Energy expenditure in wild birds

BY DAVID M. BRYANT

Avian Ecology Unit, Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA

Allometric scaling of energy metabolism is one of the most familiar and robust models in biology (Brody, 1945; Kleiber, 1975; Calder, 1984), although its cause remains contentious (West *et al.* 1997). Energy requirements of animals are often calculated assuming metabolism scales as a 0·67 or 0·75 power of body mass (Peters, 1983; Brown & Maurer, 1986). Yet, the practices and assumptions of this approach will often be inadequate if the goal is precise prediction of energy expenditure or requirements at the species level. This is because organismal and environmental influences on avian metabolism are ubiquitous, both regarding their effect on basal energy requirements (Aschoff & Pohl, 1970; Bennett & Harvey, 1987) and, more pertinently in the present context, on expenditure of energy by free-living individuals (Walsberg, 1983; Nagy, 1987; Bryant & Tatner, 1991). It is important, therefore, to identify factors, additional to those simply allied with body mass, which account for this variation.

Identification of significant categorical factors affecting energy expenditure has been a main concern to date. A study of interspecies variation in mammalian energetics, for example, showed that desert dwellers had generally low field (free-living) metabolic rates but identified no other significant factors (Nagy, 1994). Amongst birds, desert dwellers and sea-birds stand apart from others, with respectively low and high field metabolic rates (Nagy, 1987). Also, some studies have indicated that aerial-feeding birds, including hummingbirds, have a relatively high field metabolism (Walsberg, 1983). Nevertheless, very few reliable predictor variables of wide applicability are available to explain interspecies variation in energy expenditure, either for wild birds or mammals.

The present study has the general aim of accounting for interspecies variation in energy expenditure of birds. More specifically, it confirms that metabolic scaling with body mass (W) remains pre-eminent in explaining energy expenditure amongst wild birds, even when W only varies across about an order of magnitude. The main aim, however, is to identify and evaluate other factors which predict variation in energy expenditure amongst free-living birds.

METHODS

All estimates of energy expenditure used in the present study were obtained from wild birds by using the doubly-labelled water (DLW) technique (Lifson & McClintock, 1966; Nagy, 1980; Bryant, 1989; Tatner & Bryant, 1989). The technique yields reliable, direct, estimates of CO_2 production from which energy expenditure is calculated using the accepted conventions of indirect calorimetry (Brody, 1945; Blaxter, 1989, Speakman & Racey, 1988). Measurements on individual birds in the study were generally made over periods of 1–2 d; a time-span constrained by their small W. Details of field and laboratory methods may be found in the sources quoted in the Appendix.

Statistical analysis was restricted to species weighing under 150 g (Appendix), because exclusion of a wider body-size range reduced the risk of confounding the causes of variation in energy expenditure with the potentially subtle consequences of life-history

attributes (Calder, 1984; Saether *et al*. 1993; Saether, 1994). In this way, the effect of large-bodied seabirds in particular, typically with high survivorship and small families, on emergent trends in energy expenditure, was minimized (but see Trevelyan *et al*. 1990). At the same time, the effect of systematic variation in behaviour related to W was also reduced. For example, Walsberg (1983) demonstrated a negative correlation between flight activity and W, which could confound an apparent association between energy expenditure and size. Within the limited W range dealt with here, however, there was no correlation between daily flight duration (h/d) and W (r -0.11, n 33, NS).

The results presented here are based on two main analyses. The first analysis (A) employs data from all species which have been studied, and the second (B), species for which data on flight behaviour were available. In both cases, species were treated as independent data points. Generalizations derived from analysis of across-species data can yield misleading results, however, if phylogeny is not considered as a possible confounding factor (Harvey & Pagel, 1991). This is because species do not necessarily constitute fully independent data points; hence, the degrees of freedom assumed in any statistical analyses could be inflated. In the extreme case, relationships may be demonstrated which do not exist. Nevertheless, in practice, the diverse assemblage considered here and the restriction of this study to species under 150 g, substantially reduces the risk of spurious results (see p. 1029). Furthermore, two recent analyses involving interspecies analysis of avian metabolism, showed that with a wide variety of taxa, similar results emerged from conventional analyses and those based on phylogenetically-independent contrasts (Weathers & Siegel, 1995; Ricklefs & Starck, 1996). The present investigation uses the conventional approach, and goes on to check that gross taxonomic groupings could not alone determine emergent patterns. Even so, confirmation is still needed that a phylogenetically-informed analysis would yield similar results.

Studies included in the analyses mostly referred to just a single stage in the annual cycle, but some, at the other extreme, included year-round measurements on both sexes. Overall, information on the following stages was available (includes both males and females unless otherwise stated): non-breeding (excluding high-latitude winters), holding territory (males), laying (females), incubation, rearing young, attending fledged young, juveniles, moult and winter. Data on nestlings were excluded; they have been reviewed recently by Weathers & Siegel (1995). The sample of species studied included both non-passerines and passerines. They were split into six taxonomic groupings (see results, p. 1029). All species could be allocated to one of four foraging modes (see results, p. 1029).

