

ENERGETICS AND GROWTH PATTERNS OF THREE TROPICAL BIRD SPECIES

DAVID M. BRYANT¹ AND CHRISTOPHER J. HAILS²

¹Department of Biology, University of Stirling, Stirling FK9 4LA, United Kingdom, and

²Department of Zoology, University of Malaya, Kuala Lumpur, Malaysia

ABSTRACT.—Energy budgets and growth data are presented for nestlings of three species of tropical insectivores: White-bellied Swiftlets (*Collocalia esculenta*), Blue-throated Bee-eaters (*Merops viridis*), and Pacific Swallows (*Hirundo tahitica*). A comparison with temperate nestlings, matched for body size, shows that the peak energy demand in our tropical sample averaged around 60% of temperate counterparts. We attribute savings to slow growth rates, reduced thermoregulatory requirements, a low resting metabolism (in swallows only), asynchronous hatching (in bee-eaters), and low nestling activity levels. Patterns of energy storage as lipid in nestlings of the three species were similar to the pattern in temperate swallows (Hirundinidae) and swifts (Apodidae), with those species feeding at the greatest heights, and hence on the most unpredictable supplies, storing the most fat while in the nest. Received 1 February 1982, accepted 16 November 1982.

BIRDS that breed in the tropics usually have small clutches (Moreau 1944; Lack and Moreau 1965; Cody 1966, 1971; Skutch 1976), and their nestlings grow slowly (Ricklefs 1976, Oniki and Ricklefs 1981). Many nests may be lost to predators (Skutch 1967, Lack 1968, Ricklefs 1969), but, if the nest is successful, then care of fledglings is often prolonged (Fogden 1972, Skutch 1976). It has proved difficult to provide a unifying explanation for these trends, but short days (Hesse 1922, Lack 1954, Royama 1969) and poor nutrition (Snow 1976, Foster 1977) may be contributory extrinsic factors limiting clutch sizes and growth rates. Equally, high adult survival and poor offspring survival may favor low levels of reproductive effort (Williams 1966, Cody 1971, Charnov and Krebs 1974).

It is usually assumed in discussions of avian reproductive rates that the number of eggs or young (at least within taxa, matched for body size) is a valid comparative unit and that resource demands are related mainly to brood size and the duration of parental care. The individual nestling's requirement is thus perceived as relatively constant, variability in the parents' propensity or capacity for gathering food being the main limiting factor. Food requirements for breeding in the tropics, however, may be less than those for temperate birds. For example, *BMR* (basal metabolic rate) among adults is lower in many tropical birds (Weathers 1979, Hails in press), and a similar trend was evident in a sample of nestling passerines (Ricklefs 1976). Thermoregulatory demands,

too, will usually be less, and additional energy savings may follow from reduced activity by nestlings in some tropical species (Snow 1976).

In this study we examined the effect of economic factors on the overall energy demands of some tropical nestlings. By looking at three insectivorous species, we avoided many problems with nutrient deficiency, such as may apply with frugivores (Foster 1977, 1978). We made comparisons with temperate species, which are nourished almost exclusively on nutritionally rich foodstuffs, including granivorous species that generally take insects to the brood.

METHODS

We studied three species of aerial-feeding insectivores: White-bellied Swiftlets (*Collocalia esculenta*: Apodiformes, Apodidae), Blue-throated Bee-eaters (*Merops viridis*: Coraciiformes, Meropidae), and Pacific Swallows (*Hirundo rustica*: Passeriformes, Hirundinidae). All three species nested in colonies in the immediate vicinity of Kuala Lumpur, Malaysia (3°7'N, 101°42'E). We visited nests at 1–7-day intervals during April–July, at the height of the breeding season (Medway and Wells 1976). At each visit, nest contents were recorded and young weighed, and from these data breeding statistics and growth curves for body mass (*M*, g) and winglength (maximum chord) were obtained. Nestlings discovered after hatching were aged at first weighing by reference to a smaller sample of precisely aged young. All data were incorporated into the growth curves presented here. The easy accessibility of our swiftlet nests allowed daily visits and enabled us to manipulate brood sizes

TABLE 1. Breeding statistics for three tropical insectivores.^a

	White-bellied Swiftlet	Blue-throated Bee-eater	Pacific Swallow
Clutch size	2.0 ± 0.2 (240)	3.9 ± 1.0 (10)	3.0 ± 0.8 (204)
Percentage hatching	51 (469)	59 (39)	54 (250)
Young per successful nest	1.1 ± 0.8 (53)	1.8 ± 0.7 (6)	2.3 ± 0.9 (49)
Nestling period (days)	35.3 ± 1.4 (10)	28.6 ± 2.2 (7)	19–21 (10)
Number of broods per year	1–2	1	1–2

^a Means ± SD are given, with sample sizes in parentheses. For the percentage hatching, they refer to the number of individual eggs laid; for the remainder, they refer to number of broods observed.

and to explore the effects of manipulation on growth, survival, and quality of young. Data on breeding biology for the study species are summarized in Table 1.

Nestlings of all three species, as well as a small sample of House Swifts (*Apus affinis*), were collected throughout the study for carcass analysis. After weighing, the birds were sacrificed and oven dried at 60°C to constant mass, the lipid fraction was extracted (soxhlet: chloroform 20%, ether 80%), and the carcass was reweighed. From these carcass data we got water content (*W*), dry mass (*DM*), lipid mass (*L*), and lean dry mass (*LDM*) by difference. The lipid index (*L/LDM*), water index (*W/LDM*), and percentage body water (*W/M* × 100) were then calculated. Energy content of body components equals dry mass of tissue times energy density of that tissue (=20.5 kJ·g⁻¹ for *LDM*, assuming 13% ash content, and 39.7 for lipids; Kleiber 1961, Ricklefs 1974). Total energy density of live birds (*ED*) then equals the sum of the energy content of the two components (*P*), divided by the live mass (*M*). Daily $\Delta M \times ED$ then gives energy increments in growth (*G*). The metabolic rate of nestlings for all species was measured as oxygen uptake at 33 ± 1°C from a continuous-recording spirometer (Hails in press). Oxygen consumption was converted to energy expenditure, assuming RQ = 0.75: hence 1 l O₂ = 20.1 kJ. Nearly all nestlings chosen for respirometry were more than one-third grown (by age) to avoid problems caused by ineffective homeothermy in the absence of parental brooding, even though at 33°C this was unlikely to cause serious errors. Each measurement was made in darkness over 12 h during night. To obtain estimates of daytime metabolic rates, the nighttime rates were multiplied by 1.55 (after Bryant and Gardiner 1979): the sum of day (12.3 h) and night (11.7 h) then gave daily (24 h) energy expenditure (*R*). Daily metabolized energy (*DME*) for nestlings was obtained by adding daily energy expenditure (*R*) and growth increments (*G*) (Petrušewicz and Macfadyen 1970). For Pacific Swallows two additional techniques for estimating *DME*

