

SIMULTANEOUS DOUBLY LABELED WATER ( $^3\text{HH}^{18}\text{O}$ )  
AND TIME-BUDGET ESTIMATES OF DAILY  
ENERGY EXPENDITURE IN  
*PHAINOPEPLA NITENS*

WESLEY W. WEATHERS<sup>1</sup> AND KENNETH A. NAGY<sup>2</sup>

<sup>1</sup>*Department of Avian Sciences, University of California, Davis, California 95616 USA and*

<sup>2</sup>*Laboratory of Nuclear Medicine and Radiation Biology, University of California,  
Los Angeles, California 90024 USA*

ABSTRACT.—Daily energy expenditure (*DEE*) of six free-ranging Phainopeplas (*Phainopepla nitens*) was measured using doubly labeled water and simultaneously estimated from behavioral observations using Walsberg's time-budget model for free-living Phainopeplas. *DEE* measured by labeled water averaged 79.1 kJ/day, which is 2.6 times the basal metabolic rate. Estimates derived from time-budget data averaged almost 40% lower (48.1 kJ/day), demonstrating that time-budget estimates of *DEE* in birds, even if based on rates of metabolism determined in the laboratory, can involve substantial errors. An analysis of the potential sources of error in the time-budget method suggests that the influence of solar radiation on metabolism of free-living birds should be incorporated into future models. Daily water influx measured by doubly labeled water averaged 154% of the total body-water pool. This seemingly high rate is probably due to this flycatcher's unusual fruit diet. Received 2 May 1980, accepted 5 July 1980.

KNOWLEDGE of the daily energy expenditure (*DEE*) of birds is fundamental to an understanding of many life history phenomena and their adaptive variations (see review by King 1974). Many recent estimates of *DEE* have involved time-budget analyses in which the time allocated throughout the day to various categories of activity is recorded, and *DEE* calculated by multiplying the time spent in the activities by their estimated metabolic costs (reviews by King 1974, Kendeigh et al. 1977, and Walsberg in press; also see Tarboton 1978, Wakeley 1978, Ashkenazia and Safriel 1979). Although the method's simplicity makes it attractive, its accuracy depends heavily upon estimates of the energy cost of various kinds of activity in free-living animals. Due to the paucity of empirical data, these are sometimes little more than guesses. Consequently, a major limitation of the method is the lack of confidence intervals for estimates of *DEE*. An alternative technique for field studies of metabolism is the measurement of  $\text{CO}_2$  production using doubly labeled water. Once labeled, an animal may be released in its territory and left undisturbed until subsequent recapture. The average  $\text{CO}_2$  production during this interval is calculated from the turnover rates of the isotopes in the animal. Validation studies (Nagy 1980, Hails 1979) of the doubly labeled water method on 11 species of vertebrates, including birds, demonstrate that the technique provides estimates of  $\text{CO}_2$  production with a mean error of +1.2% (range: -7 to +5%). Despite its advantages, animal ecologists have been slow to adopt the doubly labeled water method since its introduction by Lifson et al. (1955), partly due to the high cost of oxygen-18 and the technical difficulties of measuring the stable isotopes  $^{18}\text{O}$  and deuterium. Recently, the method has become more attractive with the substitution of easily measured tritiated water ( $^3\text{HHO}$ ) for deuterated water ( $^2\text{H}_2\text{O}$ ), and the analysis of  $^{18}\text{O}$  by proton activation rather than by mass spectrometry (Nagy 1975, Wood et al. 1975).

In this study we compare rates of daily energy expenditure of the Phainopepla (*Phainopepla nitens*) determined simultaneously by time-budget analysis and doubly labeled water. We chose the Phainopepla because Walsberg (1977) had previously

developed a temperature-compensated time-budget model of Phainopepla *DEE* based on laboratory determinations of the energy cost of nonflight activity and maintenance metabolism. Among the various available time-budget models, Walsberg's is potentially one of the most accurate. Thus, by using his time-budget method while simultaneously measuring *DEE* by doubly labeled water, we gained insight into the accuracy of time-budget estimates of field metabolism.

