REPRODUCTIVE ENERGETICS OF TWO TROPICAL BIRD SPECIES

D. M. BRYANT,[1] C. J. HAILS,[2,3] AND P. TATNER[1]

[1]*Department of Biological Science, University of Stirling, Stirling FK9 4LA, United Kingdom; and*
[2]*Department of Zoology, University of Malaya, Kuala Lumpur, Malaysia*

ABSTRACT.—Daily energy expenditure (*DEE*) during breeding was studied in Pacific Swallows (*Hirundo tahitica*) and Blue-throated Bee-eaters (*Merops viridis*) in Malaysia. *DEE* was measured directly by the doubly labelled water ($D_2{}^{18}O$) technique and indirectly by TAL (time-activity-laboratory) methods during the time adults were feeding their young at the nest. *DEE* was 76.6 kJ/day in the Pacific Swallow and 77.4 kJ/day in the larger Blue-throated Bee-eater ($D_2{}^{18}O$ results). The relatively low *DEE*, compared to temperate-zone insectivores that also feed in flight, was attributed to the action of proximate factors, namely a more favorable thermal environment and shorter days (which results in less daytime activity). In bee-eaters, partial use of a low-cost foraging technique also contributed to their lower *DEE*. The suitability of *DEE* as a measure of reproductive effort is discussed. *Received 3 January 1983, accepted 1 September 1983.*

TROPICAL birds usually have small clutches and their nestlings grow slowly, suffer high losses, and are dependent on parents long after fledging (Lack 1954, 1968; Ashmole 1963; Lack and Moreau 1965; Cody 1966, 1971; Ricklefs 1969, 1976; Fogden 1972). The evolutionary basis for low reproductive rates among tropical birds is unclear: one view is that they are in various ways a consequence of an unfavorable environment (short days, intense predation and competition, scarce food) (Lack and Moreau 1965, Ashmole 1963, Cody 1966, Skutch 1966, Royama 1969, Ricklefs 1980). Another view is that low reproductive rates reflect an optimization of reproductive investment in relation to survival (Williams 1966, Gadgil and Bossert 1970, Charnov and Krebs 1974). In stable environments, where survival of adults is high (Fry 1980) and that of juveniles either poor or variable, low investment in breeding is favored (MacArthur and Wilson 1967, Murphy 1968, Goodman 1974, Stearns 1976, Southwood 1977). If this is the case, investment in breeding (i.e. reproductive effort) should be lower for tropical birds than for their temperate counterparts. Obtaining a realistic measure of reproductive effort to investigate this point has proved difficult, because all reproductive costs cannot be measured as a single currency (Tinkle 1969, Tinkle and Hadley 1975, Trivers 1972, Pianka and Parker 1975, Calow and Woollhead 1977, Calow 1979, Bryant 1979). In this study we examined one parameter of reproductive effort, energy expenditure during breeding. We did this to determine whether or not daily energy expenditure was lower for tropical species.

Using the doubly labelled water ($D_2{}^{18}O$) technique (Lifson and McClintock 1966), we measured daily energy expenditure in two species of tropical birds, and we draw comparisons with similar data for temperate species. Using TAL (time-activity-laboratory) techniques (Mugaas & King 1981), we attempt to identify the causes of any differences by modelling daily energy expenditure. To minimize trivial differences, which arise from inevitable dissimilarities in taxa, habitats, and habits, we compared aerially feeding insectivores from open habitats during the nestling-rearing stage.

METHODS

Study area.—Our study was carried out in the vicinity of Kuala Lumpur, Malaysia (3°07'N, 101°42'E). Study sites for Pacific Swallows (*Hirundo tahitica*, Hirundinidae) were a lakeside surrounded by secondary rain-forest (Klang Gates), a small forest clearing (Gombak), and clear-felled forest with some fish ponds (Puchong). Observations of Blue-throated Bee-eaters (*Merops viridis*, Meropidae) were made all at one site (Sungei Buloh), where nesting burrows were spread across a large lawn set amidst rubber plantations. The breeding biology of Pacific Swallows in Malaysia is described by Hails (in press) and summarized for both study species by Bryant and Hails (1983).

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[3] Present address: Botanic Gardens, Cluny Road, Singapore.

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Environment.—At hourly intervals during field observations we recorded ambient temperature in shade (T_{as}) and black-bulb temperature (T_{ab}) and relative humidity (*RH*) in exposed sites, all at 2 m above ground. We estimated sun, rainfall, and wind on 5-point scales. For the sun index (I_s): 1 = full sun, no obscuring cloud, 0900–1500; 2 = full sun, sunrise to 0900 and 1500 to sunset; 3 = sun intermittently obscured by cloud; 4 = sun frequently obscured by cloud; and 5 = no sun or full cloud cover. For the rainfall index (I_r): 1 = torrential storm; 2 = storm easing; 3 = moderate rain; 4 = drizzle; and 5 = no rain. Wind was generally light; hence, for the wind index (I_w), 1 = moderate breeze; 2 = gentle breeze; 3 = light breeze; 4 = light air; and 5 = calm (as for points 4 to 0 on the Beaufort scale). Cloud cover was recorded in oktas (eighths).

We found that I_s and T_{ab} were correlated ($r = -0.74$, $P < 0.001$) and, subsequently, that I_s was related to direct measurements of solar radidation by the following equation:

$$I_s = 4.1100 - 0.0039R, \qquad (1)$$

where R = solar radiation (W/m^2) and $r = -0.77$, $P < 0.001$ (data supplied by the Malaysian Meterological Service from their weather station at Subang International Airport, close by the Sungei Buloh site). We also monitored T_{as}, T_{ab}, and *RH* continuously at Klang Gates and Sungei Buloh throughout much of the breeding season.

