

FLIGHT COST OF A SMALL PASSERINE MEASURED USING DOUBLY LABELED WATER: IMPLICATIONS FOR ENERGETICS STUDIES

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ABSTRACT.—The metabolic cost of rest and activity ($\text{cm}^3 \text{CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) was measured for the European Robin (*Erithacus rubecula*, 18.6 g) at temperatures (T_a , °C) from -15 to $+30^\circ\text{C}$. Regressions expressing these costs are: night resting (M_{rn}) = $4.23 - 0.0733T_a$, day resting (M_{rd}) = $5.10 - 0.0807T_a$, hopping (M_{hop}) = $8.60 - 0.1256T_a$.

Daily energy expenditure (DEE) for robins held in an outdoor aviary was 64.8 kJ/day (SD = 9.2, $n = 6$), determined using the doubly labeled water technique. This was positively related to time spent in flight (t_{fly} , h) such that $\text{DEE} = 50.9 + 23.4t_{fly}$.

Flight cost for robins was estimated as 25.6 kJ/h (SD = 5.0, $n = 6$). This flight cost is about twice that predicted by various allometric equations. Robin flights in the aviary were short (3 m) and brief (0.78 s), indicating a mean flight speed (3.85 m/s) that was lower than the theoretical minimum power velocity (5.86 m/s). The European Robin has a relatively high wing loading (0.263 g/cm²) and aspect ratio (7.33). In a small bird with flapping flight these characteristics imply a high cost, particularly at low flight speeds.

The high cost of flight was offset by its short duration. During 30-min observation periods, an average of 100.2 s was spent in flight, implying a sustained energy demand of only 3.04 kJ/h ($2.7 \times$ basal metabolic rate). The exceptionally high flight cost reported here ($23 \times$ basal metabolic rate) may be typical of short, brief aerial forays. Other doubly labeled water studies reveal a positive correlation between the time spent in flight and DEE, indicating its dominant impact on energy turnover in some free-living birds. Received 17 April 1985, accepted 19 September 1985.

THE accuracy of time-activity laboratory (Mugaas and King 1981) studies for determining the daily energy expenditure (DEE) of free-living birds depends upon representative time budgets and realistic values for the energy cost of activities (Weathers and Nagy 1980, Koplín et al. 1980, Williams and Nagy 1984, Bryant et al. 1985). This was well illustrated by Weathers et al. (1984) for low-cost activities that are pursued over long periods, but it is also important for high-cost activities that usually occupy only a small proportion of the day (Mugaas and King 1981).

This study is concerned with the determination of activity costs in a small, woodland passerine, the European Robin (*Erithacus rubecula*). It employs gas-analysis respirometry to measure resting and some locomotor costs. Time budgets and doubly labeled water measurements of DEE for aviary robins were used in combination with laboratory estimates of non-flight activity to establish the cost of flight for a species that exhibits a largely nonaerial existence. It contrasts with previous studies on this topic that have focused on mainly aerial

species (Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984, Westerterp and Drent 1985).

METHODS

Energetic cost of activity.—Robins from a wooded area on Stirling University campus ($56^\circ08'N$, $3^\circ54'W$) were caught at dusk between November and March during 1983–1985. Wing dimensions and body mass were noted, and the birds were placed in a respirometer overnight to determine metabolic rate for a range of temperatures (-15°C to $+30^\circ\text{C}$). Three to five replicates were performed at 5°C intervals, each overnight trial maintaining one temperature ($\pm 0.5^\circ\text{C}$). The birds were released approximately 1 h after dawn, having completed a bout of hopping activity in the spindle-mounted respirometer. Robins were caught direct from the wild so that the respirometry results would include the effects of acclimatization to seasonal and local conditions.

The respirometer train was an open-flow system, equipped with an MSA infrared gas analyzer for monitoring CO_2 production, and a Beckman OM2 polarographic oxygen analyzer. Carbon dioxide was removed from incurrent air using Carbasorb, and air leaving the respirometer chamber was passed over

Drierite prior to gas analysis. The respirometer was enclosed in a darkened incubator. Each overnight run was divided into a series of 2-h sample periods, interspersed with ambient air sampling. During the first 2 h the bird settled down in a darkened incubator at about the time it normally went to roost, and the mean for this period was taken to indicate the cost of resting during the day (M_{rD}). Metabolism usually reached its lowest levels at about 0300. At dawn the waking period was often characterized by intermittent activity, so this and the first period were excluded when calculating the average cost of resting overnight (M_{rN}). After waking, the bird was induced to hop by revolving the spindle-mounted respirometer until a steady trace was obtained from the gas analyzers. The speed of rotation was selected such that the individual's gait resembled that of a foraging bird (1.5–2.5 m/min). The energetic cost of ground activity (including foraging) is estimated in this work from the relationship established during hopping trials (M_{hop}). Individual response to a rotating chamber was unpredictable, and it sometimes was necessary to reject trials in which birds employed bouts of hovering or clung temporarily to the chamber wall. All gas volumes were corrected to STP.

Six robins were used to determine daily energy expenditure using the doubly labeled water ($D_2^{18}O$) technique (Lifson et al. 1955). They were held during July–August 1983 for 48 h in an outdoor aviary, as groups of 3 individuals. Different birds were placed in the respirometer on successive nights to establish summertime values for night resting, day resting, and hopping. Food [blowfly larvae (*Calliphora* spp.) and cheese] was supplied with water *ad libitum*. The aviary was partly exposed to the sky, but completely shielded from the wind by fencing and woodland.

Time budgets.—In the aviary, the activity of each bird was recorded for 3–5, 30-min periods ($n = 48$) per day. Individuals were recognized by colored ring combinations and by spots of white typist's correction fluid applied to the head or breast feathers.

