

ENERGY EXPENDITURE BY FREE-LIVING DIPPERS (*CINCLUS CINCLUS*) IN WINTER

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ABSTRACT.— We measured daily energy expenditure (DEE) of free-living Dippers (*Cinclus cinclus*) during winter, using the doubly-labelled water (DLW) technique. DEE was estimated as 206 kJd⁻¹ by this method, compared to 194 kJd⁻¹ using time-activity budgets combined with laboratory estimates of metabolic costs. The latter result was most sensitive to the assumed costs of underwater-feeding (“diving”); taking lower and higher costs for this activity resulted in DEE equaling 177 and 212 kJd⁻¹, respectively. Correlation between individual estimates of DEE obtained using DLW and time-energy budgets was significant, but weak. Of 26 independent variables examined for correlation with DEE and average daily metabolic rate measured using DLW, significant results were limited to various measures of body-size and activity. None of the measured weather variables was significant. These results suggested that for any individual bird, variation in DEE in winter was largely a consequence of changes in the nature and duration of energy-costly activities. Accurate prediction of mean energy expenditure and its confidence intervals using time-budget techniques, at least in species which show a range of activities with differing costs, will depend on precise evaluation of those activity costs and their variability.

A knowledge of energy expenditure by free-living birds is important for understanding many aspects of their biology (King 1974, Walsberg 1983). Studies of avian communities (Holmes and Sturges 1973, Furness 1978), reproduction (Ricklefs 1974, Drent and Daan 1980, Bryant and Westerterp 1983), foraging (Gill and Wolf 1975, Pyke 1979), territoriality (Carpenter and MacMillen 1976, Davies and Houston 1981), and population management (Stalmaster 1983) rely on accurate estimates of the energy costs of daily activity. It is usual to estimate energy expenditure using allometric models, time-activity budgets in combination with laboratory measurements of activity costs, or related methods (Gessaman 1973, Mugaas and King 1981, Robbins 1983). Only rarely, however, are such methods assessed for their accuracy before they are used as part of a wider study. When they have been examined, limits to their precision have been revealed (Koplin et al. 1980, Weathers and Nagy 1980, Williams and Nagy 1984). In this study, we set out to measure daily energy expenditure (DEE) using the doubly-labelled water (DLW) technique (Lifson et al. 1955, Nagy 1980), and then compare the results with estimates based on other methods. Our main interest was in answering two questions: first, do direct esti-

mates of mean energy expenditure, obtained by using DLW, match predictions from allometric equations and time-energy budgets? Second, can time-energy budgets accurately describe patterns of variation in DEE under changing conditions? We assumed that the DLW technique is as accurate under field conditions as it has proved to be in laboratory trials (LeFebvre 1964, Hails and Bryant 1979, Westerterp and Bryant 1984). It thus would serve as a standard against which other methods, themselves liable to substantial errors (Travis 1982), could be assessed.

The study was carried out on the Dipper (*Cinclus cinclus*) in central Scotland, United Kingdom, during winter. Dippers were suited to the aims of the study in one main respect: they remain faithful to their roosts, which are commonly in cavities in the masonry of bridges, and can therefore be readily recaptured—an essential feature for success of the DLW technique. The biology and habits of Dippers in Scotland have been described by Hewson (1967, 1969), Shaw (1978, 1979a and b), and Galbraith and Broadley (1980). The studies of Bakus (1959) and Price and Bock (1983) on the American Dipper (*C. mexicanus*) show few substantial differences in the biology of the two species.

METHODS

LABORATORY METABOLISM STUDIES

To obtain estimates of the energy expenditure of Dippers while roosting, resting, and feeding, we used indirect calorimetry (Brody 1945). After dark in mid-winter, single birds were captured at roosts using a hand-net, and were placed in a spindle-mounted respirometer. Oxygen uptake and carbon dioxide production were measured overnight with a Beckmann OM2 polarographic oxygen analyser and MSA infra-red gas analyser, respectively. About 1 h after dawn (07:30–08:30), we lit the incubator containing the respirometer and rotated the cylindrical chamber at 0.06 m sec^{-1} to encourage walking for a period of 30 min. The speed of rotation was chosen so that the Dippers' gait resembled that of a foraging bird. A plexiglas side allowed us to confirm that, at night, birds settled immediately in the darkened chamber, and that, in the revolving chamber, activity was limited to slow pacing with occasional hops. We assumed the energy cost of walking in the chamber was the same as the cost of pecking and pacing on the river bank and in shallows. We did not attempt to measure the cost of feeding by diving (Goodge 1959), or the cost of flight (see below). We made measurements on three different birds at each 5°C mark across the temperature range to which birds could be exposed in the field (i.e., -10°C to $+25^\circ\text{C}$). After the laboratory studies each night, birds were released at their site of capture. A total of ten individuals was used in the course of the laboratory measurements. All gas volumes were corrected to standard temperature and pressure.

