

# DAILY ALLOCATION OF TIME AND ENERGY OF WESTERN BLUEBIRDS FEEDING NESTLINGS<sup>1</sup>

PATRICK J. MOCK<sup>2</sup>

*Department of Biology and Laboratory of Biomedical and Environmental Sciences,  
University of California, Los Angeles, CA 90024*

**Abstract.** The daily allocation of time and energy of adult Western Bluebirds (*Sialia mexicana*) feeding 9–12 day-old nestlings was measured using time-activity budget and doubly-labeled water methods. Components of the bluebird energy budget were estimated by extrapolating laboratory measurements of metabolic heat production to field conditions using a linear heat-transfer model and the operative temperature and wind speed experienced by the free-living bird. This model was validated with the doubly-labeled water method. Adult Western Bluebirds feeding nestlings are neither food-limited nor working maximally. Adults fulfilled their own energy requirements, and those of four to six nestlings, while actively pursuing prey for less than 10% of their active day. The daily energy requirement of a 27.5 g adult bluebird averaged 95 kJ/day ( $n = 52$ ), which is 2.6 times its nighttime basal metabolic rate. Thermostatic requirements were the most variable components of the energy budget ( $CV = 41.6\%$ ). Differential use of microhabitats by individuals accounted for some of this variability. Activity costs were less variable ( $CV = 17.6\%$ ) and accounted for less than 20% of the total energy budget. Differences in brood size resulted in a minor difference in activity costs (3kJ/day) between broods of four and six. Variation in thermostatic costs overshadowed this small brood-size effect, resulting in no significant brood-size effect on total daily energy expenditure. This study suggests that bluebirds, like several other temperate passerine species, are able to regulate their overall daily energy expenditures within definable limits through differential use of thermal environments and activity budgets. I conclude that potential food limitations on reproductive output are more likely to occur at other stages of the breeding cycle due to greater variability in weather and food conditions compared to the nestling stage.

**Key words:** *Energy budget; nestling care; Sialia mexicana; time budget; Western Bluebirds.*

## INTRODUCTION

Excess resources gained during foraging by breeding birds may be allocated to either self-maintenance or to offspring. When feeding nestlings, the demands on a parent's time and energy are high (Drent and Daan 1980). Energy shortage has been proposed by some ecologists to be a critical constraint to breeding success, while others argue that predation is the preeminent factor influencing breeding effort (for reviews, see Murphy and Haukioja 1986, Lima 1987, Martin 1987). Optimal reproductive effort should reflect a trade-off between offspring number and offspring survival due to food limitation (Lack 1968). However, it is possible that parental behavior may reflect a cost-benefit trade-off be-

tween parental survival and offspring survival (Lima 1987).

Energetics is one aspect of a life history that can be used to assess constraints on reproduction. Both time and energy have upper limits of allocation that affect reproduction. Quantification of these constraints among the allocation of time and energy to particular activities should lead to an appreciation of the evolution of a species' life-history traits. I studied the allocation of time and energy of a cavity-nesting passerine, the Western Bluebird (*Sialia mexicana*), during the nestling stage of the breeding season. I show that adult Western Bluebirds feeding young do not appear to be constrained by food availability. Bluebirds, like several other temperate-zone passerine species, regulate their overall daily energy expenditure within definable limits through adaptive modification of their activity budgets and differential use of thermal environments. I conclude that potential food limitations on reproductive output are more likely to occur at other stages of the breeding cycle due to greater

<sup>1</sup> Received 20 November 1990. Final acceptance 27 March 1991.

<sup>2</sup> Present address: ERC Environmental and Energy Services Company, 5510 Morehouse Drive, San Diego, CA 92121.

variability in weather and food conditions compared to the nestling stage.

## METHODS

From 1984 to 1986, I studied the allocation of time and energy by adult Western Bluebirds feeding 9–12 day-old young in May, June, and early July. This is the nestling age when energy requirements of the brood are maximized (Mock et al. 1991). To accomplish this, I: (1) banded a population of breeding bluebird pairs; (2) determined the amount of time allocated to various behavioral categories and microenvironments at the 9–12 day-old nestling stage; (3) measured rates of oxygen consumption in field-captured individuals; (4) assessed the birds' thermal environment under field conditions in terms of the operative temperature ( $T_o$ ), air temperature ( $T_a$ ), and wind speed ( $u$ ) experienced by the bird under observation; and (5) used the doubly-labeled water (DLW) method to measure total daily energy expenditure (DEE) of free-living bluebirds and to validate the time-energy budget (TEB) model of DEE for free-living birds not measured with DLW.

## STUDY AREA

I carried out this study at Garner Valley in the San Jacinto Mountains, Riverside County, California (33° 47'N, 116° 58'W; 1,375 m altitude). The vegetation at the study area consisted primarily of stands of Jeffrey Pine (*Pinus jeffreyi*) interspersed with wet and dry meadows dominated by native and non-native grasses and sagebrush. The bluebirds nested in boxes placed at 1.5 m above the ground on the north side of pine trees.

## TIME ALLOCATION AND HABITAT USE

I measured daily time allocation and habitat use by 31 individual bluebirds, including 15 mated pairs. These time budgets were based on 16–22 min observation periods (mean  $19.5 \pm 1.03$  min) gathered over the entire active day (05:30–20:00 local time). Throughout this paper, values are cited as mean  $\pm$  SEM. Each bird was observed for at least eight observation periods (mean  $12.4 \pm 1.65$  periods per bird). The total time of observation for each bird averaged  $241.7 \pm 35.8$  min. The activity budgets of both members of mated pairs were gathered on the same day. I collected these data from a sufficient distance so

that the bird under observation was as likely to move toward as away from the observer. This distance was usually about 30 m. I partitioned elapsed time into five activities: alert perching, preening, flying, nest attendance, and ground activity.

The Western Bluebird is primarily a "sit and wait" insectivore, with only a minor amount of time allocated to flycatching. Typically a bluebird would perch over an open area and visually search the ground for prey. Upon detecting an insect, the bird would quickly fly to the ground, capture the prey and return to a perch to consume the food. Bluebirds do not walk on the ground, but tend to hop when moving short distances ( $<5$  m) on the ground in pursuit of prey. Usually the time spent on the ground was brief ( $<5$  sec). The primary mode of locomotion for bluebirds is flight.

To monitor microhabitat use, I recorded time spent perched in the sunlight versus shade. All activity data are expressed as percent of total observation time for each individual. An arcsine-square root transformation of the percentages was performed to equalize the variance among groups prior to statistical analysis.

## BASAL AND STANDARD METABOLISM

I determined basal and thermoregulatory energy requirements by measuring the fasting oxygen consumption ( $\dot{V}O_2$ ) of nine adult bluebirds (four males and five females) resting in the dark at a stable ambient temperature between 4 and 31°C. The rate of oxygen consumption was measured by means of a closed-circuit manometric system. The closed-circuit manometric method has been validated in two previous studies (Williams and Prints 1986, Obst et al. 1987).

Bluebirds were captured the same day the metabolism measurements were conducted. Birds were released the next morning at the site of capture. Measurements were made at night, between 21:00 and 04:00 local time. Individual bluebirds that had not been fed since 18:00 were placed in a dark, air-tight, 3.8-liter container. The inner walls of the metal chamber were painted flat black to minimize reflective radiation. Ascarite and silica gel were placed in the chamber to absorb  $CO_2$  and  $H_2O$ , respectively. The chamber was immersed in a temperature-controlled water bath. Chamber temperature was monitored with a 40-gauge thermocouple placed 3 cm above the bird. Chamber temperature was con-

trolled to within 0.1°C during each measurement period.