Activities were timed using a microprocessor-based data logger, with event resolution limited only by the human response time (approximately 0.2 s). Three classes of activity were recognized: resting, flying, and ground activity. The latter category comprised principally hopping and pecking but also included occasional preening, bathing, and defecating as these activities entail broadly similar energy demands. We designated these minimal energy-demanding activities as ground activity to simplify the analysis, and because it is not yet possible to distinguish between the energy costs of these minor activities. Weathers et al. (1984) measured the energetic costs of alert perching, preening, eating, and hopping. The mean costs of each activity were ranked in the order mentioned, although there were no statistically significant differences.

The 24-h day was divided into three periods: (1)

the dark period, during which robins were resting either in the aviary or in the respirometer; (2) the handling period, during which body mass was recorded, blood samples taken, and the birds then placed in a cloth bag; and (3) the light period, when the birds were active in the aviary.

Doubly labeled water technique.—The birds received intraperitoneal injections of 0.13 ml of 10 atom % D_2O and 0.22 ml of 20 atom % $H_2^{18}O$. Initial blood samples were taken 1 h later, after which one individual was placed in the respirometer and the others returned to the aviary. On the following morning a blood sample was obtained from the robin in the respirometer, after which it was returned to the aviary. Blood samples were obtained from all individuals 48 h after initial sampling. The samples were flame-sealed in Vitrex microcapillaries (5 μ l) for later analysis. A different individual was monitored in the respirometer on the second night. Natural enrichment levels of deuterium and oxygen-18 were determined from other robins on the study site at the time of the experiment ($D = 152.82$ ppm, $^{18}O = 2,011.56$ ppm).

Blood samples were processed according to the method given in Bryant et al. (1984) and Westerterp and Bryant (1984). The theory of measuring energy expenditure using doubly labeled water ($D_2^{18}O$) is described by Lifson et al. (1955), and assumptions associated with the method are outlined by Nagy (1980). Body water content was taken as 65% (after Newton 1968) of the mean body mass, itself derived from measurements taken at the beginning and end of a sampling period.

RESULTS

Respirometry measurements.—Figure 1 shows winter metabolism during night resting (M_{rN}), day resting (M_{rD}), and hopping (M_{hop}) as a function of ambient temperature (T_a). Predictive equations were produced using regression analysis (Table 1). McNab (1980) noted that regression coefficients derived in this manner are poor representations of minimal thermal conductance if the regression lines do not extrapolate to the animal's body temperature at zero metabolism. In this work the regressions extrapolate to 57.7°C (M_{rN}), 63.2°C (M_{rD}), and 68.5°C (M_{hop}), which are all much greater than the European Robin's proventricular temperature of 40.6°C (Urdvary 1953). For this reason the mean conductance method advocated by McNab (1980) was investigated, assuming a constant body temperature of 40.6°C. However, agreement between this method and measured metabolism was poor. This may have been due to an incorrect assumption of constant body temperature. Metabolic values reported here for

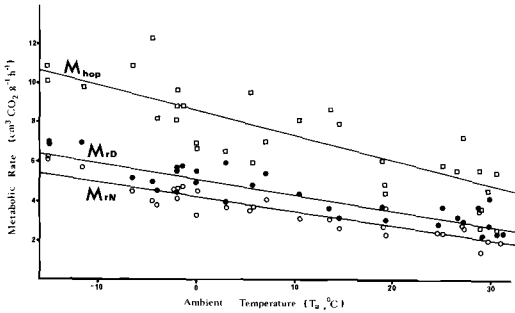


Fig. 1. Robin winter metabolism as a function of ambient temperature. M_{rN} = night resting metabolism; M_{rD} = day resting metabolism, M_{hop} = hopping metabolism. Regressions are given in Table 1.

M_{rN} are nightly averages and therefore above the lowest resting level (40% greater, Tatner unpubl. data). Thus, the thermal conductance for M_{rN} does not represent the minimal value. These limitations, together with the extent of variability in measured metabolism (Fig. 1, S_{yx} in Table 1), render the use of regression analysis most appropriate in the context of this work.

Day resting was significantly more demanding than night resting ($t = 5.42, P < 0.05$), requiring 21% [$100 \times (4.23 - 5.10)/4.23$] more energy. A comparison of the respective regression coefficients (Table 1) indicates that this difference did not vary with ambient temperature ($t = 0.736, P > 0.05$; Zar 1974). An increase of this magnitude (20–25%) between the night and day phases is a general feature of avian resting metabolism (Aschoff and Pohl 1970b, Calder and King 1974).

The respirometry trials during summer, undertaken at a mean T_a of 25°C, indicated a higher CO_2 production (Table 2) than would be predicted from the winter metabolism relationships for both M_{rN} and M_{rD} . These increases were 32% for M_{rN} (2.41 to 3.17 $cm^3 CO_2 \cdot g^{-1} \cdot h^{-1}$) and 24% for M_{rD} (3.10 to 3.85 $cm^3 CO_2 \cdot g^{-1} \cdot h^{-1}$). Summer robins also exhibited higher respiratory quotients (RQs). The difference between

RQ in summer and winter was greater over the night-resting phase (0.95 compared with 0.75; $t = 5.24, P < 0.01$) than the day-resting phase (0.88 compared with 0.75; $t = 3.27, P < 0.05$). The apparent increase in metabolic rate indicated by the elevated CO_2 production of summer robins was reduced to 12% (M_{rN}) and 11% (M_{rD}) when corresponding changes in RQ were taken into account. However, differences between summer and winter resting metabolic rate at 25°C were still statistically significant (Table 2). Summer predictions using the winter regression equations therefore were incremented by 12% for M_{rN} and by 11% for M_{rD} . The energetic cost of hopping at 25°C for summer robins was not significantly different from that predicted by the winter regression equation (Table 2).

