AN EVALUATION OF TIME-BUDGET ESTIMATES
OF DAILY ENERGY EXPENDITURE IN BIRDS

WESLEY W. WEATHERS,[1] WILLIAM A. BUTTEMER,[1]
ANITA M. HAYWORTH,[1] AND KENNETH A. NAGY[2]

[1]Department of Avian Sciences, University of California, Davis, California 95616 USA and
[2]Laboratory of Biomedical and Environmental Sciences, University of California,
Los Angeles, California 90024 USA

ABSTRACT.—We used the doubly-labeled water (DLW) technique to measure the daily energy expenditure ($\dot{H}_{TD}$) of aviary-housed Loggerhead Shrikes (*Lanius ludovicianus*). Simultaneously to our DLW measurements, we obtained a continuous 24-h record of the bird's time budget (TB) and assessed its thermal environment at 10-min intervals with an array of 23 meteorological sensors that measured the air temperature (T_a), operative temperature (T_e), and wind speed (u) experienced by the bird. From the TB and meteorological data, we estimated the birds' $\dot{H}_{TD}$ by several TB models that differed in the energy equivalents assigned to behaviors and in how thermoregulatory costs were calculated. Only a convection-adjusted, electrical-analog model provided a mean $\dot{H}_{TD}$ estimate that was identical to the mean DLW value (106 kJ/day). Values of $\dot{H}_{TD}$ for individual birds calculated by this model ranged from −8.1 to +7.5% of the DLW values and were significantly correlated with the DLW values, indicating that this method accurately gauged the $\dot{H}_{TD}$ of individual birds. Our analysis showed that this model's accuracy resulted from (1) using T_e and u to calculate thermoregulatory costs through heat transfer theory, and (2) using measured energy equivalents for the various behavior categories. $\dot{H}_{TD}$ estimates based on other commonly used TB models differed significantly from the DLW values, with mean errors ranging from −18 to +21%. *Received 19 August 1983, accepted 12 January 1984.*

OVER the past decade, much effort has been directed towards elucidating how free-living birds allocate available time and energy among the requirements for thermoregulation, foraging, territory defense, reproduction, and so on. Although quantifying time allocation is relatively easy, assessing the energy expenditure of free-living animals has proven to be difficult. One popular technique—the time-budget (TB) method—calculates daily energy expenditure ($\dot{H}_{TD}$) from the animal's observed daily activity budget by means of laboratory-derived estimates of the energy cost of various activities. This method has been used in over 40 studies of birds (reviews by King 1974; Kendeigh et al. 1977; Walsberg 1980, 1983; Dol'nik 1980). Despite its popularity, the TB method has infrequently been subjected to error analyses to examine its reliability and its sensitivity to variations in its major components (Withers 1977, Mahoney 1976, Walsberg 1977, Walsberg and King 1978a, Ashkenazie and Safriel 1979, Ettinger and King 1980, Weathers and Nagy 1980, Koplin et al. 1980, Mugaas and King 1981, Biedenweg 1983). These analyses demonstrate that: (1) the same time-budget data can give

rise to widely differing $\dot{H}_{TD}$ estimates depending upon the TB model chosen (Weathers and Nagy 1980, Koplin et al. 1980, Williams and Nagy 1984a), and (2) that, for a given TB model, $\dot{H}_{TD}$ is relatively insensitive to errors in the energy costs assigned to various activities (e.g. Withers 1977, Ettinger and King 1980). The insensitivity of the TB method to errors in activity-cost assignments led some researchers (e.g. Ettinger and King 1980, Biedenweg 1983) to suggest that their TB estimates of $\dot{H}_{TD}$ differed from true values by less than 5%. Regrettably, such optimism is unwarranted on two accounts. First, the cost of activity is frequently only a small fraction of $\dot{H}_{TD}$. Combined basal metabolic and thermoregulatory requirements typically represent 40–80% of $\dot{H}_{TD}$ (Ettinger and King 1980, Walsberg 1983), and errors in their cost assignments, not in those of activity, may contribute most to errors in the TB method (Weathers and Nagy 1980, Weathers et al. in press). Second, sensitivity analyses do not measure accuracy per se. To assess the accuracy of the TB method, $\dot{H}_{TD}$ must be measured simultaneously by an independent technique of known accuracy, such as doubly-labeled water

(DLW). Unfortunately, this has been done only a few times (Utter 1971, Weathers and Nagy 1980, Weathers et al. in press, Williams and Nagy, 1984a). Varying degrees of concordance between TB and DLW estimates were found in these studies, with some TB models yielding mean H_{TD} estimates in error by 20–40%. It is unclear why some of the TB models yielded reasonable H_{TD} estimates while others did not. It is important to improve the accuracy of the TB method, because reliable modeling of energy flow through populations depends on accurate estimates of H_{TD}. Our earlier analyses suggested that TB estimates could be improved if thermoregulatory costs were assessed by means of existing heat-transfer theory (Weathers and Nagy 1980, Weathers et al. in press). Accordingly, in this study we used DLW to test several TB models that differed in the way in which thermoregulatory costs were calculated.

Because our goal was to evaluate the reliability of the TB method, we took extraordinary steps to make our TB estimates as accurate as possible. First, we studied birds individually in a large flight aviary equipped with 23 meteorological sensors, including taxidermic mounts that measured the bird's T_e (Bakken 1976, Bakken et al. 1981). Second, we used a microcomputer to generate a continuous real-time record of the bird's behavior and position within its thermal environment throughout the 24-h study period. Confining the birds to an aviary permitted us to monitor their behavior and thermal environment more accurately than would have been possible under field conditions. Third, within a few days of the aviary studies, we measured each bird's oxygen consumption ($\dot{V}O_2$) in the laboratory, thereby establishing its basal metabolic rate, thermoregulatory costs, and rate of energy expenditure during all behavioral categories except flight. Consequently, we eliminated a major source of uncertainty in the TB method—namely, the energy costs assigned to the various behaviors.

METHODS

Animals.—The Loggerhead Shrikes (*Lanius ludovicianus*) we used were captured near Palm Desert, Riverside County, California in April 1981 (Federal Permit No. 2-1633-SC, State Permit No. 114). Between measurements they were housed individually in 0.6- × 0.3- × 0.3-m cages within an enclosed room and were provided a diet of day-old domestic chicks. The room was unheated but air conditioned to prevent its temperature from exceeding 35°C during the summer. The birds were exposed to the prevailing photoperiod, and all remained in excellent condition throughout the study. Of the six birds used in the time-budget studies, Nos. 218 and 232 were used twice; all others were used only once.

Time budgets.—Time budgets of individual birds were obtained during November 1982. The bird was labeled with $^3HH^{18}O$ and released into a large aviary to which it had been previously accustomed. The rectangularly shaped aviary (12 × 6 × 4 m) had a northeast-southwest orientation and contained a 3-m-high dead tree at each end to provide the shrikes with a variety of perches, roost sites, and locations for impaling "prey" (lean chicken breast). Each tree contained 2–3 unheated taxidermic mounts for measuring operative temperature (T_e; for theory and methods see Bakken 1976, Bakken et al. 1981). The mounts were positioned at various heights and compass headings to compensate for changes in the bird's location. Wind speed (u) and air temperature profiles were monitored at the cage's north and south ends with paired 36-gauge thermocouples and hot-ball anemometers (Buttemer 1981) mounted at heights of 0.5, 1.0, 2.0, and 3.3 m. An Eppley pyranometer measured global radiation. Outputs from the meteorological sensors were fed through a switching device to an analog to digital converter (Fluke model 8810A Digital Multimeter) and thence to a microcomputer (North Star Horizon equipped with a Mountain Computer real-time clock). The switching device was activated by the microprocessor and was programmed to scan the sensors at 10-min intervals. The microcomputer was also used to generate a continuous real-time record of the bird's behavior, which was divided into the following categories: (1) rest perch (nighttime), (2) alert perch (includes vocalizing), (3) preening, (4) eating, (5) flying, (6) hopping, and (7) other (mainly clinging to the aviary screen). Coded keys on the computer's console were assigned to the various behaviors. When the bird began a given behavior, the observer (located in a blind adjacent to the aviary) pressed the corresponding key and the computer accumulated that behavior's time (to the nearest ms) until another key was pressed. An interrupt subroutine allowed the observer to record the bird's position relative to the meteorological sensors without affecting the time recording. The behavioral, meteorological, and position data were stored in the computer's memory and periodically transferred to magnetic disks. The T_e associated with the bird's position in the aviary was obtained by noting which taxidermic mount most nearly matched the bird's height and orientation. Wind speed was obtained by interpolating between values from the two anemometers that bracketed the bird's height.

