DAILY ENERGY EXPENDITURE OF SAVANNAH SPARROWS: COMPARISON OF TIME-ENERGY BUDGET AND DOUBLY-LABELED WATER ESTIMATES

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ABSTRACT.—Using the doubly-labeled water (DLW) technique, we measured the CO_2 production of six free-living male Savannah Sparrows (Passerculus sandwichensis, mean mass 19.1 g) and found a mean (± 1 SD) of 7.28 ± 1.36 ml CO_2/h. Assuming an R.Q. of 0.85 and 24 J/ml CO_2, we calculated a mean $\dot{H}_{TD}$ (daily energy expenditure) of 80.3 ± 16.6 kJ/day. Simultaneously to our DLW measurements, we constructed time budgets for the sparrows during their normal activities with the intent of exploring the agreement between predictions of a number of time-energy budget (TEB) models from the literature and DLW measurements. Our results reveal that several models yield reasonable results, the mean value for the models of Kendeigh et al. (1977), Walsberg (1977), and Mugaas and King (1981) differing from DLW measurements by only $+4.7$, -5.6%, and $+5.7\%$, respectively. Comparisons of $\dot{H}_{TD}$ as predicted by these TEB models between species and within species between nesting phases might be made with some confidence. However, the variation in TEB estimates is not related to variation in DLW measurements within our study. This precludes statements about differences between individuals. Received 28 June 1983, accepted 1 November 1983.

A RECURRING idea in ecological literature is that the life-history strategies of animals are inextricably coupled to allocation patterns of time and energy (King 1974). To explore how species expend energy during their daily and seasonal cycles, investigators have used the time-energy budget (TEB) method. This involves categorizing and timing an animal's activity throughout the day and subsequently calculating its daily energy expenditure ($\dot{H}_{TD}$) by means of laboratory measurements or estimates of the energetic costs of various activities (Schartz and Zimmerman 1971, Utter and LeFebvre 1973, Walsberg 1977, Ettinger and King 1980, Mugaas and King 1981). As pointed out by Weathers and Nagy (1980), a major lim-

itation of this method is the lack of verification for the estimates of $\dot{H}_{TD}$.

A second method for determining $\dot{H}_{TD}$, originally developed by Lifson et al. (1955) and later revised by Nagy (1975), incorporates the use of doubly-labeled water (DLW) to measure the CO_2 production of animals. The technique involves isotopic labeling of body water with oxygen-18 and tritium or deuterium and calculating the rate of CO_2 production from the difference between the turnover rates of the two isotopes. Validation studies on 10 species of vertebrates and one invertebrate showed that the DLW method agreed within $\pm 8\%$ of direct gravimetric measurement of CO_2 production, indicating that reasonably reliable measures of

CO_2 production of free-living animals can now be obtained (Nagy 1980). An animal's $\dot{H}_{TD}$, in terms of heat production (joules or calories), can be calculated from CO_2 values through information about the chemical composition of the diet and its digestibility and with established conversion factors.

One way to ascertain the accuracy of TEB estimates of $\dot{H}_{TD}$ is to compare these with estimates made with the DLW method. Using this approach, Weathers and Nagy (1980) and Weathers et al. (in press) showed that the TEB results averaged 40% and 18% lower than DLW results for Phainopeplas (*Phainopepla nitens*) and Budgerigars (*Melopsittacus undulatus*), respectively, confined to an outdoor aviary. The study of Utter and LeFebvre (1973) of Purple Martins (*Progne subis*) showed that TEB analysis yielded values averaging 10–20% higher.

In this study, we compare $\dot{H}_{TD}$ estimates obtained with the DLW method for free-ranging male Savannah Sparrows with those derived from seven predictive models from the literature. We show that four of these models yield reasonable mean $\dot{H}_{TD}$ estimates for Savannah Sparrows, but three models do not. We conclude that some models can be valuable for comparing $\dot{H}_{TD}$ during different stages of nesting or between different species. We also show that a lack of correspondence between DLW and TEB measurements for any given individual bird precludes an analysis of differences between individuals.