#### METHODS

We began this study working with free-living Phainopeplas breeding in a dry desert wash near Palm Desert, California. After we completed measurements on one male (No. 299), however, we moved the study to a nearby large (30 × 15 × 8 m) free-flight aviary because of heavy predation by Loggerhead Shrikes (*Lanius ludovicianus*) on both adult and nestling Phainopeplas. The aviary was planted with native desert vegetation and contained a small artificial stream. Clumps of desert mistletoe (*Phoradendron californicum*) containing mature berries were hung in the aviary as a food source. Measurements were made between 21 April and 3 June 1979.

To determine metabolism by doubly labeled water ( $^3\text{HH}^{18}\text{O}$ ), we captured birds in mist nets, weighed them to the nearest 0.1 g, and gave them an intramuscular injection of either 150 or 200  $\mu\text{l}$  of water containing  $\sim 1.6$  mCi  $^3\text{H}$  and 90 atom-percent  $^{18}\text{O}$ . After allowing 1 h for the labeled water to reach equilibrium with body water (previously determined in the laboratory), we obtained a 50- $\mu\text{l}$  blood sample from the brachial vein and stored it in a flame-sealed glass microhematocrit tube for later analysis. The bird was then released on its territory or into the aviary, and the collection of time-budget data was begun. One day later the bird was recaptured, reweighed, and a second blood sample 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-POP scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of  $^{18}\text{O}$  to fluorine-18 with subsequent counting of the gamma-emitting  $^{18}\text{F}$  in a Packard Gamma-Rotomatic counting system (Wood et al. 1975). Isotope measurements were used to calculate rates of water influx and  $\text{CO}_2$  production using the equations of Lifson and McClintock (1966) as modified by Nagy (1975). *DEE* was calculated from  $\text{CO}_2$  production assuming a caloric equivalent for  $\text{O}_2$  of 20.08 kJ/l  $\text{O}_2$  and a respiratory quotient of 0.85. Assuming mixed fat and carbohydrate metabolism, *DEE* would be 10.9% higher if the respiratory quotient were 0.75 and 7.8% lower if it were 0.95.

*DEE* was estimated from time-budget data using Walsberg's (1977) method, which incorporates two assumptions on the interaction of cold and exercise thermogenesis. First, exercise metabolism at the low work levels of nonflight activity is considered additive to maintenance metabolism at ambient temperatures below thermoneutrality. Second, exercise metabolism at the high work levels of flight is assumed to substitute for cold-induced thermogenesis. Phainopeplas were observed from a distance of  $\sim 25$  m, and the time spent in flight was recorded for one half of each hour throughout the bird's active day (portion of each day the birds were awake). Phainopeplas were inactive and presumably asleep for  $8 \pm 0.5$  h of the day. Because of uncertainty in judging when birds were asleep (versus perching quietly but awake), however, we arbitrarily set the length of the sleep period at 8 h. An error of 1 h in sleep time would, on the average, result in only a 1.2% error in *DEE*. Knowledge of the time spent in flight, as well as the total time active per day, allows calculation of time spent in three activity level categories: (1) flight; (2) nonflight activity, equal to the bird's active day minus time in flight; and (3) inactive, presumably asleep. From this information *DEE* is calculated according to Walsberg's equation,

$$DEE = [(\dot{E}_f)(t_f)] + [(\dot{E}_{nfa})(t_{nfa})] + [(\dot{E}_m)(24 - t_f)],$$

where  $\dot{E}_f$  is the rate of energy expenditure in flight,  $t_f$  is the time spent in flight per day,  $\dot{E}_{nfa}$  is the rate of energy expenditure due to nonflight activity that is additional to the rate of maintenance energy expenditure,  $t_{nfa}$  is the time spent in nonflight activity per day, and  $\dot{E}_m$  is the temperature-dependent maintenance metabolism estimated for the entire day minus the time spent in flight. Following Walsberg (1977),  $\dot{E}_f$  was calculated from the bird's mass by the equation of Hart and Berger (1972) where  $\text{kJ/h} = 1.23 (\text{g})^{0.73}$ .  $\dot{E}_{nfa}$  was determined by Walsberg (1977) to be  $26.5 \text{ J} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ .  $\dot{E}_m$  was calculated from Walsberg's data relating metabolism of Phainopeplas to ambient temperature, using an adjusted mean temperature ( $T_m$ ) to predict average  $\dot{E}_m$  for nonflight periods by the relation  $\text{J} \cdot \text{g}^{-1} \cdot \text{h}^{-1} = 122.6 - 2.54T_m$ .  $T_m$  was determined from hourly determinations of air temperature by Walsberg's (1977) method. The methods and calculations we used to estimate *DEE* from time-budget data duplicated those of Walsberg

TABLE 1. Time budgets of Phainopeplas and calculated effective maintenance temperature ( $T_m$ ).