TABLE 1. Time budgets of Loggerhead Shrikes. Data are hours spent per activity.

Bird number	Run number	Perching		Eating	Preening	Flying	Hopping	Other[a]	Total
		Night	Day						
218	1	11.96	10.79	0.41	0.22	0.10	0.03	0.66	24.17
220	2	12.54	9.44	0.49	0.11	0.07	0.06	0.28	22.99
232	3	11.47	10.70	0.05	0.12	0.08	0.02	0.38	22.82
221	4	11.67	10.40	0.22	0.04	0.20	0.04	0.09	22.66
230	5	11.43	9.42	0.70	0.10	0.10	0.03	1.88	23.66
225	6	12.28	6.73	0.01	0.01	0.19	0.05	2.74	22.01
218	7	11.97	10.30	0.30	0.35	0.08	0.11	0.39	23.50
232	8	12.17	10.49	0.00	0.71	0.05	0.00	0.58	24.00
Mean		11.94	9.78	0.27	0.21	0.11	0.04	0.88	23.23
(SD)		(0.39)	(1.34)	(0.25)	(0.23)	(0.06)	(0.03)	(0.93)	(0.73)

[a] Mainly clinging to the wire sides of the aviary.

Doubly-labeled water.—To determine metabolism by doubly-labeled water (^{3}HH^{18}O), birds were weighed to the nearest 0.1 g and given an intramuscular injection of 0.25 ml of water containing 95 atom-percent ^{18}O and ~0.1 mCi ^{3}H. After allowing 1 h for the labeled water to reach equilibrium with body water, we obtained duplicate 50-μl blood samples from a brachial vein and stored them at 4°C in flame-sealed glass microhematocrit tubes for later analysis. The bird was then released into the aviary and the collection of time-budget data begun immediately. Approximately 1 day later the bird was recaptured and reweighed, and a second set of duplicate blood samples was obtained.

Blood samples were micro-distilled (Wood et al. 1975) to obtain pure water, which was assayed for tritium activity (Beckman LS 230 liquid scintillation counter, toluene-Triton X100-PPO scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of ^{18}O to fluorine-18 with subsequent counting of the gamma-emitting ^{18}F in a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Using the equations of Lifson and McClintock (1966) as modified by Nagy (1975), we calculated rates of water flux and CO_2 production by means of isotope measurements.

We validated the DLW method for birds (Buttemer et al. MS) by using the Haldane method to collect simultaneously the CO_2 produced by nine isotopically labeled Budgerigars (*Melopsittacus undulatus*). DLW measurements for individual birds ranged from −5.2 to +6.2% of Haldane values, with a mean error in the DLW method of −0.04%. In previous bird-validation studies, mean errors were around ±6% (LeFebvre 1964, Hails and Bryant 1979, Williams and Nagy 1984b). Thus, we feel that our shrike DLW values for CO_2 production of individual birds are within 6% of the true values.

Oxygen consumption.—We measured each bird's basal, thermoregulatory, and activity costs in the lab-

oratory by using an open-flow respirometry system. Details of the methods, apparatus, and calibration procedures used in the metabolism studies are presented elsewhere (Weathers et al. 1980). We determined the basal and thermoregulatory requirement by measuring fasting oxygen consumption ($\dot{V}O_2$) at various operative temperatures (T_e's) during the rest phase of the daily cycle (2100–0500). We calculated rates of metabolic heat production ($\dot{H}_m$) by assuming that 20.08 kJ of heat were produced per liter of O_2 consumed. We determined the energy cost of the various behaviors—except for flight, which was estimated by Eq. 15 of Tucker (1975)—from $\dot{V}O_2$ measurements of sustained (i.e. steady-state) activity bouts (>2 min) during the active phase of the daily cycle (0800–1600). The activity cost was taken as the mean of several separate determinations for each bird. For these measurements, fed birds were housed individually in a 14-l cylindrical plexiglass metabolism chamber that was placed in a constant temperature cabinet equipped with fluorescent lights and a one-way port for viewing behavior. The metabolism chamber contained a horizontal perch equipped with a spike on which pieces of lean chicken meat were impaled.

RESULTS

Time budgets were expressed in behavioral categories (Table 1). The length of the time-budget observation periods ranged from 22.01 to 24.17 h, or from 91.7 to 100.7% of a 24-h day. Because birds were released and recaptured during midday, departures from a true 24-h day affected only the photophase and mainly the time spent perching. Shrikes perched an average of 93.5% of their time, flew only 0.5% of the time, and spent an average of only 6% of

TABLE 2. Mean daily operative temperature (T_e), mean daily air temperature (T_a), mean nighttime air temperature (T_{na}), mean daily wind speed, and midday global radiation during time-budget observations.

Run number	Number of observations	T_e (°C)	T_a (°C)	T_{na} (°C)	Wind speed (m/s)	Global radiation[a] (W/m)
1	145	13.7	11.0	8.8	0.67	334.2
2	138	14.7	12.2	10.3	0.62	442.2
3	137	13.2	10.7	7.7	0.41	422.7
4	136	13.0	10.9	8.4	0.29	445.3
5	142	14.0	11.7	8.8	0.32	413.2
6	132	13.5	12.3	11.1	0.85	354.0
7	141	8.3	5.8	3.9	0.69	322.0
8	142	7.5	5.9	4.4	0.53	317.4

[a] Average of 24 measurements taken at 10-min intervals between 1000 and 1400.

the total time in all other nonperching activities.

Meteorological data.—Table 2 presents the mean daily T_e and wind speed (u) corresponding to the bird's position, together with mean daily T_a, mean nighttime air temperature (T_{na}), and midday global radiation. These data reveal considerable variation in meteorological conditions between runs. Average T_e's and T_a's calculated at half-hour intervals throughout the day for all runs (Fig. 1) illustrate (1) that T_e was usually slightly lower than T_a at night but was up to 9°C higher during the day and (2) that T_a was always below the bird's lower critical temperature (T_{lc}), whereas T_e exceeded T_{lc} for 2.5 h during midday. On average, mean daily T_e exceeded T_a by 2.2°C.

Basal and standard metabolism.—Figure 2 presents values for the shrikes' rest-phase metabolic heat production as a function of T_e. The shrikes' thermoneutral zone extends from 24.3 to at least 36°C. Within this zone, $\dot{H}_b$ averaged 1.79 ± 0.20 kJ/h ($n = 27$). (The equivalent mass-specific value is 10.42 ± 1.26 mW/g.) The least squares regression equation for $\dot{H}_{sm}$ as a function of T_e below 24°C is: $\dot{H}_{sm}$ (kJ/h) = 3.81 − 0.084 T_e ($r^2 = 0.610$, $S_{y \cdot x} = 0.366$, $S_b = 0.0134$, $n = 27$). This line extrapolates to $\dot{H}_{sm} = 0$ at $T_e = 45.5$°C, suggesting that thermal conductance is not constant below the T_{lc}.