MATERIALS AND METHODS

Study area and birds.—We studied male Belding's Savannah Sparrows (*Passerculus sandwichensis beldingi*) during their breeding season (April–June) in 1977. Our study area lay in the middle and upper littoral zone of a large salt marsh on the Point Mugu Naval Air Station, Pt. Mugu, California (34°07′N, 119°07′W). Vegetation at this site was dominated by *Salicornia virginica, Frankenia grandifolia, Batis maritima,* and *Monanthochloe littoralis.* Large barren salt pans and shallow tidal creeks intermixed with patches of vegetation formed a mosaic of sites used by Savannah Sparrows for foraging. Belding's Savannah Sparrows reside in the marsh year-round with breeding beginning in early April. All birds on our 2-ha study area were fitted with aluminum U.S. Fish and Wildlife bands and were color-banded to facilitate individual recognition. We selected individuals with territories containing tidal creeks or salt pans so that we could

more easily follow birds while they foraged. The males we studied were paired with females that were building nests or incubating eggs. The males participated in neither of these activities.

Doubly-labeled water.—Tritiated water injected into a pectoral muscle of Savannah Sparrows mixed completely in their body water within 1 h (Williams and Nagy in press). Prior field experience indicated that netting and then holding these birds for 1 h during daylight often caused them to leave their territories for up to several hours. Using sham injections and varying capture times, we found that males that were handled and released late in the evening would resume their normal activities (singing and territorial defense) at first light the following morning. Therefore, in this study we made initial captures only in the evening. Birds were captured by luring them into a mist net with a tape recording of another male's song. We studied one bird at a time so that full attention could be devoted to the construction of a reliable time budget.

After initial capture, birds were injected with 0.10 ml of water containing 95 atom % oxygen-18 and 30 microcuries of tritium, weighed to 0.01 g on a triple beam balance, and their identification numbers and color bands were recorded. Injections were made into a pectoral muscle with a glass syringe, which had been calibrated in the laboratory by weighing it ($\pm$0.1 mg) full and emptied of distilled water. An hour after injection, we took blood samples (ca. 0.10 ml) from a brachial vein and flame-sealed them in heparinized microhematocrit tubes and then released the birds. We observed the bird the following day (see time-budgets section). We recaptured the bird that evening or the next morning, weighed it, and took a second blood sample before releasing it. Blood samples were stored at 4°C pending analysis.

In the laboratory we micro-distilled (Wood et al. 1975) each sample to obtain pure water. We assayed the water for tritium activity with a Beckman LS 230 liquid scintillation counter (using a toluene-Triton X 100-PPO scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of 0–18 to fluorine-18 and by subsequently counting the gamma-emitting F-18 with a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Rates of CO_2 production were calculated by means of equation (2) of Nagy (1980). Throughout this paper we have assumed an R.Q. of 0.85 and a conversion factor of 24 J/ml CO_2. These factors are intermediate between those for insectivorous animals and those for herbivorous and granivorous animals (Nagy 1983), in accordance with the presumed mixed diet of Savannah Sparrows.

The DLW technique has been compared with direct measures of CO_2 production for three species of birds, including Savannah Sparrows, with results showing an average overestimate of 3–7% (Table 1). These data suggest that the DLW method can yield

TABLE 1. Summary of validation studies of the doubly-labeled water method on birds.

Species (n)	Mass (g)	Mean error (%)[a]	Range	Reference
Pigeon (10) (*Columba livia*)	380	+3.6	−12.2−+16.8	LeFebvre (1964)
House Martin (4) (*Delichon urbica*)	17.8	+3.4	?	Hails and Bryant (1979)
Savannah Sparrow (7)	16.6	+6.5	−0.2−+11.0	Williams and Nagy (in press)

[a] Calculated as (DLW-DM/DM) × 100, where DM (direct measurement) was done by trapping expired CO_2 in Ascarite or measuring CO_2 in downstream air by infrared gas analysis.

reasonable estimates of CO_2 production of free-ranging birds.

We obtained hourly weather records for air temperature (T_a), wind (m/s), solar insolation (W/m²), and relative humidity (RH) from the Pt. Mugu weather station located 1 km from our study area.

Time budgets.—Time-activity budgets were determined for each injected bird by recording its activity (every 10 s) at the moment a signal was produced by an electronic metronome (Wiens et al. 1970). We used the following eight activity categories: perch, walk-hop, sing, fly, hawk, aggression, preen, and other. Perching birds showed no movement other than head turning. Foraging birds walked and hopped along the ground. When foraging birds disappeared from view temporarily, we assumed that they continued to forage for up to 2 min. If they had not reappeared by then, recording was halted until they were again visible. Hawking birds fluttered 2–4 m above ground while catching flying insects. Aggressive behavior usually included rapid, flying chases of intruders and sometimes included physical contact. We included bathing in water in the preen category. The Other category included all other activities, such as manipulation of food items and stick carrying during courtship.

