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Active and resting metabolism in birds: allometry, phylogeny and ecology

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(With 6 figures in the text)

Variation in resting metabolic rate is strongly correlated with differences in body weight among birds. The lowest taxonomic level at which most of the variance in resting metabolic rate and body weight is evident for the sample is among families within orders. The allometric exponent across family points is 0·67. This exponent accords with the surface area interpretation of metabolic scaling based on considerations of heat loss. Deviations of family points from this allometric line are used to examine how resting metabolic rates differ among taxa, and whether variation in resting metabolic rate is correlated with broad differences in ecology and behaviour. Despite the strong correlation between resting metabolic rate and body weight, there is evidence for adaptive departures from the allometric line, and possible selective forces are discussed.

The allometric scaling of active metabolic rate is compared with that of resting metabolic rate. The allometric exponents for the two levels of energy expenditure differ, demonstrating that active small-bodied birds require proportionately more energy per unit time above resting levels than do active large-bodied birds. No consistent evidence was found to indicate that the different methods used to estimate active metabolic rate result in systematic bias. Birds require more energy relative to body size when undertaking breeding activities than at other stages of the annual cycle.

Contents

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Introduction

Basal and active metabolic rates have been measured for a number of bird species, and several authors have attempted interspecific comparisons of the relationships between measures of metabolic rate and body size (Brody & Proctor, 1932; King & Farner, 1961; Lasiewski & Dawson, 1967; Zar, 1969; Aschoff & Pohl, 1970*b*; Kendeigh, Dol'nik & Gavrilov, 1977; Walsberg, 1983; Whittow & Rahn, 1984). There is no general agreement on the way metabolic rates scale with body size. Moreover, few studies have attempted to test in a rigorous and comprehensive manner which species have higher or lower metabolic rates than expected for their size, or if this variation is associated with differences in ecology and behaviour. In this paper, we review the available data to examine four main questions as well as testing subsidiary hypotheses. First, how do metabolic rates change with body size in birds? Secondly, are there ecological correlates of metabolic rate when size and taxonomic effects are taken into account? Thirdly, do estimates of active metabolic rate vary with the method of measurement used and the time of year when the measurements are taken? Fourthly, how much greater is active than resting metabolic rate? Our analyses are more rigorous than those reported previously and our data base is more extensive.

Materials and methods

Resting metabolic rate

All data have been collected from the published literature. Data on variation in resting metabolic rate were last collated by Kendeigh *et al.* (1977) for 172 species. Many studies have appeared since then, particularly on seabirds (Adams & Brown, 1984; Brown, 1984; Ellis, 1984), and our data set includes estimates of resting metabolic rate and body weight for 399 species (see **Appendix 2**).

Estimates of what we shall term Resting Metabolic Rate (RMR) have been variously termed 'basal' or 'standard' metabolic rate. The experimental conditions under which these 2 measurements have been obtained differ. The most common conditions are that basal metabolic rate is measured on unfed, inactive birds in the dark at temperatures within the thermoneutral zone. Standard metabolic rates are usually estimates taken when the thermoneutral zone has not been defined, and thus may include some costs of thermoregulation. Both estimates have been included in **Appendix 2**, although the great majority are of basal metabolic rate. The reason that the term 'resting metabolic rate' is preferred here over the usual 'basal metabolic rate' is that the estimates are *not* all minimum estimates of oxygen consumption. Some birds have been shown to have metabolic rates below accepted basal levels. The most striking examples are provided by birds that enter torpor, such as hummingbirds Trochilidae and mousebirds Coliidae.

Estimates of RMR that were taken during the active phase of the daily cycle have been excluded from the analyses (leaving data for a total of 356 species) because they have been shown to be around 25% higher in some species (Aschoff & Pohl, 1970*a*, *b*). Many studies do not report when measurements were taken and this factor results in an unknown bias in the data. Another source of bias results from investigators using either the lowest values obtained within the thermoneutral zone, or the average of all values within the zone, to estimate RMR. In addition, there is evidence for some species that RMR differs according to season of measurement (see Weathers, 1979). As long as there is no systematic distribution in these potential sources of bias, then such measurement error should not affect our conclusions. In some cases, there has been more than one study on a particular species (see **Appendix 2**), and the estimates of RMR and the weight of animals differ between studies. In such cases, the lowest mass-specific RMR (RMR divided by body weight) was selected for analysis because RMR is the minimum value within the zone of thermoneutrality. The mass-specific RMR is only an accurate measure if the relationship between RMR and body size between individuals within species is isometric. However, ranges of intraspecific variation in body size were very small compared with differences in RMR, and so the assumption of isometry is not critical.