Cost of activity.—Table 3 presents mean values for the rate of energy expenditure associated with different activity categories. Because these measurements were made on fed birds, the energy values include not only the cost of the activity but the basal requirement, produc-

tive costs (if any), and the heat increment of feeding (SDA). The rate of energy expenditure during the four low-level activities—alert perching, preening, eating, and hopping—was similar, ranging from 2.0 to 2.3 times $\dot{H}_b$.

Doubly-labeled water.—Calculating $\dot{H}_{TD}$ from CO_2 production requires knowledge of the bird's diet, because the heat equivalent per liter CO_2 depends on the type of substrate being oxidized—averaging 21.14 kJ for carbohydrate, 27.25 kJ for protein, and 27.75 kJ for fat (King and Farner 1961). Assigning a precise heat equivalent to our shrikes' CO_2 production is difficult, because we are unsure of their actual diet. Although they were provided with strips of lean chicken breast (metabolizable dry matter: 92% protein and 8% fat), some birds also caught insects (mostly flies and bees) during our TB runs. Furthermore, because not all birds ate enough to maintain their mass, body fat catabolism must be accounted for. For a shrike that was in energy balance, each liter of CO_2 produced would be equivalent to 27.29 kJ of heat if it fed exclusively on chicken and 25.70 kJ if it ate solely on insects (Nagy 1983). We deduced each bird's diet, and the corresponding heat equivalents (Table 4), from its mass change and our behavioral observations of its food intake. Because the potential heat equivalents range only from 25.70 to 27.75 kJ/l CO_2, and because we could gauge what the shrikes ate, the error in our DLW $\dot{H}_{TD}$ estimates due to faulty diet assignment is probably less than 5%. Calculated in this way, $\dot{H}_{TD}$ averaged 105.9 kJ/day, or 2.5 times $\dot{H}_b$ (range: 2.2–2.7 times $\dot{H}_b$; Table 4).
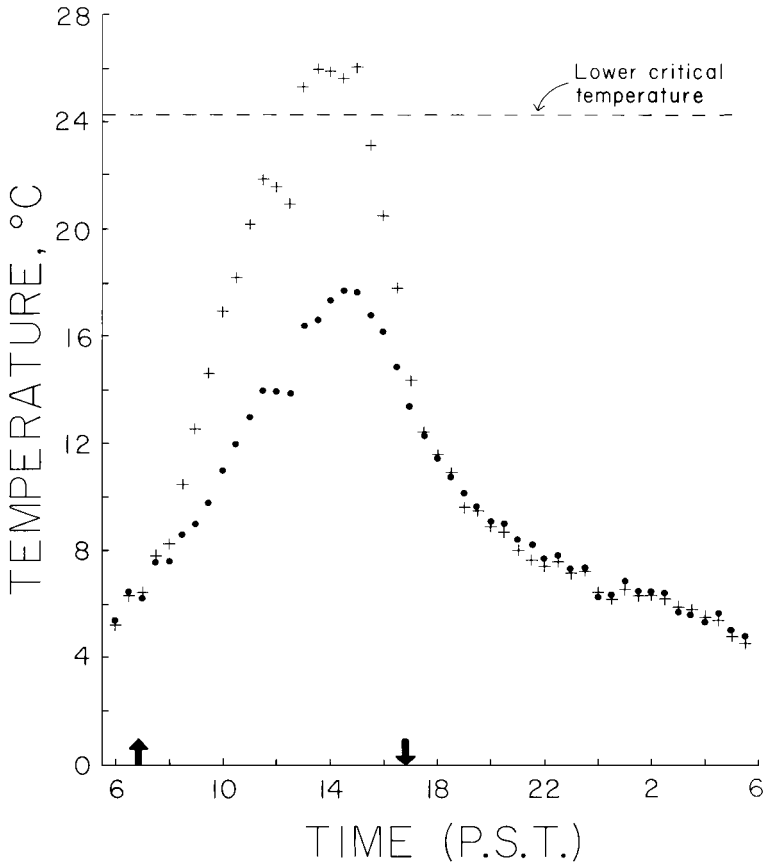
Fig. 1.   Relation of mean operative temperature (+) experienced by Loggerhead Shrikes and mean air temperature (●) measured at 2 m to time of day. Arrows indicate sunrise and sunset.
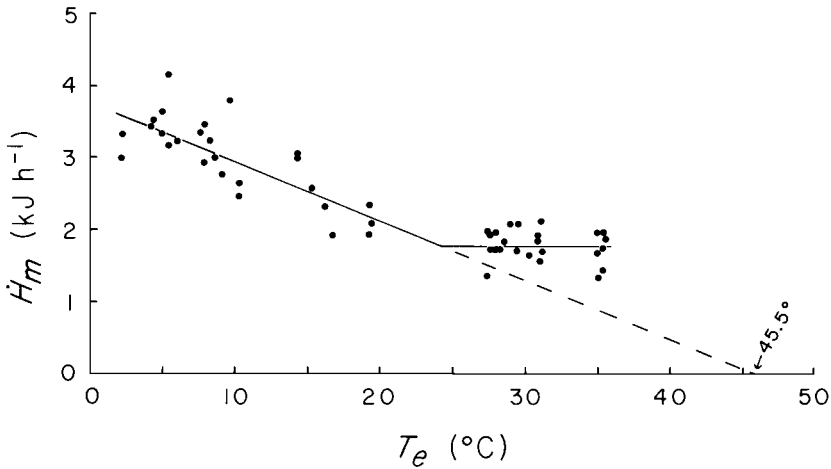

Fig. 2.   Relation of metabolic heat production ($\dot{H}_m$) of Loggerhead Shrikes to operative temperature (T_e). Each dot represents the minimal fasted $\dot{H}_m$ determined during the rest phase of the daily cycle. Line fitted to data below 25°C by method of least squares. Above 25°C, the line depicts the mean $\dot{H}_m$.

TABLE 3. Cost of activity in Loggerhead Shrikes.

	Number of shrikes	Number of observations	kJ/h[a]	Multiple of $\dot{H}_b$
Basal metabolism ($\dot{H}_b$)[b]	9	27	1.79 ± 0.20	1.0
Alert perching	6	68	3.51 ± 0.60	1.98
Preening	3	4	3.87 ± 0.71	2.18
Eating	5	21	3.87 ± 0.63	2.19
Hopping	2	5	4.05 ± 0.67	2.28
Flying[c]	—	—	23.7	13.2

[a] Values are means ± SD of thermoneutral metabolic measurements.
[b] Rest phase (ρ) determinations. Mean mass of birds during these measurements was 48.6 g.
[c] Calculated from Eq. 15 of Tucker (1975) using a mean mass of 48.6 g and a mean wing span of 0.32 m.

DISCUSSION

Previous TB estimates of $\dot{H}_{TD}$ have followed one of two contrasting approaches. One, tracing its antecedents to Kendeigh (1949) and his students, uses existence metabolism as a basis for energy assignments (e.g. Schartz and Zimmerman 1971, Wiens and Innis 1973, Koplin et al. 1980), whereas the other, initiated by Pearson (1954), bases its energy assignments on standard metabolism determined from laboratory measurements of $\dot{V}O_2$ (e.g. Stiles 1971, Walsberg 1977, Mugaas and King 1981). For brevity's sake, we refer to these two approaches as Kendeigh's method and Pearson's method. The main advantage of Kendeigh's method is that $\dot{H}_{TD}$ can be estimated from a few simple measurements and existing allometric equations that relate existence metabolism to body mass and average daily T_a. A further advantage is that Kendeigh's equations (Kendeigh et al.