Each bird was placed in the chamber and air was pumped through the chamber at the same temperature as the water bath for at least 2 hr prior to initial data collection. This procedure allowed the system to reach a temperature equilibrium and allowed the bird to become accustomed to the chamber. Following this equilibration period, the air line was disconnected, a manometer was attached to one port, and a syringe containing oxygen was attached to the other port. Depending on the chamber temperature, either 5 or 10 cm<sup>3</sup> of oxygen at room temperature and pressure were injected, resulting in an increase in chamber pressure and a displacement of the manometer. The system was left closed, and the time required for the bird to consume the injected oxygen was measured to the nearest second. This procedure was repeated five or more times at each test temperature. The mean of the three lowest  $\dot{V}O_2$  values measured was taken to be the individual's standard metabolism ( $H_{sm}$ ) for a given temperature. Temperature of the injection syringe and ambient pressure were recorded, and the injection volume was corrected to standard temperature (0°C) and pressure (760 torr). All values of  $\dot{V}O_2$  were corrected to STPD.

Successive  $\dot{V}O_2$  measurements were made at two or three temperatures using the same individual without removing the bird from the chamber between runs. Air was pumped through the chamber while the chamber temperature was changed. The system was allowed to equilibrate at the new temperature for 1 hr before data were taken. No single individual was exposed to the full range of temperatures (4 to 31°C) examined. Body temperature ( $T_b$ ) was measured immediately after removal of the bird from the chamber, using a 40-gauge thermocouple inserted about 2 cm into the cloaca. I calculated rates of metabolic heat production by assuming that 20.08 kJ of heat were produced per liter of oxygen consumed for a mixed insect diet (Schmidt-Nielsen 1979).

#### FIELD METABOLIC RATE

I estimated the daily energy expenditure (DEE) under field conditions by two independent methods. I used the doubly-labeled water (DLW) technique to determine the integrated DEE for 52 bluebirds (26 males, 26 females). I also calculated DEE of 31 individuals using the convection-adjusted, electrical analog time-energy bud-

get (TEB) model described by Weathers et al. (1984) and Buttemer et al. (1986). These previous studies validated the TEB model with the DLW method using birds enclosed in a large aviary. The present study assessed the accuracy of the TEB model by simultaneously estimating the DEE of seven free-living bluebirds with the DLW method.

#### TIME-ENERGY BUDGET MODEL

Calculating DEE of birds under field conditions requires knowledge of the  $T_e$  and  $u$  experienced by the bird, and how  $H_{sm}$  varies in relation to these meteorological parameters (see Appendix A for abbreviations). Concurrent with the gathering of behavioral observations,  $T_e$  and  $u$  were measured in two microenvironments in the study area. Unheated taxidermic mounts for measuring  $T_e$  (see Bakken 1976, Bakken et al. 1981 for theory and methods) and hot-ball anemometers (Buttemer 1981, Roer and Kjolsvik 1973) were placed at a height of 2 m in a shaded, wind-sheltered roost tree and on a fence post that was fully exposed to the sun and wind at a height of 1.5 m. The output of the sensors was monitored at 10-min intervals with a datalogger and averaged every hour. The hot-ball anemometers were calibrated in a wind tunnel with a vane anemometer.

I calculated DEE from individual activity budgets, meteorological, and laboratory metabolism data by the following equation:

$$\begin{aligned} \text{DEE} = & [t_r \cdot H_r + H_{tr}] \\ & + [t_{AP} \cdot H_{AP} + H_{ta}] \\ & + [t_F \cdot H_F + t_{NF} \cdot H_{NF}] \end{aligned} \quad (1)$$

where the  $t$ 's are activity durations (in hr),  $H$ 's are the energy requirements for a given activity (in kJ/hr; Table 1), and the subscripts designate the type of activity. The first bracketed term is the nocturnal (rho phase) energy expenditure of a sleeping bird at a roost site (basal metabolism, plus thermostatic costs). The second bracketed term represents the daytime (alpha phase) energy expenditure of an alert perched bird (3.04 kJ/hr, plus thermostatic costs). The length of the alpha phase was defined as the time between sunrise and sunset, typically 14.3 hr. The third bracketed term represents the sum of daytime costs for flying and non-flying activity other than alert perching.

The costs of various activities were assumed to be multiples of basal metabolism ( $H_b$ ) and

TABLE 1. Value of activity costs used in time-energy budget model for the Western Bluebird.

Activity	kJ/hr	Multiple of basal metabolism
Basal metabolism <sup>a</sup>	1.52	1.0
Alert perch <sup>b</sup>	3.04	2.0
Flight <sup>c</sup>	9.12	6.0
Non-flight activity <sup>b</sup>	3.50	2.3

<sup>a</sup> Mean value of thermoneutral measurements. SD = 5.23 kJ/day,  $n = 19$ ; Mean body mass: 27.5 g.

<sup>b</sup> Weathers et al. (1984), Buttemer et al. (1986).

<sup>c</sup> Flight cost calculated from Castro and Myers (1988), using body mass of 27.5 g and a wing span of 31.4 cm.

were assigned as follows (see Table 1). The cost of alert perching ( $H_{AP}$ ) was assumed to be two times  $H_b$  (3.04 kJ/hr), the approximate multiple empirically determined in two bird species (Weathers et al. 1984, Buttemer et al. 1986). The cost of all low level activity ( $H_{NF}$ , i.e., preening, activity on the ground, and nest attendance behaviors) was assumed to be 2.3 times  $H_b$  (3.5 kJ/hr; Weathers et al. 1984, Buttemer et al. 1986). Flight ( $H_F$ ) was assumed to cost 6 times  $H_b$  (9.12 kJ/hr), based on a multiple regression model which estimates flight costs as a function of body mass and wing length (Model b of Castro and Myers 1988). I calculated thermostatic costs ( $H_r$  and  $H_m$ ) by relating the laboratory measurements of  $H_m$  directly to the mean hourly  $T_e$  and  $u$ . I used the linear heat-transfer model of Robinson et al. (1976), as modified by Weathers et al. (1984). This model expresses steady-state heat exchange between an animal and its environment by the relation:

$$H_m - H_e = [\rho c_p (T_b - T_e)] / (r_b + r_e). \quad (2)$$

Evaporative heat loss ( $H_e$ ) and skin temperature were calculated from body mass or  $T_e$  (Equation 56, Calder and King 1974, Hill et al. 1980).

Maintenance metabolism was measured during the rho (inactive) phase and assumed to be 1.25 times greater in the thermoneutral zone during the alpha (active) phase (Aschoff and Pohl 1970). Estimates of  $H_m$  were converted to  $W m^{-2}$  for the heat transfer calculations (Walsberg and King 1978). Body temperature was assumed to vary between active and rest phases and was assigned the values of 41°C and 38°C, respectively (Equation 8-4, Calder 1984). The lower critical temperature ( $T_{lc}$ ) was estimated to be 21°C during the rho phase and assumed to be 5°C higher during the alpha phase (Weathers and van Riper 1982).

Using these estimates of  $T_b$ ,  $T_{lc}$ , and  $H_m$  in the thermoneutral zone for both rho and alpha phases, I calculated the relationship between  $H_m$  and  $T_e$  for  $T_e$ s below the lower critical temperature ( $T_{lc}$ ; Table 2). Estimating field  $H_m$  by Equation 2 requires calculating total, body, and equivalent heat resistances ( $r_t$ ,  $r_b$ ,  $r_e$ , respectively) from metabolism chamber data and field  $T_e$ , following the methods of Weathers et al. (1984) and Buttemer et al. (1986). The laboratory free-convection value for  $r_b$  was adjusted for the effect of wind under field conditions by the equation:

$$r'_b = r_b - [(0.12u^{0.5})r_b]. \quad (3)$$

The field total thermal resistance ( $r'_t = r'_b + r_e$ ), together with  $T_e$  and the appropriate  $T_b$ , was used to solve Equation 2 for the dry rate of heat transfer, from which field  $H_m$  was calculated (see Weathers et al. 1984) as:

$$H_m = (H_m - H_e)[1/(1 - E_r)], \quad (4)$$

with  $E_r$  calculated from Equation 56 of Calder and King (1974). The value of  $H_m$  was then transformed to units of kJ/hr.