Data points were selected for each species in the following way. Data on energy expenditure during the nestling rearing period were preferred if more than one stage in the annual cycle had been studied, because this comprised the largest homogeneous group. If data from other stages were allied to detailed time-budget data, however, and the nestling stage was not, they were used instead. This allowed analysis of the effects of flight duration (h in flight/d) to employ the largest and most consistent data-set. Data on three other factors which could affect energy expenditure (latitude, daylength and ambient temperature) could usually be extracted from published accounts, and these were also included in the analyses. If daylength data were not given in the original paper, dawn–dusk intervals were taken from published sources for each site during the study period. In the present context, therefore, daylength broadly describes the length of the 'active' period (except for the crepuscular poorwill, *Phalaenoptilus nuttallii*). In some cases mean temperatures were obtained directly from authors, or for the relevant study period from nearby weather stations.

Three complementary units of energy expenditure were adopted here: first, daily energy expenditure (DEE), expressed as a function of BMR measured on the same species (BMR_{sp}; extrapolated over 24 h); second, DEE as a function of BMR calculated from the 'resting phase' equations of Aschoff & Pohl (1970; BMR_{ap}); third, DEE relative to metabolic mass (W^b), where the exponent was derived from each data-set under review. These were termed respectively $\times BMR_{sp}$, $\times BMR_{ap}$ and $DEE : W^b$.

RESULTS

Measurements of DEE were available from 123 stages for fifty-eight species. Energy expenditure values for seven species included in the analysis have not been reported previously (Table 1). Three examples involved measurements of a single individual (as did two published examples; Weathers & Nagy, 1980; Weathers & Paton, 1997). Nevertheless, these results are likely to be adequate for the present purpose, because in four cases, parallel studies on the same species, but using different methods or conducted at different times, gave closely similar results.

A correlation between DEE and W was confirmed, even within the narrow range of W considered (Fig. 1). The relationship was described by the power equation: $DEE (kJ/d) = 15 \cdot 94 (SE 1 \cdot 17) W^{0 \cdot 53 (SE 0 \cdot 05)}$ (r 0·82, $P < 0.001$, n 58; W expressed in g). For the sub-sample of birds (B), for which flight activity data were available: $DEE (kJ/d) = 14 \cdot 57 (SE 1 \cdot 22) W^{0 \cdot 57 (SE 0 \cdot 06)}$ (r 0·85, $P < 0.001$, n 33). The desert quail appeared as an outlier within the latter analysis (also, see Fig. 3), showing a low DEE relative to W. A revised allometric equation, excluding the quail, had a higher exponent: $DEE (kJ/d) = 11 \cdot 49 (SE 1 \cdot 20) W^{0 \cdot 65 (SE 0 \cdot 06)}$ (r 0·90, $P < 0.001$, n 32).

Table 1. *Energy expenditure of some small birds measured using the doubly-labelled water technique with sample sizes and the environmental conditions prevailing during each study**

(Mean values and standard deviations where appropriate)

	Body mass (g)	ADMR (ml CO_2/g per h) Mean	SD	DEE (kJ/d)	n	%fly	Daylength (h)	Latitude (°N)	T_a (°)
Dunnock†	21·2	6·39	0·62	86	4	–	8·7	56	3·0
Blackbird‡	96·0	2·92		179	1	0·6	8·7	56	3·0
Robin§	19·5	5·08	0·54	63	11	4·2	9·0	56	4·6
Spotted flycatcher‖	14·4	5·64		52	1	9·1	17·0	56	14·2
Great tit¶	18·9	4·66		56	1	2·5	8·7	56	3·0
Bullfinch**	25·1	5·53	0·39	88	4	–	9·7	51	4·0

ADMR, average daily metabolic rate; DEE, daily energy expenditure; %fly, proportion of the daylight period spent in flight; T_a, ambient temperature.

* Bryant and Tatner (unpublished results), unless stated otherwise. Data on field metabolic rates were obtained for two additional species in Australia: Superb fairy-wren (*Malurus cyaneus*) and Clamorous reed warbler (*Acrocephalus stentoreus;* Bryant, unpublished results).

† *Prunella modularis*; winter, Scotland.

‡ *Turdus merula*; winter, Scotland.

§ European robin (*Erithacus rubecula*): winter, Scotland (Johnstone, 1994).

‖ *Muscicapa striata*; rearing young, Scotland.

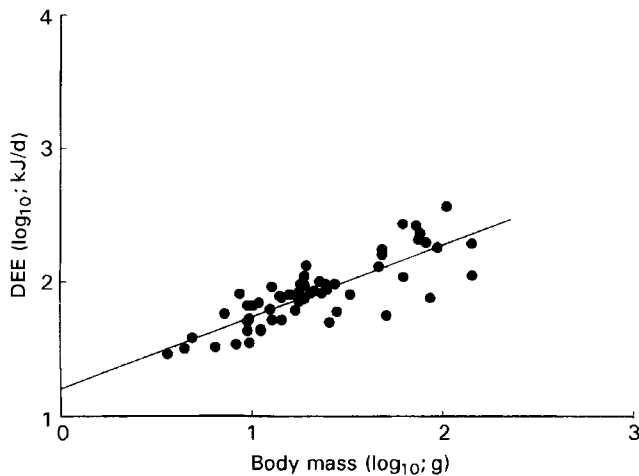¶ *Parus major*; winter, Scotland.