Active metabolic rate

Estimates of active metabolic rate (AMR) for 96 species are given in **Appendix 3.** The last review was by Walsberg (1983) who obtained estimates for 42 species. The methods used to estimate daily energy expenditure vary greatly and have been obtained on birds during different phases of the annual cycle. The codes used in **Appendix 3** to describe the various methods refer to (after King, 1974):

1. Pellet analysis
2. Crop contents
3. Single-labelled water
4. Double-labelled water
5. Time-activity combined with laboratory data on RMR
6. Extrapolations from laboratory data
7. Extrapolations from food consumption of captives
8. Observations of feeding rate and excretory rate
9. Observations of feeding rate combined with data on caloric value of food
10. Weight loss

The most commonly used techniques are 5 and 9. However, only 3 and 4 provide direct measurements of energy expenditure. The indirect methods are based on many assumptions which are only beginning to be tested. For example, Wijnandts (1984) showed that Graber's (1962) estimates based on pellet analysis for 3 owl species are incorrect because the assumption that the owls void a single pellet a day is invalid. Method 5 is commonly used and is an indirect estimate of AMR using daily activity budget data combined with laboratory derived estimates of the energy costs of the various daily activities. The energy cost of activites are either generated by obtaining expected values from allometric equations based on small samples of species or are simply guessed as some multiple of RMR. In the latter case, the ratio of AMR to RMR has been calculated for a small number of species and is used as the multiple to estimate the energy costs of activity. This ratio is only appropriate if AMR and RMR scale to body size with the same exponent. This question and a comparison of the various methods for estimating AMR will be addressed below. Because of the relative paucity of data and the heterogeneous methods that have been used to estimate AMR, the ecological correlates of size-corrected values will not be examined.

Ecological classification

Species for which information on RMR was available were classified for a number of ecological and behavioural variables (for sources see Bennett, 1986). As demonstrated below, the lowest taxonomic level

TABLE I

The ecological classification and values of relative resting metabolic rate (relative RMR, see text) for families of birds. The families are ranked from lowest to highest relative RMR. See ***Appendix 2*** *for the distribution of families within orders, and for the species which were used to derive the family values for RMR and the ecological classification. The abbreviations for the states within the ecological categories are explained in the text (see* ***Ecological classification****). The column numbers refer to: 1—Relative RMR for each family (this is the value of the deviation of the family point from the major axis across all family points); 2—Nest type; 3—Mode of development; 4—Incubating sex; 5—Nestling care; 6—Diet; 7—Habitat; 8—Stratification; 9—Locomotion; 10—Breeding latitude; 11—Migration; 12—Mode of prey location and capture; 13—Mating system; 14—Nest dispersion; 15—Activity timing*