For  $T_e$  above the  $T_{lc}$ , I assumed that  $H_m$  was

TABLE 2. Parameter values used in time-energy budget model to calculate thermostatic cost of an adult Western Bluebird.

Parameter	Active phase	Rest phase
$T_b, ^\circ C: T_e < T_{lc}$	41.0	38.0
$T_{lc}, ^\circ C$	26.6	21.0
$r_t, s m^{-1}: T_e < T_{lc}$	$258.2 + 1.64T_e$	$381.4 + 1.64T_e$
$r_b, s m^{-1}: T_e < T_{lc}$	$178.6 + 1.64T_e$	$301.8 + 1.64T_e$
$H_m, W m^{-2}: T_e > T_{lc}$	71.5	57.2
$H_m, W m^{-2}: T_e < T_{lc}$	$203.8 - 4.97T_e$	$127.8 - 3.36T_e$
$H_m - H_e, W m^{-2}: T_e = T_{lc}$	57.2	49.1
$H_m - H_e, W m^{-2}: T_e = 0^\circ C$	190.6	119.6

External surface area =  $7.397 \times 10^{-3} m^2$  (Walsberg and King 1987); Characteristic dimension ( $d$ ) = 0.035 m; Mean mass = 27.5 g.

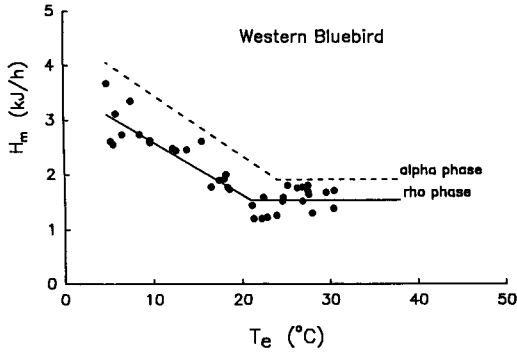


FIGURE 1. Metabolic heat production of adult Western Bluebird in relation to operative temperature ( $T_e$ ) during the rho (resting) phase of the daily cycle. Solid line indicates the rho phase relationship used in TEB model. Dashed line is the alpha (active) phase relationship used in TEB model, assumed to be 1.25 times the rho phase relationship. See text for details.

constant and minimal (Table 2). This assumption is valid for this study since field  $T_e$ s above 28°C were associated with relatively high convective conditions ( $u > 4 \text{ m s}^{-1}$ ). All activity costs other than alert perching were assumed to substitute for thermostatic costs at  $T_e$  below the  $T_{ic}$  (Paladino and King 1984, Webster and Weathers 1990).

#### DOUBLY-LABELLED WATER

In the field I followed standard procedures for the doubly-labeled water method of determining an integrated estimate of DEE (Nagy 1983). I weighed each bird to the nearest 0.25 g and injected tritiated water ( $1 \mu\text{Ci g}^{-1}$  body mass) mixed with water containing 97 atom% oxygen-18 ( $3 \mu\text{l g}^{-1}$  body mass) into the pectoral muscles using a calibrated glass syringe. After a 45–60 min equilibration period, I took a small blood sample (100  $\mu\text{l}$ ) from a vein in the wing. Blood samples were flame-sealed in heparinized microhematocrit tubes and stored at 4°C pending isotope analyses.

I injected all birds between 13:00 and 20:00 hr. Either one or two days later, the bird was recaptured, reweighed, and bled a second time. The elapsed time between initial and final blood samples averaged  $23.9 \pm 0.52$  hr for “one-day” samples ( $n = 46$ ) and  $47.8 \pm 0.83$  hr for “two-day” samples ( $n = 6$ ). All released birds behaved normally after the manipulations involved with the DLW technique. None of the released birds abandoned their nests. All young in nests at the

TABLE 3. Comparison of simultaneous estimates of daily energy expenditure (DEE) of the Western Bluebird using time-energy budget (TEB) and doubly-labeled water (DLW) methods.

Nest ID No./sex	Estimate of daily energy expenditure (kJ/day)		Percent difference <sup>a</sup>
	TEB method	DLW method	
1/M	113.1	102.1	+10.8
1/F	112.3	120.3	-6.6
19/M	96.8	104.3	-7.2
19/F	100.2	100.4	-0.2
20/M	105.0	109.2	-3.8
49/M	123.4	109.1	+13.1
49/F	119.9	113.5	+5.6
Mean <sup>b</sup>	110.1	108.4	+1.7
SEM	3.74	2.61	
% CV	9.0	6.4	

<sup>a</sup>  $[(\text{TEB} - \text{DLW})/\text{DLW}] \cdot 100$

<sup>b</sup> TEB estimate is not significantly different from DLW estimate;  $P > 0.05$ , paired, two-tailed *t*-test.

time of capture eventually fledged, with the exception of two nests that were subsequently lost to predation.

In the laboratory I microdistilled each blood sample to obtain pure water (Wood et al. 1975, Nagy 1983). The water was assayed for tritium activity with a Beckman LS 1801 liquid scintillation counter using a toluene-Triton X 100-PPO scintillation cocktail. Oxygen-18 content of the samples was determined by the proton activation of oxygen-18 to fluorine-18, with subsequent counting of the gamma emissions of fluorine-18 by a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Rates of  $\text{CO}_2$  production were calculated using Equation 2 of Nagy (1980).

The total body water (TBW) at the time of injection was estimated by the dilution method using the initial oxygen-18 level at equilibrium. Background levels of isotopes measured in blood from uninjected individuals were subtracted from all values prior to calculations. The energy equivalent of  $\text{CO}_2$  production was assumed to be 24.6 kJ/l  $\text{CO}_2$  (Williams and Prints 1986) except for seven individuals that lost more than 3% of their mean body mass during the measurement interval. For these birds, I adjusted the above energy equivalent of  $\text{CO}_2$  production for the oxidation of body fat (27.75 kJ/l  $\text{CO}_2$ ) after accounting for water loss as measured by tritium turnover (Weathers and Sullivan 1989). This was a minor correction, increasing the estimate of field metabolism an average of +2.1% (range: 0 to 4.3%).

TABLE 4. Percent of active day spent in various activities by 31 Western Bluebirds feeding 9–12 day-old nestlings.