Resting metabolism.—Swallows and bee-eaters were captured between 1600 and 1800. They were weighed and put in a metabolism chamber overnight. In the morning, birds were reweighed and released. The metabolism chamber contained 20% KOH to absorb expired carbon dioxide and was linked to a continuous recording spirometer containing oxygen. The chamber was immersed in a thermostatic water bath, and the entire apparatus was held within a constant temperature room. We measured the rate of oxygen uptake $\dot{V}(O_2)$ for 6+ h. Analysis was restricted to the 3-h period within each run that yielded the lowest mean $\dot{V}(O_2)$. This ensured that thermal equilibration was complete and birds were in a postabsorptive state. For Pacific Swallows we confined measurements to the presumed thermoneutral zone (30–35°C, see below), but for bee-eaters we recorded $\dot{V}(O_2)$ throughout the range, 20–35°C. Further details of our techniques are given by Hails (1983). All measurements of $\dot{V}(O_2)$ were corrected to S.T.P. To estimate energy expenditure, we took $RQ = 0.75$ (Hails and Bryant 1979, Bryant and Westerterp 1983) and, hence, 19.83 J/cm^3 O_2 (Brody 1945).

Time-activity budgets.—We recorded the activity of swallows and bee-eaters by scanning the study sites from vantage points with 10 × 50 binoculars. We did this from around sunrise to sunset at intervals of 10 min and recorded behavior under the following headings: perching in exposed position (i.e., open to direct solar radiation), perching in shaded position (i.e., largely shaded from sky radiation by vegetation or artefacts), perching on shaded nest or down burrow, sunbathing (i.e. adopts spread-wing posture with dorsal surface angled toward sun), preening, flying, drinking, and bathing. For successive hourly periods we estimated the proportion of individuals engaged in each activity and took this as equivalent to percentage time spent by individuals on each behavior. Pacific Swallows invariably fed in the immediate vicinity of the nest site, and so we expect no bias due to differences in behavior for birds in view and out of sight. Bee-eaters, in contrast, could often be seen leaving the colony but would drop down and feed out of view. Casual observations at nearby (<2 km) sites visited by our bee-eaters suggested that perching was still predominant to flying, as we found at the colony. In view of this we expect no serious bias to follow from basing time-activity budgets on behavior at the colony. At the time of the observations reported here (April–June), breeding was closely synchronized among bee-eaters and moderately so among swallows. Any bias arising from birds being at different stages in the breeding cycle is therefore likely to be small.

We used the TAL (time-activity-laboratory) technique to calculate daily energy expenditure (*DEE*, kJ·day^{-1}·individual^{-1}) (Ettinger and King 1980, Mugaas and King 1981).

Doubly labelled water ($D_2{}^{18}O$) technique.—Swallows were caught with a spring-trap as they visited their nests, at around 1500. They were loaded with 0.12 cm^3 $H_2{}^{18}O$ (20 atom %) and 0.08 cm^3 D_2O (10 atom %) by intraperitoneal injection and then kept in a cloth bag for 1+ h to allow equilibration of stable isotopes. Samples of blood were taken from the femoral vein and immediately sealed in fine glass capillaries. The birds were then individually color marked and released to resume normal activity. All the swallows were rearing young aged 8–15 days at the time of our observations. Time-activity data were collected throughout the following day, mainly from unmarked birds at the colony but including marked birds as encountered. Recaptures were secured as near 1600–1700 as possible, resulting in 24 ± 1-h observation periods. If recapture was at first unsuccessful, we followed birds for a further 24 h to give ≈48-h periods of observation.

Bee-eaters were caught by placing a net over the nest hole while adults were feeding their young below ground. They were loaded with $D_2{}^{18}O$ (isotope enrichments as above); injected volumes ranged from 0.20–0.25 cm^3 $H_2{}^{18}O$ and 0.12–0.16 cm^3 D_2O. We allowed 1.5 h for equilibration in the larger species, but otherwise techniques were the same as for swallows. All nestlings of bee-eaters were 10–25 days old.

For estimates of body mass (*W*) we have relied on birds captured when they had young in the nest. To measure water and fat content, we oven-dried some

TABLE 1. Body mass and carcass composition of Pacific Swallows and Blue-throated Bee-eaters during the nestling phase (means ± SD, *n* in parentheses).

	Pacific Swallow	Blue-throated Bee-eater
Body mass (g)	14.07 ± 0.75 (14)	33.81 ± 2.38 (12)
Percentage of water	63.0 ± 1.0 (4)	63.2 ± 2.0 (6)
Lipid index[a]	0.13 ± 0.04 (4)	0.24 ± 0.08 (6)

[a] Lipid index = lipid mass/lean dry carcass mass. For two temperate hirundines during the nestling phase, adult lipid indices = 0.35 ± 0.17 (*n* = 20) (Common House-Martin, *Delichon urbica*) and = 0.17 ± 0.04 (*n* = 10) (Sand Martin, *Riparia riparia*) (Bryant unpubl.).

carcasses to constant mass at 60°C. We then extracted lipids (soxhlet: chloroform 20%, ether 80%) and obtained lipid content from the difference between initial and final dry mass.

The theoretical basis of the doubly labelled water ($D_2{}^{18}O$) technique has been discussed by Lifson et al. (1949, 1955), Lifson and McClintock (1966) and Nagy (1980). Carbon dioxide output ($r\mathrm{CO_2}$, mM $\mathrm{CO_2}$/h) is:

$$r\mathrm{CO_2} = \frac{\bar{N}}{2.08}(K_\mathrm{O} - K_\mathrm{D}) - 0.015K_\mathrm{D}\bar{N}, \qquad (2)$$

where K_O, K_D = fractional turnover rates per hour of oxygen-18 and deuterium, respectively. Hence:

$$K_\mathrm{O} = \ln(S^{18}\mathrm{O}_i - S^{18}\mathrm{O}_n) - \ln(S^{18}\mathrm{O}_f - S^{18}\mathrm{O}_n)/\Delta t, \qquad (3)$$

where $S^{18}\mathrm{O}_i$ = initial ppm ^{18}O in blood sample, $S^{18}\mathrm{O}_f$ = final ppm ^{18}O in blood sample, $S^{18}\mathrm{O}_n$ = natural abundance of ^{18}O in blood sample, and Δt = interval between initial and final samples (h). For K_D, read D instead of O in Equation 3. $\bar{N}$ = body water (mM), which we obtain from:

$$\bar{N} = (Wp)/0.018, \qquad (4)$$

where W = body mass (g) and p is proportion of body mass that is water (Table 1).