DOUBLY-LABELLED WATER TECHNIQUE

We conducted the study of free-living Dippers on the River Devon, near Stirling. Birds were captured at 20:00–22:00, mainly at different roosts from those used for the laboratory studies. Stable isotopes (D_2 , ^{18}O) were administered by intraperitoneal injection, and after 1.5 h for equilibration and initial blood sampling, birds were returned to the roost. All individuals whom we checked ($n = 8$) stayed in sheltered sites at or near the point of release for the rest of the night (see Shaw 1979a). They were briefly recaptured at the same roost about 48 h after release, so that the final blood samples could be taken. All birds were color-banded for identification in the roost and on the river. Throughout the winter, twelve different birds (3 males, 9 females) were recaptured a total of 32 times over all months from October to February. Because no individual was sampled twice in a month, and because weather and day-

length were changing throughout the course of the study, we felt justified in treating each recapture as an independent result for subsequent statistical analysis. While the birds were being handled, we measured body mass, wing length (maximum chord), tarsus length, and sternal (keel) length.

The doubly-labelled water technique for measuring energy expenditure of free-living animals has been described by Lifson and McClintock (1966), Mullen (1973), and Nagy (1980). Our field protocol and analytic procedures were the same as those used by Hails and Bryant (1979), Bryant and Westerterp (1980), and Bryant et al. (1984). We assumed that body water was 63% of body mass for all individuals.

TIME-ACTIVITY BUDGETS

We gathered sample time-activity budgets throughout the day on one or both of the days during which isotope-loaded birds were at liberty, with the initial aim of determining the budgets of all experimental individuals. Since the daily range of movement often proved to be extensive (up to 4 km from roosts to feeding sites), however, it was often difficult to find or to follow any marked bird for long. We therefore gathered data from all individuals, including DLW-loaded birds, as we encountered them. Samples on each of these days involved 10–19 birds for 1–30 min each. These observations were made over 29 days in fourteen sessions (i.e., 2–3/month). Overall, DLW-loaded birds comprised 20% of individuals included in the time-activity budget samples. Additional observations on activity were made on other days to quantify average activity patterns through the winter.

Activity during daytime was recorded under four headings: resting, foraging, diving, and flying. Resting at night is referred to as "roosting." "Resting" denotes the time spent stationary during daytime; including not only standing quietly and alert, but also preening, singing, food manipulation, and the characteristic bobbing action of Dippers. "Foraging" includes all walking activity, which was almost exclusively devoted to pacing and pecking while feeding. During these activities, the birds were either fully exposed in the air, or were wading in shallow water and were putting just their heads below the surface. All subsurface foraging is termed "diving." Birds were watched from a distance of 30–100 m with binoculars or telescope, and cumulative times for each activity were recorded on a set of stopwatches.

Weather records were taken at Stirling, 29 km from the study site, throughout all field sessions. On other occasions, weather data were

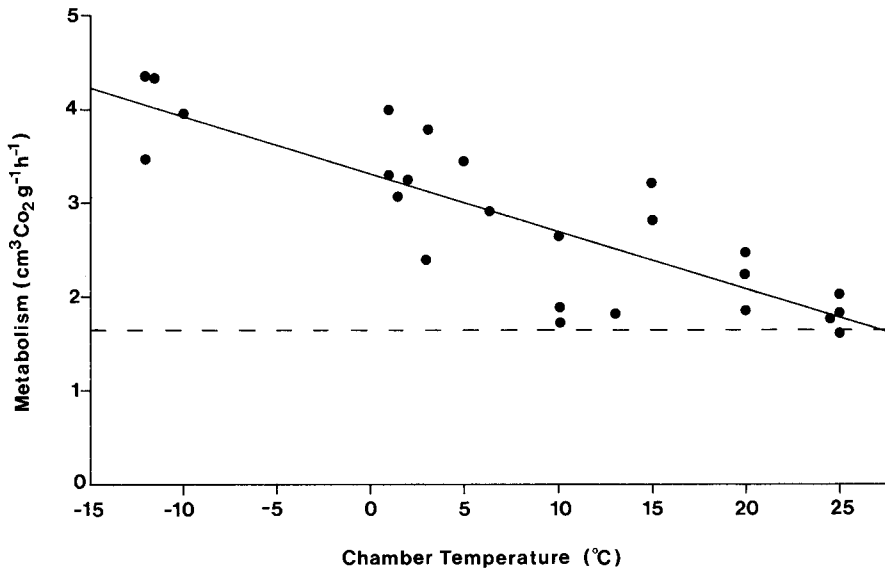


FIGURE 1. Metabolic rates of Dippers (closed symbols, solid line) in relation to chamber temperature during nighttime rest. Basal metabolism (dashed line) is derived from the equations of Aschoff and Pohl (1970) (see text).

collected beside the river and at roosts to examine micro-climate variation. Temperatures used for calculating monthly energy budgets refer to the averaged 40-year means (1941–1970) for Perth, Glasgow, and Edinburgh, which lie in the general area of study, in central Scotland (data from Meteorological Office, United Kingdom). River depth and flow rate were recorded continuously at one site on the study river.