** *Pyrrhula pyrrhula*; winter, England.

Fig. 1. The relationship between daily energy expenditure ($\log_{10}$ DEE; kJ/d) and body mass ($\log_{10}$; g) for fifty-eight species of small bird. The equation for the fitted line is: DEE (kJ/d) $= 15\cdot94$ (SE $1\cdot17$)$W^{0\cdot53}$ (SE $0\cdot05$) (r $0\cdot82$, $P<0\cdot001$, n 58). For details of species and sources of data, see Appendix.

Stage of annual cycle

Energy expenditure data were available for ten stages of the annual cycle; however, for only five of these stages were mean expenditures obtained from more than four species. Accordingly, analysis is limited to these stages to avoid conclusions which rely on small, and hence potentially biased, samples of species. Analysis of variance (ANOVA) confirmed that 'stage' had a significant effect (F $4\cdot9$, $P<0\cdot01$) on DEE, when W was entered as a covariate (F $322\cdot9$, $P<0\cdot001$). Comparisons of energy costs between stages, however, sometimes gave inconsistent results. On the basis of DEE : W^b, parents rearing nestlings had the highest energy costs, followed by incubating females and males holding territory. The lowest costs were for non-breeders and birds during winter (Table 2). Yet, when $\times BMR_{ap}$ was taken as a measure of energy costs, non-breeders showed the highest costs. This is probably related to the inclusion of hummingbirds in this category (n five of thirteen), since when they were absent (as with $\times BMR_{sp}$), energy costs were relatively low. The effect of phylogenetic correction on this result deserves particular attention. There was a close consistency between $\times BMR_{sp}$ and DEE : W^b, suggesting that they provided the most generally applicable rankings.

Foraging mode

The sample of species was split into four foraging modes. Three of these ('hover', 'flight feed' and 'sit and wait') were in a minority, comprising nineteen species in total. The remainder were placed in a group of arboreal and ground foragers, embracing tits to honeyeaters, and involving most of the species studied (n 39). Highest energy expenditures were for the two 'aerial' groups (Table 3). Progressively lower expenditures were typical for arboreal and ground and 'sit and wait' foragers. These results are consistent with the highly significant differences (ANOVA; F $95\cdot4$, $P<0\cdot001$) in flight activity between foraging modes (see p. 1029), which, as expected, reached its lowest level amongst the least active 'sit and wait' foragers.

Table 2. *Energy expenditure* of small birds (<150 g) for ten stages during the annual cycle*

(Mean values and standard deviations)

| | $\times BMR_{sp}$ | | $\times BMR_{ap}$ | | $DEE:W^b$ | | |
	Mean	SD	Mean	SD	Mean	SD	n
Non-breeding	2·4	0·7(6)†	3·8	2·3	14·7	4·8	14
Holding territory (m)	2·8	0·3	3·2	0·6	18·2	3·7	5
Laying (f)‡	2·8	0·6	3·0	0·7	16·0	6·2	3
Incubating (f)‡	3·0	0·6(18)†	3·3	1·1	18·3	4·9	22
Incubating (m)‡	3·5	0·8	2·7	0·3	13·6	4·2	2
Rearing young	3·2	0·7(46)†	3·4	0·7	19·7	4·8	54
Attending fledglings	–		2·9	–	17·2	–	1
Juveniles	2·4	0·2	3·0	0·1	21·7	0·3	2
Moulting	2·4	0·2	3·1	0·3	20·3	2·1	3
Wintering	2·4	0·4(15)†	2·6	0·6	15·2	4·6	18

* Energy expenditure is given as a multiple of: (1) measured BMR ($\times BMR_{sp}$), (2) calculated BMR ($\times BMR_{ap}$; after Aschoff & Pohl, 1970); and as (3) daily energy expenditure (DEE) expressed as a function of metabolic mass (W^b, where b derived from the current data-set is 0·53). For further details, see p. 1027.

† Sample sizes where they differ from those shown.

‡ Males (m) and females (f) are indicated; otherwise both sexes are represented.

Table 3. *Energy expenditure* of small birds with different foraging modes†*

(Mean values and standard deviations)

| | $\times BMR_{sp}$ | | $\times BMR_{ap}$ | | $DEE:W^b$ | | |
	Mean	SD	Mean	SD	Mean	SD	n
Hover§	3·5	– (1)‡	6·2	1·4	18·7	4·4	6
Flight feed	4·4	0·7(5)‡	3·8	0·7	21·7	3·4	7
Glean	2·7	0·6(28)‡	3·0	1·0	16·4	5·3	39
Sit and wait	2·7	0·3(5)‡	2·6	0·6	13·8	4·1	6

* Energy expenditure is shown as a multiple of: (1) measured BMR ($\times BMR_{sp}$), (2) calculated BMR ($\times BMR_{ap}$; after Aschoff & Pohl, 1970); and as (3) daily energy expenditure (DEE) expressed as a function of metabolic mass (W^b, where b derived from the current data-set is 0·53). For further details, see p. 1027.