of nestlings were used. The number of feeds delivered per day (*n_f*) was obtained from an earlier study at the same sites (Hails in prep) and multiplied by the mean dry mass (*m_f*) of each feed. Assuming that assimilation efficiency (*a*) of swallow nestlings = 0.70 (Bryant and Westerterp 1980, Turner 1982) and the energy content of insects (*e_i*) = 23.0 kJ·g⁻¹ (Bryant 1973, Turner 1980), then

$$DME = n_f \times m_f \times a \times e_i. \quad (1)$$

The third technique involved collecting fecal pellets (including uric acid) produced by broods. For nestlings of 10 days or more nearly all fecal pellets dropped onto the trays placed below the nests. The number of pellets carried away by parents at this time was recorded by direct observation (see results). Feces were dried and weighed (*F*, *g*), and the energy density (*e_f*) was determined by bomb calorimetry. Then,

$$DME = F \left(\frac{a}{1-a} \right) \times e_f. \quad (2)$$

RESULTS

Nestling growth.—Live mass (*M*) growth curves for all three species (Fig. 1) were fitted by the logistic equation (Ricklefs 1967, 1968a). The logistic equation takes the form:

$$M(t) = A \{1 + \exp[-K(t - t_i)]\}^{-1} \quad (3)$$

where *A* = peak nestling mass, *K* = growth rate constant (days⁻¹), *t* = nestling age (days), and *t_i* = age at point of maximum growth rate. From this we obtained growth constants (*K*) for comparing growth rates between species (Table 2).

Two species, the bee-eater and the swallow, showed a marked mass recession (Ricklefs

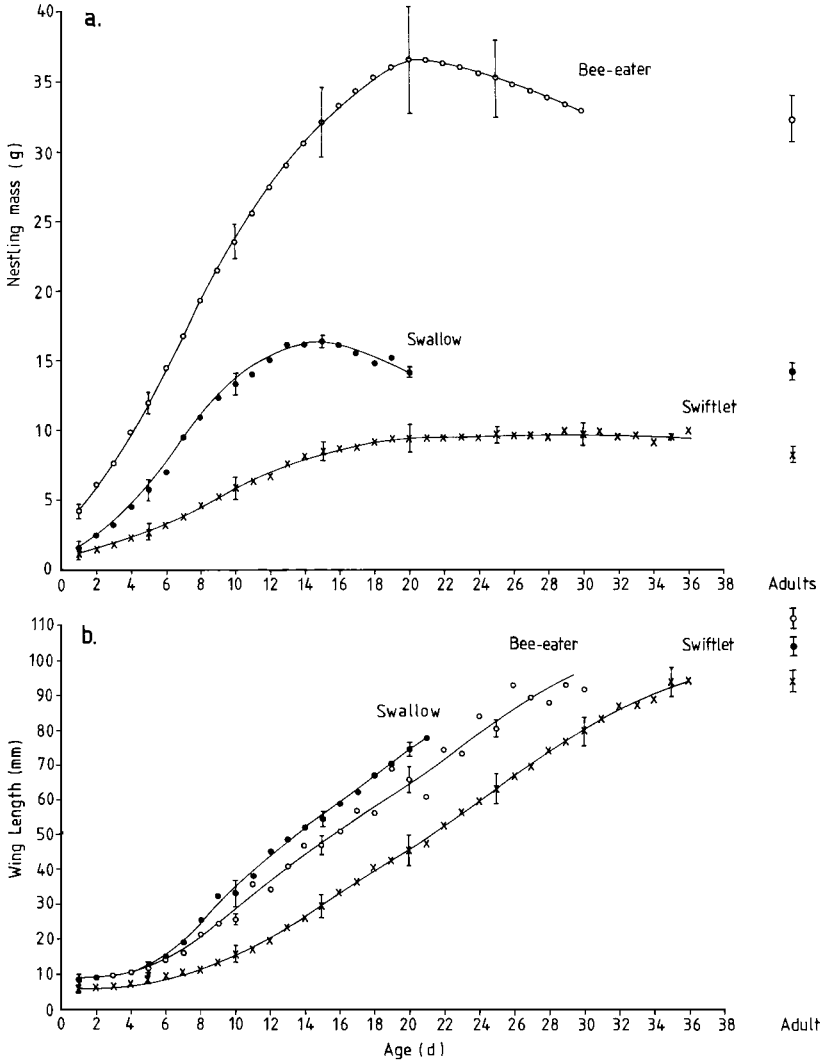


Fig. 1. Growth curves for three tropical birds. A. live mass, B. winglengths (maximum chord). Symbols show means (\pm SD at every 5th day). Curves are fitted by eye. For Blue-throated Bee-eaters sample size for nestlings = 86 nestling-days; for Pacific Swallows, $n = 146$; and for White-bellied Swiftlets, $n = 467$. Means (\pm SD) for adults of each species are shown for comparison.

1968b) after the peak, involving the loss of 15–16% body mass before fledging (Fig. 1a, Table 2). The swiftlet showed no recession, a pattern similar to that of another swiftlet in Malaysia (*Collocalia fuciphaga*) (Langham 1980).

The growth of the wing was approximately linear for all three species during the middle stages of growth (Fig. 1b).

Nestling composition.—Body-mass changes among nestlings can be considered in terms of three principal components: water content, the

lean dry fraction, and total lipid. In all three species the water index (and percentage of water) declined throughout the nestling period, levelling off prior to fledging (at an index value of 2–3) (Fig. 2). The lean dry component (principally the protein fraction plus ash) increased linearly during the early growth stages in the three species but tended to level off in swiftlets before they left the nest (Figs. 3 and 4). The lipid index showed the most striking differences between species: in bee-eaters and

TABLE 2. Nestling growth parameters^a for three tropical birds.

	White-bellied Swiftlet	Blue-throated Bee-eater	Pacific Swallow
M_{ad} (g)	8.1	34.1	14.1
M_f (g)	9.7	33.0	14.6
A (g)	9.46	37.7	16.3
R_{ad}/R_f	1.17/0.97	1.11/1.14	1.16/1.12
K	0.28	0.29	0.42
t_{10-90}	15.78	15.36	10.46
r^2	0.99	0.07	0.98
Sample size ^b	48	5	25

^a M_{ad} and M_f denote body mass of adults and fledglings, respectively; A = peak nestling mass; R_x = ratio of A/M_{ad} and A/M_f , respectively; K = growth constant in logistic equation; t_{10-90} = time taken to grow from 10 to 90% of A (see Ricklefs 1967).