Natural abundance of ^{18}O in the body water of Pacific Swallows was 2,025.7 ppm and of deuterium, 149.9 ppm. There is no reason why Blue-throated Bee-eaters in the same area should differ significantly from swallows, and so we assumed the same natural abundances applied to them. To convert $\mathrm{CO_2}$ (mM) to *ADMR* (average daily metabolic rate, $\mathrm{cm^3\ CO_2 \cdot g^{-1} \cdot h^{-1}}$) we use the following:

$$ADMR = (r\mathrm{CO_2} \times 22.4)/\bar{W}, \qquad (5)$$

where $\bar{W}$ = mean body mass = $(W_i + W_f)/2$ g, measured at time of first capture (W_i) and on recpature (W_f). Finally, to estimate energy expenditure, we again take $RQ = 0.75$ and, hence, assume 26.44 J/cm^3 $\mathrm{CO_2}$.

To determine isotope concentrations in samples of blood, we adopted the following procedure. For deuterium analyses, blood samples were released under vacuum. Blood water was reduced by passing it through a uranium furnace and then collecting hydrogen/deuterium on activated carbon. We determined concentration of deuterium in the gas sample by using a VG Micromass 602 Mass Spectrometer and ensuring that correction was made for triatomic hydrogen ions ($\mathrm{H_3^+}$) formed at the source. In ^{18}O analyses, blood water was frozen down in a tube containing guanidium chloride and sealed under vacuum. Heating in a muffle furnace yielded $\mathrm{CO_2}$ (Boyer et al. 1961). Residual ammonium products were absorbed using phosphoric acid. The $\mathrm{CO_2}$ sample was then analyzed on a VG Micromass 903 Mass Spectrometer. Validation trials using the same analysis procedure have been carried out previously (Hails and Bryant 1979, Westerterp and Bryant in prep.).

RESULTS

Resting metabolism.—Pacific Swallows had a nighttime metabolism of 45.29 ± 0.001 $\mathrm{J \cdot g^{-1} \cdot h^{-1}}$ (mean ± SD, $n = 6$; Table 2). Because the swallows were postabsorptive and resting in the dark and T_a (32–35°C) was within the presumed thermoneutral zone, we call this the

TABLE 2. Metabolic parameters[a] for Pacific Swallows and Blue-throated Bee-eaters.

	Pacific Swallow[b]	Blue-throated Bee-eater[b]
Basal (M_b, night, $\mathrm{J \cdot g^{-1} \cdot h^{-1}}$)	45.29 ± 0.001 (6)	31.62 ± 4.52 (9)
Basal (M_b, day, $\mathrm{J \cdot g^{-1} \cdot h^{-1}}$)	59.78	41.74
Lower critical temperature (T_{lc}, °C)	30	33
Conductance ($\mathrm{J \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}}$)	4.389	1.513 (22)

[a] Basal metabolism was measured at T_a = 32–35°C for swallows and 32–34°C (see Fig. 1) for bee-eaters. M_b, night, is equivalent to the resting phase (ρ) of Aschoff and Pohl (1970), and M_b, day, to the active phase (α). M_b, day, is calculated from M_b, night, using a 1.32 multiplier (Hails 1983).

[b] Sample sizes in parentheses where appropriate.

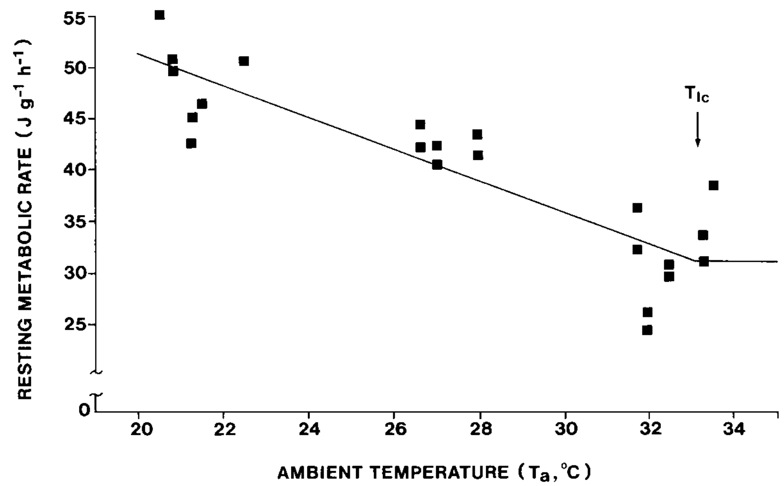

Fig. 1. The relationship between nighttime metabolic rate and ambient temperature, T_a, for adult Blue-throated Bee-eaters (see text for equation of fitted line, equation 9). The lower critical temperature (T_{lc}) is shown.

basal metabolic rate (M_b, ρ phase) (Aschoff and Pohl 1970). We discarded two runs where marked variations in recorded oxygen uptake indicated that birds were active in the chamber. We did not measure metabolism below thermoneutrality in swallows and hence make use of results from other studies to derive lower critical temperature (T_{lc},°C) and conductance (C, $\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}\cdot{}^\circ\text{C}^{-1}$).

Among tropical birds, T_{lc} is usually around 30°C (Scholander et al. 1950; Lasiewski et al. 1967, 1970; Yarbrough 1971; Weathers 1977; Hails unpubl.). Conductance varies consistently with body mass and can be predicted from the equation of Lasiewski et al. (1967). Hence:

$$C = 16.816W^{-0.508} \qquad (6)$$

where W is body mass (g). In some wholly tropical species, conductance is lower than predicted by equation 6 (Weathers 1977; also see equation 9); yet in others, it has been found to be higher (Yarbrough 1971, Hails unpubl.). In the absence of any consistent pattern among tropical birds, we therefore calculate conductance as 4.389 $\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}\cdot{}^\circ\text{C}^{-1}$ for a 14.07-g bird from equation 6 (Table 2). This yields the following equation for resting metabolism of swallows at ambient temperatures below thermoneutrality (hereafter called M_r, $\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$), assuming T_{lc} = 30°C and $M_b(\rho) = 45.29\ \text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$:

$$M_r = 176.96 - 4.389T_a. \qquad (7)$$

The cost of thermoregulation alone (TR, $\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) is then:

$$TR = 131.67 - 4.389T_a. \qquad (8)$$

In Blue-throated Bee-eaters, $M_b = 31.62 \pm 4.52$ $\text{J}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ ($n = 9$) (Table 2). Direct measurements showed that M_r below the observed T_{lc} (= 33°C) is predicted by the following equation:

$$M_r = 81.717 - 1.513T_a \qquad (9)$$

($r = -0.88$, $P < 0.001$, $n = 22$, Fig.1). Hence:

$$TR = 50.097 - 1.513T_a. \qquad (10)$$

Time-activity budgets.—Activity among aerial insectivores in Malaysia begins, on average, 13 min before sunrise and finishes 7 min after sunset (Hails in press). The active day is thus daylength (sunrise-sunset) plus 20 min. During the breeding season (March-June), mean daylength was 12.23 h; the "active" day was therefore 12.56 h and the nighttime roost period 11.44 h.