1977) seemingly account for several of the variables that affect $\dot{H}_{TD}$: photoperiod, taxon, season, and temperature. The major disadvantages of the method are that (1) it calculates the thermoregulatory requirement from T_a alone and (2) existence metabolism includes the cost of cage activity, which may vary considerably (King 1974). Consequently, Kendeigh's method may yield unreliable $\dot{H}_{TD}$ estimates under those conditions in which T_a is a poor measure of the thermal environment or in which field activity levels differ markedly from those of caged birds. Pearson's method, in contrast, has the potential for accurately estimating thermoregulatory costs by means of recently developed biophysical models, with the attendant disadvantage of requiring extensive quantification of many variables. Below, we use our TB and meteorological data to calculate $\dot{H}_{TD}$ by both methods, and we include five iterations of the Pearson method that differ in the

TABLE 4. Body mass and water content, CO_2 production, and daily energy expenditure ($\dot{H}_{TD}$) determined by doubly-labeled water.

Run number	Mean body mass (g)	Body water (%)	CO_2 production ($cm^3 \cdot g^{-1} \cdot h^{-1}$)	Diet[a]	Caloric equivalent (kJ/l CO_2)	Fraction of 24 h[b]	$\dot{H}_{TD}$ (kJ/day)
1	43.3	65.1	3.70	C + I	26.50	1.007	102.6
2	47.8	62.8	3.42	C + I + F	26.92	0.958	101.2
3	42.5	61.2	3.46	F	27.75	0.951	93.1
4	44.2	62.3	3.69	I + F	26.73	0.944	98.8
5	46.1	64.2	3.77	C + I	26.50	0.986	109.0
6	43.2	62.5	4.15	F	27.75	0.917	109.5
7	46.8	61.7	3.88	C + I + F	26.92	0.979	114.9
8	49.9	58.5	3.54	F	27.75	1.000	117.7
Mean	45.5	62.3	3.70	—	27.10	0.968	105.9
(SD)	(2.6)	(2.0)	(0.24)		(0.56)	(0.031)	(8.4)

[a] Substance catabolized during measurement period: C = chicken; I = insects; F = body fat.
[b] Proportion of 24-h day upon which TB estimate of $\dot{H}_{TD}$ was based.

way in which thermoregulatory and activity costs are calculated.

An animal's $\dot{H}_{TD}$ is partitioned among the requirements for maintenance, production (growth, gametogenesis, etc.), physical activity, thermoregulation, and the heat increment of feeding (SDA). To be robust, a TB model must account explicitly for each of these categories, although this has not always been done in the past. In our study, production was excluded, because we studied nonmigratory, nonbreeding birds in November (well after their postnuptial molt) and because our birds did not gain mass during the TB measurements. [For models that include production see Mugaas and King (1981) or Ashkenazie and Safriel (1979).]

PEARSON'S METHOD

The essence of Pearson's method is a temperature-dependent model by which laboratory-derived measurements of $\dot{H}_m$ at various temperatures are extrapolated to the field. Before the mid-1970s, heat transfer between an animal and its environment was usually described by a biological interpretation of "Newton's Law of Cooling" (Scholander et al. 1950) in which T_a alone characterized the thermal environment. This simplistic model has been superseded by electrical-analog models that integrate animal properties with radiative and convective characteristics of the environment (see Bakken and Gates 1975, Bakken 1976, Robinson et al. 1976, Mahoney and King 1977). Electrical-analog models accurately describe heat transfer under laboratory conditions (Mahoney and King 1977, Bakken 1980) and have been used in conjunction with TB data to estimate $\dot{H}_{TD}$ of birds under field conditions (e.g. Walsberg and King 1978a, Mugaas and King 1981, Biedenweg 1983). They should provide accurate estimates of thermoregulatory costs and, hence, of $\dot{H}_{TD}$. These models quantify the energy expended on thermoregulation by extrapolating laboratory measurements of $\dot{H}_m$ made at various stable T_e's to field conditions. Laboratory measurements are usually made under free-convective conditions, whereas forced convection often prevails in the field. Therefore, extrapolating laboratory data to the field necessitates accounting for the affect of wind on heat loss (Bakken 1976). To do this, we used a heat-transfer model (see Appendix), based on T_e and thermal resistance, that is formally sim-

ilar to the model of Robinson et al. (1976) but differs from other field applications of this model (Walsberg and King 1978a, Mugaas and King 1981, Biedenweg 1983) in how body resistance (r_b) is estimated (for details and rationale see Buttemer et al. MS).

Values for $\dot{H}_{TD}$ calculated by this convection-adjusted electrical-analog model (TB-1) are listed in Table 5. The mean TB-1 estimate (105.7 kJ/day) is virtually identical to the mean DLW estimate (105.9 kJ/day), with individual TB-1 estimates ranging from -8.1% to $+7.5\%$ of the individual DLW values—about the same as the limits of accuracy of the DLW method. This level of agreement equals or exceeds that attained in previous studies, which estimated $\dot{H}_{TD}$ simultaneously by TB and DLW methods (Table 6). Furthermore, in previous studies (except that of *Melopsittacus undulatus*, which used the same methods), TB and DLW estimates were not significantly correlated, indicating that the other TB models lacked elements necessary to track the energy expenditure of individual birds. In contrast, our DLW and TB-1 estimates are significantly correlated (Fig. 3), demonstrating that our TB model is robust enough to gauge the $\dot{H}_{TD}$ of individual birds accurately.
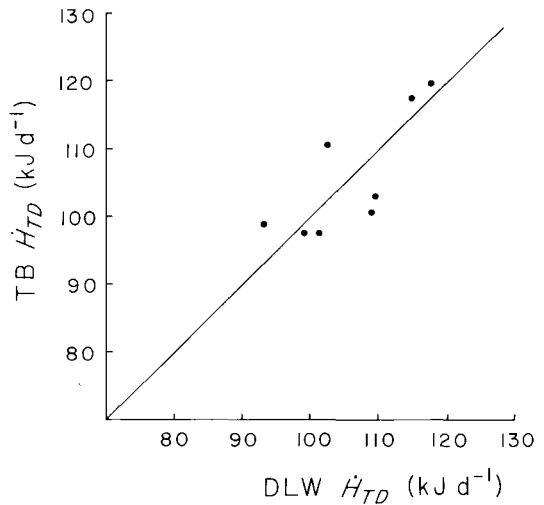

Fig. 3. Relation of daily energy expenditure ($\dot{H}_{TD}$) calculated by the convection-adjusted electrical-analog time-budget model (TB-1) to corresponding $\dot{H}_{TD}$ values measured with doubly-labeled water (DLW). The points fall along the line of equality. The least squares equation for the relation (line not shown) is $Y = 15.8 + 0.85X$ ($r = 0.791$; $P < 0.05$).

TABLE 5. Comparison of doubly-labeled water (DLW) and time-budget estimates of daily energy expenditure in Loggerhead Shrikes.

| | | Pearson's method[a] | | | | | Kendeigh's method | |
| | | | | | | | Kendeigh | |
Run number	DLW	TB-1	TB-2	TB-3	TB-4	Utter (1971)	et al. (1977)	Koplin et al. (1980)
1	102.6	110.1	119.8	91.6	133.6	87.9	121.4	115.8
2	101.2	97.6	108.1	82.2	121.4	86.0	125.6	113.6
3	93.1	98.9	109.4	87.5	120.6	81.1	120.7	108.3
4	98.8	97.6	109.4	88.6	120.6	84.9	122.9	112.2
5	109.0	100.9	110.7	89.5	123.8	90.4	124.1	116.1
6	109.5	103.0	110.0	85.1	125.5	78.7	118.5	105.0
7	114.9	117.5	125.6	98.6	143.7	88.9	137.2	126.6
8	117.7	119.8	129.5	101.8	143.9	94.5	141.6	133.0
Mean[b]	105.9	105.7	115.3*	90.6*	129.1*	86.6*	126.5*	116.3*
(SD)	(8.4)	(9.0)	(8.4)	(6.6)	(10.0)	(5.1)	(8.3)	(9.3)
% difference[c]		−0.1	+9.1	−14.2	+22.2	−18.0	+19.8	+10.1

[a] TB-1 = convective TB based on T_e and measured activity costs; TB-2 = convective TB based on T_a and measured activity costs; TB-3 = nonconvective TB based on T_e and measured activity costs; TB-4 = convective TB based on T_e and metabolic data of Cunningham (1979).