^b Sample size refers to the number of broods from which nestling growth data were collected. See legend of Fig. 1.

swallows it was low, in general ranging from 0.1–0.4 in nestlings that were more than half grown (hereafter called mature nestlings) (Fig. 3). In swiftlets the mean ($\bar{x} \pm SD$) was 0.66 \pm 0.17 for mature nestlings, and in a sample of House Swifts it was even higher, at 0.97 \pm 0.14 (Fig. 4). Only in the two swifts (Apodidae), however, did the lipid index show a progressive rise to fledging.

In White-bellied Swiftlets, for which the largest sample of nestlings was available, we compared carcass condition with live mass in mature nestlings (≥ 20 days). There was a positive correlation between the lipid index and body mass ($r = 0.43$, $P < 0.05$, $n = 50$), showing that heavy fledglings carried the largest lipid reserves (see O'Connor 1976, Bryant and Gardiner 1979).

Increases in live energy density reflect underlying changes in the composition of nestlings, the lipid component with its high energy value exerting an effect disproportionate to its mass. All species showed a typical linear increase through the nestling period (Ricklefs 1974) (Fig. 5). The highest level at fledging, nearly twice that of breeding adults, was found in swiftlets, whereas in fledgling bee-eaters and swallows energy density was similar to adult levels (Fig. 5). Despite the marked mass recession in two species, and the long period in the nest for swiftlets when they showed no changes in body mass, growth continued throughout the nestling period for all species. This is reflected in the linear rise in energy density and the progressive increases (albeit slowing in

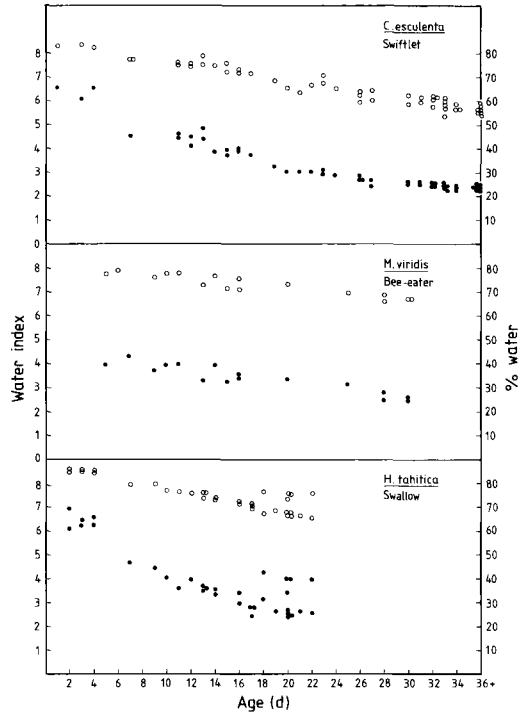


Fig. 2. Changes in the water index (W/LDM) and percentage body water in relation to nestling age. Closed circles = water index; open circles = percentage water.

swiftlets) of the lean dry component up to the time of fledging (Figs. 3, 4, and 5).

Nestling metabolism.—The oxygen uptake, and hence estimated energy expenditure for nighttime rest and biosynthesis, was derived from small samples of nestlings (Table 3). We did not find any relationship between oxygen uptake and body mass but recognize that for larger samples, especially those that contain a greater spread of sizes, a relationship may be demonstrable. If this is the case, then an effect on our estimates of age-specific energy expenditure would be expected. The magnitude of this effect can be demonstrated by example. New estimates of mass-specific metabolic rates, for Pacific Swallow nestlings were calculated from the daytime and resting phase equations of Aschoff and Pohl (1970a, b). These estimates of nestling metabolism were adjusted ($\times 0.706$) to allow for the lower mean metabolic intensity shown by our direct measurements (Table 3). Then, daytime metabolism was multiplied by 1.55, as previously, and estimates of daily en-

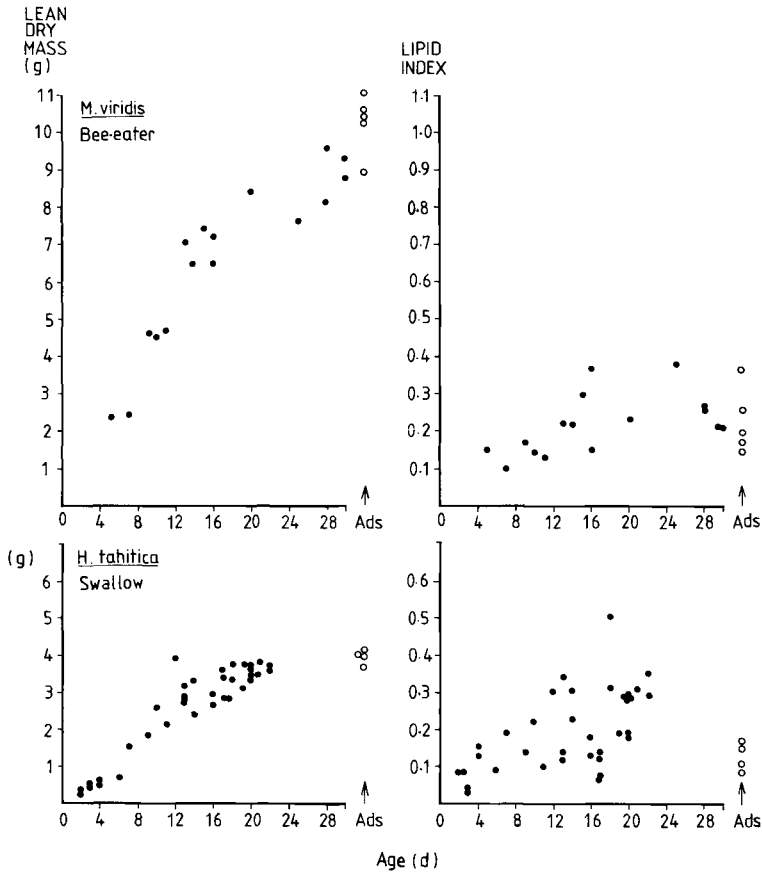


Fig. 3. Changes in lean dry mass (LDM) and lipid index (L/LDM) for nestling Blue-throated Bee-eaters and Pacific Swallows. Adult data (open symbols) are given for comparison with fledgings.

ergy expenditure obtained. Calculated in this way (and therefore assuming metabolic allometry), mean daily energy expenditure for days 7–15 (see below) was 7% greater than the original estimate, which assumed metabolic constancy.