Pacific Swallow: During the nestling period, adults spent most time in flight, mainly foraging and visiting the nest (Table 3). Next in importance was perching, either on exposed sites or in shade. Less frequent activities such as bathing and drinking took place during flight, whereas sunbathing and preening occurred while perched. Our results (Table 3) were sim-

TABLE 3. Time-activity budgets[a] for Pacific Swallows and Blue-throated Bee-eaters.

	Pacific Swallow		Blue-throated Bee-eater	
	Day (%)	Time (h)	Day (%)	Time (h)
Perch (exposed position)	21.89	2.749	53.05	6.663
Perch (shaded position)	9.81	1.232	19.21	2.413
Perch (nest or burrow)	4.22	0.530	2.03	0.255
Sunbathe	0.38	0.048	0.92	0.116
Preen	5.83	0.732	3.80	0.477
Fly	55.57	6.980	20.94	2.630
Drink	0.88	0.111	<0.01	0
Bathe	1.69	0.212	0.05	0.006
Roost (night)	—	11.440	—	11.440
n^b		1,781		4,381

[a] Percentages are for daytime only (12.56 h). Total time perched is 5.29 h (42%) for swallows and 9.93 (79%) for bee-eaters. Total flying is 7.30 h (58%) for swallows and as given in the table for bee-eaters (note that bee-eaters bathe while perched, swallows during flight). Hails (1983) found the following daytime time-activity budgets in Pacific Swallows: ♂♂ = 59% flying, 41% perching; ♀♀ = 66% flying, 34% perching.

[b] Refers to number of individual records included in time-budget observations. Data for swallows were gathered on 6 days, bee-eaters on 12 days.

ilar to those of Hails (in press), which were based on timings of focal individuals. The proportion of swallows engaged in each activity showed some changes through the day (Fig. 2). None of these changes, however, was correlated with concurrent environmental conditions or weather indices.

Blue-throated Bee-eater: The commonest daytime activity was perching (Table 3), usually in places open to the sky. Flying occupied 21% of the day and mainly involved foraging, but included nest-visiting, perch-shifting, and other activities. Most behaviors showed some small frequency variations throughout the day (Fig. 3). Only one was correlated with concurrent conditions: the percentage of birds in flight was lower when T_{ab} was high ($r = -0.56$, $P < 0.001$).

Daily energy expenditure: TAL technique.—The equation for calculating *DEE* (kJ/day)(modified after Ettinger and King 1980) is:

$$\begin{aligned} DEE = \{&[11.44(M_{b(\rho)} + TR)] \\ &+ [12.56(M_{b(\alpha)} + TR)] \\ &+ [0.5M_{b(\alpha)}(t_{pe} + t_{ps} + t_{pn})] \\ &+ [0.8M_{b(\alpha)}(t_{pp})] \\ &+ [M_{fly}(t_f)]\}W, \end{aligned} \tag{11}$$

where $M_{b(\rho)}$ and $M_{b(\alpha)}$ denote basal metabolism ($J \cdot g^{-1} \cdot h^{-1}$) in the resting and active phases, and M_{fly} is the cost of flying less $M_{b(\alpha)}$ (see below). The symbols t_{pe}, t_{ps}, t_{pn}, t_{pp}, and t_f refer respectively to time (h) spent at rest on exposed perches, at rest on shaded perches, in nests, in preening, and in flying. In bee-eaters t_{pp} includes perch-bathing in rain as well as preening. *TR*, the thermoregulatory component, is calculated from equations 8 and 10 according to time spent at $T_a < T_{lc}$ (see below).

For both species we used our direct measurements of $M_{b(\rho)}$ (Table 2). Hails (1983) has shown for a large sample of Malaysian birds that $M_{b(\alpha)} = M_{b(\rho)} \times 1.32$. We used this 1.32 multiplier to calculate $M_{b(\alpha)}$ (Table 2). We took the cost of daytime rest as $M_{b(\alpha)} \times 1.5$ and that of preening (and bathing in bee-eaters) as $M_{b(\alpha)} \times 1.8$ (see King 1974, Mugaas and King 1981). The form of equation 11 requires the increment above basal to be partitioned; hence, day resting cost less $M_{b(\alpha)}$ becomes 0.5 $M_{b(\alpha)}$, and the cost of preening becomes 0.8 $M_{b(\alpha)}$.

We assumed that energy expenditure for Pacific Swallows during flight was the same as for the Sand Martin (or Bank Swallow, *Riparia riparia*), which has a similar body mass (13.7 g). Measurements with the doubly labelled water technique showed the energy expenditure of Sand Martins during flight to be 418.51 $J \cdot g^{-1} \cdot h^{-1}$ (Westerterp and Bryant in prep.). Flight costs for bee-eaters have not been studied in detail, nor are data available for other species that often forage by sally-flycatching. We therefore predicted flight metabolism from the equation of Hails (1979) (Table 4). The total cost of flying, less $M_{b(\alpha)}$, gives $M_{fly} = 358.73$ for swallows and 476.93 $J \cdot g^{-1} \cdot h^{-1}$ for bee-eaters. Following Tucker (1968) and Berger and Hart (1974), we assume that flight costs are independent of T_a. All other activities incur a thermoregulatory cost below T_{lc}. For estimating *TR* (equations 8, 10), we used mean T_a for our two continuously monitored sites during nighttime and mean T_a obtained during daytime at the