Nest ID No./sex	Brood size	Hours active	Alert perch		Flight	Non-flight <sup>a</sup> activity
			Sun	Shade		
1/M <sup>b</sup>	6	14.0	37.5	9.6	24.1	28.8
1/F <sup>b</sup>	6	14.0	35.9	21.0	20.4	22.7
19/M <sup>b</sup>	4	14.3	21.8	57.7	11.1	9.4
19/F <sup>b</sup>	4	14.3	24.9	46.4	15.7	13.0
20/M <sup>b</sup>	5	14.4	14.7	46.4	21.4	13.5
49/M <sup>b</sup>	5	13.8	29.8	44.5	16.7	9.3
49/F <sup>b</sup>	5	13.8	34.0	44.3	12.6	8.6
8/M	4	14.4	30.2	33.9	13.4	22.6
8/F	4	14.4	41.4	22.9	13.4	22.3
9/M	6	14.4	49.5	27.9	12.9	9.7
9/F	6	14.4	39.7	24.2	20.0	16.1
12/M	5	14.3	41.1	34.6	14.5	9.7
12/F	5	14.3	33.5	30.4	17.4	18.6
21/M	4	14.4	35.3	34.7	17.4	12.6
21/F	4	14.4	22.1	39.2	20.9	17.9
29/M	6	14.4	31.4	39.9	15.4	13.3
29/F	6	14.4	40.6	27.3	16.1	16.0
36/M	5	14.4	22.2	54.8	14.4	8.6
36/F	5	14.4	27.4	47.7	16.0	8.9
51/M	4	14.4	18.7	59.7	14.2	7.4
51/F	4	14.4	25.7	53.2	13.3	8.8
61/M	6	14.4	37.7	32.2	18.2	11.9
61/F	6	14.4	43.1	32.2	15.3	9.4
67/M	5	14.3	23.4	51.0	17.2	8.4
67/F	5	14.3	29.2	45.3	17.0	8.5
84/M	6	14.4	33.2	38.7	17.4	10.7
84/F	6	14.4	31.2	39.3	17.4	12.1
89/M	4	14.4	35.9	34.4	16.4	13.3
89/F	4	14.4	37.5	29.8	16.1	16.6
98/M	4	14.3	22.0	59.3	14.6	4.0
98/F	4	14.3	24.7	53.6	15.2	6.5
Mean			31.5	39.2	16.3	12.9
SEM			1.47	2.21	0.51	1.01

<sup>a</sup> Includes ground activity, preening, nest attendance.

<sup>b</sup> Individuals used in DLW validation of time-energy budget model.

## RESULTS

### BASAL AND STANDARD METABOLISM

Mean mass of nine bluebirds (four males and five females) used in the metabolism measurements was 27.5 g. The Western Bluebird's thermoneutral zone in the rho phase extends from approximately 21°C to above 33°C (Fig. 1). Within this zone,  $H_b$  averaged  $1.52 \pm 0.05$  kJ/hr ( $n = 19$ ). The least squares regression for  $H_{sm}$  as a function of  $T_c$  below 21°C is:  $H_{sm}$  (kJ/hr) =  $3.54 - 0.898T_c$  ( $r^2 = 0.725$ ,  $n = 19$ ). This regression line extrapolates to  $H_{sm} = 0$  at  $T_c = 39.4^\circ\text{C}$ . The mean  $T_b$  of bluebirds at the conclusion of each measurement period was  $40.4 \pm 0.21^\circ\text{C}$  and ranged from 38.5 to 41.7°C. The extrapolated  $T_b$

is within the measured range of  $T_b$ , suggesting that thermal conductance is relatively constant and minimal below the  $T_{lc}$ .

### VALIDATION OF THE TIME-ENERGY BUDGET MODEL

The mean TEB estimate of seven bluebirds simultaneously labeled with DLW (110.1 kJ/day) is within 2% of the mean DLW estimate (108.4 kJ/day; Table 3). Individual TEB estimates of DEE ranged from -7.2% to +13.1% of the individual DLW estimates. The mean TEB estimate was slightly more variable than the mean DLW estimate as indicated by the coefficient of variation (Table 3). This level of agreement is concordant with the validation studies of similar



FIGURE 2. Non-perching activity during three daily time periods for male and female members of 12 mated Western Bluebird pairs feeding 9–12 day-old nestlings. Asterisk indicates significant difference between sexes for that period of the day ( $P < 0.05$ ).

TEB models of two bird species housed in a large aviary (Weathers et al. 1984, Buttemer et al. 1986).

TIME ALLOCATION

Daily time budgets were calculated as percent of a bird's active day for each activity category. Western Bluebirds feeding 9–12 day-old nestlings spent, on average, 70% of their active day perching, and allotted 11 to 24% of the active day to flight (mean = 16.3%; Table 4). Time allotted to intermediate levels of activity, such as ground activity, preening, and nest attendance, accounted for between 4 and 29% of the active day (mean = 12.9%).

The sample of time budget observations for

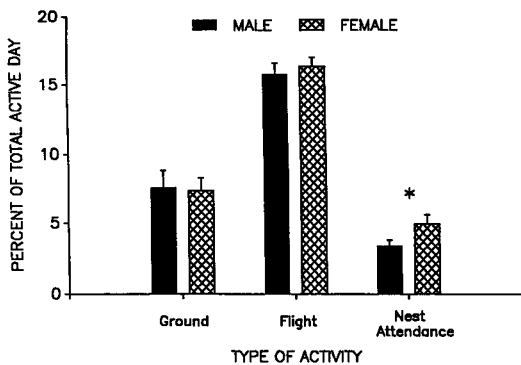


FIGURE 3. Comparison of components of non-perching activity between individuals of mated pairs of Western Bluebird feeding 9–12 day-old nestlings. Asterisk indicates significant difference between sexes ( $P < 0.05$ ).

TABLE 5. Energy expenditures (kJ/day) of 31 Western Bluebirds feeding nestlings calculated from time-energy budget model.

ID/sex	Activity costs	Thermostatic costs	Daily energy expenditure	Multiple of $H_b$
1/M <sup>b</sup>	27.5	27.8	113.1	3.10
1/F <sup>b</sup>	23.4	31.3	112.3	3.08
19/M <sup>b</sup>	12.7	25.9	96.8	2.65
19/F <sup>b</sup>	18.0	24.0	100.2	2.75
20/M <sup>b</sup>	24.4	22.2	105.0	2.88
49/M <sup>b</sup>	18.1	47.8	123.4	3.38
49/F <sup>b</sup>	13.7	48.7	119.9	3.29
8/M	16.2	6.4	81.0	2.22
8/F	16.2	6.5	81.1	2.22
9/M	14.7	13.2	86.3	2.37
9/F	23.0	13.0	94.4	2.59
12/M	16.4	27.3	102.0	2.80
12/F	20.1	25.3	103.6	2.84
21/M	19.8	23.4	101.6	2.79
21/F	24.1	23.5	106.0	2.91
29/M	17.8	19.9	96.1	2.63
29/F	18.7	18.9	96.0	2.63
36/M	16.4	20.3	95.1	2.61
36/F	18.1	20.0	96.5	2.65
51/M	16.0	9.8	84.2	2.31
51/F	15.2	10.1	83.7	2.29
61/M	20.7	18.4	97.5	2.67
61/F	17.3	19.9	95.6	2.62
67/M	19.3	33.6	111.1	3.05
67/F	19.1	32.8	110.1	3.02
84/M	19.7	27.3	105.4	2.89
84/F	19.8	27.7	105.9	2.90
89/M	18.8	23.9	101.1	2.77
89/F	18.7	23.7	100.8	2.76
98/M	16.2	31.5	105.9	2.90
98/F	16.9	30.4	105.5	2.89
Mean	18.6	23.7	100.6	2.76
SEM	0.59	1.77	1.87	0.05
% CV	17.6	41.6	10.3	10.1

<sup>a</sup>  $H_b = 36.5$  kJ/day.

<sup>b</sup> Individuals used in DLW validation of time-energy budget model.

12 of the 15 pairs observed was sufficiently uniform throughout the active period to allow for examining the effects of time of day and sex within each pair (Fig. 2). Activity budgets varied significantly with time of day ( $F = 14.5, P < 0.005$ ). Non-perching activity, which involved mostly flight, ground activity, and nest attendance, showed a distinct bimodal distribution with a lull in activity at mid-day.

Within each mated pair, the time of day significantly interacted with sex ( $F = 12.2, P < 0.005$ ). Males were significantly less active than their mates during the middle and late part of the day (Fig. 2; paired  $t$ -test,  $P < 0.03$  and  $0.05$ , respectively). Females allocated a significantly

TABLE 6. Brood-size effects on time allocation and energy costs of the Western Bluebird feeding nestlings. All categories presented as mean ( $\pm$  SEM). Within each category, means sharing the same letter are not statistically different using Tukey HSD test ( $P < 0.05$ ). An arcsine-square root transformation was applied to all percentages prior to statistical testing.