Animal number	Sex	$T_m$ (°C)	Hours/day spent		
			In flight	In nonflight activity	Inactive
299	♂	23.65	0.99	15.01	8.0
202	♂	25.68	1.09	14.91	8.0
203	Immature	25.90	0.49	15.51	8.0
204	♂	23.40	0.46	15.54	8.0
205	♀	23.44	0.12	15.88	8.0
1	Immature	25.77	0.27	15.73	8.0

(1977), except that we used the bird's actual mass in the calculation of metabolism rather than an assumed mass of 24 g.

### RESULTS

Because the values determined for the one field animal (No. 299) fall within the range of values for aviary birds, the data from both have been combined. Time budgets, expressed in behavioral categories, and associated temperature data, which provide the basis for calculating *DEE*, are presented in Table 1. Phainopeplas spent a mean of 0.57 h/day in flight (Table 1), which is similar to the value of 0.63 h/day found for winter birds from the same locality (Walsberg 1977).

Rates of  $\text{CO}_2$  production and water influx determined by  $^3\text{HH}^{18}\text{O}$  are presented in Table 2. Water flux was much more variable than  $\text{CO}_2$  production and showed no correlation with  $T_m$  or time spent in flight. The mean rate of total water influx ( $945 \text{ ml} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ ) is  $9\times$  the rate of pulmocutaneous water loss predicted for a resting 22.7-g bird (Crawford and Lasiewski 1968). Because total body water volume (determined by  $^{18}\text{O}$  dilution space) equaled 61.5% of body mass, water influx was equivalent to 154% of the body water pool per day.

Rates of *DEE* determined by  $^3\text{HH}^{18}\text{O}$  are compared with rates calculated by time-budget analysis in Table 3. *DEE* determined by  $^3\text{HH}^{18}\text{O}$  averaged 79.1 kJ/day, which is 2.6 times the observed basal metabolic rate (Walsberg 1977). Walsberg's (in press) equation (1) for metabolism of free-living birds predicts a *DEE* of 79.2 kJ/day for a 22.7-g bird, essentially identical to the observed rate. In contrast, *DEE* estimated by time-budget analysis averaged 39.2% lower than rates measured by labeled water and is only 1.8 times the basal metabolism.

TABLE 2. Rates of  $\text{CO}_2$  production and water influx of Phainopeplas determined by doubly labeled water.

Animal number	Body mass (g)	Water influx ( $\text{ml} \cdot \text{kg}^{-1} \cdot \text{day}^{-1}$ )	$\text{CO}_2$ production ( $\text{cm}^3 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ )
299	22.8	1,152	6.85
202	24.2	802	5.67
203	23.1	1,203	5.85
204	23.2	816	6.74
205	21.6	1,130	6.18
1	21.1	567	5.63
Mean $\pm$ SD	22.7 $\pm$ 1.13	945 $\pm$ 255	6.15 $\pm$ 0.53

TABLE 3. Comparison of rates of daily energy expenditure (*DEE*) measured by doubly labeled water ( $^3\text{HH}^{18}\text{O}$ ) with rates calculated by time-budget analysis (TB).

Animal number	<i>DEE</i> (kJ/day) <sup>a</sup>		Percentage error in TB estimate
	$^3\text{HH}^{18}\text{O}$	TB	
299	88.7	53.8	39.3
202	77.8	55.1	29.2
203	76.6	46.3	39.5
204	88.7	49.7	44.0
205	75.7	43.0	43.2
1	67.4	40.5	39.9
Mean $\pm$ SD	79.1 $\pm$ 8.25	48.1 $\pm$ 5.85	39.2 $\pm$ 5.28

<sup>a</sup> To convert kJ/day to kcal/day divide by 4.184.