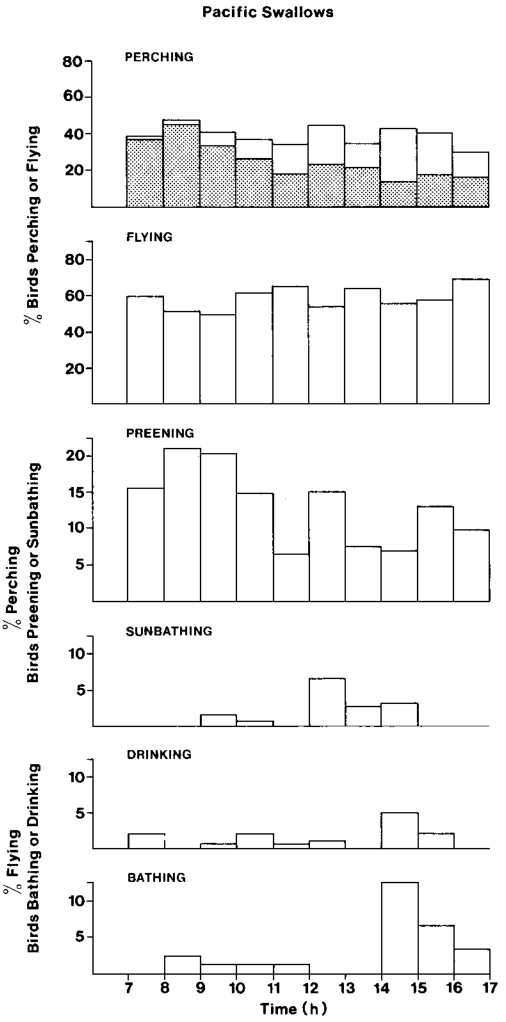

Fig. 2. Diurnal activity pattern of Pacific Swallows. Note different scale for lower four figures. In top figure upper bars denote overall percentage and lower bars percentage on exposed perches (stippled).

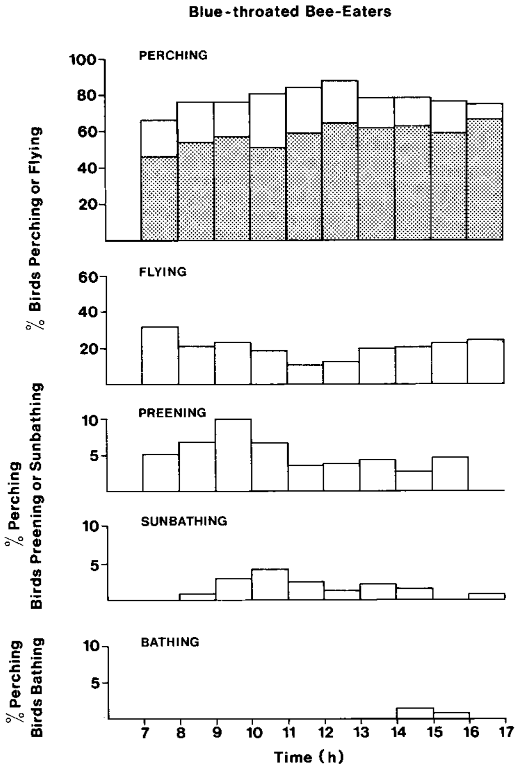

Fig. 3. Diurnal activity pattern of Blue-throated Bee-eaters. Note different scale for lower three figures. In top figure upper bars denote overall percentage and lower bars percentage on exposed perches (shaded).

time of our $D_2{}^{18}O$ experiments (Table 4). At night, Pacific Swallows roosted under bridges or in their nesting cave (26.2°C), sheltered from wind and rain. They experienced both exposed and shaded conditions during the day (33.5°C and 29.8°C, respectively). Mean T_a in the nesting cave during the day was 26.6°C. By making nighttime inspections of bee-eater burrows, we found most nests held two (unsexed) adults. We therefore assumed that pairs normally spent the night in their burrows. Hence, night T_a and daytime nest visits were at the mean burrow temperature of 29.6°C. Daytime T_a for bee-eaters was the same as for swallows (Table 4). Calculated *DEE* was 60 kJ/day for Pacific Swallows and 86 kJ/day for Blue-throated Bee-eaters (Table 4). We examined the sensitivity of *DEE* estimates to errors in component energy costs by changing each in turn by +10%. For both species, *DEE* was most sensitive to changes in flight costs (+5 to 6% *DEE*). For all other costs, changes increased *DEE* by $\leq$ 2%.

Daily energy expenditure: $D_2{}^{18}O$ technique.—For swallows and bee-eaters we obtained results for six individuals (Table 5). The sample of swallows comprised 4 males and 2 females. In view of overlap between sexes, we lumped our data to give *DEE* = 76.6 kJ/day for a 14.07-g Pacific Swallow (Table 5). The sample was too small for analysis of intraspecific trends in relation to concurrently measured weather and activity variables.

We sexed six Blue-throated Bee-eaters by dissection but found no other morphological sex-

TABLE 4. Data for calculation of daily energy expenditure (*DEE*) of Pacific Swallows and Blue-throated Bee-eaters using TAL methods.

	Pacific Swallow			Blue-throated Bee-eater		
Activity	Symbol	T_a (°C ± SD)	Energy cost[a] ($J \cdot g^{-1} \cdot h^{-1}$)	Symbol	T_a (°C ± SD)	Energy cost[a] ($J \cdot g^{-1} \cdot h^{-1}$)
Perch (exposed)	t_{pe}	33.5 ± 3.9	89.67	t_{pe}	33.5 ± 3.9	62.61
Perch (shaded)	t_{ps}	29.8 ± 2.2	89.67	t_{ps}	29.8 ± 2.2	62.61
Perch (nest)	t_{pn}	26.6 ± 1.2	89.67	t_{pn}	29.6 ± 0.5	62.61
Sunbathe	t_{pe}	33.5 ± 3.9	89.67	t_{pe}	33.5 ± 3.9	62.61
Preen[b]	t_{pp}	31.7	107.60	t_{pp}	31.7	75.13
Fly[c]	t_f	33.5 ± 3.9	418.51	t_f	33.5 ± 3.9	518.73
Drink[d]	t_f	33.5 ± 3.9	418.51	—	—	—
Bathe[d]	t_f	33.5 ± 3.9	418.51	t_{pp}	29.8 ± 2.2	75.13
Roost (night)	t_r	26.2 ± 0.9	45.29	t_r	29.6 ± 0.5	31.62
Calculated *DEE* (kJ day)			59.9			86.1

[a] Energy costs exclude the thermoregulatory component (*TR*). This was calculated using equations 8 and 10, according to T_a (see above) and time (h) (see Table 3). *TR* is included in the estimate of *DEE* (see equation 11). For swallows *TR* (night) = 16.7 $J \cdot g^{-1} \cdot h^{-1}$ and *TR* (day) = 0.7 $J \cdot g^{-1} \cdot h^{-1}$. For bee-eaters *TR* (night) = 5.3 $J \cdot g^{-1} \cdot h^{-1}$ and *TR* (day) = 1.2 $J \cdot g^{-1} \cdot h^{-1}$. Overall, *TR* comprises 4.7% *DEE* in swallows and 2.9% *DEE* in bee-eaters.