† 'Hover', foraging flights which routinely include hovering while searching for prey (pied kingfisher) or feeding (hummingbirds); 'flight feed', aerial feeding swallows (Hirundinidae); 'glean' includes a wide range of birds which forage on aerial vegetation or on the ground, typified, for example, by the Paridae; 'sit and wait' foraging involves periods of static searching, usually followed by a sally to snatch mobile prey on the ground or in the air. Here, the category includes the poorwill, bee-eater, bluebird and flycatchers (see Appendix).

‡ Sample sizes where they differ from those shown.

§ ANOVA on DEE with W as a covariate showed the main effect (foraging mode) was significant (F 3·4, df 3, P 0·025).

Taxonomic groups

Thirteen taxonomic groupings had slightly different energy expenditures. Combining these in turn into two and six larger entities, the former comprising non-passerines and passerines and the latter non-passerines plus five passerine groupings (Table 4), allowed variation across taxa to be examined in more detail. ANOVA on DEE, with taxon (split two or six ways) as main effects and W as a covariate, however, showed no significant effect of taxon in either analysis (in both cases, $F<1$, $P>0.5$).

Table 4. *Mean energy expenditures* of categories of small birds included in the study†*
(Mean values and standard deviations)

	× BMR$_{sp}$		× BMR$_{ap}$		DEE:W^b		
	Mean	SD	Mean	SD	Mean	SD	n
Galliformes	2·2	–	1·5	–	7·1	–	1
Charadriiformes	3·9	0·5	5·5	0·7	23·7	4·6	3
Columbiformes	2·1	–	0·9	–	6·3	–	1
Psittaciformes	2·1	0·5	2·6	0·1	10·9	1·4	3
Caprimulgiformes	2·6	–	1·6	–	6·3	–	1
Apodiformes	3·5	– (1)‡	6·6	1·3	17·7	4·6	5
Coraciiformes	3·2	– (1)‡	3·8	0·8	15·2	5·0	2
Piciformes	2·8	–	4·0	–	17·2	–	1
P: Crow relatives	2·7	0·1(3)‡	2·8	0·5	13·9	3·0	6
Thrush relatives	2·9	0·5(9)‡	3·0	0·6	17·9	4·5	11
OW insect-eaters	3·4	1·1(10)‡	3·2	0·8	16·5	4·3	17
Weaver relatives	2·3	0·1(2)‡	2·8	1·1	14·6	4·6	4
Nine-primaried Oscines	2·8	0·5	3·0	0·4	15·8	2·3	3

P, Passeriformes; OW, Old World.
* Energy expenditure is shown as a multiple of: (1) measured BMR (× BMR$_{sp}$), (2) calculated BMR (× BMR$_{ap}$); appropriate non-passerine and passerine equations from Aschoff & Pohl (1970) were used to derive BMR multiples; and as (3) daily energy expenditure (DEE) expressed as a function of metabolic mass (W^b, where b derived from the current data-set is 0·53). For further details, see p.1027.
† Taxonomic categorization is after Gill (1990), which largely followed Storer (1971) for non-passerines and Sibley & Ahlquist (1985) for passerines. Nine-primaried Oscines include Savannah Sparrow and two junco species (see Appendix).
‡ Sample sizes where they differ from those in the final column.

Energy expenditure and environmental factors

Three environmental factors and W were entered into a stepwise multiple-regression analysis with DEE as the dependent variable. Three factors were significant. W, as expected, explained most variation (66%), but both daylength (Fig. 2) and ambient temperature (mean 24 h; °; squared transformation) entered as significant using a forward stepwise procedure. Together, they explained 72% of the variation in DEE (Table 5, analysis A).

Energy expenditure and flight activity

Time spent in flight was significantly correlated with energy expenditure (Fig. 3); W and flight time together explained 77% of variation in DEE (Table 5, analysis B). In this analysis, daylength and temperature did not enter as significant. ANOVA, with 'aerial' or 'non-aerial' foraging habits as the main effect (F 0·5, P > 0·4) and with W (F 110·1, P < 0·001) and flight time entered as covariates, confirmed the latter was significant (F 11·0, P < 0·01). It follows that the dependence of energy expenditure on flight activity should follow a broadly predictable path; DEE should differ between species mainly according to unit flight costs and differences in the time spent flying.