Time budgets.—Activity timed using the data logger was expressed in terms of the proportion of the 30-min sample devoted to resting, ground activity, or flying. These proportions were normalized using an arcsine transformation (Zar 1974) prior to statistical analysis. The values for each individual were determined on a daily basis and used to apportion the daylight period spent in the aviary (Table 3). Analyses of variance on pooled data showed that the three categories of activity occurred in similar proportions during each hour of daylight, indicating that diel activity rhythms were absent. The average proportion of time spent in flight was the only time-budget variable that differed significantly between individuals (one-way ANOVA, $F = 5.96, P < 0.05$). Flights were short, as the birds tended to fly from one side of the aviary to the other (3 m), landing on the sides only momentarily before making a return flight. Cumulative flight time as a function of the number of flights in a sampling period is shown in Fig. 2. Because the slope of the regression was significant ($t = 16.97, P < 0.001$), the duration of a single flight was taken as 0.78 s. During this time the bird flew approximately 3 m, so we necessarily considered the cost of

TABLE 1. Robin winter metabolism as a function of ambient temperature (T_a , °C).

	CO_2 production ($cm^3 \cdot g^{-1} \cdot h^{-1}$)	S_{yx}	r^2 ($\times 100$)	n
Resting night metabolism (M_{rN})	4.23 - 0.0733 T_a	0.52	81.2	32
Resting day metabolism (M_{rD})	5.10 - 0.0807 T_a	0.65	77.4	32
Hopping metabolism (M_{hop})	8.60 - 0.1256 T_a	1.40	79.7	30

TABLE 2. Robin metabolism in winter and summer at 25°C.^a

	Night resting (M_{rn})			Day resting (M_{rd})			Hopping activity (M_{hop})		
	\bar{x}	(SD)	<i>n</i>	\bar{x}	(SD)	<i>n</i>	\bar{x}	(SD)	<i>n</i>
Summer									
cm ³ CO ₂ ·g ⁻¹ ·h ⁻¹	3.17	(0.18)	6	3.85	(0.34)	6	4.81	(0.98)	4
RQ	0.95	(0.08)	6	0.88	(0.08)	6	0.94	(0.07)	4
J·g ⁻¹ ·h ⁻¹	69.55	(4.06)	6	89.63	(5.69)	6	106.45	(21.63)	4
Winter ^b									
cm ³ CO ₂ ·g ⁻¹ ·h ⁻¹	2.41	(0.13)	31	3.10	(0.16)	31	5.46	(0.41)	29
RQ	0.75	(0.03)	19	0.75	(0.05)	19	0.82	(0.10)	17
J·g ⁻¹ ·h ⁻¹	63.46	(3.38)	31	81.70	(4.28)	31	134.38	(10.17)	30
Summer vs. winter									
Difference (J·g ⁻¹ ·h ⁻¹)	6.09			7.93			-27.93		
<i>t</i> (df) ^c	3.45**	(6.41)		3.24**	(6.14)		2.45 ^{NS}	(3.19)	

^a J·g⁻¹·h⁻¹ calculated using standard heat equivalents for CO₂ as follows (units J/cm³ CO₂): 21.95 at respiratory quotient (RQ) = 0.95, 23.30 at RQ = 0.88, 22.13 at RQ = 0.94, 26.44 at RQ = 0.75, 24.62 at RQ = 0.82 (Brody 1945).

^b cm³ CO₂·g⁻¹·h⁻¹ calculated from the regression equations in Table 1; standard deviations of predicted values were calculated using MINITAB regression (Ryan et al. 1976). RQ mean values are based on pooled data collected over the temperature range -15°C to +30°C.

^c ** = *P* < 0.01, NS = not significant.

short, brief flights. This type of flight resembles that performed by the European Robin in its natural habitat when it moves short distances between a perch and the ground, or between bushes.

Nonflight daily energy expenditure (DEE) was calculated for aviary robins using the time-activity laboratory (TAL) method (after Mugaas and King 1981). For each individual, the costs of the five categories of activity (Table 3)

were calculated on a daily basis and then averaged (*n* = 2 days) to derive the figures given in Table 4. Energy costs were determined using the results of the winter respirometry, but taking into account the observed summer differences (Table 2). The appropriate equations are given in Table 4. It was not possible to measure flight cost directly, so for the present, the period spent in flight is assigned an energy expenditure equivalent to the day-resting level.

TABLE 3. Activity budgets for aviary robins.

Individual	Day	Average temperature (°C)		Night-time rest (h)	Daytime rest		Daytime ground activity		Daytime flying		Disturbance ^b (h)
		Day	Night ^a		% of day	No. of hours	% of day	No. of hours	% of day	No. of hours	
RB35	1	18.7	23.0	8.67	87.3	11.19	6.9	0.88	5.8	0.74	2.51
	2	21.9	15.6	5.62	78.2	13.20	20.3	3.43	1.5	0.25	1.50
RB36	1	18.7	12.7	5.85	94.9	15.56	2.1	0.34	3.0	0.49	1.75
	2	21.9	25.0	10.23	88.0	11.24	7.6	0.97	4.4	0.56	1.00
RB37	1	18.7	12.7	6.1	89.0	14.15	4.2	0.67	6.8	1.08	2.00
	2	21.9	15.6	5.62	75.7	13.16	15.0	2.60	9.3	1.62	1.00
RB41	1	17.7	25.0	11.13	84.0	9.87	3.7	0.43	12.3	1.45	1.12
	2	20.1	11.2	8.75	86.9	12.18	6.2	0.87	6.8	0.95	1.23
RB42	1	17.7	14.4	8.45	99.1	14.88	0.8	0.12	0.1	0.02	0.53
	2	20.1	25.0	10.33	98.7	12.46	1.1	0.14	0.2	0.03	1.05
RB43	1	17.7	14.4	8.28	88.3	13.20	5.2	0.78	6.5	0.97	0.77
	2	20.1	11.2	8.04	87.0	13.01	8.5	1.27	4.5	0.67	1.01

^a Night temperatures above 22°C indicate that the bird spent this period in the respirometer.