	Brood Size ( <i>n</i> )		
	4 (12)	5 (9)	6 (10)
Allocation of time (%)			
Percent of active day spent:			
Alert perch, sun	28.4 <sup>A</sup> (2.15)	28.3 <sup>A</sup> (2.56)	38.0 <sup>B</sup> (1.78)
Alert perch, shade	43.7 <sup>A</sup> (3.69)	44.3 <sup>A</sup> (2.53)	29.2 <sup>B</sup> (2.99)
Flight	15.1 <sup>A</sup> (0.72)	16.4 <sup>AB</sup> (2.48)	17.7 <sup>B</sup> (1.00)
Non-flight activity <sup>1</sup>	12.9 <sup>AB</sup> (1.74)	10.5 <sup>A</sup> (1.15)	15.1 <sup>B</sup> (1.97)
Energy expenditure (kJ/day)			
TEB estimates:			
Activity costs	17.4 <sup>A</sup> (0.81)	18.4 <sup>AB</sup> (0.99)	20.3 <sup>B</sup> (1.15)
Thermostatic costs	19.9 <sup>A</sup> (2.63)	30.9 <sup>B</sup> (3.66)	21.7 <sup>A</sup> (1.53)
TEB DEE estimate	95.7 <sup>A</sup> (2.92)	107.4 <sup>B</sup> (3.23)	100.3 <sup>AB</sup> (2.71)
DLW DEE estimate <sup>2</sup>	91.8 <sup>A</sup> (3.87)	100.8 <sup>B</sup> (3.10)	92.9 <sup>A</sup> (3.49)

<sup>1</sup> Includes ground activity, preening, and nest attendance.

<sup>2</sup> *n*'s for brood sizes 4, 5, 6 were 17, 16, 19, respectively.

greater proportion of their active day to nest attendance than their mates (Fig. 3; paired *t*-test,  $P < 0.05$ ). Nest attendance usually involved feeding the brood and nest sanitation.

#### ENERGY ALLOCATION

The mean DEE estimated from the TEB model for 31 adult Western Bluebirds feeding 9–12 day-old nestlings was  $100.6 \pm 1.87$  kJ/day or 2.8 times  $H_b$  (range: 2.2 to 3.4 times  $H_b$ ; Table 5). The TEB estimate is not statistically different from the mean DLW estimate of  $95.0 \pm 2.07$  kJ/day ( $n = 52$ : 26 males, 26 females; mean body mass = 27.4 g). Statistical differences in the activity budgets of individuals within each pair did not translate into statistical differences in the TEB estimate of DEE. Males and females within each pair had about the same TEB estimate of DEE (paired *t*-test;  $P > 0.05$ ). However, males used in DLW measurements had significantly higher body masses than their mates at this stage of the breeding cycle (males = 27.5 g, females = 27.2 g; mean difference between mates = 0.6 g; paired *t*-test,  $P < 0.05$ ).

The cost of non-perching activity averaged 18.6 kJ/day, but varied substantially among individuals (CV = 17.6%; Table 5). Small, but statistically significant, differences in the daily cost of activity were related to brood size (Table 6). Bluebirds feeding broods of four spent less time in flight than those birds tending six young. This

difference in time allocation resulted in a small increase (averaging about 3 kJ/day) in activity-related energy expenditure for individuals feeding six nestlings as compared to those feeding four nestlings.

Thermostatic costs averaged 23.7 kJ/day and were much more variable than activity costs (CV = 41.6%; Table 5). The thermostatic costs of three bluebird pairs (pairs 8, 49, and 51) were very different from the remainder of the TEB estimates (Table 5). Time budgets of Pairs 8 and 51 were taken on fairly warm days with moderate wind speeds (mean  $T_a$  in shade = 23.5° C, mean  $u = 1.9$  m/sec). These two pairs had the lowest estimated thermostatic costs. Conversely, Pair 49 experienced cold and windy weather on the day that TEB observations were taken (mean  $T_a$  in shade = 8.7° C, mean  $u = 2.5$  m/sec), thus, producing the highest estimated thermostatic costs.

The sample of individuals tending broods of five nestlings had significantly higher thermostatic costs than either sample tending broods of four or six nestlings (Table 6). These group differences were due to corresponding differences in the thermal environment between groups. The mean  $T_a$  in the shade was significantly lower for the sample of birds tending five young compared to either sample with four or six nestlings. Adult bluebirds tending six nestlings also tended to perch in the sun significantly more than adults



tending smaller brood sizes, thereby reducing their thermoregulatory costs (Table 6).

Brood-size-related variation in DEE was inconsistent in the sample of birds labeled with DLW (Table 6). Bluebirds feeding five nestlings had significantly higher DEE than birds feeding broods of four or six young. Brood size was not a significant parameter ( $F = 0.75$ ,  $P = 0.48$ ) when included in an analysis of covariance model that used  $\text{CO}_2$  production as the dependent variable, brood size as the independent variable, with mean body mass and maximum and minimum  $T_a$  as covariates. Given the large variation in thermoregulatory costs estimated from TEB estimates of DEE, it is likely that variability in thermostatic costs overshadows most potential differences in activity costs that may be related to brood size. Therefore, I attempted to correct for variation in temperature to further examine brood-size effects on DEE. The DLW estimate of DEE varied inversely with maximum  $T_a$  ( $r^2 = 0.30$ ,  $P = 0.001$ ). Variation in body mass and minimum  $T_a$  did not contribute significantly to the step-wise regression model. Observed DLW values were corrected for temperature by adding the mean DEE (95.0 kJ/day) to the residuals of the regression model. This correction failed to modify the outcome of the brood size comparison of the DLW estimates of DEE. There were no significant differences in temperature-corrected DLW estimates of DEE related to brood size.

## DISCUSSION

### BASAL METABOLISM AND METABOLIC CAPACITY

The Western Bluebird appears to be a typical passerine species in terms of its metabolic capacities. Measured values for  $H_b$ ,  $T_{lc}$ ,  $T_b$ , and thermal conductance are within 5% of their allometrically predicted values for a passerine species during the summer (Kendeigh et al. 1977). Garner Valley is a typical sub-temperate coniferous forest community, with relatively cool weather conditions during the early spring months (March through early May), but generally favorable thermal conditions during the period when nestlings are most abundant (late May through early July). Because of this coincidence of good weather and the peak nestling period, few nest failures result from brief depressions in food availability associated with poor weather conditions (Mock 1990). Other studies have documented this optimal timing of breeding with good

weather conditions (e.g., Bryant 1978, Quinney et al. 1986).

### ACCURACY OF THE TIME-ENERGY BUDGET METHOD

In this study, the TEB estimate of daily energy expenditure of Western Bluebirds was similar to the DLW estimate; the difference between the two estimates averaged +1.7% and ranged from +13.1 to -7.2. The accuracy of the TEB method is highly dependent upon several important components of the TEB model (see Goldstein 1988 and Nagy 1989 for reviews). The most critical portions of the TEB method are: (1) a detailed description of the animal's thermal environment, involving the field measurement of  $T_c$  and wind speed in the microhabitats that the animal inhabits (Bakken 1985, Weathers et al. 1984, Buttemer et al. 1986); (2) a detailed activity budget of the animal's time allocation to primary thermal environments (i.e., exposed to or sheltered from sun and wind; Mugaas and King 1981) and the allocation of time to various levels of activity; and (3) laboratory measurement of standard metabolism of recently captured individuals during the appropriate time of the year (Goldstein and Nagy 1985, Buttemer et al. 1986).