The birds were observed from a portable blind that had been placed in their territories 2 days before injection of isotopes. Occasionally, it was necessary to

follow birds on foot (at distances greater than 30 m) while observing them through binoculars. Beginning at sunrise, we watched birds for 2-h periods with 1-h breaks until the birds were recaptured.

Models.—From the literature we selected five TEB models, one allometric equation, and one temperature-based model that predict $\dot{H}_{TD}$ (Table 2), adapted them to fit our data, and compared their predictions with the more direct DLW method. Symbols that we used are explained in Table 3.

Schartz and Zimmerman (1971) employed multiples of existence metabolism ($\dot{H}_{em}$), defined as the energy used by caged birds in maintaining a constant weight (±2%) over a period of days at various temperatures (Kendeigh 1949, 1970), to generate $\dot{H}_{TD}$ values for male Dickcissels (*Spiza americana*). In our use of this model, metabolism during sleep and perching both equaled 1.0 × $\dot{H}_{em}$, while $\dot{H}_{w-h}$, $\dot{H}_{sg}$, $\dot{H}_{fl}$, $\dot{H}_{pr}$, and $\dot{H}_{ot}$ were converted by 1.3, 1.1, 8.0, 1.1, and 1.1 × $\dot{H}_{em}$, respectively. These are the original conversion factors of Schartz and Zimmerman, except that they did not include a category for preen or other activity. We have assigned a value of 1.1 to $\dot{H}_{pr}$ and $\dot{H}_{ot}$, based on the assumption that their energy cost is probably above that of perching and similar to that of singing. For the flight category we have combined time spent by Savannah Sparrows in aggression, hawking, and flight. To calculate the existence metabolism of Savannah Sparrows, we applied the equation of Wil-

TABLE 2. Seven models that predict $\dot{H}_{TD}$.

Model	Source
$\dot{H}_{TD} = (t_{fl}\dot{H}_{fl}) + (t_{w-h}\dot{H}_{w-h}) + (t_p\dot{H}_p) + (t_{sg}\dot{H}_{sg}) + (t_{pr}\dot{H}_{pr}) + (t_{ot}\dot{H}_{ot})$ $\quad + (t_{sl}\dot{H}_{sl})$	Schartz and Zimmerman (1971)
$\dot{H}_{TD} = (t_{sl}\dot{H}_{sl}) + (t_{fl}\dot{H}_{fl}) + (t_{nfa}\dot{H}_{nfa})$	Utter and LeFebvre (1973)
$\dot{H}_{TD} = (t_{fl}\dot{H}_{fl}) + (t_{nfa}\dot{H}_{nfa}) + (24 - t_{fl}\dot{H}_m)$	Walsberg (1977)
$\dot{H}_{TD} = [134.2 - 0.923 \, T_a]\dot{H}_{em}$	Kendeigh et al. (1977)
$\dot{H}_{TD} = (t_{fl}\dot{H}_{fl}) + (t_{w-h}\dot{H}_{w-h}) + (t_p\dot{H}_p) + (t_{sg}\dot{H}_{sg}) + (t_{sl}\dot{H}_{sl}) + (t_{pr}\dot{H}_{pr})$ $\quad + (t_{ot}\dot{H}_{ot}) + SDA$	Holmes et al. (1979)
$\log \dot{H}_{TD} \text{ (kJ/day)} = \log 11.87 + 0.608 \log W \text{ (g)}$	Walsberg (1980)
$\dot{H}_{TD} = (t_p\dot{H}_p) + (t_{w-h}\dot{H}_{w-h}) + (t_{sg}\dot{H}_{sg}) + (t_{fl}\dot{H}_{fl}) + (t_{sfl}\dot{H}_{sfl}) + (t_{pr}\dot{H}_{pr})$ $\quad + (t_{ot}\dot{H}_{ot}) + (t_{TR}\dot{H}_{TR}) + (t_{sl}\dot{H}_{sl})$	Mugaas and King (1981)

TABLE 3. Symbols used in calculating $\dot{H}_{TD}$.