TIME-ACTIVITY-LABORATORY (TAL) METHOD

The use of time-activity budgets, along with laboratory measurements of activity costs, to estimate DEE, has been called the TAL (time-activity-laboratory) method by Mugaas and King (1981). Time-activity budget data were grouped by day or by month, as appropriate, irrespective of the identity, sex, or age of the birds. The following equation was then used for deriving DEE ($\text{kJd}^{-1} \text{ind}^{-1}$, after Bryant et al. 1984):

$$\text{DEE} = \{[t_N(M_{bN} + \text{TR}_N)] + [t_D(M_{bD} + \text{TR}_D)] + [t_{re} \cdot M_{re} + t_{fo} \cdot M_{fo} + t_{di} \cdot M_{di} + t_a \cdot M_a]\} W \quad \text{Eq. 1}$$

In Equation 1, t and M denote time (h) and metabolism ($\text{kJg}^{-1} \text{h}^{-1}$), respectively, and the subscripts are defined thus: rest (re), foraging (fo), diving (di), and flying (fl). Daylength (the "active" day) is t_D , night is t_N , and W is body mass (g). Basal metabolic rate (M_b) is calculated from Aschoff and Pohl (1970) for night (M_{bN}) and day (M_{bD}) phases. The thermoregulatory component (TR) is the difference between calculated M_b and resting metabolism

as measured by indirect calorimetry. Because all activities occurred at ambient temperatures (i.e., -4°C to $+11^\circ\text{C}$) below the presumed lower critical temperature (27°C), the use of calculated M_b , rather than a directly measured value, actually had no effect on our metabolism estimates for resting birds. For calculating total thermoregulatory costs during daytime, we excluded the time spent flying. For simplicity, Equation 1 does not include this assumption. Net costs for each activity [i.e., total energy expenditure less ($M_b + \text{TR}$)] are given in the Results.

RESULTS

LABORATORY METABOLISM STUDIES

Oxygen uptake and carbon dioxide production were measured simultaneously for four Dippers. The mean respiratory quotient (RQ) was 0.74 ± 0.04 (SD, $n = 7$). Hence, for calculations of energy expenditure, we held that $1 \text{ cm}^3 \text{ CO}_2 = 26.73 \text{ J}$ (Brody 1945), although we lack direct evidence that the same RQ applies during diving and flying.

The relationship between nighttime metabolism (M_{rN} , $\text{cm}^3 \text{ CO}_2 \text{ g}^{-1} \text{ h}^{-1}$) and chamber temperature (T_a , $^\circ\text{C}$) was based on mean CO_2 output during overnight runs (12 + h) on 25 occasions (Fig. 1):

$$M_{rN} = 3.331 - 0.0616T_a \quad \text{Eq. 2}$$

($r = -0.84$, $P < 0.01$).

Expressed in units of energy ($\text{Jg}^{-1} \text{ h}^{-1}$), this converts to the following:

$$M_{rN} = 89.03 - 1.646T_a \quad \text{Eq. 3}$$

TABLE 1. Estimates of basal metabolic rate and net costs of activity for Dippers.

| | Symbol | Metabolic cost* J g ⁻¹ h ⁻¹ | Method |
|----------------------------|-----------------|--|---|
| Basal (night) | M _{bN} | 43.89 | Aschoff and Pohl (1970) |
| Basal (day) | M _{bD} | 57.37 | Aschoff and Pohl (1970) |
| Roosting (night) | M _{ro} | 0 + TR | Present experiments |
| Resting (day) ^b | M _{re} | 32.01 + TR | Interpolated (see text) |
| Foraging ^c | M _{fo} | 64.01 + TR | Present experiments |
| Diving ^d | M _{di} | 219.45 + TR | Inferred from published data (see text) |
| Flying | M _f | 374.63 | Calculated after Hails (1979) |

* All metabolic costs are exclusive, hence M_{ro}, M_{re}, M_{fo}, M_{di}, and M_f are net costs which exclude basal metabolism, M_{bN} or M_{bD}. Thermoregulatory costs are additional where indicated by +TR.

^b Rest (day) includes non-locomotor activities such as preening (see text).

^c Foraging includes all non-diving feeding activity.

^d Refers to subsurface-foraging by diving.

The thermoregulatory component (TR_N, Jg⁻¹ h⁻¹) was then obtained by subtracting calculated basal metabolism from observed resting metabolism. Hence:

$$TR_N = 45.14 - 1.646T_a \quad \text{Eq. 4}$$

Data for daytime metabolism (M_{rD}, Jg⁻¹ h⁻¹) were taken from the 1 + h interval between dawn and "light-on" in the incubator. Treating them in the same way as Equation 2 gives:

$$M_{rD} = 125.87 - 2.630T_a \quad \text{Eq. 5}$$

$$(r = -0.71, P < 0.01, n = 24).$$

Then:

$$TR_D = 68.50 - 2.630T_a \quad \text{Eq. 6}$$

The metabolism of Dippers in the rotating chamber (M_{aD}, Jg⁻¹ h⁻¹) was:

$$M_{aD} = 189.06 - 2.431T_a \quad \text{Eq. 7}$$

$$(r = -0.67, P < 0.01, n = 24).$$

Analysis of covariance showed that the regression coefficients for Equations 3, 5, and 7 did not differ significantly ($P > 0.05$), but that their intercepts did ($P < 0.05$). This result suggests that heat produced during activity did not substitute for the thermoregulatory component. We therefore took the net energy cost of foraging (M_{fo}) to be constant (=64.01 Jg⁻¹ h⁻¹). It was calculated, by difference, from Equations 5 and 7, at the mean temperature recorded during DLW measurements (=4.1°C), and was equivalent to 1.46 M_{bN} (Table 1). To

estimate the net cost of daytime rest, which included some non-locomotor activity such as preening, we assumed a mid-point value between basal metabolism (M_{bD}) and metabolism while foraging (hence, M_{re} = 32.01 Jg⁻¹ h⁻¹ = 0.73M_{bN}). These activity cost coefficients compare closely with those proposed by Dolnik (1982) and others (King 1974).

In winter, Dippers usually feed by diving to the stream bed. We know of no data for the metabolic cost of this activity, either for Dippers in Europe or for their relatives. In the Mallard (*Anas platyrhynchos*), the net cost of surface swimming ranges from 2.5–5.6 M_{bN} (Prange and Schmidt-Nielsen 1970: Table 2). It is likely that the vigorous behavior shown by diving Dippers, involving both wing and leg action while in the water (Goodge 1959: see below) would put the cost of diving around, or above, the highest value for Mallards, which use the feet alone. In the Jackass Penguin (*Spheniscus demersus*), the net cost of foraging at sea is estimated as 5.9 M_{bN} and of diving alone as 9.3 M_{bN} (Nagy et al. 1984). In this example, the thermoregulatory component was probably greater than in the Mallard, because air and water temperatures were lower. While direct extrapolation from these examples is not possible, it seems likely that the net cost of diving by Dippers falls in the range 3–7 M_{bN}. This is assumed to include any cost of thermoregulation in water, additional to that normally incurred in air (Prange and Schmidt-Nielsen 1970), which results from the greater

TABLE 2. Metabolism of two swimming birds.

| Species | Body mass (g) | Basal metabolism (Jg ⁻¹ h ⁻¹) | Metabolic cost ^b | Temperature (°C) | Reference |
|--|---------------|--|-----------------------------|------------------|-----------------------------------|
| Mallard (<i>Anas platyrhynchos</i>) | 1,081 | 13.36 | 2.5–5.6 | 24 | Prange and Schmidt-Nielsen (1970) |
| Jackass Penguin (<i>Spheniscus demersus</i>) | 3,167 | 9.46 | 5.9–9.3 | 15 | Nagy et al. (1984) |

* Basal metabolism (M_{bN}) is calculated from Aschoff and Pohl's (1970) resting phase equation.

^b Metabolic costs, expressed as multiples of M_{bN}, are given as net costs (i.e., total metabolism while swimming less M_{bN}). The range denotes minimum and maximum costs given in the original papers. Estimated costs differ slightly from those in the original publications because both used the equation of Lasiewski and Dawson (1967), rather than that of Aschoff and Pohl used here.

TABLE 3. Time-activity budgets* for Dippers during the non-breeding season. Data show percentage time for each activity (a) during daylight only and (b) over 24-h day.

| | October | November | December | January | February |
|---------------------------------|---------|----------|----------|---------|----------|
| (a) Daytime budgets | | | | | |
| Resting | 31.4 | 28.0 | 24.0 | 25.7 | 50.0 |
| Foraging | 52.5 | 37.5 | 9.5 | 21.8 | 8.4 |
| Diving | 13.4 | 31.4 | 62.7 | 50.2 | 33.6 |
| Flying | 2.7 | 3.1 | 3.8 | 2.3 | 8.1 |
| (b) 24-h day budgets | | | | | |
| Roosting | 53.6 | 60.8 | 66.8 | 63.0 | 56.4 |
| Resting | 14.6 | 11.0 | 8.0 | 9.5 | 21.8 |
| Foraging | 24.2 | 14.8 | 3.2 | 8.1 | 3.7 |
| Diving | 6.4 | 12.1 | 20.8 | 18.6 | 14.5 |
| Flying | 1.2 | 1.2 | 1.3 | 0.9 | 3.6 |
| <i>n</i> observations | 38 | 57 | 27 | 30 | 61 |
| <i>n</i> minutes of observation | 75.3 | 178.8 | 70.6 | 143.4 | 197.5 |

* For calculations of input parameters for Equation 1, t_w , t_o , t_{di} , and t_p equal 24 (% 24 h/100). Daylength t_D = sunrise + 1 h, t_N (night) is 24 - t_D (see Results).

convective heat losses underwater. For our main calculations, we took the mid-point of this range (5 M_{bN}) for estimating diving costs (M_{di}) (Table 1). We also examined the effect of taking higher or lower estimates of M_{di} .