No attempt was made to account for energy expenditure on thermoregulation. Ambient temperatures (T_a) were high during the study (24 h, mean $T_a = 28^\circ\text{C}$; midday shade, mean $T_a = 37.5$, bee-eater burrow, mean $T_a = 29^\circ\text{C}$), however, and hence close to or within the thermoneutral zone for huddled young in the nest. We did not observe panting, which would have indicated heat stress. Additional thermoregulatory costs must therefore have been negligible.

The swiftlets were noticeably quiet in the nest, rarely moving except when parents made their infrequent visits. Activity costs must have

been low for this species. Swallows and bee-eaters were fed more frequently, and nestling activity costs would have been greater. For many tropical birds, nestling activity may be low mainly to avoid attracting predators (Snow 1976). Daylength during the study (12.3 h) was shorter than that of a typical temperate breeding season (15–18 h), and this would further reduce nestling activity costs compared to those of temperate species.

Measurements of resting metabolism of adults of the three species were very similar to the mean values for nestlings presented here (Bryant and Hails in prep).

Nestling energy budgets.—In the White-bellied Swiftlet daily metabolized energy (DME) reached a plateau at 12 days and then stayed roughly constant until fledging (Fig. 6). To allow comparisons between species, a 10-day period that yielded the highest mean DME was

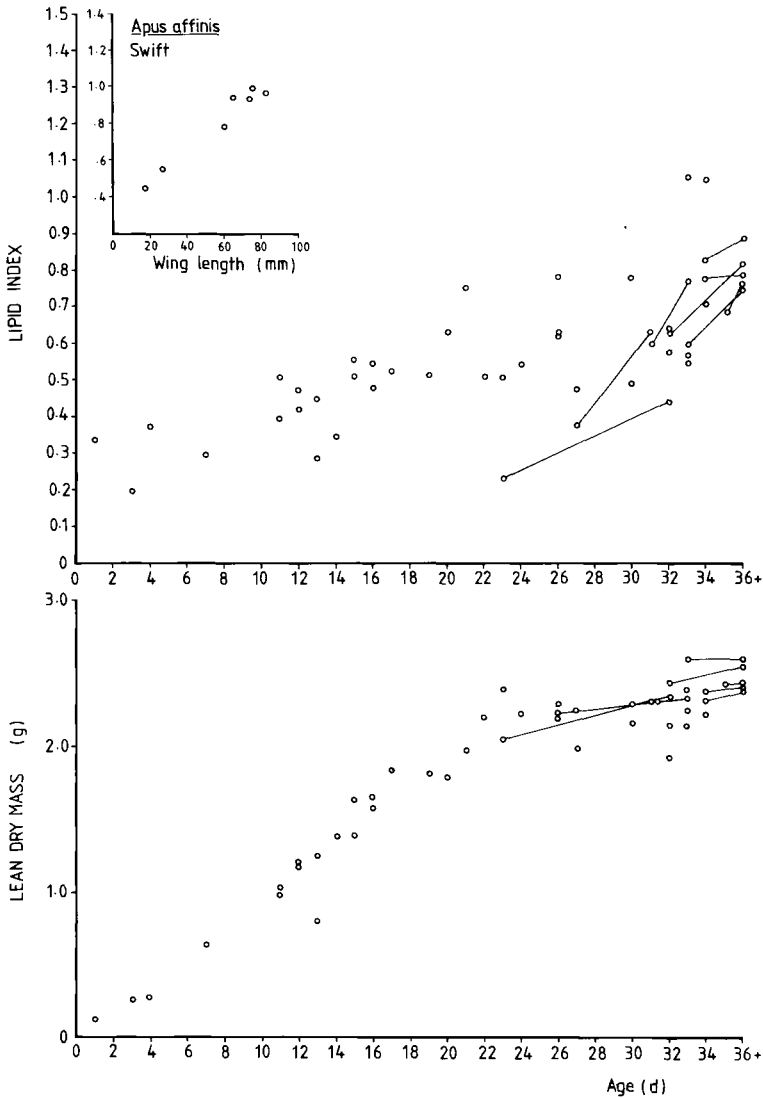


Fig. 4. Lean dry mass (*LDM*) and lipid index (*L/LDM*) in relation to age for nestling White-bellied Swiftlets. Lines join siblings, showing the similar *LDM* but relatively lower lipid index in younger siblings compared to older (see text). Also shown are values for lipid index in House Swifts (*Apus affinis*) in relation to winglength (taken as an index of nestling age).

chosen (= *DMEp*); invariably this included the day of maximum *DME*. Mean *DME* for this period was $18.91 \pm 1.49 \text{ kJ} \cdot \text{day}^{-1}$ (days 15–24).

In the Blue-throated Bee-eater *DME* rose to a peak on day 17 and declined until fledging. *DMEp* for days 13–22 was $54.36 \pm 2.23 \text{ kJ} \cdot \text{day}^{-1}$ (Fig. 6). The fall off in nestling demand may be slightly shallower than indicated, because during the last days in the burrow the youngsters came repeatedly to the burrow entrance to take food from incoming parents. This moderate

level of activity would raise the overall costs to bee-eater young relative to the young of swiftlets and swallows, which remained within the nest cup.

In the Pacific Swallow *DME* reached a peak by days 10–12 and then, as for bee-eaters, declined until fledging (Fig. 6). *DMEp* for days 7–16 was $28.58 \pm 2.94 \text{ kJ} \cdot \text{day}^{-1}$.

The sensitivity of our estimates of *DMEp* to assumptions about nestling metabolism can be demonstrated by example. If it is assumed that

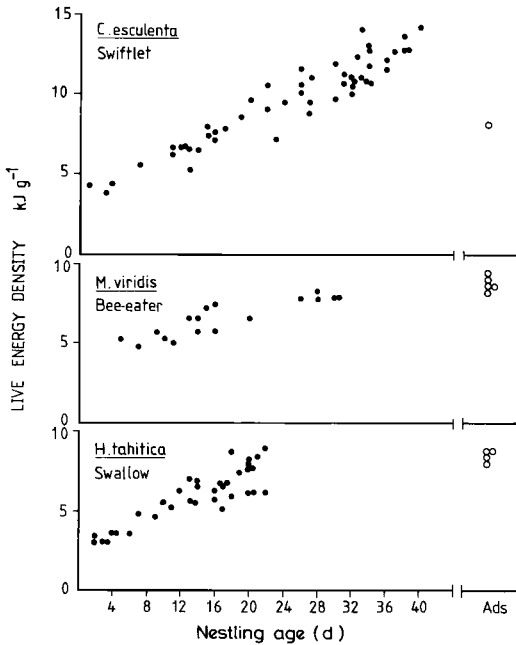


Fig. 5. Live energy density (ED) for three tropical birds. Data for adults (open symbols) are given for comparison (*C. esculenta* mean from Hails in prep.). The trends in energy density in relation to nestling age (d) are described by the regression equations (for all, $P < 0.01$): White-bellied Swiftlet: $ED = 3.626 + 0.243 d$; $r = 0.95$, $n = 51$; Blue-throated Bee-eater: $ED = 4.235 + 0.129 d$; $r = 0.89$, $n = 16$; Pacific Swallow: $ED = 2.330 + 0.283 d$; $r = 0.96$, $n = 29$.