[b] * = significantly different from DLW values; $P < 0.05$, paired, two-tailed t-test.

[c] $[(TB − DLW)/DLW] \cdot 100$; mean of individual values.

There are two reasons why method TB-1 provides excellent $\dot{H}_{TD}$ estimates. First, it appears to assess the thermoregulatory requirement accurately, and, second, it uses measured rather than assumed metabolic costs for behavioral assignments. Under the cool conditions that prevailed during our study, shrikes expended an average of 42% of their total $\dot{H}_{TD}$ on thermoregulation (44.2 kJ/day). Accurately assessing this component requires knowledge of the T_e and u experienced by the bird as well as reasonable estimates of r_b under field conditions. Thus, when we used T_a rather than T_e in our calculations, the resulting $\dot{H}_{TD}$ estimate differed sig-

nificantly from that of DLW, averaging 9.1% greater (Column TB-2, Table 5). $\dot{H}_{TD}$ estimates based on T_a overestimated the thermoregulatory component, because, unlike T_e, T_a did not exceed T_{lc} during part of the day. In contrast, $\dot{H}_{TD}$ estimates for White-crowned Sparrows (Zonotrichia leucophrys; Mahoney 1976) and Budgerigars (Buttemer et al. MS) were not significantly different when T_a was substituted for T_e.

For our shrikes, accurately assessing thermoregulatory costs required knowledge not only of T_e but also of how wind affected heat loss. This is illustrated by method TB-3, which was identical to TB-1 except that wind was ig-

TABLE 6. Comparison of simultaneous time-budget (TB) and doubly-labeled water (DLW) estimates of daily energy expenditure in birds.

| Species | Number of observations | Percentage difference between TB and DLW estimates[a] | | Source |
		Mean	Range	
Mimus polyglottos	6	+5.2	−31.1 to +45.4	Utter (1971)
Phainopepla nitens	6	−39.2	−44.0 to −29.2	Weathers & Nagy (1980)
Passerculus sandwichensis	6	+2.7	−19.8 to +18.3	Williams & Nagy (1984)
Lanius ludovicianus	8	−0.1	−8.1 to +7.5	This study (TB-1)
Melopsittacus undulatus				Buttemer et al. (MS)
Winter	6	−0.3	−12.9 to +8.4	
Summer	6	+0.8	−13.3 to +11.8	

[a] Calculated as $[(TB − DLW)/DLW] \cdot 100$.

nored in the calculation of field r_s. The mean $\dot{H}_{TD}$ estimated by TB-3 (Table 5) was 14.2% lower than the DLW estimate (range: -22.3 to -6.0%), indicating that 14.2% of the shrikes' $\dot{H}_{TD}$ was required to offset the increased heat loss caused by wind. The thermoregulatory requirement estimated by method TB-3, 28 kJ/day, is 37% less than the value obtained by TB-1. Thus, the percentage error in the thermoregulatory cost estimate is 2.6 times the percentage error in the mean $\dot{H}_{TD}$ estimate. Clearly, studies that seek to partition $\dot{H}_{TD}$ among the requirements for maintenance, production, activity, and thermoregulation should use the convection-adjusted electrical-analog model (TB-1) to accommodate heat-transfer components.

Pearson's method requires knowledge of how $\dot{H}_{sm}$ relates to temperature. Because obtaining these data empirically is tedious, many previous TB studies employed data derived from the literature or allometric equations. Intraspecific measurements of $\dot{H}_m$ in small birds, however, can vary by up to 50% between populations or seasons (Weathers and Caccamise 1978, Ettinger and King 1980). Thus, relying on literature values of $\dot{H}_m$ can result in erroneous $\dot{H}_{TD}$ estimates. This is illustrated by method TB-4 (Table 5), in which we used the convection-adjusted electrical-analog model (method TB-1) to calculate $\dot{H}_{TD}$ but substituted $\dot{H}_{sm}$ data obtained for another shrike population (Cunningham 1979) for our empirical data. $\dot{H}_{TD}$ calculated in this way averaged 22.2% higher than the DLW estimate. Cunningham's data differed from ours mainly in the value of $\dot{H}_{sm}$ below T_{lc}. His $\dot{H}_b$ value for shrikes was only 2.7% higher than ours (1.84 versus 1.79 kJ/h), whereas the slope of $\dot{H}_{sm}$ below T_{lc} in his study was 11.9% higher than ours (0.094 versus 0.084 kJ·h^{-1}·°C^{-1}). These seemingly minor differences in $\dot{H}_m$ translate into major differences in $\dot{H}_{TD}$, because most of the time our shrikes were not in thermoneutrality. Such effects may partly account for the poor agreement between TB and DLW estimates obtained for *Phainopepla nitens* (Weathers and Nagy 1980).

To emphasize further the importance of using measured energy equivalents and accurately accounting for thermoregulatory costs, we estimated $\dot{H}_{TD}$ by Utter's (1971) TB model, which does not account for thermal effects and calculates $\dot{H}_b$ from the equation of Lasiewski and Dawson (1964). The mean $\dot{H}_{TD}$ estimated by this model was 86.6 kJ/day, an error of -18%. Ut-

ter's model worked reasonably well with Mockingbirds (*Mimus polyglottos*, Utter 1971) but not with Savannah Sparrows (*Passerculus sandwichensis*, Williams and Nagy 1984a), for which it underestimated simultaneous DLW measurements by 50%. We further evaluated Utter's model by calculating the Phainopepla's $\dot{H}_{TD}$ with the data of Weathers and Nagy (1980) and found that Utter's model again underestimated $\dot{H}_{TD}$, this time by an average of 15%. Thus, in three out of the four studies in which $\dot{H}_{TD}$ was estimated simultaneously by DLW, Utter's model underestimated the DLW value by 15–50%. Clearly, accurate quantification of $\dot{H}_{TD}$ by the TB method requires concurrent measurement of the species' $\dot{H}_{sm}$ as well as quantification of thermoregulatory costs. Earlier TB studies that used assumed $\dot{H}_{sm}$ versus T_a data should be interpreted with caution, as their estimates may be in error by ± 20–40%.

KENDEIGH'S METHOD

Koplin et al. (1980) presented a variant of the Kendeigh method that is adaptable to our winter shrikes. Inputs to their model include: (1) body mass, (2) time spent in flight and nonflight activity, (3) the power required for flight, (4) mean daily air temperature, (5) photoperiod length, and (6) mean nocturnal air temperature. In brief, their method uses the equations of Kendeigh et al. (1977) to calculate $\dot{H}_{em}$ for the nonflight portion of the photophase from the bird's mass and mean air temperature. The power required for flight is added to this value to obtain the energy expended during the day. The nighttime energy requirement is calculated as the standard metabolic rate ($\dot{H}_{sm}$) predicted from the mean nighttime T_a and the bird's mass. Details of the model are presented in the Appendix.