Energy expenditure during flight (M_{flying} , $\text{kJg}^{-1} \text{h}^{-1}$) was calculated from the equation of Hails (1979), where:

$$M_{flying} = 1.785W^{-0.351} \quad \text{Eq. 8}$$

The net cost of flight (M_f) was then 374.63 $\text{Jg}^{-1} \text{h}^{-1}$ (i.e., M_{flying} less M_{bD}).

CALCULATING THE TAL ESTIMATE OF DEE

Input parameters for Equation 1 are derived from data in Tables 1 and 3. To obtain "active-day" and "night-roost" durations, we noted the time of movements into ($n = 6$) and out of ($n = 4$) roosts in winter, and compared them with times of sunset and sunrise, respectively. Mean arrival time at roost cavities was at sunset + 29.3 min and departure at sunrise - 29.5 min. The "active-day," called daylength (t_D), is thus sunrise to sunset + 1 h.

Most activity categories could be easily distinguished in the field. In the case of diving, however, the fact that that activity was underwater usually precluded detailed observations. Nevertheless, on eight occasions, Dippers were clearly seen during diving sessions in natural sites. In all instances, the birds swam down to the stream bed, using their wings for propulsion, and rarely held onto the river bed using their feet. Work under captive conditions confirms this to be the predominant underwater behavior (Goodge 1959; Bryant, unpubl.). Most activities occurred in bouts. Thus, in winter, diving bouts involved many brief dives (mainly <6 s) alternating with surface swimming, or perching on a nearby rock, while items were swallowed. Diving bouts were fol-

lowed by resting or by short flights or walks to other feeding sites.

Body mass for the individuals in the sample of DLW-loaded birds was 56.94 ± 4.47 (SD, $n = 32$) g. To minimize differences between methods which arise simply from body mass differences, we took this same mass for all calculations of DEE by Equation 1. The result of this, of course, is to eliminate any effect of sex differences and of seasonal changes in mass on DEE (Galbraith and Broadley 1980).

Accurate accounting of thermoregulatory costs depends on precise description of the thermal environment (Mugaas and King 1981). Relying on mean air temperatures only approximates conditions experienced by birds in the wild. Roost cavity temperatures and, more surprisingly, water temperatures were, however, similar to bankside (shade) temperatures measured at the same time and to temperatures recorded at the Stirling weather station ($\pm 2^\circ\text{C}$). Certainly, the shallowness of the river allowed rapid thermal equilibration (Smith 1981). Furthermore, any ameliorating effect of solar radiation (Lustick 1969, 1970; Walsberg 1977) could only apply to resting or foraging birds in daytime. As sunshine during October-February averages 1.84 h d^{-1} in the study area, and birds often rest under cover anyway, they had little exposure to direct solar radiation. The effect of wind on metabolism is potentially more important (Porter and Gates 1969, Hayes and Gessaman 1980). At night, however, Dippers were fully sheltered in their roosting cavities (Shaw 1979a), and, in daytime, they were often out of the wind. This was because the river lay 1-2 m below the level of adjacent ground (the banks thus offered some shelter), and because, in high winds, resting birds actively sought shelter behind rocks. Therefore, the thermal environment experienced by the birds, except when they were diving, was often

TABLE 4. Correlations for (a) Daily energy expenditure (DEE) and (b) Average daily metabolic rate (ADMR) of Dippers in relation to individual attributes, environment, and activity-budgets.*

| | Individual ^b attributes | Environment | Activity |
|-----------------------|--|-----------------------------|--|
| (a) DEE correlations: | Body mass 0.33* (32) Wing length 0.35* (32) Keel length 0.36 (24) | No significant correlations | % day resting -0.35* (29) |
| (b) ADMR correlations | No significant correlations | River depth 0.30* (32) | % day resting -0.46** (29) % 24 h resting -0.36* (29) % 24 h active 0.37** (29) % 24 h feeding 0.37* (29) |

* Data for DEE and ADMR were derived using DLW technique. Additional independent variables included in correlation analysis were: Individual attributes: Age (years), Tarsus length; Environment: River flow rate, Daylength, Temperature (Maximum, minimum, and mean), Rain (daytime), Windspeed (daytime), Sunshine, Cloud cover; Activity: % day diving, % day flying, % day foraging, % day feeding (i.e., foraging + diving), % 24 h diving, % 24 h flying, % 24 h foraging. Where $n < 32$, in parentheses, data sets were incomplete. * $P < 0.05$, ** $P < 0.01$.

^b Wing length is maximum chord (mm); keel length denotes length of sternum along keel (mm). All four body size measures were highly correlated ($P < 0.01$).

broadly similar to that indicated by ambient temperature measurements alone. Nevertheless, precise evaluation of the effects of solar radiation and wind on Dipper metabolism, ideally, using equivalent black body temperature as an index of the thermal environment (Robinson et al. 1976, Mugaas and King 1981), requires further investigation.