The energetic costs of locomotion can make up a substantial fraction of a bird's TEB. The sensitivity of the TEB model to errors in assigned costs for activity is highly dependent upon the proportion of time allocated to each activity (Ettinger and King 1980). Western Bluebirds spend less than 10% of their time in flight and about 8% of their day is involved in energetically less intense locomotor activities (Fig. 4). Substantial errors in the estimated costs of activity would be expected to produce significant differences between the TEB and DLW estimates. An accurate determination of flight costs is more critical for TEB estimates of aerial foraging species (Williams 1988, Goldstein 1988). This study demonstrates that the TEB method can yield reliable results that are comparable to the DLW method if the individual's use of the thermal environment and allocation of time is carefully measured.

The TEB and DLW methods complement each other and should be used in concert to obtain a detailed description of how a species allocates time and energy (Goldstein 1988, McNab 1989, Nagy 1989). The TEB method is most appropriate for bird species sensitive to handling during certain stages of the breeding cycle (e.g.,

## Western Bluebird

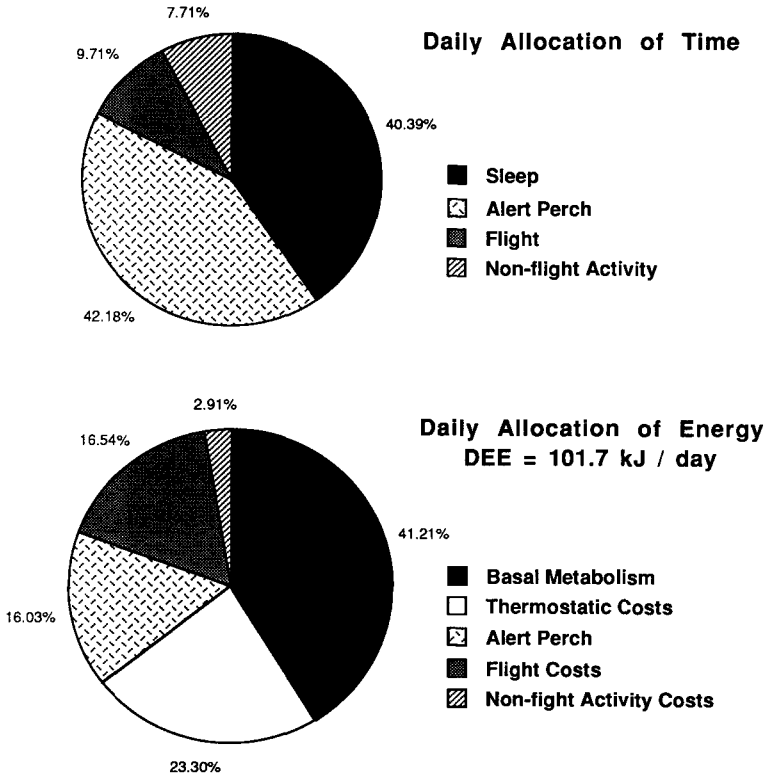


FIGURE 4. Average daily allocation of time and energy by adult Western Bluebird feeding 9–12 day-old nestlings. Proportions are for a 24-hour day with 14.3-hour alpha phase.

egg-laying and incubation) and which readily abandon the nest in response to disturbance (e.g., Williams 1987). The behavioral ecology of a species (e.g., nocturnality, large home range) may preclude the documentation of an individual's activity and use of varying thermal environments. If the species can be reliably recaptured at the nest or roost, then the DLW method may be superior even though an accurate dissection of the energy budget into various components could not be done. Both methods should be applied simultaneously whenever possible to account for any shortcomings of either method (McNab 1989, Nagy 1989).

#### VARIATION IN DAILY ENERGY EXPENDITURE

The coefficients of variation (CV) for DLW and TEB estimates of DEE of Western Bluebirds feeding nestlings were 15.7% and 10.3%, respectively. These were surprisingly low given the pos-

sible sources of variation in the contributing factors. The DLW method is accurate to  $\pm 8\%$  in free-living endotherms (Nagy 1989), but this inaccuracy is small compared to the variation in the components of the energy budget. Individual variation in measures of basal metabolism (CV = 14.0%) can also contribute to the variability in DEE.

Weather is the greatest contributor to variation in DEE. About 30% of the variation in DLW estimate of DEE was explained by variation in maximum  $T_a$ . Estimates of DEE using the TEB method indicate high variation in thermoregulatory demand (CV = 41.6%). However, birds can behaviorally moderate their thermostatic costs by differential utilization of habitats that differ greatly in  $T_e$  (Walsberg 1985, Buttemer et al. 1986, Williams 1987). Bluebirds feeding six nestlings perched in the sun to a greater extent than birds feeding smaller broods and they were

TABLE 7. Doubly-labeled water estimates of daily energy expenditure (kJ/day) of nine passerine species feeding young during the second half of the nestling period.

Species	Mass	n	kJ/day	SD	% CV	Source
<i>Riparia riparia</i>	12.9	10	92.2	12.2	13.2	Bryant and Westerterp (1984)
<i>Delichon urbica</i>	18.2	56	94.5	16.2	17.1	Bryant and Westerterp (1980)
<i>Tachycineta bicolor</i>	18.7	13	131.6	19.3	14.7	Williams (1988)
<i>Hirundo rustica</i>	19.1	14	109.6	19.6	17.9	Bryant and Westerterp (1984)
<i>Junco phaeonotus</i>	19.1	13	74.0	8.2	11.1	Weathers and Sullivan (1989)
<i>Passerculus sandwichensis</i>	19.2	26	84.8	12.7	14.8	Williams (1987)
<i>Oenanthe oenanthe</i>	23.5	13	84.8	12.0	14.2	Moreno (1989)
	24.5	24	95.3	17.0	17.8	Tatner (1990)
<i>Sialia mexicana</i>	27.4	52	95.0	14.9	15.7	This study
<i>Sturnus vulgaris</i>	75.1	11	309.6	36.2	11.7	Ricklefs and Williams (1984)

more active, thereby further reducing the thermoregulatory component of their DEE through metabolic substitution (Paladino and King 1984, Webster and Weathers 1990). The cost of activity for bluebirds with six young was only moderately increased (about 3 kJ/day) compared to birds feeding four nestlings. Most of the additional activity involved non-flight behaviors that are relatively inexpensive (2.3 times  $H_b$ ) compared to the cost of flight (6 times  $H_b$ ). Significant brood-size effects on DEE were not evident in the sample of birds involved with the DLW method.

It is likely that low variation in measures of DEE during the nestling stage of the breeding cycle reflects the complex interaction between variable thermal conditions, individual metabolic capacities, and differential use of distinct thermal environments, as well as potential individual variation in foraging efficiency and proficiency. If foraging skills or variation in food availability were positively correlated with brood size, then potentially adverse brood size effects on DEE would be limited to periods with poor weather conditions. Weather conditions in Garner Valley were relatively favorable during the measurement of DEE. There was almost no rainy weather when these data were collected. Most birds maintained their body mass during the measurement of DEE and adequately provided for their broods, suggesting that individuals were not constrained by the availability of food at this stage of the breeding cycle. The egg-laying interval appears to be the time period when food availability has its greatest effects on the reproductive output of Western Bluebirds (Mock 1990).

Studies of other passerine species have produced variable results in examining the effects of brood size on DEE. Hails and Bryant (1979) found

brood size was not significantly correlated with DEE of House Martins (*Delichon urbica*), but DEE of male House Martins varied significantly with brood mass. This suggests that parental effort of male House Martins may be influenced by the developmental stage of the brood rather than by the size of the brood. Using analysis of covariance to correct for variation in adult body mass, Williams (1987) detected a significant brood size effect on DEE in Savannah Sparrows (*Passerculus sandwichensis*). Mass-independent metabolism of Savannah Sparrows feeding six young was about 25% higher than birds attending two nestlings. Other studies of passerine birds utilizing the DLW method have failed to detect noticeable brood size effects on DEE (Ricklefs and Williams 1984, Moreno 1989, Weathers and Sullivan 1989, Tatner 1990).