## DISCUSSION

Time-budget estimates of Phainopepla *DEE* averaged nearly 40% lower than estimates based on doubly labeled water. Similar results have been obtained with howler monkeys (*Alouatta palliata*), in which time-budget estimates of *DEE* (Coelho et al. 1976) were 40% lower than  $^3\text{HH}^{18}\text{O}$  values (Nagy and Milton 1979), and with three-toed sloths (*Bradypus variegatus*), where the time-budget value (McNab 1978) was only 67% of the  $^3\text{HH}^{18}\text{O}$  measurement (Nagy and Montgomery 1980). These studies suggest that for some species the time-budget method may lead to significant underestimates of *DEE*. The only previous study that simultaneously estimated *DEE* by doubly labeled water and time-budget analysis is that of Utter (1971) on the Mockingbird (*Mimus polyglottos*). Using time-budget data, he calculated daily energy expenditure by the relation

$$DEE = [(\dot{E}_f)(t_f)] + [(\dot{E}_{nf})(t_{nf})] + [(\dot{E}_s)(t_s)],$$

where  $\dot{E}$  is rate of energy expenditure,  $t$  the amount of time per day spent in a given category of activity, and  $f$ ,  $nf$ , and  $s$  refer to flight, nonflight, and sleep, respectively. Lacking empirical values for the energetic cost of the three categories of activity, Utter assumed that (1) the energy cost of sleep was equal to the rate of basal metabolism (predicted from the bird's mass by the equation of Lasiewski and Dawson 1967), (2) the energy requirement of all nonflight activity was twice the basal metabolism, and (3) the cost of flight was 12 times basal metabolism. Each of these estimates involves a degree of uncertainty, the potential magnitude of which is known only for basal metabolism, for which observed values differ from predicted values by an average of  $\pm 15\%$ . Lack of empirical data on the metabolic cost of the model's activity categories should produce inaccurate estimates of *DEE*. Furthermore, unlike Walsberg's (1977) model, Utter's time-budget model does not account for the effect of temperature on metabolism. Thus, it is probably fortuitous that the mean difference between time-budget and  $\text{D}_2^{18}\text{O}$  estimates in Utter's six Mockingbirds was 17.2%, and, because the range of differences for individual birds was from  $-31.2\%$  to  $+45.2\%$ , the results are equivocal.

In contrast with Utter's time-budget study, Walsberg (1977) empirically determined the energy cost of nonflight activity and maintenance metabolism, thereby reducing two sources of error. Hence, it is surprising that the agreement between  $^3\text{HH}^{18}\text{O}$  and time-budget estimates of Phainopepla *DEE* is not better. Assuming Walsberg's time-budget model is correct, there are numerous factors that could

contribute to the observed discrepancy between time-budget and labeled water estimates. These include (but are not limited to) erroneous assumptions about the energy cost of flight, differences in the maintenance metabolism of Phainopeplas in our study versus Walsberg's that are attributable to seasonal or acclimation effects, and increases in nonflight activity costs of free-ranging versus laboratory birds. Because King (1974) presented an in-depth consideration of the use of time and energy resources by birds, including the factors that affect metabolic rate, we will restrict our analysis to reconciling our time-budget and labeled water estimates of *DEE* within the context of Walsberg's model.

Time-budget and labeled water estimates of *DEE* in this study can be made to agree by assuming higher metabolic costs for the activity categories in one of three ways. First, the cost of any one activity category could be increased as follows: increase the cost of flight 5.6-fold, or increase the cost of nonflight activity 4.4-fold, or increase maintenance metabolism 2-fold. Second, the cost of all three activity categories could be increased but by smaller amounts. Thus,  $^3\text{HH}^{18}\text{O}$  and time-budget estimates would agree if the cost of flight and nonflight activity were doubled and maintenance metabolism were increased 1.5-fold. Third, any two of the cost estimates could be increased, the third being unchanged. For example, increasing the cost of nonflight activity 2-fold and maintenance metabolism 1.68-fold makes the *DEE* estimates agree. All these methods of reconciliation illustrate that for the Phainopepla errors in the estimation of maintenance metabolism contribute most to the overall error in the time-budget estimate. This would not necessarily be true for other species, especially those spending more time in flight than the Phainopepla.