DEE, calculated from Equation 1 for the average conditions and activity budgets recorded during our studies with doubly-labelled water (see below), where mean $T_a = 4.1 \pm 3.0$ (SD)°C, was 194 ± 24 (SD) kJd^{-1} . If lower or higher estimates of the cost of diving are assumed, then estimated DEE changes to 177 kJd^{-1} (where $M_{\text{di}} = 3M_{\text{bN}}$) or to 212 kJd^{-1} (where $M_{\text{di}} = 7 M_{\text{bN}}$). At long-term mean monthly temperatures, and including all available time-budget data, DEE ranged from 170 in October to 207 kJd^{-1} in February (mean = 195 ± 16 (SD) kJd^{-1}).

The sensitivity of DEE estimates to input values for metabolic costs (all those listed in Table 1) was examined by changing each in turn by +10% and recalculating DEE (Equation 1). Resulting changes in estimated DEE were all less than 0.5%, except for M_{di} , where DEE increased by 2.3%.

DOUBLY-LABELLED WATER TECHNIQUE

Carbon dioxide production by Dippers, measured using the DLW technique, was 5.64 ± 1.26 (SD) $\text{cm}^3\text{CO}_2\text{g}^{-1} \text{h}^{-1}$ ($n = 32$). We call this the average daily metabolic rate (ADMR). This yields an estimated DEE of 206 ± 49 (SD) kJd^{-1} . Expressed as a multiple of basal metabolic rate, $\text{DEE} = 3.43 M_{\text{bN}}$.

Differences in the body mass and size of individuals, the conditions they experienced, or the behavior they showed accounted for some of the observed variation in DEE and ADMR (Table 4). The most important factors, as indicated by significance level in a correlation matrix, were body size (for DEE only; Fig. 2) and the amount of resting or feeding activity during the day (Table 4). Significant correlations between DEE and three size measures, yet none for ADMR with the same measures, suggest that the critical factor is the mass of metabolizing tissue and not a systematic difference in the activity or environment of

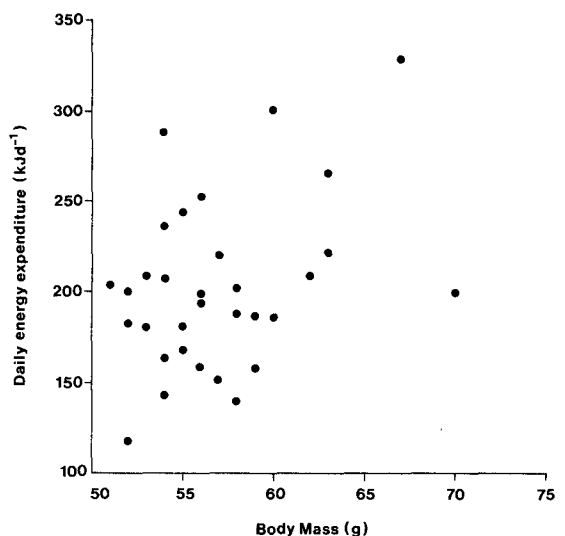


FIGURE 2. Daily energy expenditure (DEE) of individual Dippers in relation to their body mass ($r = 0.33$, $P < 0.05$).

TABLE 5. Models for predicting DEE: comparison of prediction with DLW estimate (called standard).

| Predicted DEE kJd ⁻¹ | Method* | Reference |
|---------------------------------|---------------------------|--|
| 206 | DLW | Standard, present study |
| 194 | TAL* | Equation 1, present study |
| 176 | Regression | King (1974) |
| 175 | Regression | Present study (non-breeding passerines, Equation 10) |
| 156 | Regression | Kendeigh et al. (1977) |
| 155 | Regression | Present study (non-breeding) |
| 154 | Regression | Dolnik and Kinzhewskaja (1980) |
| 153 | TAL* | Dolnik (1982) |
| 151 | Regression | Walsberg (1983) |
| 146 | TAL* | Koplin et al. (1980) |
| 144 | TAL* | Walsberg (1977) |
| 130 | TAL | Yom-Tov and Hilborn (1981) |
| 114 | M _b multiplier | Drent and Doornbos (in Drent and Daan 1980) |

* Time-energy budget methods which make provision for thermoregulation and vigorous non-flight activity are marked, *.

birds of different size. For both DEE and ADMR, the highest correlation among the activity factors examined was for the proportion of each day spent resting (Table 4). The con-

sequence of an increase in river depth was to encourage diving at the expense of foraging. Because diving was the most energetically costly method of feeding, mass-specific energy costs were likely to be higher when diving was more frequent. The absence of a similar correlation for percentage diving itself may imply that change in river depth can be a better predictor of average daytime activity patterns than certain elements from our time-activity budgets. An attempt to examine further the relative importance of individual, environmental, and activity factors by step-wise multiple regression was unsuccessful, because no partial effects were significant (i.e., $P > 0.05$).