Despite the many potential sources of variation in energy expenditure, the various components of the energy budget of passerine birds are adjustable so that the overall DEE of the bird is confined within relatively narrow limits. The coefficient of variation of DLW estimates of DEE during the second half of the nestling period ranges between 11 and 18% for nine passerine species (Table 7). This low variation in DEE suggests that individuals are able to closely regulate their daily energy expenditures through behavioral and physiological adjustments. Increased demands of large broods do not substantially influence the DEE of many adult passerines, except during poor weather conditions.

Because of the low variation in DEE, allometrically predicted estimates of DEE for temperate passerine birds during the breeding season are likely to be within the 95% confidence limits of empirically derived estimates. An allometric equation of DLW estimates for DEE of nine pas-

serine species feeding nestlings predicts a DEE of 117.8 kJ/day for a 27.5-g bluebird (Weathers and Sullivan 1989). This is a 24% over-estimate of the mean DLW estimate of DEE for the Western Bluebird, yet it is still within the 95% confidence limits of the mean. Therefore, accurate estimates of DEE can be derived from the allometric relationship of DLW values of DEE. When empirical data are lacking, allometric models can be useful in predicting the food requirements of breeding bird populations (Nagy 1987). Variation in DEE during the non-breeding season is likely to be much larger compared to the breeding season due to the greater variation in weather conditions and food availability. Such environmental variability is likely to make allometric predictions of DEE during the non-breeding season less reliable. This is unfortunate, since the non-breeding season is the time of year when energetic constraints may cause increased mortality in many temperate passerine populations (Ricklefs 1969, Fretwell 1972, Gessaman and Worthen 1982).

#### PARENTAL EFFORT AND REPRODUCTIVE SUCCESS

Food shortage has been proposed as a critical constraint limiting reproductive rates of altricial birds (Drent and Daan 1980, Martin 1987). The nestling stage is often cited as the period when breeding adults have the highest food requirements because they must gather sufficient food for their rapidly growing young in addition to providing for themselves. A 9–12 day-old bluebird nestling requires about 65 kJ/day of metabolizable energy (Mock et al. 1991). This energy requirement translates into about 93 g of insects that must be delivered to the nest to meet the daily food requirements for a brood of 6 bluebird nestlings. An adult bluebird requires about 23 g of insects to remain in energy balance. Assuming that a female bluebird provides 60% of the brood's food requirements (Fig. 3), she must gather nearly 3.5 times the amount of food required to sustain herself. If the less attentive male provides 40% of the brood's food requirements, he must gather about 2.6 times more food to maintain body mass. Based on the amount of time bluebirds spend in active pursuit of prey (8% of the active day), prey capture by a pair would have to be only 25 to 30% efficient to meet the needs of the family.

Drent and Daan (1980) proposed that an en-

ergetic plateau equal to about 4 times  $H_b$  exists for optimal reproductive performance; a higher level of energy expenditure might result in serious physiological stress and decreased body condition. The ratio of DEE to  $H_b$  for Western Bluebirds feeding nestlings ranged from 1.8 to 3.4 and averaged 2.8 times  $H_b$ , which suggests that Western Bluebirds do not need to work at a maximal sustainable level to provide adequately for the largest observed brood size. Experiments manipulating brood size indicate that most bluebirds can raise at least one additional nestling without any substantial effect on fledgling mass or adult mass (Mock 1990). Weathers and Sullivan (1989) reviewed the literature on parental effort and concluded that few species approach the proposed upper limit of sustainable working capacity. The DEE values of aerial-foraging species are closest to this upper limit due to the large allocation of time to flight. Ground-foraging species and "sit and wait predators" such as bluebirds spend relatively little time in flight, thus minimizing energy expenditures associated with activity. Ground-foraging species appear to work at maximal capacity only during periods of inclement weather (King and Murphy 1985).

Food limitation is likely to occur at stages of the breeding cycle when conflicts in the allocation of time between foraging and reproductive behaviors occur. The frugal foraging behavior of the Western Bluebird suggests that the late nestling stage of the breeding cycle is rarely limited by food availability. Critical periods when food availability and weather conditions consistently combine to constrain reproductive success are likely to occur during egg-laying, when nestlings require brooding, and when fledglings become independent of their parents (Mock 1990, Clark 1988, Clark and Ricklefs 1988, Weathers and Sullivan 1989, Sullivan 1988). Studies of reproductive energetics that concentrate on these potentially critical periods of the breeding cycle are needed to elucidate energetic constraints on reproductive output.

#### ACKNOWLEDGMENTS

I thank the Lake Hemet Water District, Garner Ranch, and the U.S. Forest Service for kindly allowing access to their properties. The U.S. Forest Service also provided logistical support. T. M. Hilleary, B. Johnson, M. Khubesrian, D. M. Larcheveque, M. Gold, E. Flint, and B. S. Obst assisted in the field. G. A. Bartholomew kindly provided much of the equipment to measure metabolism and operative temperature. I thank T. R.

Howell, K. A. Nagy, B. M. Wenzel, G. E. Walsberg, and an anonymous reviewer for comments on the manuscript. T. M. Hilleary provided unwavering moral support and editorial advice throughout the study. This study was funded in part by the Ecological Research Division of the Department of Energy (Contract DE-AC03-76-SF00012) to the University of California. Additional support included grants from the North American Bluebird Society, Eldorado Audubon Society, Sigma Xi, Frank M. Chapman Research Fund, and UCLA Department of Biology. Final preparation of the manuscript was supported by the Biological Resources Group, ERC Environmental and Energy Services Company.