Two simple time–energy budgets were constructed to assess this proposition: the first (model 1) consisted of only two components; 'flight' time (t_{fly}; based on field time-budgets from original publications) and 'rest' time (t_{rest}; assumed to be at BMR$_{ap}$; where $t_{total} = t_{fly} + t_{rest}$). Flight costs were predicted from the allometric equation of Masman & Klaassen (1987; E_{flight} (watts) = 0·305 M$^{0·756}$), or from an equation I derived from data they collated relating to 'extremely aerial species'; (E_{flight} = 0·344 M$^{0·512}$; taking one
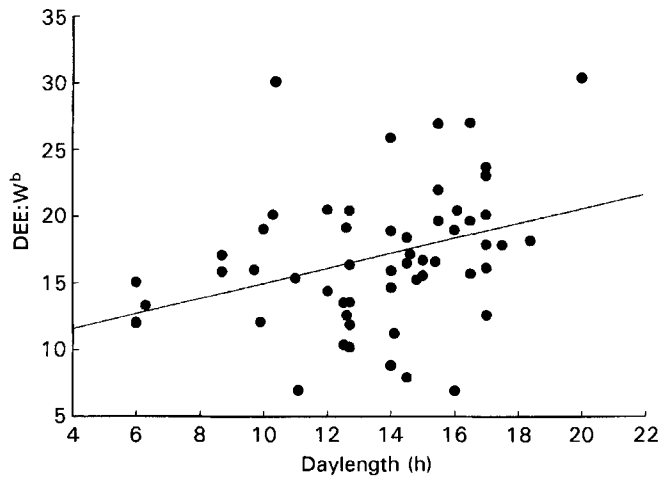
Fig. 2. The relationship between mass-specific energy expenditure amongst small birds (daily energy expenditure (DEE; kJ/d) : metabolic mass (W^b, where b 0·53)) and daylength. The regression for the fitted line is: $y = 9·33 + 0·56 x$ (r 0·35, $P<0·01$, n 57). No data on daylength were available for one species (*Zosterops lateralis*). For details of species and sources of data, see Appendix.
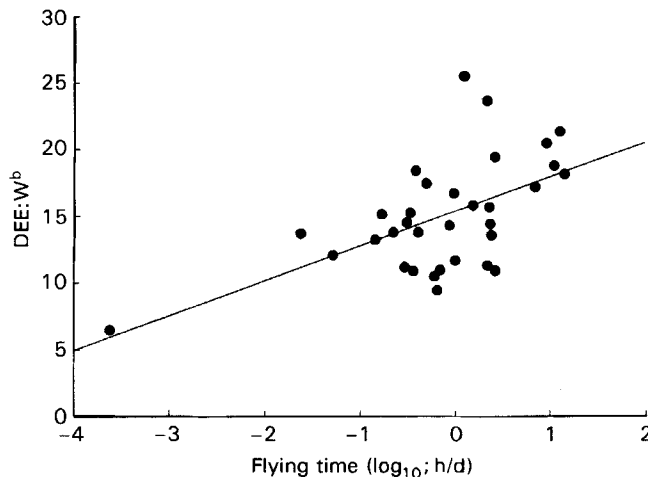

Fig. 3. The relationship between mass-specific energy expenditure amongst small birds (daily energy expenditure (DEE; kJ/d) : metabolic mass (W^b where b 0·57)) and time spent in flight ($\log_{10}$; h/d). The regression for the fitted line is: $y = 15·35 + 2·61x$ (r 0·56, $P<0·001$, n 33). Removal of the outlier (*Callipepla gambelii*), lower left, had little effect ($y = 15·33 + 2·75x$; r 0·46, $P<0·01$, n 32). For details of species and sources of data, see Appendix.

datum per species, n 6, $P<0·05$). A lack of morphological data for most of the species considered prevented more precise flight cost estimates being made using Masman & Klaassen's (1987) equation 6. The second energy budget (model 2) included flight costs, night-time costs at BMR_{ap}, plus an arbitrary allowance for daytime costs (apart from flight) at $2 \times BMR_{ap}$ (model 2a). Predictions from models were then compared with observed daily mass-specific energy costs (although hummingbirds were excluded, because hovering flight costs could not be calculated). Both models indicated that energy expenditure would rise progressively with increases in flight time at about the same rate as was observed.

Table 5. *Multiple-regression analyses of daily energy expenditure (DEE; kJ/d) by small birds*

(A forward stepwise procedure was used to select significant variables. Analysis A, one data point from all species; analysis B, only species for which flight activity was known)

Variable	Partial *b*	*Beta*	*t*	Statistical significance: *P*
A (all species)				
Log_{10} body mass (W; g)	0·529	0·82	11·0	<0·001
Daylength (h)	0·014	0·18	2·5	0·01
Ambient temperature ($T^2*;°$)	$-0·137 \times 10^{-3}$	$-0·17$	2·3	0·02
Constant	1·064		11·8	<0·001
B (flight data)				
$Log_{10}W(g)$	0·571	0·86	10·2	<0·001
Flying (h/d)	0·015	0·24	2·9	<0·01
Constant	1·121		14·3	<0·001

Analysis A: multiple R^2 (adjusted 72%, *F* 48·0, df_1 53, *P*<0·0001. Rejected variables (*P* > 0·05) were latitude and T.
Analysis B: multiple R^2 (adjusted) 77%, *F* 55·4, df_1 2, df_2 30, *P*<0·0001. Rejected variables were daylength, latitude and T. Dependent variable is DEE in both analyses
* Squared transformation of T.