nestling metabolism is an allometric function of body mass (see Nestling metabolism) then $DMEp$ for swallows is increased by 9.2%. Alternatively, if tropical nestlings are indeed more quiescent than temperate species, then a night : day multiplier of $1.3 \times$ nighttime metabolism may be more appropriate than the value of 1.55 used here. This would lead to a 7.5% reduction in $DMEp$.

The energy losses via the feces could not be measured for all growth stages because of frequent losses to predators amongst our study broods. At the time of peak nestling demand, however, fecal output averaged 0.74 dry $g \cdot \text{nestling}^{-1} \cdot \text{day}^{-1}$ (see below). To derive this figure, we measured the daily accumulation below a sample of nests ($n = 8$) and estimated the proportion of fecal pellets carried away by parents. In the early stages of nestling growth, all feces were carried away, but after 10 days, only a small proportion was removed. During

17.1 h of observation at four nests, parents carried away 1.14 ± 0.79 ($\bar{x} \pm SD$) pellets $\cdot \text{nestling}^{-1} \cdot \text{day}^{-1}$ and added none of their own (see Bryant and Gardiner 1979). As each pellet weighed 0.101 g dry ($n = 72$), this represented a loss of 0.115 $g \cdot \text{day}^{-1}$. The mean energy value of feces (including the uric acid component) measured by bomb calorimetry was 14.16 ± 0.63 $\text{kJ} \cdot \text{g}^{-1}$ in five samples from different nests. The overall energy value of fecal losses per nestling is therefore the nestling output on the trays (0.625 ± 0.104 g) and the share taken away by parents times the energy density and equals 10.48 $\text{kJ} \cdot \text{day}^{-1}$. We can then calculate $DMEp$ per nestling from Equation 2 ($= 24.37$ $\text{kJ} \cdot \text{day}^{-1}$).

The rate at which Pacific Swallows in the study area fed their broods was monitored throughout the day at three nests with 12–14 day-old young ($n = 10$ nest-days) (Hails in prep). Mean feeding rate ($\pm SD$) was 65.5 ± 5.6 feeds $\cdot \text{nestling}^{-1} \cdot \text{day}^{-1}$ for well-nourished young (i.e. their growth pattern conformed with mean growth curves). At another sample of nests ($n = 8$), boluses were obtained by neck collaring over 6 days. The mean bolus mass was 23.43 ± 11.97 mg ($n = 106$). This yields 377.7 joules per feed. Then, applying equation 1, $DMEp = 24.74$ $\text{kJ} \cdot \text{day}^{-1}$.

The three techniques used for estimating DME in nestling Pacific Swallows yielded broadly similar results for the middle portion of the nestling period (28.58, 24.37, 24.74), with an overall mean of 25.90 ± 2.33 $\text{kJ} \cdot \text{day}^{-1}$. Although the close similarity could have been fortuitous, we can safely conclude that any metabolism costs we failed to account for in our energy budget calculations were rather small. As the swallows were moderately active in the nest at this stage and the thermal environment was similar for all species, unidentified energy losses were probably small for the swiftlet and bee-eater as well.

Nestling competition.—Competition for food between siblings is expected if parental feeding is inadequate (Lack 1968, O'Connor 1978). It is possible to infer sibling competition indirectly from the condition of nestlings, without knowledge of energy balance as a whole, by showing that some, but not all, nestlings are undernourished (Bryant 1978a).

Swiftlet nestlings: Asymptotic mass (between days 20–30) of second-hatched and first-hatched or single chicks was not significantly different (1st = 9.48 ± 0.18 g, $n = 36$; 2nd =

TABLE 3. Nestling metabolism for three tropical species.

Species	Nestling age (days)	Nestling mass (g)	T_a (°C)	Resting metabolism ($\text{kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$)
White-bellied Swiftlet	16	8.62	32	0.0588
	16	7.98	31	0.0438
	18	8.15	33	0.0495
	22	9.45	33	0.0420
	28	9.38	32	0.0819
Mean \pm SD		8.72 \pm 0.68		0.0552 \pm 0.0163
Blue-throated Bee-eater	5	12.35	34	0.0441
	11	26.13	32	0.0445
	16	31.45	34	0.0411
	25	33.55	34	0.0429
Mean \pm SD		25.87 \pm 9.54		0.0432 \pm 0.0015
Pacific Swallow ^a	9	10.50	34	0.0495
	11	11.07	32	0.0520
	14	12.07	34	0.0525
	17	10.65	34	0.0404
Mean \pm SD		11.07 \pm 0.71		0.0486 \pm 0.0056

^a Basal metabolic rate for passerines (resting phase) = $0.133 M^{0.728} \text{ kJ} \cdot \text{h}^{-1}$ (Aschoff and Pohl 1970b). For an 11.07-g Pacific Swallow, estimated BMR = $0.0688 \text{ kJ} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. Hence, observed metabolism = estimated BMR \times 0.706 (see under Nestling metabolism).

$9.68 \pm 0.62 \text{ g}$, $n = 18$). In contrast, the condition of second-hatched young was poorer. By comparing body composition in a sample of eight broods of two young, we found that, whereas the lean dry component was similar for both groups, the lipid indices of second nestlings were always lower ($P < 0.05$) than those of their siblings (Fig. 4). The magnitude of the difference, however, was related to age differences. If the lipid indices (LI) of the younger siblings are increased to adjust for age differences, using the equation: $LI = 0.249 + 0.0136 d$ ($P < 0.01$), where d = nestling age in days (see Fig. 4), then differences between first- and second-hatched young were nonsignificant, although in 7 (88%) cases the second nestling still had a lower LI .

Twenty-two broods in which nestlings were less than 10 days old were enlarged from the normal maximum brood of two by adding a similarly aged youngster. In no case did all three young survive; nestlings usually died after a period of starvation. The overall productivity of enlarged broods was 1.0 young·nest⁻¹ reared to fledging ($n = 22$), a lower mean production ($P < 0.05$) than for unmanipulated (control) broods of two young 1.31 young·nest⁻¹, $n = 32$).