The mean $\dot{H}_{TD}$ estimated by the method of Koplin et al. differs significantly from the DLW estimate, with individual TB estimates averaging 10.1% higher than the DLW values (range: -4.1 to $+16.3\%$; Table 5). The DLW and TB estimates are significantly correlated ($r = 0.727$), however, suggesting that this method tracks the energy expenditure of individual shrikes, but with a positive bias. A somewhat different result was obtained by Koplin et al. (1980). They obtained excellent agreement between mean $\dot{H}_{TD}$ estimates based on their method and simultaneous measurements of food consump-

tion but poor correspondence between values for individual birds. Similarily, in free-living Savannah Sparrows, Williams and Nagy (1984a) found that $\dot{H}_{TD}$ estimated by Kendeigh's method differed from simultaneous DLW measurements by only +4.7%. Here too, however, the TB estimates were not correlated with the DLW measurements. Based on the available studies, the Kendeigh method would seem to provide reasonable mean estimates of $\dot{H}_{TD}$ (mean errors are usually <10%) but unreliable estimates for individual birds. For shrikes, however, the good agreement is largely fortuitous. Approximately 14% of the shrikes' $\dot{H}_{TD}$ represents increased heat production needed to compensate for the heat loss caused by wind. Had there been no wind during our study, the shrikes' $\dot{H}_{TD}$ would have been lower, while $\dot{H}_{TD}$ calculated by the model of Koplin et al. would have been unchanged. Under these conditions, the model of Koplin et al. would have overestimated $\dot{H}_{TD}$ by 28% instead of 10%.

ALLOMETRIC APPROXIMATIONS

As an alternative to the time-budget method, $\dot{H}_{TD}$ can be estimated allometrically. Kendeigh et al. (1977: 182) presented equations based on H_{em} that permit a bird's $\dot{H}_{TD}$ to be approximated given only its mass and the mean daily T_a. Their equation for winter passerines produces $\dot{H}_{TD}$ values for shrikes that average 20% higher than the DLW values (Table 5). Similarily, Walsberg's (1983) allometric equation, which calculates $\dot{H}_{TD}$ from mass alone, yields mean values for shrikes (131 kJ/day) that average 24% higher than the DLW values. Apparently, both of these allometric techniques provide only rough approximations.

CONCLUSIONS

Using the doubly-labeled water technique, we show that accurate time-budget estimates of daily energy expenditure ($\dot{H}_{TD}$) are possible but depend upon: (1) the use of measured energy equivalents for the various behaviors and (2) the extrapolation of laboratory measurements of oxygen consumption to field conditions by means of heat-transfer theory such as that based on T_e and thermal resistances. The latter prerequisite requires detailed knowledge of the thermal conditions surrounding the bird. Although TB estimates based on existence metab-

olism (Kendeigh's method) may provide reasonable $\dot{H}_{TD}$ estimates (±10%) under some conditions, the reliance of this method upon mean daily T_a to characterize the bird's thermal environment makes it susceptible to large errors. TB estimates that assign to behaviors energy equivalents that have been derived from the literature rather than empirically are subject to errors of 20–40% and, thus, may be no better than approximations that use existing allometric equations to predict $\dot{H}_{TD}$ from the bird's body mass alone (Walsberg 1983) or from its mass and the mean daily air temperature (Kendeigh et al. 1977).

LITERATURE CITED

ASHKENAZIE, S., & U. N. SAFRIEL. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow Alaska. Ecology 60: 783–799.

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.

———. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. Physiol. Zool. 53: 108–119.

———, & D. M. GATES. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology and evolution. Pp. 255–290 *in* Perspectives of biophysical ecology (D. M. Gates and R. B. Schmerl, Eds.). New York, Springer-Verlag.

———, W. A. BUTTEMER, W. R. DAWSON, & D. M. GATES. 1981. Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. Ecology 62: 311–318.

BIEDENWEG, D. W. 1983. Time and energy budgets of the Mockingbird (*Mimus polyglottos*) during the breeding season. Auk 100: 149–160.

BUTTEMER, W. A. 1981. The thermal significance of winter roost-site selection by American Goldfinches (*Carduelis tristis*). Unpublished Ph.D. dissertation. Ann Arbor, Michigan, Univ. Michigan.

CUNNINGHAM, K. G. 1979. Bioenergetics of the Log-

gerhead Shrike: relation between lifestyle and metabolism. Unpublished M.S. thesis. Irvine, California, Univ. California.

DOL'NIK, V. R. 1980. Time and energy budgets in free-living birds [In Russian]. Acad. Sci. U.S.S.R., Proc. Zool. Instit. 133: 3–37.

ETTINGER, A. O., & J. R. KING. 1980. Time and energy budgets of the Willow Flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533–546.

HAILS, C. J., & D. M. BRYANT. 1979. Reproductive energetics of a free-living bird. J. Anim. Ecol. 48: 471–482.

KENDEIGH, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. Auk 66: 113–127.

———, V. R. DOL'NIK, & V. M. GAVRILOV. 1977. Avian energetics. Pp. 127–204 in Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). New York, Cambridge Univ. Press.

KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4–85 in Avian energetics (R. A. Paynter, Ed.). Publ. Nuttall Ornithol. Club No. 15.

———, & D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215–288 in Biology and comparative physiology of birds, vol. 2 (A. J. Marshall, Ed.). New York, Academic Press.

KOPLIN, J. R., M. W. COLLOPY, A. R. BAMMANN, & H. LEVENSON. 1980. Energetics of two wintering raptors. Auk 97: 795–806.

LASIEWSKI, R. C., & W. R. DAWSON. 1964. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13–23.

LEFEBVRE, E. A. 1964. The use of D_2O^{18} for measuring energy metabolism in Columba livia at rest and in flight. Auk 81: 403–416.

LIFSON, N., & R. McCLINTOCK. 1966. Theory and use of the turnover rates of body water for measuring energy and material balance. J. Theor. Biol. 12: 46–74.

MAHONEY, S. A. 1976. Thermal and ecological energetics of the White-crowned Sparrow (Zonotrichia leucophrys) using the equivalent black-body temperature. Unpublished Ph.D. dissertation. Pullman, Washington, Washington State Univ.

———, & J. R. KING. 1977. The use of the equivalent black-body temperature in the thermal energetics of small birds. J. Thermal Biol. 2: 115–120.

MITCHELL, J. W. 1976. Heat transfer from spheres and other animal forms. Biophys. J. 16: 561–569.

MUGAAS, J. N., & J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie: a study of thermal and behavioral energetics. Studies in Avian Biol. No. 5.

NAGY, K. A. 1975. Water and energy budgets of free-living animals: measurement using isotopically labeled water. Pp. 227–245 in Environmental physiology of desert organisms (N. F. Hadley, Ed.). Stroudsburg, Pennsylvania, Dowden, Hutchinson and Ross.

———. 1983. The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. Publ. No. 12-1417. Los Angeles, Univ. California.

PALADINO, F. V., & J. R. KING. In press. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows (Zonotrichia leucophrys gambelii). Physiol. Zool.

PEARSON, O. P. 1954. The daily energy requirements of a wild Anna Hummingbird. Condor 56: 317–322.

ROBINSON, D. E., G. S. CAMPBELL, & J. R. KING. 1976. An evaluation of heat exchange in small birds. J. Comp. Physiol. 105: 153–166.

SCHARTZ, R. L., & J. L. ZIMMERMAN. 1971. The time and energy budget of the male Dickcissel (Spiza americana). Condor 73: 65–76.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, & L. IRVING. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99: 259–271.

STILES, F. G. 1971. Time, energy, and territoriality of the Anna Hummingbird (Calypte anna). Science 173: 818–821.

TUCKER, V. A. 1975. Flight energetics. Pp. 49–63 in Avian physiology (M. Peaker, Ed.). London, Academic Press.

UTTER, J. M. 1971. Daily energy expenditure of free-living Purple Martins (Progne subis) and Mockingbirds (Mimus polyglottos) with comparison of two northern populations of Mockingbirds. Unpublished Ph.D. dissertation. New Brunswick, New Jersey, Rutgers Univ.

VEGHTE, J. H., & C. F. HERREID. 1965. Radiometric determination of feather insulation and metabolism of arctic birds. Physiol. Zool. 38: 267–275.