Coefficients of determination (r^2) for models and observations were 57 and 63% respectively for models 1 and 2a. An alternative equation for deriving flight costs (Dolnik, 1982), allowed that increasingly aerial species had progressively lower flight costs. This energy budget (model 2b) generated changes in daily costs which more closely matched the observed pattern (r^2 69%). These results suggest that a knowledge of flight costs, even in the absence of other components of the energy budget, makes a substantial contribution to explaining variation in DEE.

Patterns of energy expenditure in small birds

Comparisons between rates of energy expenditure by different species are conventionally made by expressing energy expenditure relative to BMR. The largest sample is available when BMR is calculated from an allometric equation. This showed energy expenditure averaged 3·42 (SD 1·40) × BMR_{ap} (range 0·90–8·56; *n* 58). It has been argued (Bryant & Tatner, 1991), however, that more appropriate comparisons can be made using BMR measured on each species in question (BMR_{sp}). This apparently has some value here, since it eliminates some questionable outliers. Such BMR data, however, are not always available, thus the sample of species is necessarily smaller. This analysis showed energy expenditure averaged 2·96 (SD 0·81) × BMR_{sp} (range 1·49–5·06; *n* 39).

DISCUSSION

Variation in energy expenditure during the course of the annual cycle has been studied in relatively few species (King, 1974). In general, changes in mean expenditure within single species have been found to lie within rather narrow bounds (Bryant & Westerterp, 1980; Bryant & Tatner, 1988a; Weathers & Sullivan, 1993). The present analysis has shown that a similar pattern emerges when comparisons are made between species. For the five stages considered here in detail, the highest mean energy cost, while rearing young, was only 28% above the lowest cost (amongst non-breeders). The difference is somewhat greater

when all stages, including those represented by few data points, are compared (37 % difference); juveniles apparently incur the highest costs (Weathers & Sullivan, 1991). This contrast excludes migratory flights, of course, for which costs would undoubtedly be higher, but otherwise spans the main stages in the annual cycle. Even so, differences in energy expenditure over a wide range of environmental conditions, activities and species, are more striking for their consistency than their variability. This can be compared with patterns at the level of individuals in some species, where the highest expenditures at a given stage may be more than double the lowest values (Bryant & Westerterp, 1980; Bryant & Tatner, 1988b, 1991).

Three predictor variables were significantly related to DEE in the first analysis (A): W, daylength and temperature. W, as expected from earlier analyses of DLW results (Nagy, 1987), explained much of the variation in daily costs. The significance of daylength probably arose because longer days allowed more extended periods of activity, which was relatively more costly than alternative behaviours, such as resting. The negative effect of temperature seems likely to reflect the lower thermostatic costs incurred under higher ambient temperatures (Williams, 1987). The non-linear form of this relationship matches a similar result from an earlier study (Bryant, 1989). When the time spent in flight was incorporated into the analysis, it proved to be a better predictor than the two environmental factors, which then became non-significant under the stepwise procedure (analysis B). This accords with the variation apparent across species with contrasting foraging modes, particularly with respect to the frequency of flights during foraging. For example, the highest costs, for species which characteristically feed when flying, were 68 % greater (based on $DEE:W^b$) than the DEE of 'sit and wait' species with their relatively low daily activity costs. These patterns suggest that the frequency of costly activities has a marked effect on living costs amongst wild birds.

Flight is amongst the most energetically expensive of animal activities (Pedley, 1977; Norberg, 1990; Casey, 1992); direct measurements at times exceed $20 \times BMR$ (Tatner & Bryant, 1986; Masman & Klaassen, 1987). Its potential impact on DEE, therefore, is considerable. A simple energy budget incorporating flying and resting costs alone accounted for the rise in DEE of small birds with increasing time in flight. Some of the residual variation will be due to methodological errors in the DLW technique (Speakman & Racey, 1988), imprecision inherent in time budgets of flight activity, and factors apart from flight having an impact on energy expenditure of wild birds. In particular, non-flight activity will inevitably have affected observed expenditures to a degree (Bryant & Tatner, 1991). When energetically-costly non-flight behaviours are frequent, the slope of the regression of energy costs v. flight time will substantially underestimate flight expenditures (Tatner & Bryant, 1986; Wilson & Culik, 1993). The question also remains as to whether the effects of flight on energy expenditure shown in this analysis would have been as marked if phylogenetically-independent contrasts had been applied.