^b Disturbance = when birds were handled.

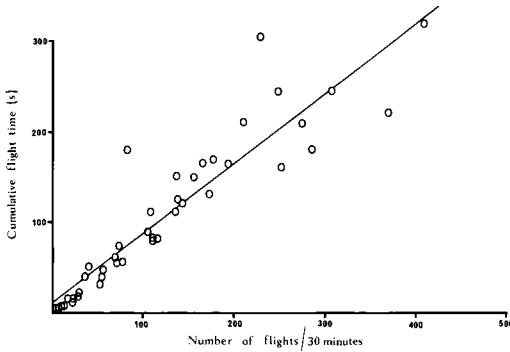


Fig. 2. Robin flight activity in an aviary during time budgets of 30 min. Regression slope = 0.777 (SD = 0.046, $t = 16.97$, $P < 0.01$), regression constant = 8.35 (SD = 7.17, $t = 1.16$, NS); $r^2 = 86.2$, $n = 47$.

Doubly labeled water results.—The average daily metabolic rate for aviary robins was $5.46 \text{ cm}^3 \text{ CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (SD = 0.67, $n = 6$), ranging from 4.21 to $6.07 \text{ cm}^3 \text{ CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ (Table 5). At an RQ of 0.75, this gives a daily energy expenditure of 64.8 kJ/day for an 18.6-g robin, which is $2.42 \times \text{BMR}$ (where $\text{BMR} = 2.26 \text{ cm}^3 \text{ CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ for an 18.6-g passerine; Aschoff and Pohl 1970a). Four overnight respirometry trials at 25°C with D_2^{18}O -loaded birds gave an average metabolic rate of 3.33 (SD = 0.50) $\text{cm}^3 \text{ CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, which was not significantly different from the 3.76 (SD = 0.27) $\text{cm}^3 \text{ CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ obtained simultaneously using infrared gas analysis.

Cost of flight.—Daily energy expenditure determined using the doubly labeled water (DLW) technique was significantly related to time spent in flight (Fig. 3A). This is described by the relationship $\text{DEE} = 50.9 + 23.4t_{\text{fly}}$, where DEE is daily energy expenditure (kJ/day) and

t_{fly} is time spent in flight per day (h). When no time was spent in flight the regression predicted DEE to be 50.9 kJ (SD = 4.3). This is 16% greater than the mean nonflight DEE of 44.0 kJ (SD = 2.3) estimated using the TAL method (Table 4). The regression equation also predicted that for every hour of the day that robins spent in flight there was an increment in DEE of 23.4 kJ (SD = 4.98, $n = 6$). At the same time, there was a corresponding reduction in the daytime nonflight DEE of 2.2 kJ [$1/16 \times (70 \times 50.9/100)$]. This is based on an average of 30% nonflight DEE devoted to nighttime rest (Table 4), occurring over an average of 8 h (Table 3), during which time robins do not fly. Thus, the flight cost of aviary robins was 25.6 kJ/h.

Flight cost can also be calculated using the TAL estimates of nonflight DEE (Table 4). These estimates do not include an estimate of flight cost, the period spent in flight having been allocated a cost equivalent to day resting. Thus, the difference between the DLW estimate of DEE and the TAL estimate may be regarded as the net energy devoted to flight (i.e. the energetic demand above the day-resting level). Figure 3B shows this difference as a function of the time spent in flight. Although the regression coefficient was significantly different from 0 ($t = 4.05$, $P < 0.05$), the constant was not ($t = 2.06$, $P > 0.05$). Hence, this regression predicted a net energy requirement of only 20.50 kJ when 1 h/day was spent in flight. The extra amount required to convert this figure to gross flight energy is the cost of day resting for 1 h at the mean daytime temperature during the experiment (19.6°C), which is 3.52 kJ/h. Hence, a second estimate of flight cost is 24.02 kJ/h. It

TABLE 4. Energetic costs for aviary robins based on two 1-day TAL predictions (kJ/day).^a

Bird	Disturbance			Ground activity	Flight period at $M_{r,D}$ level	Nonflight DEE
	Night resting	cost	Day resting			
RB35	10.46	3.26	22.10	5.59	0.92	42.33
RB36	12.71	2.47	27.06	1.86	1.05	45.15
RB37	10.84	2.67	27.13	4.60	2.65	47.89
RB41	15.37	1.95	21.18	1.80	2.35	42.65
RB42	13.92	1.29	26.26	0.36	0.05	41.88
RB43	14.11	1.43	24.43	2.76	1.54	44.27
Mean	12.90	2.18	24.69	2.83	1.43	44.03
(SD)	(1.94)	(0.76)	(2.57)	(1.94)	(0.96)	(2.26)

^a Energy cost ($\text{J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$): night resting ($M_{r,N}$) = $111.84 - 1.938T_a$, plus 12% for summer metabolism; day resting ($M_{r,D}$) = $134.84 - 2.134T_a$, plus 11% for summer metabolism; ground activity (M_{hop}) = $211.73 - 3.102T_a$. Disturbance cost (blood sampling, weighing, transit, etc.) taken as $M_{r,D}$ at 25°C, plus 12%.

TABLE 5. Metabolic rate of aviary robins during summer determined using doubly labeled water ($D_2^{18}O$).