Symbol	Description
$\dot{H}_b$	Basal metabolic rate taken to be the minimal metabolic rate of a post absorptive bird at night in a thermoneutral environment (kJ/h)
$\dot{H}_{bd}$	Basal metabolic rate during the normal active phase, considered here to be $1.25 \times \dot{H}_b$
$\dot{H}_{em}$	Existence metabolism (kJ/g·day)
$\dot{H}_{fl}$	Energy cost of flight (kJ/h)
$\dot{H}_m$	Minimal metabolic rate of a fasting bird resting at a specified T_a
$\dot{H}_{nfa}$	Energy cost of nonflight activity (kJ/h)
$\dot{H}_{ot}$	Energy cost of other activities (kJ/h)
$\dot{H}_p$	Energy cost of perching (kJ/h)
$\dot{H}_{pr}$	Energy cost of preening (kJ/h)
$\dot{H}_{sfl}$	Energy cost of short flight (kJ/h)
$\dot{H}_{sg}$	Energy cost of singing (kJ/h)
$\dot{H}_{sl}$	Energy cost of sleeping (kJ/h)
$\dot{H}_{TD}$	Total daily energy expenditure (kJ/day)
$\dot{H}_{TR}$	Energy cost of thermoregulation (kJ/h)
$\dot{H}_{w\text{-}h}$	Energy cost of walking and hopping (kJ/h)
SDA	Heat increment due to feeding (kJ/day)
T_a	Ambient temperature (°C)
t_{fl}	Time spent in flight (h)
t_{ot}	Time spent in other activities (h)
t_p	Time spent perching (h)
t_{pr}	Time spent preening (h)
T_s	Mean temperature (°C) during the summer (we used mean daily temperature in our calculations)
t_{sg}	Time spent singing (h)
t_{sl}	Time spent sleeping (h)
t_{TR}	Time during which ambient temperature was below the lower critical temperature for Savannah Sparrows (h)
$t_{w\text{-}h}$	Time spent walking and hopping (h)

liams and Hansell (1981), kJ·g^{-1}·day^{-1} = 5.1 − 0.10 (°C). Our walk-hop category equals the foraging category of Schartz and Zimmerman.

The model of Utter and LeFebvre (1973), constructed to predict $\dot{H}_{TD}$ for Purple Martins, included three levels of activity: sleep, flight, and nonflight activity (Table 2). The energetic cost of these activities equaled $1.0 \times \dot{H}_b$, $5.78 \times \dot{H}_b$, and $1.5 \times \dot{H}_b$, respectively. Again we lumped hawking, aggression, and flying into the flight category. As our estimate of $\dot{H}_b$ for Savannah Sparrows in this and all other models, we have used the value of 1.48 ± 0.07 kJ·g^{-1}·day^{-1} measured by Williams and Hansell (1981) on postabsorptive Savannah Sparrows at night in their zone of thermoneutrality. As noted by these authors, this value is indistinguishable from predictions of the allometric equations of either Lasiewski and Dawson (1967) or Aschoff and Pohl (1970).

Walsberg (1977) altered the model of Utter and

LeFebvre (1973) by adding a thermoregulatory requirement to calculate the $\dot{H}_{TD}$ of the Phainopepla. He derived flight metabolism from the equation of Hart and Berger (1972; kcal/h flight = 45.5 kg$^{0.73}$), $\dot{H}_{nfa}$ from the difference between $\dot{H}_{em}$ and $\dot{H}_b$ at thermoneutral temperatures, and $\dot{H}_m$ as the minimal metabolic rate of a fasting bird during the day resting at a specified temperature. Because Walsberg used the basal metabolic rate ($\dot{H}_{bd}$) during normal active hours in his calculation and because Aschoff and Pohl (1970) demonstrated that daytime resting rates can be higher than at night, we have multiplied our $\dot{H}_b$ by 1.25 to obtain the $\dot{H}_{bd}$ for Savannah Sparrows (1.85 kJ·g·day). The rate of metabolism, which includes a thermoregulatory requirement (TR) for Savannah Sparrows, is given by the equation of Williams and Hansell (1981): kJ·g^{-1}·day^{-1} = 4.5 − 0.10 (°C). Note that one of the assumptions in this model is that flight metabolism totally substitutes for TR.

Kendeigh et al. (1977) added the costs of various energy-demanding activities such as flight, walking, feeding young, etc. to the $\dot{H}_{em}$ of the House Sparrow (Passer domesticus) in a number of localities to formulate an equation for $\dot{H}_{TD}$ expressed as a percentage (PC) of $\dot{H}_{em}$:

$$PC = 134.2 - 0.923\ T_s \pm 0.9,$$

where T_s equals the mean temperature during summer. To use this equation for Savannah Sparrows, we calculated the PC increase in $\dot{H}_{em}$ at a given mean daily and mean nightly temperature for each male.