Bee-eater nestlings: The body-size hierarchy was conspicuous in all five broods studied in detail. The establishment of a hierarchy prob-

ably depends on the hatching interval (Howe 1977, Bryant 1978b). In our bee-eaters the interval was 5.2 ± 2.3 days (range, 3–9 days) from first to last hatching.

Of 15 young hatching in the five burrows fitted with inspection doors, 5 were taken for carcass analysis and 3 died in the nest (none within 11 days of opening the burrows, indicating minimal disturbance effects). All three were the smallest in the brood at time of death (Fig. 7). One brood of three fledged successfully: the largest on record (Medway and Wells 1976). The hatching spread of this brood was unusually long (9 days). We propose that this wide spread facilitated the rearing of the brood by spacing out the peak energy requirement of individual nestlings (see Hussell 1972, Bryant and Gardiner 1979). The overall reduction in peak energy demand can be demonstrated by comparing $DMEp$ in synchronous broods and our asynchronous example.

Growth curves for the asynchronous brood are shown in Fig. 7. Using these, we calculated $DMEp$ for individual nestlings as previously. Overall brood requirements were then obtained by adding daily metabolized energy for all three chicks. The body condition of the 2nd- and 3rd-hatched young was checked immediately after fledging by carcass analysis and found to be within one standard error of the regression line (Fig. 5). $DMEp$ for synchronous

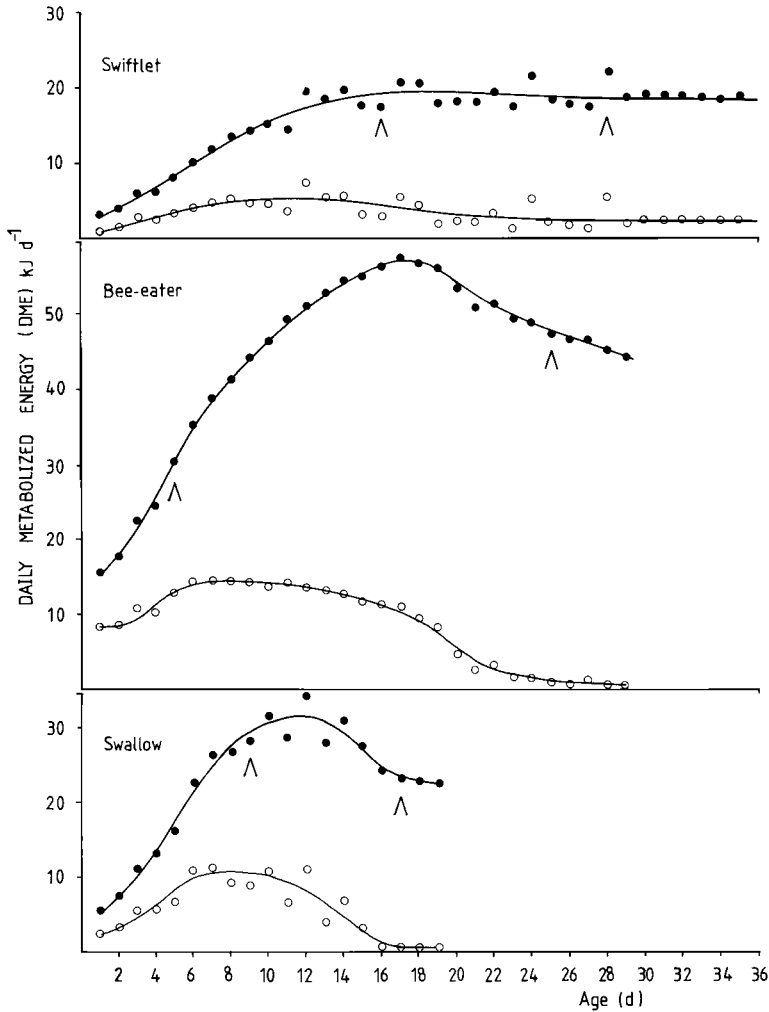


Fig. 6. Daily metabolized energy ($DME\text{ kJ}\cdot\text{nestling}^{-1}\cdot\text{day}^{-1}$) for three tropical birds in relation to age (d). Closed symbols indicate DME (i.e. $G + R$), open symbols energy devoted to growth (G) alone. Curves are fitted by eye. Direct measurements of nestling metabolism were made for sections of DME curve between arrows.

broods with three young was $163.1 \pm 6.7\text{ kJ}\cdot\text{day}^{-1}$ (i.e. 54.36×3) and for the asynchronous brood was $149.1 \pm 9.2\text{ kJ}\cdot\text{day}^{-1}$. The overall energy saving for the 10-day period of peak demand was thus 9%. Energy demand exceeded an arbitrary value of $150\text{ kJ}\cdot\text{day}^{-1}$ for 11 days in synchronous broods but for only 4 days (36%) in the asynchronous brood. This period may have been slightly underestimated in asynchronous broods if nest activity just before fledging adds significantly to daytime metabolism (see Nestling energy budgets).

DISCUSSION

Nestling growth.—Values for K , the growth constant in the logistic equation, were all within the typical range for tropical birds of less than 100 g (0.278–0.520) (Ricklefs 1976). The values for the White-bellied Swiftlet and Blue-throated Bee-eater (both aerial-feeding non-passerines) closely resembled those for two swifts in Ricklefs' sample (0.281), and the value for the Pacific Swallow was close to the mean for three neotropical Swallows (0.398). We con-