Bird	Body mass (g)	Metabolism ($cm^3 CO_2 \cdot g^{-1} \cdot h^{-1}$)	DEE ^a (kJ/day)	DEE ($\times BMR^b$)
RB35	17.9	6.07	70.32	2.67
RB36	19.7	5.50	68.83	2.48
RB37	19.5	6.02	74.68	2.70
RB41	18.4	5.55	65.07	2.46
RB42	18.2	4.21	48.61	1.85
RB43	17.8	5.39	61.07	2.36
Mean	18.6	5.46	64.76	2.42
(SD)	(0.8)	(0.67)	(9.17)	(0.31)

^a Using $RQ = 0.75$, $1 cm^3 CO_2 = 26.44 J$ (Brody 1945).

^b Predicted from body mass, $BMR = 1.11 kJ/h$ (night phase; Aschoff and Pohl 1970a).

may be argued that resting during the day includes a high proportion of alert behavior that may have a higher cost than indicated by M_{rD} . An estimate of the alert cost was made using the upper confidence limit of the M_{rD} regression ($M_{rD} + tS_{yx}$, t at 95%), which is equivalent to an addition of 0.4 BMR ($0.85 cm^3 CO_2 \cdot g^{-1} \cdot h^{-1}$). Recalculating the nonflight TAL prediction of DEE gave a mean value of 53.98 kJ/day ($SD = 3.21$), which is close to that predicted above (50.9 kJ/day). Using these higher values of nonflight DEE produced only a slight change in the predicted flight cost, which was 23.47 kJ/h ($19.95 + 3.52$).

DISCUSSION

Winter/summer metabolism.—The winter metabolism results may be compared with those obtained by Gavrilov (*in* Kendeigh et al. 1977) for Russian robins of slightly lower average body mass (17.6 g). His equation for winter robins (night resting metabolism, $cm^3 CO_2 \cdot g^{-1} \cdot h^{-1} = 5.84 - 0.1460T_a$) indicates a much greater increase in energy requirement as T_a declines than we found (Table 1). Possibly, this was due to an adjustment of the relationship undertaken to ensure that metabolic rate was zero when the ambient and bird's body temperatures were equal (see Kendeigh et al. 1977: appendix 5.1). A similar procedure was investigated here (see Methods), and it produced the following equation for night resting metabolism: $cm^3 CO_2 \cdot g^{-1} \cdot h^{-1} = 5.34 - 0.1315T_a$. Although this is similar to Gavrilov's result, it was not acceptable because it overestimated

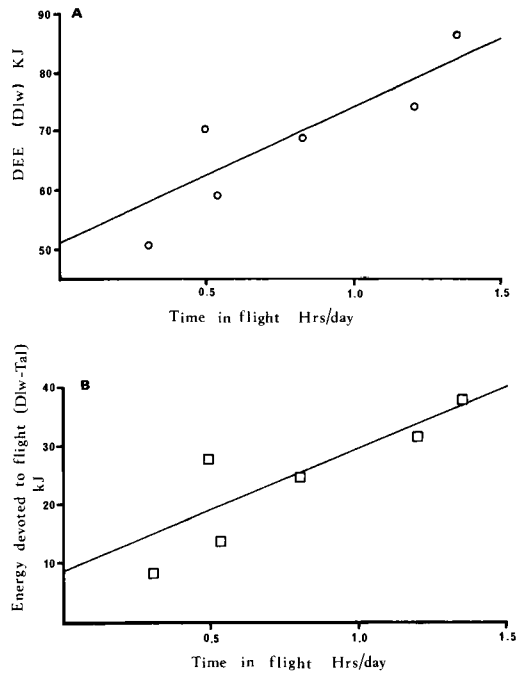


Fig. 3. Robin energy expenditure as a function of time spent in flight. (A) Regression slope = 23.4 ($SD = 4.98$, $t = 4.69$, $P < 0.01$), regression constant = 50.9 ($SD = 4.29$, $t = 11.85$, $P < 0.01$); $r^2 = 80.8$, $S = 5.46$. (B) Regression slope = 20.5 ($SD = 5.07$, $t = 4.05$, $P < 0.05$), regression constant = 8.98 ($SD = 4.37$, $t = 2.06$, $P > 0.05$); $r^2 = 75.5$, $S = 5.55$. Dlw = Doubly labeled water.

metabolism at low temperatures. Differences in the slope of metabolic equations for summer and winter given by Gavrilov indicate a reduction in conductance of 7%, probably due to thicker winter plumage. In Moscow, robin plumage increased from 7% of the body mass (14.0 g) to 9.1% of the body mass (17.2 g) between summer and winter (Shilov 1968). Seasonal shifts in thermoregulatory metabolism are well documented (Calder and King 1974) and have been related to body mass (Kendeigh et al. 1977). Regression coefficients for SMR (Kendeigh et al. 1977: 135) of an 18.6-g passerine, calculated for summer and winter, indicate a 12% increase in summer energy requirements [i.e. winter temperature coefficient (b) = 1.490 $kJ \cdot bird^{-1} \cdot day^{-1} \cdot ^\circ C^{-1}$, compared with summer temperature coefficient (b) = 1.676 $kJ \cdot bird^{-1} \cdot day^{-1} \cdot ^\circ C^{-1}$]. Elevated resting metabolic rates therefore are expected for summer robins, in accordance with the 11–12% increase we observed.

The reason for the higher RQ values for summer robins in this study is rather obscure. Work on substrate concentrations and turnover in birds has demonstrated that in some winter-acclimatized species there is a reduced reliance on carbohydrate as a metabolic fuel, although this was observed only for elevated rates of thermogenesis (Marsh and Dawson 1982, Marsh et al. 1984).