[b] Preening is assumed to be split, half in exposed sites and half in shade (therefore T_a = 31.7°C).

[c] Flight costs for bee-eaters were calculated from Hails (1979), where flight metabolism ($kJ \cdot g^{-1} \cdot h^{-1}$) = $1.785\ W^{-0.351}$.

[d] Pacific Swallows drink and splash-bathe during flight. Bee-eaters bathe during rainstorms while perched.

ing criterion. We therefore calculated *DEE* for an average 33.81-g bee-eater, which was 77.4 kJ/day (Table 5).

DISCUSSION

Comparison of methods for estimating DEE.—The match between *DEE* measured directly using $D_2{}^{18}O$ and predicted using TAL budgets differed between our two study species. In Blue-throated Bee-eaters agreement was closest, with the TAL estimate 11% greater than that of the $D_2{}^{18}O$ technique. In Pacific Swallows the TAL prediction was 22% lower than the mean $D_2{}^{18}O$ estimate. A comparable discrepancy (40%) was found by Weathers and Nagy (1980) for the Phainopepla (*Phainopepla nitens*). There, too, the time-budget estimate was lower than that obtained using doubly labelled water. Our $D_2{}^{18}O$ estimates, however [with coefficients of variation (CV) of 35% for swallows and 15% for bee-eaters], differed from the TAL estimate by less than ±1 SD. The discrepancy between methods might therefore be explained by a combination of small $D_2{}^{18}O$ sample sizes and and inherent variability of daily energy expenditure. A high level of variation in *DEE* has also been shown in the temperate Common House-Martin (*Delichon urbica*; CV = 17% when rearing nestlings, Bryant and Westerterp 1980, 1983).

It is useful to consider other factors that could cause divergence between TAL and $D_2{}^{18}O$ estimates of *DEE*. First, TAL estimates of *DEE* are usually most sensitive to the costs of flight (Results, Utter and Lefebvre 1970, Mugaas and King 1981). Pacific Swallows took larger insects than Sand Martins (Waugh 1978, Waugh and Hails 1983, pers. obs.), and, following the example of the Common House-Martin (Bryant and Westerterp 1983), we would expect this to raise energy costs of foraging. Our estimate of flight costs, based on Sand Martin data, may therefore underestimate the true cost for Pacific Swallows. By substituting the $D_2{}^{18}O$ estimate for *DEE* (Table 5) in equation 11, we can derive a new and higher estimate for flight metabolism in Pacific Swallows (581 $J \cdot g^{-1} \cdot h^{-1}$). A similar calculation for the bee-eaters yields an estimate of flight metabolism (421 $J \cdot g^{-1} \cdot h^{-1}$) that is lower than the original. In this case, our initial estimate (519 $J \cdot g^{-1} \cdot h^{-1}$) was probably too high because aerially feeding birds have relatively low flight costs compared to other species with a similar body mass (Hails 1979). Also, our bee-eaters often used cheap (Baudinette and Schmidt-Nielsen 1974) gliding flight while foraging (=59% of flying time, compared to 25% in Pacific Swallows).

Second, behavior of individuals measured with the $D_2{}^{18}O$ technique may have differed from those included in our time-activity budgets. Unfortunately, we rarely recognized our experimental birds away from their nests (2% total observations) and, therefore, cannot compare activity in the two groups. Data on feeding rates at the nest were extensive but unsuit-

TABLE 5. Daily energy expenditure (*DEE*) of Pacific Swallows and Blue-throated Bee-eaters based on $D_2^{18}O$ technique.

Bird	Sex	Body mass (g)	Brood size[a]	*ADMR* (cm^3 $CO_2 \cdot g^{-1} \cdot h^{-1}$)	*DEE* (kJ/day)
		Pacific Swallows			
1	♂	14.85	3	4.64	43.7
2	♀	13.05	5	12.05	99.8
3	♂	14.30	3	5.80	52.6
4	♂	14.30	5	8.99	81.6
5	♂	13.90	1	12.75	112.4
6	♀	14.00	1	7.81	69.4
Mean				8.67	76.6
SD				3.27	26.7
		Blue-throated Bee-eaters			
1		32.75	1	4.02	83.5
2		34.55	2	3.44	75.4
3		30.45	1	3.07	59.3
4		33.50	1	3.33	70.8
5		33.60	1	4.34	92.5
6		38.65	1	3.38	82.9
Mean				3.60	77.4
SD				0.48	11.6

[a] Broods of swallows 2 and 4 were enlarged from an original brood size of 4. Feeding rates, however, remained at the level typical for a brood of 4. All other broods of swallows and bee-eaters were of their original size.

able as a guide to general activity levels, because they showed no correlation with *DEE*. This was not surprising, as earlier work with Common House-Martins and Barn Swallows (*Hirundo rustica*) also showed that feeding rate was a poor predictor of *DEE* (Bryant and Westerterp 1980, 1983; Westerterp and Bryant in prep.). Those observations we were able to make, both at the nest and nearby, did suggest, however, that the behavior of experimental birds was similar to that of nonexperimental individuals at the same sites.

Only the first of these factors may alone account for the discrepancy between TAL and $D_2^{18}O$ estimates of *DEE*. Taken together, they would obviously permit close agreement between TAL and $D_2^{18}O$ estimates for both species. As the error in TAL methods can be large (Travis 1982), we therefore attach no special importance to the failure of our estimates to match exactly the mean *DEE* obtained by $D_2^{18}O$. Instead, we take the opportunity to revise the estimates of flight metabolism, the most likely source of discrepancy, allowing us to model with greater accuracy the consequence of changes in other costs (see below). In view of these points we refer in further discussion to our direct ($D_2^{18}O$) measure of mean *DEE*.