The model of Holmes et al. (1979) included the following conversion factors: flight = $10 \times \dot{H}_{bd}$, walk-hop = $5 \times \dot{H}_{bd}$, perch = $1.5 \times \dot{H}_{bd}$, sing = $2 \times \dot{H}_{bd}$, sleep = $\dot{H}_{bd}$ at a specified ambient temperature (T_a), other = $1.3\ \dot{H}_{bd}$ (a category not included in their original model), and SDA = $0.3 \times \dot{H}_{bd}$. They did not consider thermoregulatory costs during the daylight hours to be important, because, presumably, T_a was near the thermoneutral zone, and because muscular exercise might compensate for any additional heat needs.

Walsberg (1980) combined a number of methodologically heterogenous studies of birds of different sizes to find an allometric relationship for $\dot{H}_{TD}$ (kJ/day), which we have used to predict $\dot{H}_{TD}$ of male Savannah Sparrows.

For Mugaas and King's (1981) model, we used the conversion factors: perch = $1.7 \times \dot{H}_b$; walk-hop = $2.0 \times \dot{H}_b$; sing = $1.9 \times \dot{H}_b$; fly = $11.0 \times \dot{H}_b$, which also includes aggression in the case of the Savannah Sparrow; short flight = hawk = $6.0 \times \dot{H}_b$; preen = $1.8 \times \dot{H}_b$; and other = $1.3 \times \dot{H}_b$. Conversion factors for sing, preen, and other were not included in their original model, and we have assigned values to them based in part on other studies from the literature. For example, King (1974) discussed the rationale for using a factor of $1.9 \times \dot{H}_b$ to convert time spent singing to energy cost. We arrived at a factor of 1.8 for preen-

TABLE 4.   Rates of CO_2 production and $\dot{H}_{TD}$ for six male Savannah Sparrows.

Animal number	Mean body mass (g)	Body water (%)	ml $CO_2 \cdot g^{-1} \cdot h^{-1}$	kJ/day	$\times \dot{H}_b$	t (days)[b]
141-A	18.10	66.7[a]	6.67	69.5	2.59	1.38
144	19.75	68.3	6.20	70.4	2.41	0.89
139	18.15	63.8	5.76	60.4	2.25	1.40
148	19.60	66.7[a]	8.89	100.4	3.46	0.90
141-B	19.55	65.4	7.21	81.4	2.81	0.91
132	19.26	66.7	8.97	99.5	3.49	1.06
$\bar{x}$	19.07	66.3	7.28	80.3	2.84	1.09
(SD)	(0.75)	(1.5)	(1.36)	(16.6)	(0.53)	0.24

[a] Body water for these two males was estimated from the mean of 10 males injected during 1979 ($\bar{x} = 66.7\%$, SD = 1.67). Other total body water estimates were made using oxygen-18 dilution space for each individual.
[b] Time (days) elapsed during measurement period.

ing, with the idea that it must be slightly more energetically expensive than perching (1.7). Additionally, our perching category was considered tantamount to their alert perching. We considered sleep to be equal to $\dot{H}_b$ when birds experienced temperatures above their lower critical temperature (T_{lc}) or to $\dot{H}_b + TR$ at lower temperatures. All activities except flight were considered additive to TR; flight was considered substitutive. In this model SDA (heat increment due to feeding) was ignored because of the lack of apparent uniformity of response between species.

Statistics.—Differences between means were examined for statistical significance using a t-test or a paired t-test (Zar 1974) as appropriate. Linear least squares regression analysis and an F-test were used to determine correlations between variables.

RESULTS AND DISCUSSION

The CO_2 production for the six males averaged 7.28 ± 1.36 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ and ranged

from 5.76 to 8.97 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$ (Table 4). These sparrows produced CO_2 at a somewhat higher rate than the similar-sized House Martin (body mass 18.8 g; 5.54 ± 0.69 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$; $t = 2.32$; $P < 0.05$) (Bryant and Westerterp 1980), even though House Martins spent more of their time in flight. The production of CO_2 by sparrows was not significantly higher than that by male Phainopeplas [22.7 g mass; 6.42 ± 0.65 ml $CO_2 \cdot g^{-1} \cdot h^{-1}$; $t = -1.01$; $P > 0.3$ (Weathers and Nagy 1980)], which spent most of their time perching (Walsberg 1977).

Male Savannah Sparrows at Point Mugu became active about 30 min before sunrise and roosted 30 min after sunset. During daylight hours, they allocated a large component of their time to foraging (walking, hopping, and hawking) and perching, which together accounted for over 80% (ca. 12 h) of their nonroosting time (Table 5). Flying consumed only about 5% of their time. During a comparable period when

TABLE 5.   Time budgets of male Savannah Sparrows during daylight hours. Values are precentage of total number of instantaneous observations (n). Time spent in each activity was calculated by multiplying fraction of observations (percentage/100) by hours active.