The absence of a significant metabolic difference between summer and winter hopping trials may be due to the small sample size and high degree of inherent variability. Pohl and West (1973) reported a greater heat production during forced exercise for Common Redpolls (*Carduelis flammea*) in winter compared with summer.

Daily energy expenditure.—Robins in the aviary spent a high proportion of the daylight period resting, with relatively little time devoted to activities akin to foraging (Table 3). These aspects of their daily behavior may be different from robins in their natural habitat at this time of year, as East (1982) has shown that robins forage for approximately 20% of the time at temperatures greater than 10°C. The proportion of time spent in flight also may be lower than the free-living level. Walsberg's equation relating percentage of active day spent in flight to body mass (Walsberg 1983; Eq. 11) predicts a figure of 7.6% (± 1 SD, 3.1–18.7%) for an 18.6-g bird, compared with a mean of 4.3% (± 1 SD, 1.1–9.2%) found here. So, it is likely that the mean DEE estimate (DLW; 64.76 kJ/day) reported in this study will be low compared with free-living individuals. This suggestion is in accordance with a DEE prediction of 76.40 kJ/day for an 18.6-g nonbreeding passerine (Bryant et al. 1985), which is 18% above the value we observed.

Flight costs.—Bird flight is recognized as a costly but highly efficient form of locomotion (Tucker 1970). Determination of flight costs has been approached using a variety of techniques, including material balance (Kespaik 1968, Lyuleeva 1970), flight mechanics (Pennycuik 1968, 1975; Tucker 1968; Greenewalt 1975; Rayner 1979a), and doubly labeled water (LeFebvre 1964, Utter and LeFebvre 1970, Hails 1979, Flint and Nagy 1984). The theoretical approach predicts a U-shaped curve relating power requirements to flight speed (Pennycuik 1975), but in studies of DEE the cost of flight usually is taken as a multiple of BMR (see Williams and Nagy

TABLE 6. Wing characteristics of small birds.

	Body mass (g)	Wing area (cm ²)	Wing loading (g/cm ²)	Aspect ratio (wing-span ² /wing area)
<i>Erithacus rubecula</i> ^a	18.6	70.8	0.263	7.33
<i>Lanius excubitor</i> ^b	31	144	0.215	—
<i>Parus major</i> ^b	14.5	62	0.234	—
<i>Emberiza</i>				
<i>gubernatrix</i> ^b	25.5	100	0.255	—
<i>Passer domesticus</i> ^b	28.3	76	0.372	—
<i>Spizella a. arborea</i> ^b	18	90	0.200	—
<i>Anthus spinoletta</i> ^b	19	109	0.174	—
<i>Parus ater</i> ^c	9.1	53.8	0.169	6.02
<i>Parus montanus</i> ^c	10.9	61.9	0.176	5.53
<i>Parus cristatus</i> ^c	12.2	60.2	0.203	5.75
<i>Regulus regulus</i> ^c	5.9	35.4	0.167	5.94
<i>Certhia familiaris</i> ^c	9.1	62.4	0.146	5.72

^a Measured, $n = 21$.

^b Greenewalt 1962.

^c Norberg 1979.

1984). There is an implicit assumption that the flight speed adopted coincides with the minimum power speed (base of the U power curve). However, the energetic cost of flight is likely to reflect a compromise between flight speed and flight gait, both being influenced by the current demands on a bird's time and activity budget (Norberg 1981, Pyke 1981). There is also likely to be an inverse relationship between the cost associated with the flight gait and the time spent in the air. Hails (1979) showed that avian aerial insectivores, which spend most of their life in the air, exhibit flight costs that are 49–73% lower than predicted on the basis of body mass for nonaerial species. More recently, a similar result was reported for a larger, nonpasserine seabird (Flint and Nagy 1984). Our study considers the opposite end of the spectrum in terms of adaptation to an aerial existence. For most of the year robins spend only a small proportion of their time in flight. Thus, during 172 h of time budgeting this species, East (1982) obtained such small sample sizes for birds in flight that it was necessary to pool the information with other activities of short duration or infrequent occurrence. The European Robin's mode of foraging involves hopping, although there are often short flights between perches and the ground (East 1980). The wing loading and aspect ratio of a robin are high compared with most other birds with a similar body mass or wing area (Table 6). A high aspect

TABLE 7. Predictions of European Robin flight cost.^a

Source	Flight cost (kJ/h)	Method
Pennycuick 1975 (Eq. 25)	5.69	Body measurements and flight speed
Tucker 1973 (Eq. 49)	6.43	Body measurements and flight speed
Greenewalt 1975 ^b	5.61	Body measurements and flight speed
Hart and Berger 1972	10.23	Body mass
Kendeigh et al. 1977	14.66	Body mass
Hails 1979	11.90	Body mass

^a Robin measurements ($n = 21$): body mass = 18.6 g (0.182 N), wingspan = 228 mm, wing area = 70.78 cm², flight speed = 3.85 m/s, air density = 1.18 kg/m³ (Hodgman 1959).

^b Eq. 23 (1.09 kJ/h) \times 4 (muscular efficiency 25%) + SMR (=1.24 kJ/h; Lasiewski and Dawson 1967).

ratio indicates relatively long wings, which may improve maneuverability, but this could be a disadvantage in a small bird that exhibits flapping flight because of the increased wing inertia. These characteristics suggest that the flight cost of foraging robins may be high.

Predictions of flight cost in the robin vary from 5.61 to 14.66 kJ/h (Table 7). The lowest estimates, derived using aerodynamic theory (Pennycuick 1975), indicated a flight cost of only $5.1 \times$ BMR. This calculation is likely to have underestimated induced power for robins in this study, as the very short flight duration meant that a proportion of the time was probably very similar to hovering. Rayner (1979b: 751) noted that induced power is better predicted at low flight speeds using a model for hovering. The observed flight speed (3.85 m/s) was lower than the theoretical minimum power speed (5.86 m/s, Pennycuick 1975). This would also increase observed flight cost relative to the theoretical prediction. Limitations associated with the models of flight mechanics employed here are discussed by Rayner (1982).