DISCUSSION

THERMOREGULATION

Accurate predictions of DEE using time-energy budgets depend on the validity of several assumptions. Whether heat production during exercise can substitute for thermoregulatory production is questionable, since the results of earlier studies are inconsistent (Kontogiannis 1968, Mugaas and King 1981). We found no evidence for this substitution in Dippers, at least while they walked slowly in a treadmill, and have therefore treated foraging costs and

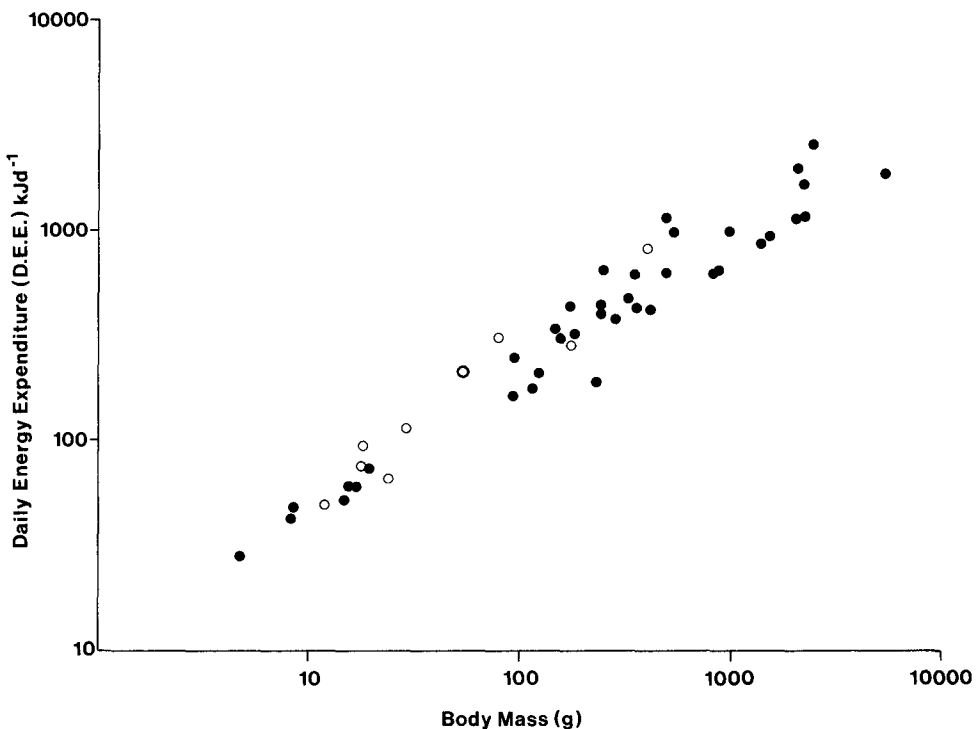


FIGURE 3. Daily energy expenditure (DEE) of non-breeding birds in relation to body mass. Open symbols show passerines, closed symbols, non-passerines. The large open symbol denotes the Dipper. Equations are as follows: DEE (All species) = $11.954W^{0.634}$, $F = 667$, $df\ 2 = 45$, $P < 0.01$ (Eq. 9); DEE (Passerines) = $8.732W^{0.742}$, $F = 86$, $df\ 2 = 6$, $P < 0.01$ (Eq. 10); DEE (Non-passerines) = $11.649W^{0.635}$, $F = 516$, $df\ 2 = 37$, $P < 0.01$ (Eq. 11); where DEE is $\text{kJ ind}^{-1} \text{d}^{-1}$ and W is body mass (g).

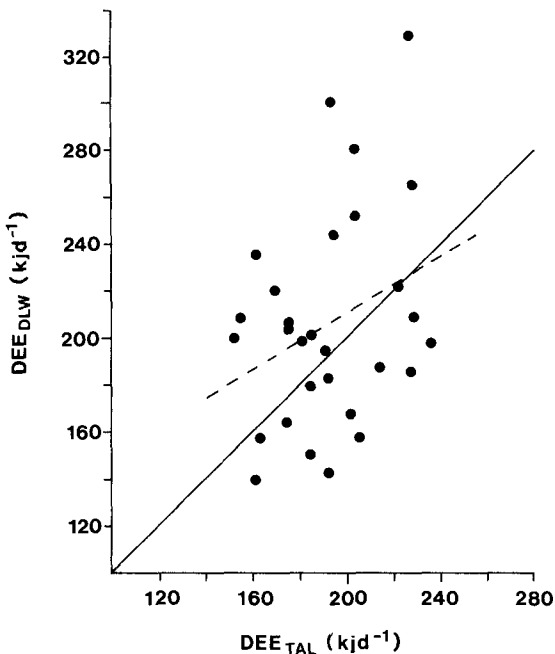


FIGURE 4. Daily energy expenditure of Dippers measured using the doubly-labelled water technique (DEE_{DLW}) in relation to DEE estimated by time-energy budgets (DEE_{TAL}) ($r = 0.32$; $P < 0.05$). The solid line shows where $DEE_{DLW} = DEE_{TAL}$. The fitted regression is shown by the dashed line ($DEE_{DLW} = 90.29 + 0.60DEE_{TAL}$).

thermoregulatory costs as additive. We assumed the same situation applied to diving Dippers, and that thermoregulatory costs under water could be predicted from our equation for Dippers in air, plus an unknown component included in the net diving cost (see Results). It also remains unresolved whether substitution occurs in flying birds (Schuchmann 1979, Mugaas and King 1981), but since Dipper flights were brief (Table 3), effects on calculated DEE will nevertheless be limited. The close agreement between DEE measured using DLW and time-energy budgets is consistent with our assumptions being correct or introducing no major errors, but in itself provides little or no support for any given assumption.