WALSBERG, G. E. 1977. Ecology and energetics of contrasting social systems in Phainopepla nitens (Aves: Ptilogonatidae). Univ. Calif. Publ. Zool. 108: 1–63.

———. 1980. Energy expenditure in free-living birds: patterns and diversity. Pp. 300–305 in Acta 17th Congr. Internal. Ornithol., vol. 1 (R. Nohring, Ed.). Berlin, Deutschen Ornithologen-Gesellschaft.

———. 1983. Avian ecological energetics. in Avian biology, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

———, & J. R. KING. 1978a. The energetic consequences of incubation for two passerine species. Auk 95: 644–655.

———, & ———. 1978b. The relation of the external surface area of birds to skin surface area and body mass. J. Exper. Biol. 76: 185–189.

WEATHERS, W. W., W. A. BUTTEMER, & K. A. NAGY. In

press. Simultaneous estimates of daily energy expenditure using time-budget analysis and doubly labeled water. Proc. 18th Intern. Ornithol. Congr. (Moscow), 1982.

———, & D. F. CACCAMISE. 1978. Seasonal acclimatization to temperature in Monk Parakeets. Oecologia 35: 173–183

———, & K. A. NAGY. 1980. Simultaneous doubly labeled water (^{3}HH^{18}O) and time-budget estimates of daily energy expenditure in *Phainopepla nitens*. Auk 97: 861–867.

———, C. J. SHAPIRO, & L. B. ASTHEIMER. 1980. Metabolic responses of Cassin's Finches (*Carpodacus cassinii*) to temperature. Comp. Biochem. Physiol. 65A: 235–238.

WIENS, J. A., & G. S. INNIS. 1973. Estimation of energy flow in bird communities. II. A simulation model of activity budgets and population bioenergetics. Proc. Summer Computer Simulation Conference, Montreal: 739–752.

WILLIAMS, J. B., & K. A. NAGY. 1984a. Daily energy expenditure of Savannah Sparrows: comparison of time-energy budget and doubly-labeled water estimates. Auk 101: 221–229.

———, & ———. 1984b. Validation of the doubly labeled water technique for measuring energy metabolism in Savannah Sparrows. Physiol. Zool. 57: 325–328.

WITHERS, P. C. 1977. Energetic aspects of reproduction by the Cliff Swallow. Auk 94: 718–725.

WOOD, R. A., K. A. NAGY, N. S. MACDONALD, S. T. WAKAKUWA, R. J. BECKMAN, & H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. Anal. Chem. 47: 646–650.

APPENDIX

PEARSON'S METHOD

We calculated $\dot{H}_{TD}$ by the following equation:

$$\dot{H}_{TD} = [t_{RP}\dot{H}_{RP}] + [t_\alpha\dot{H}_{AP}] \\ + [t_E(\dot{H}_E - \dot{H}_{AP1}) + t_P(\dot{H}_P - \dot{H}_{AP1}) \\ + t_F(\dot{H}_F - \dot{H}_{AP1}) + t_H(\dot{H}_H - \dot{H}_{AP1})], \quad (1)$$

where t's are activity durations (h), $\dot{H}$'s are the energy equivalents for various activities (kJ/h), and the subscripts identify the activity (see List of Symbols). The first bracketed term, the energy expended by a shrike during the night, consists of basal plus thermoregulatory requirements. The second bracketed term, the energy expended by a shrike perched during the day (photophase), consists of basal plus thermoregulatory costs, the activity cost associated with perching, and SDA. The third set of bracketed terms concerns the energy cost of activities that are additive to the cost of alert perching.

Three categories of input data are required by this model: physiological, morphological, and meteorological. The physiological inputs are T_b, T_s, $\dot{H}_m$, and $\dot{E}$. Of these we measured only $\dot{H}_m$. We used Cunningham's (1979) data for $\dot{E}$ of Loggerhead Shrikes to calculate the fraction of metabolic heat production lost evaporatively (E_f) as a function of T_a. We used Cunningham's (1979) values for T_b and calculated T_s from the equation of Veghte and Herreid (1965). The heat-transfer calculations require that $\dot{H}_m$ be expressed in units of W/m². To convert our $\dot{H}_m$ data (Fig. 2) to these units, we calculated surface area from the equation of Walsberg and King (1978b), using the shrikes' mean mass (45.5 g). The morphological inputs are m and d. Because shrikes typically perched with their long axis normal to the wind, d was taken as the body diameter at the widest point (0.05 m). The meteorological inputs required by the model are the u, T_a, and T_e experienced by the bird. These were determined at 10-min intervals throughout the 24-h day as described in materials and methods.

Nighttime energy expenditure.—When T_e exceeded the lower critical temperature (T_{lc}), we assumed $\dot{H}_{RP}$ equaled $\dot{H}_b$ regardless of the wind speed. At T_e's < T_{lc}, $\dot{H}_{RP}$ was assumed to vary with both T_e and u. Finding the value of $\dot{H}_{RP}$ at any u when $T_e < T_{lc}$ involved two steps. First, we solved Eq. (2) for r_t at 0°C and T_{lc}, using values for $\dot{H}_m$ from Fig. 1 together with the T_b and E_f data from Cunningham (1979).

$$\dot{H}_m - (E_f\dot{H}_m) = \rho c_p(T_b - T_e)/r_t. \quad (2)$$

Using these r_t values, we calculated the body resistance (r_b) of shrikes in the metabolism chamber at 0°C and T_{lc} from the relation (Robinson et al. 1976):

$$r_b = r_t - r_e,$$

where

$$r_e = r_r r_a/(r_r + r_a)$$

and

$$r_r = \rho c_p/4\sigma\epsilon T_a^3.$$

The convective resistance (r_a) component of r_e was calculated as the parallel sum of a forced-convective resistance, r_{fo}, and a free-convective resistance, r_{fr}:

$$r_a = r_{fo}r_{fr}/(r_{fo} + r_{fr}),$$

where

$$r_{fo} = 310\sqrt{d/u}$$

and

$$r_{fr} = 820[d/(T_s - T_a)]^{0.25},$$

where d is in meters, T in °C, and u in m/s. T_s was estimated from the relation $T_s = 12.5 + 0.7\ T_a$ (Veghte and Herreid 1965). We included a forced convective component ($u = 0.05$ m/s) in our calculation of metabolism chamber r_e. We measured the wind speed

that attended our metabolic measurements by using a heated taxidermic mount of a Budgerigar as a thermoanemometer (Buttemer et al. MS). The electrical power (P in W) required to maintain the mount's T_b at 36°C was measured in a wind tunnel (0.5 × 0.5 m; turbulence intensity = 0.10; T_e = 24.0°C) at wind speeds from 0.07 to 6.0 m/s. The mount was then placed in the metabolism chamber used for our physiological measurements and provided the same rate of airflow (750 cm³/min; T_e = 24.0°C). Based on the regression of P on u (r^2 = 0.99; n = 8), the value of P in the metabolic chamber corresponded to a wind speed of 0.05 m/s. Using a high-precision Alnor thermoanemometer, Mahoney (1976) measured metabolism chamber wind speeds of 0.1–0.2 m/s at airflow rates similar to ours. The difference is probably due to differences in the design of the metabolism chambers used in the two studies.

