparable to that of the foregut-fermenting

Hoatzin (*Opisthocomus hoazin*; Pacheco et al. 2004). It remains to be seen whether these are avenues of nutritional importance.

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