The rationale for considering flight costs mainly in terms of flight duration is often pragmatic; energy expenditure during flight is difficult to quantify directly, whereas time spent in flight and morphology are more widely available for modelling flight energetics. In practice, therefore, multiples of BMR (King, 1974; Dolnik, 1982), allometric equations predicting flight costs from W (Kendeigh et al. 1977; Hails, 1979; Butler, 1981), or estimates derived from combinations of mass and morphology (Masman & Klaassen, 1987; Castro & Myers, 1988) and aerodynamics-based models (Greenwalt, 1962; Tucker, 1973; Pennycuick, 1989; Rayner, 1993), are in routine use to estimate energy costs for flight. While level flapping flight is often an implicit assumption, a few studies have considered the effect of detailed changes in flight behaviour on flight energetics. They confirm that an

assumption of sustained flapping flight is unrealistic for many trivial flights because gliding and soaring often reduce expenditure during free-flights (Hails, 1979; Bryant & Westerterp, 1980; Masman & Klaassen, 1987; Furness & Bryant, 1996). Trivial flights (as opposed to migratory flights) within a home range or territory, whether seeking food, deterring competitors or avoiding predators, are likely also to involve actions which generate costs greater than for level flapping flight. Specifically, the cost of take-off and acceleration, turning, load carrying, landing, plus post-flight costs, should be considered. In addition, attributes peculiar to individuals or species should be allowed for, such as plumage wear or damage, or elongate tails (Thomas, 1993). Were data of this type to be available, more accurate predictions of trivial flight costs and, hence, field energy expenditure over extended periods would be feasible.

Activity costs in birds, of which trivial flights are normally a part, may govern choice of behavioural strategy, via their impact on the net benefits of alternative behaviours. Yet other costs, such as mortality risks, could also be involved in regulating behavioural strategies, and thereby energetic costs (Bryant, 1988), because costs of different types are intimately linked (McNamara & Houston, 1986; Ricklefs, 1991). For example, a bird which is hungry may take greater risks in other respects to secure food, most obviously with accidents, competitors, predators or diseases. Cuthill & Guilford (1990) showed that starlings (Sturnus vulgaris) took a riskier flight path when they were deprived of food. Equally, when conditions are severe, it pays to store fat, even though it has negative consequences for flight performance (Lima, 1986; Houston et al. 1993). While trade-offs of this kind are intuitively credible, their elucidation can be problematic because they are not readily explored using a single currency. Theoretical treatments, however, predict that patterns of behaviour will change as environments or reserve status shifts (McNamara & Houston, 1986, 1987). Clearly, when flight behaviour or mode changes, then flight energetics and, hence, DEE could also be affected.

When viewed in the context of daily energy budgets, flight behaviour and costs, as suggested previously, may have an important effect on variation in energy expenditure, whether examined within (Bryant & Tatner, 1991) or, as here, across species. That flight costs themselves have wider repercussions and, therefore, could help to explain average levels of energy expenditure, is suggested by studies of avian flight attributes in relation to components of fitness. Feinsinger & Chaplin (1975) and Carpenter et al. (1993) showed how wing-disc loading affected dominance relationships amongst hummingbirds. Johnstone (1994) demonstrated a correlation between the size of territory occupied and wing-disc loading in robins (Erithacus rubecula). Moller (1991) reduced song–flight time by skylarks (Alauda arvensis) through wing-feather manipulations while Evans & Hatchwell (1992) reduced flight time and hawking efficiency of sunbirds by tail elongation. Saether et al. (1993) added weights to petrels and induced a reduction in breeding success, possibly due to an increase in flight costs. All these studies suggest that behavioural, reproductive and survival strategies may be related to, and perhaps in part governed by, limitations on energy expenditure, including that devoted to flying (Bryant, 1988, 1991). While they mostly demonstrate intraspecies patterns, they also allow for comparable interspecies effects. Furthermore, since the energetic cost of trivial flights may be exceptionally high, these effects are not necessarily limited to species obliged to spend most of their day in flight.

Comparisons of energy expenditures can be made across species by expressing energy costs relative to BMR (Drent & Daan, 1980). The largest data-set, incorporating all fifty-eight species, was available when an allometric equation was used to derive BMR. In this context, calculated BMR serves as a standard against which all species could be compared.

What it did not do was allow for variation in BMR which was associated with factors apart from W; such as latitude (Weathers, 1979; Hails, 1983), habitat (Nagy, 1987) or taxon (Bennett & Harvey, 1987). Nor was the exponent (b 0·73) appropriate to the data-set under review (where b 0·53). The effect of this would be to depress energy expenditure: BMR values amongst relatively large species. This would not occur if energy expenditure were expressed relative to BMR measured in the same species, although suitable data were not always available. In spite of these problems, there was broad agreement, in that DEE averaged approximately 3–3·4 × BMR whichever BMR measure was used. The upper limits of expenditure, however, seem to have been inflated by using a calculated BMR, since they otherwise lay below about 5 × BMR when using measured BMR_{sp}. A similar pattern was evident when intra-species variation was considered (Bryant & Tatner, 1991).