We used the r_b's calculated at 0°C and T_{lc} to estimate the value of r_b at intermediate T_e's. For extrapolation to field conditions, one must adjust these r_b's for the affect of wind. Previous field applications have assumed that r_b is not influenced by wind (e.g. Mugaas and King 1981). Elsewhere, we show that this assumption is incorrect for small birds (Buttemer et al. MS). Accordingly, we calculated the value for r_b under field conditions by the relation:

$$r_b' = r_b - [(0.10\sqrt{u})r_b],$$

where u is the wind speed (m/s) to which the bird was exposed. This adjustment in r_b (see Buttemer et al. MS) derives from two studies of the metabolic response of small passerines to forced convection (Robinson et al. 1976, Buttemer 1981). In both studies, r_b decreased approximately 10–15% for each unit increase in $\sqrt{u}$. Although r_b appears to be affected more by wind as temperature increases (Robinson et al. 1976, Buttemer 1981), we chose the fraction 0.10 for all r_b adjustments. The adjusted r_b' is combined with the value for r_e calculated from the field T_e, T_a, and u data to obtain r_t under field conditions. [To account for wind turbulence under field conditions (Mitchell 1976), we assumed $r_{fo} = 246\sqrt{d/u}$.] This field r_t, together with the field T_e and nighttime T_b (40°C), was used to solve Eq. (2) for the rate of dry heat transfer ($\dot{H}_m - E_f\dot{H}_m$) under field conditions, from which $\dot{H}_{RP}$ was calculated as

$$\dot{H}_{RP} = [\dot{H}_m - (E_f\dot{H}_m)] [1/(1 - E_f)].$$

Using the above method and the data for T_e and u corresponding to the bird's position, we calculated $\dot{H}_{RP}$ at 10-min intervals throughout the night.

Daytime energy expenditure.—This is the sum of the second and third terms in Eq. (1). The second bracketed term, $[t_a \dot{H}_{AP}]$, is the cost of perching during the day. It is obtained by extrapolating laboratory measurements of $\dot{H}_m$ (made on fed shrikes perching in the light during the day) to the field. $\dot{H}_{AP}$ can be calculated in the same way as $\dot{H}_{RP}$, provided the cost

of alert perching has been determined as a function of T_e. We measured $\dot{H}_{AP}$ only within the thermoneutral zone (where $\dot{H}_{AP} = 1.98\dot{H}_b$) and, thus, have estimated a value for $\dot{H}_{AP}$ at 0°C to calculate r_b at 0°C. Based on our measurements of Budgerigars (Buttemer et al. MS), we assigned alert perching a value of $3.18\dot{H}_b$ at 0°C. As with the nighttime determinations, $\dot{H}_{AP}$ was calculated at 10-min intervals throughout the photophase from the field T_e and u data.

Calculating the contribution of physical activity to $\dot{H}_{TD}$ (the third set of bracketed terms in Eq. 1) is potentially complicated, because the heat produced by intense activity may substitute for thermoregulatory requirements. This presumably applies to flight at all temperatures and to running at low temperatures (Mugaas and King 1981, Paladino and King in press) but not to moderate activities such as perching, preening, eating, or hopping. Because our shrikes did not run and spent little time flying, we made the simplifying assumption that flight costs did not substitute for the thermostatic requirement. Thus, the energy cost of the various activities was obtained by subtracting the cost of alert perching measured in the metabolism chamber (3.51 kJ/h) from the measured activity costs (Table 3) and multiplying the difference by the time spent in the activity. $\dot{H}_O$ was set equal to $\dot{H}_{AP}$ and t_O added in with t_a.

KENDEIGH'S METHOD

Modifying Eq. 1 of Koplin et al. (1980) and converting the allometric equations of Kendeigh et al. (1977) to units of kJ/h, the model can be summarized as:

$$\dot{H}_{TD} = t_{NF}\left[\frac{t_T(\dot{H}_{em_{Ta}}) - t_{RP}(\dot{H}_{sm})}{t_T - t_{RP}}\right]$$
$$+ t_r(\dot{H}_r) + t_{RP}(\dot{H}_{sm}),$$

where t_{NF} = duration of daytime nonflight activities as a proportion of the photophase ($t_{NF} = 1 - t_r$),

t_T = duration of the total observation period,

t_{RP} = time spent rest-perching (duration of night),

t_r = duration of flight as a proportion of photophase ($t_r = 1 - t_{NF}$);

$\dot{H}_{em_{Ta}}$ = existence metabolism of passerine birds during winter as a function of the average daily (24-h) air temperature (T_a):

$$\dot{H}_{em_{Ta}} = \dot{H}_{em_{0°C}} + (T_a)(b),$$

where $b = 1/30(\dot{H}_{em_{30°C}} - \dot{H}_{em_{0°C}})$,
$\dot{H}_{em_{30°C}} = 0.269m^{0.660}$,
$\dot{H}_{em_{0°C}} = 0.774m^{0.522}$;

$\dot{H}_{sm}$ = standard metabolism of passerine birds during the winter at night as a

function of the average nighttime air temperature (T_{na}):

$$\dot{H}_{sm} = \dot{H}_{sm_{0^\circ C}} - (h)(T_{na}),$$

where $\dot{H}_{sm_{0^\circ C}} = 0.539m^{0.531}$
and $h = 0.0127m^{0.543}$.

When $T_a > T_{lc}$, $\dot{H}_{sm} = \dot{H}_{b}$,

where $\dot{H}_b = 0.194m^{0.658}$

$\dot{H}_F$ = power requirement of flight, assumed to = $12\dot{H}_b$.

LIST OF SYMBOLS

c_p	specific heat of air ($10^3 J \cdot kg^{-1} \cdot {}^\circ C^{-1}$)
d	characteristic dimension (m)
$\dot{E}$	evaporative heat loss
E_f	fraction of metabolic heat production lost evaporatively
$\dot{H}_{AP}$	cost of alert (daytime) perching (kJ/h) calculated for field conditions
$\dot{H}_{AP1}$	cost of alert perching in thermal neutral zone (3.51 kJ/h)
$\dot{H}_b$	basal metabolic rate (kJ/h)
$\dot{H}_E$	cost of eating (kJ/h)
$\dot{H}_{em}$	existence metabolism (kJ/h)
$\dot{H}_F$	cost of flight (kJ/h)
$\dot{H}_H$	cost of hopping (kJ/h)
$\dot{H}_m$	metabolic heat production
$\dot{H}_O$	cost of other activities (kJ/h)
$\dot{H}_P$	cost of preening (kJ/h)
$\dot{H}_{RP}$	cost of rest (nighttime) perching (kJ/h)
$\dot{H}_{sm}$	standard metabolic rate (kJ/h)
$\dot{H}_{TD}$	total daily energy expenditure (kJ/day)
h	coefficient of heat transfer ($kJ \cdot h^{-1} \cdot {}^\circ C^{-1}$)
m	body mass (g)
r_a	boundary layer resistance (s/m)
r_b	whole-body thermal resistance (s/m)
r_b'	field whole-body thermal resistance (s/m)
r_e	equivalent resistance (s/m)
r_{fo}	forced-convective resistance (s/m)
r_{fr}	free-convective resistance (s/m)
r_r	radiative resistance (s/m)
r_t	total resistance (s/m)
T_s	surface temperature (${}^\circ C$)
T_a	air temperature (${}^\circ C$)
T_e	operative temperature (${}^\circ C$)
T_{lc}	lower critical temperature (${}^\circ C$)
T_{na}	nighttime air temperature (${}^\circ C$)
t	time (h)
t_α	duration of daylight period (h)
t_{AP}	time spent alert perching (h)
t_E	time spent eating (h)
t_F	time spent in flight (h)
t_H	time spent hopping (h)
t_{NF}	time spent in non-flight activities (daytime) (h)
t_P	time spent preening (h)
t_{RP}	time spent rest perching (h)
$\dot{V}O_2$	oxygen consumption (ml/min)
u	wind speed (m/s)
ϵ	emissivity of animal's surface (≈ 0.98)
σ	Stefan-Boltzmann constant ($5.67 \times 10^{-8} W \cdot m^{-2} \cdot {}^\circ K^{-4}$)
ρ	density of air (1.2 kg/m^3 at 20°C)