The flight cost predictions based on body mass (Table 7) are much greater than those derived using theoretical flight mechanics, probably because the latter underestimate the physiological requirements of flight (Rayner 1982) and the increase in power required for low-speed flight in small birds (Tucker 1973: fig. 1, Westerterp and Drent 1985: fig. 4). Mechanical predictions of energy requirements for flight do not make provision for the cost of take-off, which is presumably greater than that of sustained flight and which assumes a high significance in the present work. Allometric equations relating body mass to physiological measures of flight metabolism tend to utilize data based on protracted flight duration, and therefore may reflect minimum power require-

ments. Teal (1969) provided data on the cost of brief flights ($\bar{x} = 68$ s, SD = 42, $n = 56$) in small birds based on direct measurement of CO₂ production. His passerine results are shown in Fig. 4, from which it can be determined that flight cost (cm³ CO₂/h) = $53.70M^{1.03}$, where M is body mass (g). This relationship predicts that flight cost for an 18.6-g robin will be 30.14 kJ/h (assuming RQ = 0.71; Torre-Bueno 1977), rather higher than we observed.

The cost of flight for robins in this study was extremely high at 25.6 kJ/h [$23 \times$ BMR (night) = 1.11 kJ/h; Aschoff and Pohl 1970b]. This demand operates for only very short periods, however, as the average flight duration was 0.78 s. During the 30-min time-budgeting periods cumulative flight time for robins averaged 100.2 s. In this instance, 712.5 J would be required for flight, plus 866.3 J for the remaining period, assuming it was at the average nonflight level (Table 4; 44.03 kJ/day or 0.51 W). Hence, the overall average sustained energy demand may have been only 3.16 kJ/h ($2.8 \times$ BMR). The maximum cumulative time spent flying in a 30-min bout was 320 s; even when flying for three times as long, the sustained energy demand would not be exceptional (6.06 kJ/h, $5.46 \times$ BMR; see Westerterp and Bryant 1984).

Energy demand for a single flight (0.75 s) is 5.3 W, of which 0.51 W may be accounted for by resting metabolism, leaving 4.79 W associated with flight activity. Maximum sustained output of striated muscle is estimated to be 250 W/kg of muscle tissue (Weis-Fogh and Alexander 1977). In the European Robin the pectoralis muscles weigh 3.0 g, implying a mechanical power output of up to 0.75 W. Assuming 23% muscle efficiency (Pennycuick 1975), the maximum power consumption of the flight muscles will be 3.26 W. This leaves a

shortfall of 1.53 W, which could be accounted for by the muscular activity of the legs during take-off and landing. If this is correct, the energy requirements during short forays can be partitioned as 61% flight, 29% take-off and landing, and 10% resting metabolism.

For sustained flight, most allometric predictions are based on body mass^{0.75}, which indicates that sustained power requirements in flight are a multiple of basal metabolic rate (Hart and Berger 1972). Hence, larger birds use proportionally less power in continuous flight. Theoretical aerodynamic predictions indicate a more direct proportionality with body mass ($M^{1.17}$ in Hart and Berger 1972, $M^{1.10}$ in Rayner 1979a). These calculations are based on structural and mechanical features and therefore are more likely to reflect the ability for maximal power output, the duration of which probably is limited in the longer term by physiological constraints, including substrate availability and oxygen debt. Maximal power output in flight is therefore likely to be greater than sustained output, and might be expected to occur during short, brief flights such as those documented by Teal (1969), Westerterp and Drent (1985: fig. 3), and the present study. This is in accordance with the reanalysis of Teal's data, which indicate power requirements that are proportional to body mass ($M^{1.03}$; see Fig. 4).

The high cost of flight (23.4 kJ/h) reported here for the European Robin is a consequence of the short flight duration. It is thought to provide a realistic estimate for the cost of non-migratory flights because the gait exhibited was similar to that observed in the natural situation. As mentioned, structural aspects of the robin's wing and the slow flight speed indicate that short flights are likely to involve high cost.

Implications for energetics studies.—The discussion of flight cost indicates that attention should be paid to the foraging mode employed by the species when constructing a TAL budget. Thus, aerial-foraging species are adapted for low-cost flights of $2.9\text{--}5.7 \times \text{BMR}$ (Hails 1979) or $4.8 \times \text{BMR}$ (Flint and Nagy 1984), whereas foraging that involves many short flights may involve costs as high as $21 \times \text{BMR}$ (this study), or even higher because the cost is not proportional to basal metabolism (Fig. 4). Current allometric flight equations (Hart and Berger 1972, Ken-deigh et al. 1977, Hails 1979) employed to predict flight costs in TAL studies give estimates that are intermediate between these extremes.