The energy cost of flight was the only one of the three activity categories in Walsberg's model for which empirical data were unavailable. It is unlikely that error in the estimation of  $\dot{E}_f$ , however, contributed significantly to the lack of agreement between time-budget and labeled water estimates of *DEE* for the following reasons. First, flight time averaged only 2.4% of the day (Table 1). Hence, even though flight is metabolically more expensive than the maintenance and nonflight activity categories, its contribution to total *DEE* is less. Second, for data on 16 species presented by Hails (1979, excluding swifts and swallows, which have a lower  $\dot{E}_f$  than other species), observed and predicted values of  $\dot{E}_f$  differ on the average by only 16.5%. Hence, it seems unlikely that the energy cost of flight in Phainopeplas would be 560% of that predicted. Apparently the maintenance and/or nonflight activity components of the time-budget model need correction. Consistent with this is the observation that the fractional error in estimates based on time budgets (Table 3) is negatively correlated with time spent in flight ( $r = -0.75$ ;  $0.10 > P > 0.05$ ). This correlation, while not statistically significant, does at least suggest that the major source of error in the time-budget model is in the nonflight components.

Calculation of the contribution of the maintenance component ( $\dot{E}_m$ ) to *DEE* is based on laboratory measurements of oxygen consumption ( $\dot{V}\text{O}_2$ ) made in the dark. This method does not take into account the effect that solar radiation can have on  $\dot{V}\text{O}_2$ . DeJong (1976) found that in White-crowned Sparrows (*Zonotrichia leucophrys*) exposed to simulated solar radiation ( $70 \text{ mW/cm}^2$ ), the thermal neutral zone extended from 10 to 20°C. Above 20°C  $\dot{V}\text{O}_2$  increased rapidly, reaching 162% of the basal rate at 30°C and even higher at higher irradiation levels. In contrast, the  $\dot{V}\text{O}_2$  of White-crowned Sparrows measured in the dark does not increase until  $T_a$  exceeds 37°C (King 1964). Hence, overlooking the potential influence of solar radiation on

$\dot{E}_m$  when air temperature is high could lead to underestimation of *DEE*. During our study, daytime  $T_a$  usually exceeded 20°C, and during two measurement periods it exceeded 35°C for 5 h. Moreover, our Phainopeplas were frequently exposed to solar radiation, and at these times  $\dot{V}O_2$  was probably elevated above thermal neutral levels. We lack the necessary data to determine whether taking the influence of solar radiation on  $\dot{E}_m$  into account would result in complete agreement between  $^3\text{HH}^{18}\text{O}$  and time-budget estimates of *DEE*, but it should decrease the discrepancy.

*Water flux calculations.*—Water influx rates in our Phainopeplas averaged 945 ml·kg<sup>-1</sup>·day<sup>-1</sup> (Table 2), or nearly 95% of their body mass in water flux each day. This seemingly high rate is probably due to this flycatcher's unusual diet: they fed exclusively on berries of desert mistletoe during our study. Our measurements probably underestimate actual water fluxes in the field, however, for the following reasons. Mistletoe berries contain about 79% water by mass (Walsberg pers. comm.), and about 49%, or 2.27 kJ/g fresh berry, of the chemical potential energy in them is metabolizable (Walsberg 1975). A Phainopepla eating these berries to meet its energy needs (79.1 kJ/day, from Table 3) would have to consume 34.8 g of berries per day (79.1 kJ metabolized/day divided by 2.27 metabolizable kJ/g fresh berry), which would provide 27.5 ml of water/day (34.8 g berries/day times 0.79 ml H<sub>2</sub>O/g of berry). This amounts to 121% of body mass/day in dietary water input alone, which is higher than our estimated total input of 95%/day. Actual total inputs must have been even greater than 121%/day because of the production of "oxidation" water during energy metabolism (which we estimate from energy metabolism to be about 8%/day) and because of drinking free water (several of our birds were seen drinking during measurement periods). The most likely reason for this error is the unusual digestive physiology of Phainopeplas. Their foreguts are adapted to extrude the berry's seed and pulp from the exocarp, and the food is processed and eliminated within 12–45 min after ingestion (Walsberg 1975). This short residence time probably does not allow the tritium in body water to equilibrate completely with all the water in the berries, especially that in the seeds. Accordingly, water flux rates measured with tritiated water should underestimate actual water fluxes in these birds. This error, however, has little effect on the accuracy of measurements of metabolic rate by  $^3\text{HH}^{18}\text{O}$  (Nagy 1980).

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