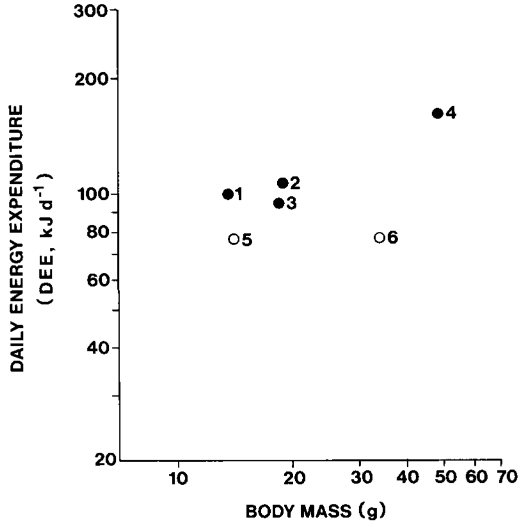

Fig. 4. The relationship between mean *DEE* during the nestling phase and body mass for four temperate (●) and two tropical (○) insectivores, measured using the doubly labelled water ($D_2^{18}O$) technique. (1) Sand Martin (*Riparia riparia*), $n = 10$; (2) Barn Swallow (*Hirundo rustica*), $n = 14$; (3) Common House-Martin (*Delichon urbica*), $n = 50$; (4) Purple Martin (*Progne subis*), $n = 4$; (5) Pacific Swallow (*Hirundo tahitica*), $n = 6$; and (6) Blue-throated Bee-eater (*Merops viridis*), $n = 6$. Data for 1, 2, and 3 from Bryant and Westerterp (1980, 1983) and Westerterp and Bryant (in prep.). Data for 4 from Utter and Lefebvre (1970). The equation for temperate hirundines ($n = 4$) is $DEE = 29.717\ W^{0.433}$ ($P < 0.05$).

Tropical-temperate comparisons of DEE.—*DEE* of Pacific Swallows and Blue-throated Bee-eaters was lower than that of four temperate hirundines also studied using $D_2^{18}O$ (Mann-Whitney, $P < 0.01$, Fig. 4). *DEE* of swallows was 82% and of bee-eaters 56% of that predicted (equation 12, Fig. 4) for a temperate hirundine of similar body mass. The greater difference for bee-eaters arose partly from their foraging habits; sally-flights were shared with more sustained flight-foraging, which meant bee-eaters spent less time than hirundines in the most energy-expensive activity, flight. Taking the evidence of our $D_2^{18}O$ measurements, as well as our TAL estimates of *DEE*, we suggest that aerial insectivores in the tropics have a lower mean *DEE* than do their temperate counterparts.

There are several proximate factors that would cause the *DEE* of tropical birds to differ

TABLE 6. Effect of a simulated temperate basal metabolism and temperate environment on *DEE* of two tropical birds.

	Pacific Swallow		Blue-throated Bee-eater	
Factor	*DEE* (kJ/day)	Δ%[a]	*DEE* (kJ/day)	Δ%
Basal metabolism (M_b)[b]	82.6	+8	77.4	0[c]
Ambient temperature (T_a)[d]	91.5	+19	96.0	+24
Daylength[e]	95.9	+25	93.8	+21
All	113.9	+49	110.9	+43

[a] Δ% = [*DEE* (simulated) − *DEE*(D_2O)/*DEE*(D_2O)]100, equation 13. See Table 5 for *DEE*(D_2O).

[b] Basal metabolism $M_{b(p)}$ derived from Aschoff and Pohl (1970).

[c] No percentage change (Δ%) because observed $M_{b(p)}$ was the same as predicted from Aschoff and Pohl (1970; nonpasserine equation).

[d] Ambient temperature = 17°C day, 11°C night. Thermoregulatory costs are only incurred for nonflying activities.

[e] Daylength = 16.91 h.

from that of their temperate counterparts. Some of these factors might cause *DEE* to be relatively high (i.e. work done to dissipate heat stress), but most would lead to a low *DEE*. These include low basal metabolic rates (Weathers 1979, Hails 1983), higher ambient temperatures, more solar heating, less wind (see Landsberg 1972), and shorter daylengths and, hence, "active" periods. If tropical birds carry less fat than similar temperate species (Table 1), then flight costs would be slightly cheaper in birds of similar dimensions (Pennycuick 1968, 1969). We can evaluate the contribution of three of these factors (M_b, T_a, and "active" daylength) using our TAL models of *DEE*. To do this we compared the observed *DEE* in the two species with the *DEE* that would occur under simulated temperate conditions (comparisons are made with a study area in central Scotland, UK; Bryant and Westerterp 1980, 1983).

Aschoff and Pohl's (1970) passerine equation for basal metabolism is based on temperate species and the nonpasserine equation on temperate species plus the domestic fowl. In Blue-throated Bee-eaters (and temperate hirundines, Hails 1977, Bryant and Westerterp 1980, Westerterp and Bryant in prep.), $M_{b(p)}$ was exactly as predicted by Aschoff and Pohl's equations. In contrast, Pacific Swallows were only 70.3% of the predicted value. This was not a consequence of a high (nonmetabolizing) fat content, because lipid indices were similar to those of temperate hirundines (Table 1). Comparing $M_{b(p)}$ for Pacific Swallows with the prediction from Hails (1983) equation for tropical passerines shows a close match (104%).

The significance of a lower M_b for *DEE* was assessed by calculating TAL budgets, which used $M_{b(p)}$ derived from Aschoff and Pohl (1970). The revised estimates of flight costs (see above) are incorporated in these calculations. A temperate value for M_b caused *DEE* for Pacific Swallows to increase by 8% (Table 6). Next, by taking daytime $T_a = 17°C$ and night $T_a = 11°C$ and assuming no microclimate variation, we found that *DEE* rose by 19% for swallows or 24% for bee-eaters. Finally, when daylength was increased to 16.91 h (mean May–August) and proportional increases were allowed for all daytime activities, *DEE* increased by 25% for swallows and 21% for bee-eaters. Under these conditions the proportion of a 24-h day spent flying was 41% for swallows and 15% for bee-eaters, compared to over 50% for Common House-Martins (Bryant and Westerterp 1980), Barn Swallows, and Sand Martins (Turner 1980) rearing young in a temperate environment. The TAL models of *DEE* suggest that differences between our tropical and temperate aerial insectivores were largely a consequence of differences in thermal conditions and the total time spent on more costly activities such as flight. Differences in M_b were of more limited significance.