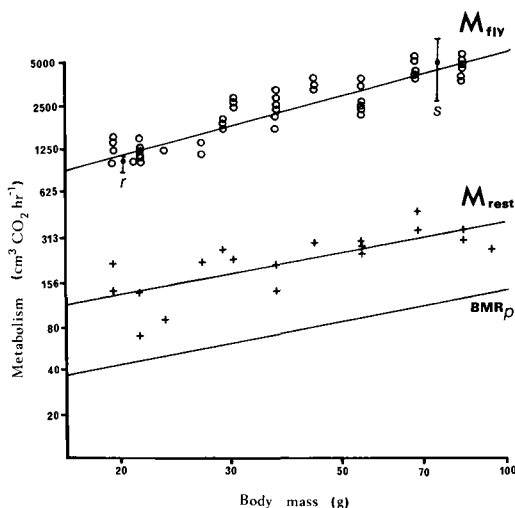


Fig. 4. Metabolic rate ($\text{cm}^3 \text{CO}_2/\text{h}$) as a function of body mass (g). Flight (circles) and resting (crosses) values are passerine data from Teal (1969). Robin flight cost ($\pm 1 \text{SD}$) = r . Starling flight cost ($\pm 1 \text{SD}$) = s (after Westerterp and Drent 1985). Regression equations are: Flight metabolism (M_{fly}) = $53.70M^{1.03}$ (slope = 1.03, $\text{SD} = 0.05$, $t = 19.12$, $P < 0.001$; \log_{10} constant = 1.74, $\text{SD} = 0.09$, $t = 20.01$, $P < 0.001$; $r^2 = 86.9$, $\log_{10} S = 0.09$). Resting metabolism (M_{rest}) = $16.98M^{0.69}$ (slope = 0.69, $\text{SD} = 0.14$, $t = 4.93$, $P < 0.001$; \log_{10} constant = 1.23, $\text{SD} = 0.22$, $t = 5.45$, $P < 0.001$; $r^2 = 55.1$, $\log_{10} S = 0.14$). Night basal metabolism (BMR) = $5.03M^{0.726}$ (after Aschoff and Pohl 1970a). Body mass (g) = M .

Although accurate predictions of flight and other costs are important when constructing TAL estimates of DEE, they must be considered in conjunction with limitations of the time-budget technique. It is noteworthy that in most doubly labeled water studies where it was relatively easy to obtain an accurate estimate for time spent in flight as a result of its conspicuousness or duration, this has correlated well with the DEE (Table 8). There will be no variation in DEE due to the flight component, however, unless there is a significant difference between individuals in the amount of time they spend in flight. A priority in future studies of this type should be to ensure that the flight component is accurately sampled, even though it may form only a small proportion of the daily activity.

Interest in the field of free-living energetics studies has centered on obtaining a TAL model that will accurately predict DEE as revealed by

TABLE 8. Correlation between DEE and flight parameters.

Source	Species	Correlation (r)	Flight parameter
Flint and Nagy 1984	Sooty Tern (<i>Sterna fuscata</i>)	0.92	Time in flight
Bryant and Westerterp 1980	House Martin (<i>Delichon urbica</i>)	0.49	Percentage of period in flight
Westerterp and Bryant 1984	Barn Swallow (<i>Hirundo rustica</i>)	0.85	Percentage of period in flight
	Bank Swallow (<i>Riparia riparia</i>)	0.82	Percentage of period in flight
Westerterp and Drent 1985	European Starling (<i>Sturnus vulgaris</i>)	0.94	Time in flight
Weathers and Nagy 1980	Phainopepla (<i>Phainopepla nitens</i>)	None	Time in flight
Williams and Nagy 1984	Savannah Sparrow (<i>Passerculus sandwichensis</i>)	None	Time in flight
Weathers et al. 1984	Loggerhead Shrike (<i>Lanius ludovicianus</i>)	None	Time in flight
Nagy et al. 1984	Jackass Penguin (<i>Spheniscus demersus</i>)	0.88	Distance swum
This study	European Robin (<i>Erithacus rubecula</i>)	0.90	Time in flight

the doubly labeled water method (Weathers and Nagy 1980, Williams and Nagy 1984, Weathers et al. 1984, Bryant et al. 1985). Weathers et al. (1984) emphasized the importance of obtaining an accurate estimate of the operative temperature (T_e ; Bakken 1976) and using measured energy equivalents for various behaviors. The latter aspect was endorsed here by the comparison of resting metabolism results for Scottish and Russian robins. Operative temperature was not determined in the present study because the birds were sheltered from the effects of sun and wind. This may have affected the nonflight estimates of DEE (Table 4), but the similarity in predictions of flight cost indicate that this was of minor significance. Williams and Nagy (1984) published an analysis of DEE for the Savannah Sparrow (*Passerculus sandwichensis*) in which

they concluded that three of the TAL models examined yielded mean estimates comparable to those given by the DLW method, but that there was no correspondence in the variability. When their DLW results are plotted as a function of TAL predictions, there are no significant correlations (Table 9). This lack of correlation appears to be due to a single individual (No. 144), which was the least intensively observed. Exclusion of this bird reveals an improved level of correlation between DLW and TAL results (Table 9), to the extent that the model of Holmes et al. (1979) provides a significant correlation. Although it is of questionable validity to have excluded individual 144, this reinterpretation does offer some encouragement for accurate prediction of intraspecific DEE variability using TAL methods. It also indicates the importance of both increasing the number of individuals sampled in each study and obtaining an accurate measure of time spent in brief but costly activities if the conclusions in this type of study are to withstand critical appraisal.

TABLE 9. Correlation between DLW and TAL measures of daily expenditure for the Savannah Sparrow (after Williams and Nagy 1984).

Model	Coefficient of determination (r^2) %	
	All data	Excluding bird No. 144
Schwartz and Zimmerman 1971	0	0
Utter and LeFebvre 1973	24	53
Walsberg 1977	0	12
Kendeigh et al. 1977	0	0
Holmes et al. 1979	11	89*
Walsberg 1980	19	60
Mugaas and King 1981	5	73

* Significant at 1%.

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ERRATA

In the memorial to Edmund W. Mudge (1985, *Auk* 102: 869), "Edmund W. Mudge" should read "Edmund W. Mudge, Jr."

There is an error in the article by Spencer G. Sealy (1985, *Auk* 102: 889-892). At the end of paragraph 2 on page 889, the sentence beginning "In 1979 a single 9-day-old cuckoo gradually assumed an erect posture . . ." should read "In 1985 . . ."