COMPARISON OF METHODS FOR ESTIMATING DEE

Validation of the doubly-labelled water method against other techniques under laboratory conditions has yielded differences ranging from 3% to 13% (Lifson et al. 1955, McClintock and Lifson 1958a and b, Lee and Lifson 1960, LeFebvre 1964, Mullen and Chew 1973, Little and Lifson 1975, Randolph 1980, Gettinger 1983, Williams and Nagy 1984). Our own validation trials have shown differences between CO_2 production, measured simultaneously by infra-red gas analysis and with DLW, of 3% (Hails and Bryant 1979) and 2% (Westerterp

and Bryant 1984). Thus, although the DLW technique can overestimate or underestimate CO_2 production, its mean error rarely exceeds 10% (Nagy 1980).

Comparing, for Dippers, the mean DEE, estimated using DLW and predicted from Equation 1, showed the TAL estimate was 6% lower, but within ± 1 SD of the DLW mean (206 ± 49 kJd^{-1}). Further comparisons with a range of predictive equations showed that the TAL model used here predicted more accurately than the others, which gave estimates ranging from 176 kJd^{-1} to 114 kJd^{-1} (Table 5). Among these, the closest prediction was by the regression equation of King (1974), which was compiled from twelve earlier studies of free-living birds. We surmised that even greater accuracy might be achieved with an allometric equation of this type, by restricting input data to those for non-breeding birds, as well as by including material additional to those available to King (1974). This new regression equation for non-breeding birds failed, however, to yield a more accurate prediction, perhaps because the vigorous diving habits of the Dipper in winter led to a rather high DEE (Fig. 3). That activity indeed markedly affects variation in DEE, and exceeds any effects due to changes in prevailing temperature, is implied by the correlation between daily activity patterns and DEE as well as the absence of significant correlations with weather variables (Table 4). Clearly, temperature was not the principal factor causing variation in DEE of Dippers in winter. For any given individual whose size will be constant, it is likely that changes in activity pattern are the main factor causing energy expenditure to vary (Table 4). A full analysis of the relative importance of these effects, however, requires more detailed study of the micro-climate experienced by Dippers relative to gross weather changes, as well as more comprehensive time-activity budgets.

Some models for predicting energy expenditure by free-living birds specifically include time devoted to flight—the most energy-demanding of their activities. Models that include both flight costs and thermoregulatory demands generally yield the most accurate predictions of DEE for Dippers (Table 5). Few models, however, allow for vigorous non-flight activity. In Dolnik's review (1982), for example, $1.6M_{bN}$ was the highest cost assumed for non-flying birds. Dippers are certainly not unusual in including some high-cost non-flight activity in their behavioral repertoire; examples of activities likely to require much energy include: probing by sandpipers (Scolopacidae), hammering by oystercatchers (*Haematopus* spp.) and gulls (Laridae), burying food by crows

(Corvidae), and running by plovers (Charadriidae) and wagtails (*Motacilla* spp.) Accurate budgets for species such as these may require explicit recognition of non-flight net activity costs greater than 1–2 M_{bn} , especially if they are frequent or are used over long periods.

INTRASPECIFIC VARIATION IN DEE

DEE, measured using the DLW technique, was correlated with estimates calculated using Eq. 1 for each individual in the sample for which time-budget data were available (Fig. 4). The coefficient of determination, however, was only 10%. The variance of the calculated sample was less than that for the DLW sample, probably because we did not distinguish time-activity budgets for individuals on the same day, and because mass-specific costs of thermoregulation, maintenance, and activity were assumed to be the same for all birds. While the accuracy of time-budgets could be improved with a greater success in finding and following our marked birds, it would be difficult to model the observed variation in the constituent energy costs (see Results) without first identifying the causes of variation consistently found in laboratory studies of metabolism (at least some of which, presumably, persist under natural conditions). At present, therefore, time-energy budget methods can give satisfactory estimates of mean DEE, yet are unlikely to mimic natural patterns of variation without first incorporating a stochastic element into the input parameters. Finally, it should be recognized that the low level of correlation between DLW and time-energy budgets will also follow, in part, from errors inherent in the theory and practice of the DLW technique (Lifson et al. 1955, LeFebvre 1964, Nagy 1980).

CONCLUSION

Time-activity budgets in conjunction with laboratory estimates of metabolism, as well as regression equations relating DEE to body mass, can be helpful for obtaining crude estimates of DEE. These can prove adequate for ecosystem studies where the wide range of habits shown by members of a community will reduce the significance of interspecific differences. By contrast, in studying a single species, it will usually be necessary to make explicit allowance for the main energy-demanding activities, as well as for quantifying the demands of thermoregulation, in order to accurately predict mean values for DEE, and thus demonstrate variation linked to changing behavior, seasons, or climate. Even so, it is unlikely that such methods will realistically reflect the variance of energy budgets that are likely to occur in free-living birds.

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