## LITERATURE CITED

- ASCHOFF, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* 69A:611-619.
- ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 111:38-47.
- BAKKEN, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60:337-384.
- BAKKEN, G. S., W. A. BUTTEMER, W. R. DAWSON, AND D. M. GATES. 1981. Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. *Ecology* 62:311-318.
- BAKKEN, G. S., W. R. SANTEE, AND D. J. ERSKINE. 1985. Operative and standard operative temperature: tools for thermal energetics studies. *Am. Zool.* 25:933-943.
- BRYANT, D. M. 1978. Environmental influences on growth and survival of nestling House-Martins *Delichon urbica*. *Ibis* 120:16-26.
- BRYANT, D. M., AND K. R. WESTERTERP. 1980. The energy budget of the House-Martin (*Delichon urbica*). *Ardea* 68:91-102.
- BUTTEMER, W. A. 1981. The thermal significance of winter roost-site selection by American Goldfinches (*Carduelis tristis*). Unpublished Ph.D. diss. Univ. Michigan, Ann Arbor, MI.
- BUTTEMER, W. A., A. M. HAYWORTH, W. W. WEATHERS, AND K. A. NAGY. 1986. Time-budget estimates of avian energy expenditure: physiological and meteorological considerations. *Physiol. Zool.* 59:131-149.
- CALDER, W. A. 1984. Size, function and life history. Harvard University Press, Cambridge, MA.
- CALDER, W. A., AND J. R. KING. 1974. Thermal and caloric relations of birds, p. 259-413. *In* D. S. Farner and J. R. King [eds.], *Avian biology*, Volume 4. Academic Press, New York.
- CASTRO, G., AND J. P. MYERS. 1988. A statistical method to estimate the cost of flight in birds. *J. Field Ornithol.* 59:369-380.
- CLARK, L. 1987. Thermal constraints on foraging in adult European Starlings. *Oecologia* 71:233-238.
- CLARK, L., AND R. E. RICKLEFS. 1988. A model for evaluating time constraints on short-term reproductive success in altricial birds. *Am. Zool.* 28:853-862.
- ETTINGER, A. O., AND J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (*Empidonax traillii*) during the breeding season. *Auk* 97:533-546.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ.
- GESSAMAN, J. A., AND G. L. WORTHEN. 1982. The effects of weather on avian mortality. Unpublished annotated bibliography, Biology Department, Utah State University, Logan, UT.
- GOLDSTEIN, D. L. 1988. Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *Am. Zool.* 28:829-844.
- HAILS, C. J., AND D. M. BRYANT. 1979. Reproductive energetics of a free-living bird. *J. Anim. Ecol.* 48:471-482.
- HILL, R. W., D. L. BEAVER, AND J. H. VEGHTE. 1980. Body surface temperatures and thermoregulation in the Black-capped Chickadee (*Parus atricapillus*). *Physiol. Zool.* 53:305-321.
- KENDEIGH, S. C., V. R. DOLNIK, AND V. M. GAVILOV. 1977. Avian energetics, p. 127-204. *In* J. Pinnowski and S. C. Kendeigh [eds.], *Granivorous birds in ecosystems*. Cambridge Univ. Press, Cambridge, England.
- LACK, D. 1988. Ecological adaptations for breeding in birds. Methuen, London.
- LIMA, S. L. 1987. Clutch size in birds: a predation perspective. *Ecology* 68:1062-1070.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.* 18:457-487.
- MCNAB, B. K. 1989. Laboratory and field studies of energy expenditure of endotherms: a comparison. *Trends Ecol. Evol.* 4:111-112.
- KING, J. R., AND M. E. MURPHY. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? *Am. Zool.* 25:955-964.
- MOCK, P. J. 1990. Energetics of growth and reproduction of the Western Bluebirds *Sialia mexicana*. Ph.D. diss. Univ. California, Los Angeles.
- MOCK, P. J., M. KHUBESRIAN, AND D. M. LARCHEVEQUE. 1991. Energetics of growth and maturation in sympatric passerines that fledge at different ages. *Auk* 108:34-41.
- MORENO, J. 1989. Variation in daily energy expenditure in nesting Northern Wheatears (*Oenanthe oenanthe*). *Auk* 106:18-25.
- MUGAAS, J. N., AND J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie. *Stud. Avian Biol.* 5:1-78.
- MURPHY, E. C., AND E. HAUKIOJA. 1986. Clutch size in nidicolous birds. *Curr. Ornithol.* 4:141-180.
- NAGY, K. A. 1980. CO<sub>2</sub> production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* 238:R466-473.
- NAGY, K. A. 1983. The doubly labeled water (<sup>3</sup>H<sup>18</sup>O) method: a guide to its use. UCLA Publication Number 12-1417, Univ. California, Los Angeles.

- NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57:111-128.
- NAGY, K. A. 1989. Field bioenergetics: accuracy of models and methods. *Physiol. Zool.* 62:237-252.
- NAGY, K. A., AND D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238:R454-R465.
- OBST, B. S., K. A. NAGY, AND R. E. RICKLEFS. 1987. Energy utilization by Wilson's Storm-petrel (*Oceanites oceanicus*). *Physiol. Zool.* 60:200-210.
- PALADINO, F. V., AND J. R. KING. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). *Physiol. Zool.* 57:226-236.
- QUINNEY, T. E., D.J.T. HUSSEL, AND C. D. ANKNEY. 1986. Sources of variation in growth of Tree Swallows. *Auk* 103:389-400.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contr. Zool.* 9:1-48.
- RICKLEFS, R. E., AND J. B. WILLIAMS. 1984. Daily energy expenditure and water turnover of adult European Starlings (*Sturnus vulgaris*) during the nesting season. *Auk* 101:707-716.
- ROBINSON, D. E., G. S. CAMPBELL, AND J. R. KING. 1976. An evaluation of heat exchange in small birds. *J. Comp. Physiol.* 105:153-166.
- ROER, P., AND M. KJOLSVIK. 1973. Equipment for measuring low air velocity. *Agric. Meteorol.* 12:281-296.
- SCHMIDT-NIELSEN, K. 1979. *Animal physiology*. Cambridge Univ. Press, New York.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in Yellow-eyed Juncos: adaptation to ecological constraints. *Ecology* 69:118-124.
- TATNER, P. 1990. Energetic demands during brood rearing in the Wheatear *Oenanthe oenanthe*. *Ibis* 132:423-435.
- WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection, p. 389-414. *In* M. L. Cody [ed.], *Habitat selection in birds*. Academic Press, Orlando, FL.
- WALSBERG, G. E., AND J. R. KING. 1978. The relation of the external surface area of birds to skin surface area and body mass. *J. Exp. Biol.* 76:185-189.
- WEATHERS, W. W., W. A. BUTTEMER, A. M. HAYWORTH, AND K. A. NAGY. 1984. An evaluation of the time-budget estimates of daily energy expenditure in birds. *Auk* 101:459-472.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.* 59:223-246.
- WEATHERS, W. W., AND C. VAN RIPER III. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). *Auk* 99:667-674.
- WEBSTER, M. D., AND W. W. WEATHERS. 1990. Heat produced as a by-product of foraging activity contributes to thermoregulation by Verdins *Auriparus flaviceps*. *Physiol. Zool.* 63:777-794.
- WILLIAMS, J. B. 1987. Field metabolism and food consumption of Savannah Sparrows during the breeding season. *Auk* 104:277-289.
- WILLIAMS, J. B. 1988. Field metabolism of Tree Swallows during the breeding season. *Auk* 105:706-714.
- WILLIAMS, J. B., AND A. PRINTS. 1986. Energetics of growth in nestling Savannah Sparrows: a comparison of doubly labeled water and laboratory estimates. *Condor* 88:74-83.
- WOOD, R. A., K. A. NAGY, S. MACDONALD, S. T. WAKAKUWA, R. J. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Anal. Chem.* 47:646-650.

## APPENDIX A

List of symbols	
$c_p$	specific heat of air (kJ/kg °C)
$d$	characteristic dimension (m)
DEE	daily energy expenditure (kJ/day)
$E_r$	fraction of metabolic heat production lost evaporatively
$H_{AP}$	cost of alert (daytime) perching (kJ/hr)
$H_c$	evaporative heat loss (kJ/hr)
$H_f$	cost of flight (kJ/hr)
$H_b$	basal metabolism (kJ/day)
$H_m$	maintenance metabolism (kJ/hr)
$H_{NF}$	cost of non-flight activity (kJ/hr)
$H_r$	rho (rest) phase basal metabolism (kJ/hr)
$H_{sm}$	standard metabolism (kJ/hr)
$H_{ta}$	alpha (active) phase thermostatic cost (kJ)
$H_{tr}$	rho (rest) phase thermostatic cost (kJ)
$\rho$	density of air (1.2 kg/m <sup>3</sup> at 20°C)
$r_b$	body thermal resistance (s/m)
$r'_b$	body thermal resistance in field (s/m)
$r_e$	equivalent thermal resistance (s/m)
$r_t$	total thermal resistance (s/m)
$r'_t$	total thermal resistance in field (s/m)
$T_a$	air temperature (°C)
$T_b$	body temperature (°C)
$T_e$	operative temperature (°C)
$T_{lc}$	lower critical temperature (°C)
$t_{AP}$	duration of daylight period (hr)
$t_f$	time spent in flight (hr)
$t_{NF}$	time spent in non-flight activities (hr)
$t_R$	duration of nighttime period (hr)
$\dot{V}O_2$	oxygen consumption (ml/min)
$\mu$	wind speed (m/sec)