Changing weather conditions can affect metabolic rates independently of T_a: solar radiation and wind are usually considered to be the most important (Porter and Gates 1969, Calder and King 1974, Mount 1979, Mugaas and King 1981). The effect of exposure to solar radiation, intense for an average of 6.2 h/day (Hails unpubl.), would be to increase absorbed radiation at the body surface (Marder 1973, Mugaas and King 1981). Presumably, shade seeking, leg-exposure during flight, and other thermoregulatory behaviors (Bryant 1983) generally had the effect of holding equivalent blackbody temperature, T_e (Robinson et al. 1976, Mugaas and King

1981), below the upper critical temperature. Otherwise, shade seeking at midday would have been more marked and the proportion of birds on exposed perches lower (Bryant 1983). Also, such winds as occurred were apparently exploited beneficially for cooling (Bryant 1983). Because the sensitivity of *DEE* estimates to variation in costs of nonflight activity (including thermoregulation) is small (Results), it is unlikely that our failure to examine all avenues of heat exchange has much significance for our conclusions.

Ricklefs (1971) suggested that the reduced flight activity of Mangrove Swallows (*Iridoprocne albilinea*) in Central America during the middle of the day was a response to radiational heat stress. Our analysis of time-activity budgets showed a small reduction in flight frequency for bee-eaters under strong sun. A greater effectiveness of heat dissipation (Bryant 1983) apparently allowed swallows to continue foraging through the hottest part of the day. Even so, we cannot reject the possibility that both species would have foraged yet more frequently in the absence of intense solar heating. Heat stress, then, may be an additional constraint on activity, leading to a lower *DEE* in some tropical species of open habitats.

To conclude, we found *DEE* was lower in two tropical insectivores than in four temperate species with broadly similar habits. In the Pacific Swallow the difference could be explained as the result of higher T_a and shorter days in the tropics. For the Blue-throated Bee-eater, partial use of a less costly foraging technique (sally-flycatching) also contributed to their lower *DEE*. Therefore, the difference in *DEE* between tropical and temperate insectivores can be accounted for by the action of proximate factors alone.

Significance of DEE for reproductive effort.—Interspecific comparisons of energy expenditure can also be made using the ratio, DEE/M_{ab} (where M_{ab} = basal metabolism, ρ phase, over 24 h) (Utter 1971, Drent and Daan 1980, Mugaas and King 1981). Hirundines in temperate environments have a mean ratio of 3.6–4.3 M_{ab} during breeding (Westerterp and Bryant in prep.). The same ratio for Purple Martins (*Progne subis*) in North America is 3.0 M_{ab} (Utter and Lefebvre 1970). Making a similar comparison for our tropical species gave 5.1 ± 1.9 M_{ab} for swallows and 3.0 ± 0.4 M_{ab} for bee-eaters. If used as one measure of reproductive effort, therefore, the DEE/M_{ab} ratio does not indicate a consistent difference between our tropical and temperate insectivores.

The theoretical minimum *DEE* equals the sum of energy expenditure on maintenance, thermoregulation, and any foraging activity that just permits energy balance. Upward variation of *DEE* is a consequence of facultative behaviors that presumably increase fitness but at the same time change daily energy costs. It is easy to see how fitness might be enhanced by more foraging if net energy gain also increased (i.e. it leads to greater breeding success), even if this entailed a higher *DEE*. Under these conditions, comparative values for *DEE* might be used as one measure of reproductive effort, ideally in conjunction with data on the other costs of breeding. It is feasible, however, that fitness might increase as a result of time investments in maintenance or vigilance activities, which, being energetically cheaper than foraging, would reduce *DEE*. For example, perching near the nest to discourage intruders or watch for predators could increase the chance of successful nesting. The consequence of investing an extra hour in activities of this type, at the expense of foraging flights, is to reduce *DEE* by 9% for Pacific Swallows and 15% for Blue-throated Bee-eaters (calculations based on data in Table 4 but using revised flight costs). Interspecific variation in *DEE* (and hence DEE/M_b) is therefore unlikely to reflect in any consistent way differences in reproductive effort. In circumstances of this kind, more complex indices of reproductive effort, such as those that include energy inputs and outputs for foraging (Hirshfield and Tinkle 1975, Calow 1979) could also be misleading. In view of these points, the reduced *DEE* of our tropical insectivores compared to that of similar temperate species cannot be assumed to imply a lower investment in breeding. Instead, we view it as a consequence of selection pressures acting mainly on time-activity budgets to increase fitness (Mugaas and King 1981) and proximate factors governing metabolic function.

ACKNOWLEDGMENTS

We are grateful to Dr. Siew for the facilities of the Zoology Department, University of Malaya. The Royal Society, through its Commonwealth Bursary Scheme and the University of Stirling, gave financial support to D.M.B. The support of the University of Malaya research grant F9/78 to C.J.H. is gratefully acknowledged. The Malaysia Meteorological Service supplied weather data, and the office of the Prime Minister's Department and the Rubber Research Institute kindly gave permission for research and site access, respectively. We analyzed our stable isotope samples at the Scottish Universities Research and Reactor Centre (SURRC) at East Kilbride with support from NERC grant GR3/4185. We are most grateful for the advice of the staff of the Stable Isotope Unit, A. Fallick, J. Borthwick, and T. Donnelly. H. Biebach, J. Mugaas, R. Prys-Jones, and K. Westerterp made valuable comments on the manuscript.

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The **Herbert and Betty Carnes Research Award** will provide one or two grants of $500-2,000 in 1984. Awards are given on the basis of scientific merit, importance, and originality. Particularly favored are studies that aim to *expand* the design of field or laboratory work or to explore *new* methods of data analysis. Women are particularly encouraged to apply. Proposals must be submitted by 1 March 1984. Guidelines may be secured by writing: **Dr. J. W. McIntyre, Utica College of Syracuse University, Utica, New York 13502.**