Animal number	Perch	Walk-hop	Sing	Fly	Hawk	Agg.	Preen	Other	n[a]	Hours active	Hours sleep	$\bar{T}_a$ day	$\bar{T}_a$ night	Date (1977)
141-A	9.9	78.7	0.2	3.6	3.2	3.3	1.0	0.1	1,660	14.87	18.29	16.4	11.1	4/13–15
144	10.1	68.9	4.7	5.2	—	9.8	0.9	0.4	553	12.92	8.40	14.8	10.5	5/3–4
139	10.1	73.5	8.5	4.4	0.3	2.8	0.2	0.2	635	16.72	16.87	16.5	15.4	5/25–27
148	20.1	62.9	5.1	6.2	0.4	4.6	0.7	0.1	1,626	13.15	8.43	16.3	12.1	5/30–31
141-B	27.7	48.5	12.0	5.4	0.1	4.4	1.9	0.1	1,504	13.00	8.75	17.2	15.8	5/31–6/1
132	20.1	71.5	2.9	2.3	0.4	1.9	0.9	0.1	2,069	16.68	8.65	19.5	15.9	6/7–8
Mean	20.0	63.2	5.6	4.8	1.0	4.3	1.1	0.1	1,566	14.56	11.57	—	—	—

[a] n equals the total number of observations made at each signal from an electronic metronome.

TABLE 6. A comparision of the estimates of the $\dot{H}_{TD}$ of male Savannah Sparrows generated by using DLW and TEB models.

Animal number		Daily energy expenditure (kJ/day)						
	DLW	Schartz and Zimmerman (1971)	Utter and LeFebvre (1973)	Walsberg (1977)	Kendeigh et al. (1977)	Holmes et al. (1979)	Walsberg (1980)	Mugaas and King (1981)
141-A	69.5	91.3	36.9	61.1	82.0	115.9	69.0	77.4
144	70.4	104.2	42.6	85.6	91.3	135.1	72.8	92.6
139	60.4	81.9	36.4	68.3	76.1	110.7	69.2	73.9
148	100.4	101.3	43.3	79.6	85.1	129.8	72.5	85.2
141-B	81.4	94.2	42.9	77.3	79.6	115.2	72.4	75.8
132	99.5	82.7	40.6	69.4	71.4	128.6	71.7	90.3
$\bar{x}$	80.3	92.6	40.5	73.6	80.9	122.6	71.3	82.5
(SD)	(16.6)	(9.2)	(3.1)	(18.9)	(7.0)	(9.85)	(1.7)	(7.9)
Mean % diff.[a]		+19.1	−48.3	−5.6	+4.9	+57.0	−8.3	+6.0
SD of % diff.		24.1	8.3	19.9	23.7	27.5	17.3	20.5
Paired t value		1.68	−6.54	−0.97	0.08	7.34	−1.27	0.38
Significance		N.S.	$P < 0.005$	N.S.	N.S.	$P < 0.001$	N.S.	N.S.

[a] % difference calculated as [TEB − DLW/DLW] × 100.

females incubated their eggs, Custer (1974) reported that male Lapland Longspurs (*Calcarius lapponicus*), breeding near Barrow, Alaska, foraged about 6–11 h of the day and perched about 6–9 h. From data taken throughout the breeding season, Wiens (1969) calculated that male Savannah Sparrows in Wisconsin foraged about 20% (ca. 3 h) of their time and perched over 50% (ca. 8 h) during daylight hours, results that are very different from ours.

The model of Schartz and Zimmerman (1971) varied from our DLW measurement of $\dot{H}_{TD}$, with a mean difference of +19.1%, although the mean values are not distinguishable statistically (Table 6). The reason for the lack of reliability of this model in predicting the energetics of individual birds could arise from questionable conversion factors relating activities to energy consumption. For example, Schartz and Zimmerman used the increment of $1.3 \times \dot{H}_{em}$ for the cost of foraging, a value apparently derived from the work of Uramoto (1961), in which little empirical evidence is given to justify such a number for birds living in their natural environment. Kahl (1965) cited the work of Uramoto (1961) as evidence that birds in their natural environment required 30% more energy than did captive birds, but he did not use the correction factor in his work relating existence metabolism to field energetics in the Marsh Wren (*Cistothorus palustris*), because

"captive wrens were extremely active in their cages and hopped or flew incessantly." The difficulty in relating unknown levels of activity in small cages to the activity metabolism of individuals in the field restricts the utility of this model to some degree. Furthermore, using $\dot{H}_{em}$ to represent the power requirements of a roosting bird at night may be inappropriate, because $\dot{H}_{em}$ contains a significant activity component.