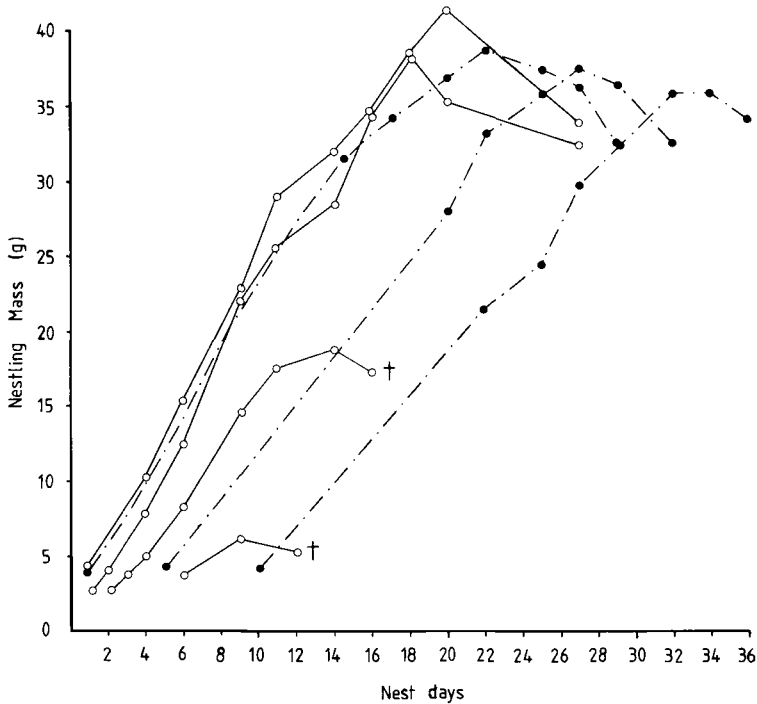


Fig. 7. Growth curves for two broods of Blue-throated Bee-eaters. Open symbols (○) show a nest of four chicks with brood reduction, resulting in successive death (†) of the two smallest young. The two remaining chicks fledged. The other curves (dashed) show growth of a brood of three chicks in which asynchrony at hatching was extreme (i.e. 9-day hatching spread). In consequence, development and peak body masses were widely spaced (see text for explanation and analysis).

clude that our three study species are typical of tropical birds with respect to their slow growth rates and are representative of their respective taxa.

Lack (1968) contended that the shape of the growth curves of many seabirds and aerial-feeding insectivores (increase to peak, followed by a decline) reflected the accumulation and subsequent use of lipid reserves. Several authors have shown that, amongst aerial feeders, the decline in body mass just prior to fledging is due to loss of water, not lipids, mainly from the drying out of the integument (Ricklefs 1968b, O'Connor 1977, Bryant and Gardiner 1979). In most examples, however, the species with a marked mass recession also accumulate large fat reserves. The White-bellied Swiftlet, and presumably the Edible-nest Swiftlet as well (Langham 1980), proved to be an exception; there was no mass recession, and yet the lipid index reached a high level. Presumably, water losses from the drying of the

integument were offset by the progressive rise in both the lean dry content and (unusual for aerial-feeding birds) the lipid content during the later phase of growth.

The size of the lipid store in each species increased with increasing feeding height, a pattern also detected in temperate aerial feeders (Turner and Bryant 1979) (Fig. 8). The height of feeding is related to the variance or unpredictability of food supplies (Medway 1962, Lack 1968, Bryant 1973, Waugh 1978, Turner 1980), because insects in higher aerial strata are more affected by bad weather (Johnson 1969, Waugh 1978). Hence the "insurance" fat of the nestlings closely matches the risk of food shortages. Presumably, the lower lipid indices of the tropical species (for any given height) are related to the greater predictability of their environment. It is difficult to isolate the effect of an additional factor, the opportunity for post-fledging care. If postfledging care is frequent, such as in bee-eaters and swallows, fledglings

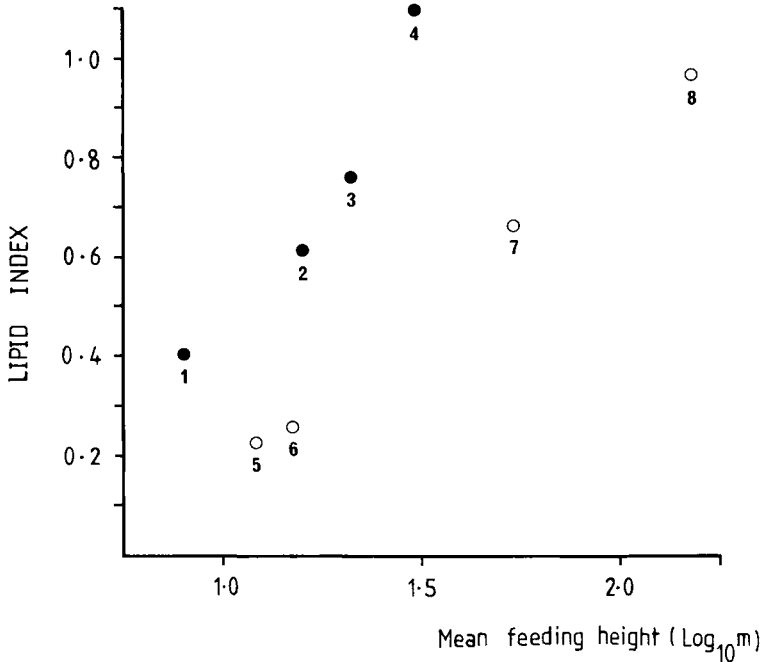


Fig. 8. Lipid indices for mature nestlings of various aerial insectivores in relation to average feeding height (feeding data from Bryant 1973, Waugh 1978, Waugh and Hails in press; lipid indices for temperate species from Koskimies 1950, Bryant and Gardiner 1979, Turner and Bryant 1979). Temperate species, closed circles: 1. *Hirundo rustica*, 2. *Riparia riparia*, 3. *Delichon urbica*, 4. *Apus apus*. For these $r = 0.95$, $P = 0.05$. Tropical species, open circles: 5. *Hirundo tahitica*, 6. *Merops viridis*, 7. *Collocalia esculenta*, 8. *Apus affinis*. For these $r = 0.99$, $P < 0.01$.

are not as fat when they leave the nest, but, where there is little or no contact between fledglings and parents (i.e. swifts), then a relatively large fat store is typical, to allow the youngster time to become a proficient hunter (Lack 1968, Bryant and Gardiner 1979).

Nestling metabolism.—The metabolic rate of tropical birds has been the subject of much controversy. Scholander et al. (1950), Kendeigh et al. (1977), and Vleck and Vleck (1979) were unable to accept a systematic difference between tropical and temperate birds, and it was not until the more extensive measurements and analyses of Weathers (1979) and Hails (in press) that the pattern of low *BMR* for certain tropical birds was confirmed. Hails' sample of adult passerines in Malaysia yielded an average 30–35% reduction in *BMR* when compared with predictions from Aschoff and Pohl's (1970a, b) passerine equation (resting phase), which is based on mainly temperate species. A similar reduction was found in adult Pacific Swallows

(Bryant and Hails in prep.). There has been no treatment of nestling metabolism like that of Aschoff and Pohl (1970a, b) for adult birds, and so comparisons between tropical and temperate nestlings are difficult. Among nestlings of four temperate residents, however, resting metabolism was 1.03 *BMR* (Table 4), where *BMR* was calculated after Aschoff and Pohl (1970b). A similar comparison for nestling Pacific Swallows gave 0.71 *BMR*, a result close to that of Ricklefs (1976) for several nestling passerines from the Neotropics. In contrast, nestling metabolism for swiftlets and bee-eaters had values of 1.22 and 1.27 *BMR*, respectively (based on Aschoff and Pohl's nonpasserine equation), and so any general trend for tropical nestlings to have a low resting metabolism is unlikely. We do not imply by these comparisons with predicted *BMR* that growing nestlings at rest meet all criteria for a state of basal metabolism. Instead, we use estimates of mass-specific adult metabolism as points of reference. Judged on