The general pattern, at least amongst small birds, therefore, is that mean energy expenditure is usually below 5 × BMR and averages substantially less. Hammond & Diamond (1997) suggested that physiological limits (Stearns, 1992) prevent energy expenditure rising to much higher levels. Yet evidence from studies of wild birds presented here indicates that levels are invariably lower than would be likely to result from physiological limits alone. Indications that high levels of energy expenditure are associated with fitness costs, offers another route by which higher rates of energy expenditure may be constrained. Drent & Daan (1980) suggested that 4 × BMR was a maximum sustainable metabolic rate amongst endotherms. Evidence from wild birds suggests that high rates of energy expenditure are indeed linked to fitness costs (Bryant, 1991; Daan *et al.* 1996), as well as benefits, and this may be why mean expenditures amongst bird species usually lie within a rather narrow range and approximately conform (Bryant & Tatner, 1991) to Drent & Daan's (1980) rule.

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Appendix. *Bird species and sources included in this study**

Species		Reference
Desert quail	*Callipepla gambelii*	Goldstein & Nagy (1985)
Ringed plover	*Charadrius hiaticula*	Tatner & Bryant (1993)
Common sandpiper	*Actitis hypoleucos*	Tatner & Bryant (1993)
Turnstone	*Arenaria interpres*	Piersma & Morrison (1994)
Spinifex pigeon	*Geophaps plumifera*	Williams *et al.* (1995)
Budgerigar	*Melopsittacus undulatus*	Williams *et al.* (1991)
Rock parrot	*Neophema petrophila*	Williams *et al.* (1991)
Port Lincoln parrot	*Barnardius zonarius*	Williams *et al.* (1991)
Poorwill	*Phalaenoptilus nuttallii*	Thomas *et al.* (1996)
Anna's hummingbird	*Calypte anna*	Powers & Nagy (1988)
Crowned woodnymphs	*Thalurania colombica*	Weathers & Stiles (1989)
Bronze-tailed plumeleteers	*Chalybura urochrysia*	Weathers & Stiles (1989)
Blue-throated hummingbird	*Lampornis clemenciae*	Powers & Conley (1994)
Black-chinned hummingbird	*Archilochus alexandri*	Powers & Conley (1994)
Pied kingfisher	*Ceryle rudis*	Reyer & Westerterp (1985)
Blue-throated bee-eater	*Merops viridis*	Bryant *et al.* (1984)
Acorn woodpecker	*Melanerpes formicivorus*	Weathers *et al.* (1990)
New Holland honeyeater	*Phylidonyris novaehollandiae*	Weathers *et al.* (1996)
Eastern spinebill	*Acanthorhynchus tenuirostris*	Weathers *et al.* (1996)
Crescent honeyeater	*Phylidonyris pyrrhoptera*	Weathers *et al.* (1996)
Splendid fairy-wren	*Malurus splendens*	Weathers & Paton (1997)
		Weathers & Stiles (1989)
White-throated treecreeper	*Cormobates leucophaeus*	Weathers & Paton (1997)
Purple martin	*Progne subis*	Utter (1971)
Sand martin	*Riparia riparia*	Westerterp & Bryant (1984)
Barn swallow	*Hirundo rustica*	Westerterp & Bryant (1984)
Pacific swallow	*Hirundo tahitica*	Bryant *et al.* (1984)
House martin	*Delichon urbica*	Bryant & Westerterp (1980, 1983)
Tree swallow	*Tachycineta bicolor*	Williams (1988)
Cliff swallow	*Petrochelidon pyrrhonota*	Gauthier & Thomas (1993)
White-eye	*Zosterops lateralis*	Weathers & Stiles (1989)
Phainopepla	*Phainopepla nitens*	Weathers & Nagy (1980)
Dipper	*Cinclus cinclus*	Bryant & Tatner (1988*b*)
Mockingbird	*Mimus polyglottos*	Utter (1971)
Wheatear	*Oenanthe oenanthe*	Tatner (1990)
Pied flycatcher	*Ficedula hypoleuca*	Moreno & Carlson (1989); Moreno & Sanz (1994)
Collared flycatcher	*Ficedula albicollis*	Moreno *et al.* (1991)
Western bluebird	*Sialia mexicana*	Mock (1991)
Coal tit	*Parus ater*	Moreno *et al.* (1988)
Blue tit	*Parus caeruleus*	Tatner & Bryant (1993)
Crested tit	*Parus cristatus*	Moreno *et al.* (1988)
Great tit	*Parus major*	Tatner & Bryant (1993)
Willow tit	*Parus montanus*	Moreno *et al.* (1988); Carlson *et al.* (1993)
Black-capped chickadee	*Parus atricapillus*	Karasov *et al.* (1992)
Siberian tit	*Parus cinctus*	Carlson *et al.* (1993)
Verdin	*Auriparus flaviceps*	Webster & Weathers (1990)
Orange-breasted sunbird	*Nectarinia violacea*	Williams (1993)
Savannah sparrow	*Passerculus sandwichensis*	Williams (1987)
Starling	*Sturnus vulgaris*	Westerterp & Drent (1985)
Sociable weaver	*Philetairus socius*	Williams & Du Plessis (1996)
Yellow-eyed junco	*Junco phaeonotus*	Weathers & Sullivan (1989, 1991)
Dark-eyed junco	*Junco hyemalis*	Weathers & Sullivan (1993)

* Seven additional species and an additional season for Great tit are listed, with their sources, in Table 1.