The model of Utter and LeFebvre (1973) grossly underestimated the $\dot{H}_{TD}$ of male Savannah Sparrows as measured by DLW (Table 6), a surprising result considering that they originally found less than a 10% disparity for females between TEB and DLW estimates and a 20% disparity for males. For Budgerigars, Weathers et al. (in press) also compared the predictions of $\dot{H}_{TD}$ of this method with DLW estimates and found that the estimate of the model averaged only 34% that of DLW. One could argue that the conversion factor for $\dot{H}_{nfa}$ of Purple Martins markedly differs from Savannah Sparrows, because perching accounts for most of the *nfa* for martins but foraging is the major component of *nfa* in male Savannah Sparrows. The energy cost of these two *nfa* is almost certainly not at parity. Additionally, aerially feeding birds may expend less energy during flight than ground-foraging birds (King 1974); thus, the conversion factor for flight ($5.78 \times \dot{H}_b$) may be inappropriate for sparrows,

resulting in an underestimate of $\dot{H}_{TD}$. Therefore, we altered the model by assuming that the energetic cost of *nfa* should equal $2.0 \times \dot{H}_b$ and of flight $9.0 \times \dot{H}_b$ and recalculated $\dot{H}_{TD}$. The results showed a mean estimate of 50.8 ± 4.3 kJ/day for our six sparrows, which is only 63% of our DLW estimates, indicating that even with more appropriate conversion factors the model still falls short in predicting the $\dot{H}_{TD}$ of Savannah Sparrows. We agree with Walsberg (1977) that one likely source of error in their model is the omission of a thermoregulatory requirement. We cannot explain the close agreement between their TEB and DLW estimates, unless for some reason the *TR* of Purple Martins was low during their experiment. Indeed, some studies, such as the work of Lasiewski (1963), Tucker (1968), and Berger and Hart (1974), indicate that exercise metabolism at the high-work levels of flight substitutes for cold-induced thermogenesis, and so the fact that Purple Martins forage in flight may explain the apparent discrepancy.

When we followed the methods of Walsberg (1977), TEB estimates agreed more closely with DLW estimates, with a mean error of -5.6% (Table 6). Again the variance around the mean error appeared high (range -30.3 to $+21.6\%$), suggesting that the model lacks elements to map the energy expenditure of an individual bird accurately during any given time period. When Weathers and Nagy (1980) compared the $\dot{H}_{TD}$ of one free-living and five aviary-confined Phainopeplas by means of DLW and, simultaneously, TEB analysis via the Walsberg (1977) model, they reported that estimates derived from TEB analysis averaged almost 40% lower. Furthermore, they suggested that the model did not account for the effect of solar insolation on $\dot{H}_{TD}$ in Phainopeplas. Because the ideas of Ohmart and Lasiewski (1971), DeJong (1976), and Lustick et al. (1980), certainly seem to support the notion that solar radiation can influence energy expenditure in birds, we tried to correlate $\dot{H}_{TD}$ as measured by DLW with mean hourly solar insolation (W/m²), but we failed to find any relationship ($R^2 = 0.20$, $F = 0.99$, N.S.).

The model of Holmes et al. (1978) overestimated the $\dot{H}_{TD}$ obtained by the DLW method (Table 6), primarily, we think, because of the unrealistic assumption that hopping costs $5 \times \dot{H}_{bd}$. In support of this view, Paladino (1979) found that White-crowned Sparrows (*Zono-trichia leucophrys*) forced to hop on a treadmill at the highest treadmill speed (0.13 m/s, which is probably faster than Savannah Sparrows normally walk while foraging) in a thermoneutral environment increased their metabolic heat production by a factor of 1.5 above resting levels. Moreover, Mugaas and King (1981), using the data of Fedak et al. (1974), estimated that Black-billed Magpies (*Pica pica*) expended energy at a level $2.0 \times \dot{H}_b$ while walking. Because the above suggests that the cost of walking and hopping for male Savannah Sparrows is nearer $1.5-2.0 \times \dot{H}_b$, we recalculated $\dot{H}_{TD}$ using the Holmes model with the altered conversion factor of $2 \times \dot{H}_{bd}$ for the cost of walking and hopping and found that TEB predictions agreed more closely with DLW estimates ($\bar{x} = 82.2$ kJ/day; $t = 0.31$, $P > 0.7$, mean % error = $+5.6\%$), but the range ($+25.4$ to -21.1%) and the variance for the percentage difference remained high. The model also does not account for thermoregulatory costs (Williams and Hansell 1981) during daylight hours, which we consider to be important for Savannah Sparrows at the air temperatures they experienced in this study. When we added *TR* costs to the model, however, the values increased, averaging 12.0% higher than DLW measurements, although they were not significantly different ($t = 1.84$, $P > 0.1$).