TABLE 4. Resting metabolism (RMR) of nestling passerines from temperate environments.^a

Species	Nestling age (days)	Body mass (g)	RMR (kJ·g ⁻¹ ·h ⁻¹)	$\frac{RMR}{BMR}$	Reference
Blue Tit (<i>Parus caeruleus</i>)	11–18	11.0	0.0633	0.92	O'Connor (1975)
Great Tit (<i>Parus major</i>)	12–15	16.1	0.0695	1.12	Mertens (1977)
House Sparrow (<i>Passer domesticus</i>)	9–15	21.91	0.0513	0.90	O'Connor (1975)
House Sparrow (<i>Passer domesticus</i>)	7–17	21.91	0.0666	1.17	Blem (1975)
Starling (<i>Sturnus vulgaris</i>)	9–16	61.40	0.0434	1.01	Westerterp (1973)

^a BMR was calculated using Aschoff and Pohl's (1970b) equation for passerines (resting phase); see Table 3. In all studies quoted, conditions were thermoneutral, and in Mertens' (1977) and Westerterp's (1973) studies the young were huddled in broods of three and four, respectively.

this basis, Pacific Swallows have a lower resting metabolism than that found among temperate residents. In the other two study species we cannot attribute any energy savings to a low resting metabolism; indeed the converse may apply.

For all three species, metabolic intensity in the earliest stages of growth might differ from our estimates based on measurements of older nestlings (see results). Myrcha et al. (1973) and Mertens (1977) have shown that mass-specific metabolism for the full nestling period is best described by allometric equations, indicating a modest increase in metabolic intensity for older nestlings. In the Bank Swallow (*Riparia riparia*), however, Marsh (1979) found no systematic change in mass-specific metabolism between day 3 and fledging at T_a 's of 32–38°C (calculated from Marsh's Fig. 6). O'Connor (1975) obtained a similar result for the House Martin (*Delichon urbica*) and two other small passerines. In view of these results for passerine nestlings in the thermoneutral zone, we expect our assumption of metabolic uniformity during development will have caused, at worst, only small errors in our calculations. We do restrict our detailed comparisons to the growth periods for which we made direct measurements of metabolism, the period when demands for brood rearing reached the highest level.

Nestling energetics.—The agreement between three different techniques for measuring daily metabolized energy in Pacific Swallows provides support for the reliability of our principal technique based on energy budgets. Compar-

isons of daily metabolized energy ($DMEp$) in three tropical species with published data for growing temperate nestlings (Kendeigh et al. 1977) show a substantially lower energy requirement for our tropical sample: $DMEp$ averaged only 55.5% of that of temperate nestlings (Table 5). Similarly, taking Drent and Daan's (1980) data, which are restricted to nidicolous young, a broadly similar result is obtained (64.0%) (using a line fitted by eye to their Fig. 9). Slow growth rates, reduced thermoregulatory requirements, low levels of nest activity, and, in swallows only, a low resting metabolism probably contributed to the reduced daily metabolized energy of our tropical insectivores. It is also suggested that asynchronous hatching further depressed peak energy demands in large broods of bee-eaters by spacing out the requirements of individual nestlings (Hussel 1972, Bryant and Gardiner 1979). There were two more energetic advantages of asynchronous hatching: to reduce the period of exceptional demand and to provide an opportunity to undernourish or starve the youngest nestling selectively should demands exceed supply. One consequence of slow growth and asynchronous hatching is a longer period of nestling care, which would usually lead to a greater cumulative energy demand for brood rearing. We argue here, in the context of energetic limits to brood size, that it is the upper level of brood demands (estimated here as $DMEp$) that restricts brood productivity and not the total for the nestling period. Any further extension of the nestling period, however, is probably selected against in order to reduce

TABLE 5. A comparison of nestling DME (daily metabolized energy), estimated from the equation^a of Kendeigh et al. (1977) and observed in this study.

	White-bellied Swiftlet	Blue-throated Bee-eater	Pacific Swallow
Nestling mass ^b (g)	9.24	34.30	14.31
Predicted DME (kJ·day ⁻¹)	34.59	100.61	49.38
Observed DME _p (kJ·day ⁻¹)	18.91	54.36	28.58
Observed/predicted percentage ^c	54.7	54.0	57.9

^a Kendeigh et al. (1977) predict DME from their equation (5.78): DME = 5.661 M^{0.814} kJ·day⁻¹.

^b Mean body mass for the period of peak nestling energy demand.

^c Observed DME_p expressed as a percentage of predicted DME. Mean = 55.5%.

predation risks, to avoid deteriorating food supplies or weather, or to allow for multiple laying or other factors (Clark and Wilson 1981).

Lowering nestling quality (i.e. reducing lipid indices) can also be viewed as a means of economizing energy demands for growth (Drent and Daan 1980). In White-bellied Swiftlets, the youngest nestling in surviving broods of two was invariably of lower quality. The effect was confounded by age differences, however, and further study is needed. More drastic reductions in brood requirements, involving selective starvation of the youngest nestling (Lack 1954, Ricklefs 1965, O'Connor 1978), were observed in both swiftlets and bee-eaters. We conclude that parent swiftlets will not nourish enlarged broods of three and that there is evidence from nestling mortality that bee-eaters, as well as swiftlets, may experience difficulty in nourishing their largest broods.

There will naturally be some temperate breeding species with exceptionally well-insulated nests, low growth and metabolism requirements, or other factors reducing energy demands. The House Martin, breeding in the temperate zone but wintering in the tropics, may be such an example (O'Connor 1975, Bryant and Gardiner 1979). Nevertheless, a pattern emerges for reduced peak energy costs for rearing offspring in tropical environments. Against this must be set the more prolonged care due to slow growth (Ricklefs 1976) and extended postfledging attention (Fogden 1972). In the context of limitations to reproductive rates, however, it is likely to be the maximum

demand during breeding that regulates clutch size (Lack 1954, 1966), and this generally occurs during the time the young are in the nest (Ricklefs 1974, Bryant and Westerterp 1980).

Whatever the basis for reduced reproductive rates among many tropical birds, this study suggests that their small broods exert even lower demands than a simple comparison of brood-size would suggest. The enigma of small clutches at low latitudes is thereby intensified and deserves further examination.

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