The model given by Mugaas and King (1981) yielded estimates close to those given by the DLW method (Table 6). This model includes a thermoregulatory requirement, differences in the basal metabolic rate between the day and night phase, and more realistic conversion factors relating energetic costs of activities in the field with laboratory data. Still, the range ($+31.5$ to -23.8) and high variance for the percentage error (SD = 20.5) indicate that their model, as we used it, lacks important components to track the $\dot{H}_{TD}$ of a given individual. We did not use the equivalent blackbody temperature (T_e) as an index of the thermal environment as they did, but rather ambient temperature (T_a). Use of T_e obtained by taxidermic mounts (Bakken et al. 1981) may decrease the variance around the mean for the percentage error, a possibility that we shall explore in the future. Clearly, weather variables influence T_e, but we did not detect any relationship between $\dot{H}_{TD}$ and wind ($r^2 = 0.38$, $F = 2.50$, N.S.), T_a ($r^2 = 0.22$, $F = 1.19$, N.S.), or, as stated before, solar insolation.

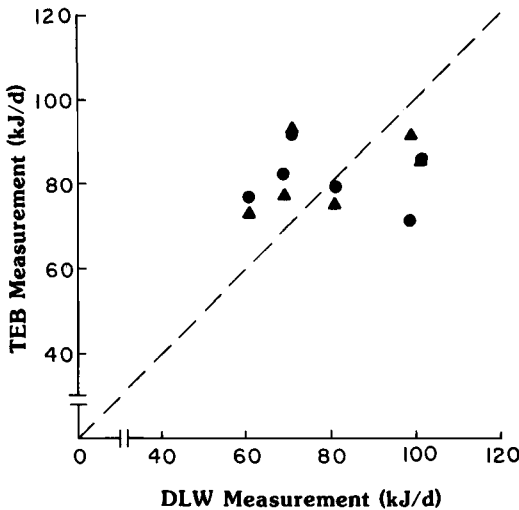We have also compared estimates of $\dot{H}_{TD}$ gen-

Fig. 1. A graphical analysis showing the lack of correspondence between DLW and TEB estimates of $\dot{H}_{TD}$. The dashed line represents a 1:1 agreement. Circles are values as predicted by the model of Kendeigh et al. (1977); triangles represent values as predicted by the model of Mugaas and King (1981).

deigh et al. (1977) differs widely in approach from that of Mugaas and King (1981). Our analysis points out that the variation does not correspond between the two measures of $\dot{H}_{TD}$. This lack of correspondence emphasizes to us that TEB measurements are as yet inadequate to measure the $\dot{H}_{TD}$ of any given individual reliably. This is not surprising, because several of the models incorporate mean values for metabolic costs in the first place, thereby artifically reducing expected variation among individuals.

erated by the equations of Kendeigh et al. (1977) and Walsberg (1980) for Savannah Sparrows as measured by the DLW method (Table 6). Kendeigh's equation yielded estimates closer to those of DLW than did Walsberg's, but data from both equations contained a large variance, with standard deviations equaling ±23.2 and ±21.9, respectively.

In summary, we found that the models of Kendeigh et al. (1977), Walsberg (1977), and Mugaas and King (1981) yielded mean estimates comparable to those given by the DLW method. Our analysis of these methods suggests that comparisons of average $\dot{H}_{TD}$ between species, or between nesting phases within a species, might be made with some measure of confidence. Although mean estimates are in reasonable agreement, the variance around the mean percentage error is high for all models, suggesting that measurements with TEB of $\dot{H}_{TD}$ of individuals may vary widely from those with DLW. To emphasize this point, we have plotted the relationship between DLW measurements with TEB estimates for the models of Kendeigh et al. (1977) and Mugaas and King (1981) (Fig. 1). We chose these two models because of their close agreement, on average, with DLW measurements, even though the model of Ken-

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