Family	Common Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Podargidae	Frogmouths	−0·523	A	SA	F	MF	IN	WO	AR	F	2	4	PG	M	SP	N
Caprimulgidae	Nightjars	−0·503	G	SA	MF	MF	IN	GR	TR	F	1–5	3	AA	M	SP	N
Apterygidae	Kiwis	−0·495	H	P	M	M	IN	FT	TR	NF	1	3	GG	M	SP	N
Thinocoridae	Seedsnipes	−0·489	G	P	F	MF	FR	GR	TR	F	2	3	GG	M	SP	D
Fregatidae	Frigatebirds	−0·321	G	A	MF	MF	LV	MR	AE	F	1	4	AS	M	CO	D
Strigidae	Typical owls	−0·305	H	SA	F	MF	IN/HV	FT	AR	F	2	1–4	AG/PG	M	SP	N/DN
Meropidae	Bee-eaters	−0·253	H	A	MF	MF	IN	SC	AR	F	4	4	AA	M	CO	D
Struthionidae	Ostrich	−0·251	G	P	MF	MF	FO	GR	TR	NF	3	4	GG	P	SP	D
Pycnonotidae	Bulbuls	−0·225	A	A	MF	MF	OM	WO	AR	F	1	4	PP	M	SP	D
Columbidae	Pigeons	−0·216	A	A	MF	MF	FR	WO	AR	F	2	2–4	GG	M	SP	D
Trogonidae	Trogons	−0·190	H	A	MF	MF	IN	FT	AR	F	1	4	AA	M	SP	D
Nectariniidae	Sunbirds	−0·186	A	A	MF	MF	NE	FT	AR	F	1	4	PP	M	SP	D
Anhingidae	Darters	−0·185	A	A	MF	MF	LV	FW	AQ	F	2	4	WU	M	CO	D
Accipitridae	Hawks/eagles/vultures	−0·176	A	SA	F/MF	MF	AN	FT	AR	F	1–5	2/3	AG/AA	M	SP	D
Charadriidae	Plovers	−0·152	G	P	MF	MF	IN	TU	TR	F	5	2	GG	M	SP	D
Irenidae	Leafbirds	−0·138	A	A	MF	MF	FR	GR	AR	F	1	4	PP	M	SP	D
Upupidae	Hoopoe	−0·115	H	A	F	MF	IN	GR	AR	F	3	2–4	GG	M	SP	D
Cracidae	Curassows	−0·109	A	SP	F	MF	FR	FT	AR	F	1	4	PP	M	SP	D
Cinclidae	Dippers	−0·105	G	A	F	MF	IN	FW	AQ	F	1	3/4	PW	M	SP	D
Cacatuidae	Cockatoos	−0·093	H	A	MF	MF	FR	GR	AR	F	1	3	PP	M	SP	D
Apodidae	Swifts	−0·088	H	A	MF	MF	IN	LD	AE	F	5	1–3	AA	M	CO	D
Rallidae	Rails	−0·077	G	SP	F/MF	MF	OM	GR/FW	TR/AQ	F	4	3	GG/WU	M	SP	D
Estrildidae	Estrildid finches	−0·076	A	A	MF	MF	FR	GR	TR	F	2	4	GG	M	SP	D
Cathartidae	New World vultures	−0·074	G	SA	MF	MF	CA	TU	AE	F	1	3	AG	M	SP	D
Phasianidae	Grouse/quail/pheasant	−0·073	G	P	F	MF	OM	FT	TR	F	1	1–4	GG	M/P	SP	D
Dendrocolaptidae	Woodcreepers	−0·073	H	A	F	F	IN	FT	AR	F	1	4	PP	PR	SP	D
Anhimidae	Screamers	−0·062	G	SP	MF	MF	FO	MA	TR	F	1	4	PW	M	SP	D
Alcedinidae	Kingfishers	−0·057	H	A	MF	MF	LV	FW	AQ	F	3	2–4	AW/PG	M	SP	D
Parulidae	Wood warblers	−0·056	H/G/A	A	F	MF	IN	WO/GR/MA	AR	F	4	2–4	PP	M	SP	D
Falconidae	Falcons	−0·053	H/A	SA	F/MF	MF	AN	GR	AE	F	3	1–4	AG/AA	M	SP	D
Casuariidae	Cassowary	−0·052	G	P	M	M	FR	FT	TR	NF	1	4	GG	M	SP	D
Cuculidae	Cuckoos	−0·046	A	A	MF/PA	MF/PA	OM	WO/SC/GR	AR	F	1–5	2–4	GG/PP	M/PR	SP	D
Gruidae	Cranes	−0·041	G	SP	MF	MF	OM	GR/MA	TR	F	4	3	GG	M	SP	D
Dromaiidae	Emu	−0·035	G	P	M	M	FR	GR	TR	NF	3	3	GG	M	SP	D

TABLE I (*cont*)

Family	Common name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pipridae	Manakins	−0·029	A	A	F	F	FR	FT	AR	F	1	4	AA	P	SP	D
Ploceidae	Weavers	−0·028	H/A	A	F/PA	MF/PA	FR	GR	TR	F	1	2–4	GG	M/PR	CL	D
Muscicapidae	Flycatchers/thrushes	−0·017	H/G/A	A	F/MF	MF	IN									

Anhimidae	Screamers	−0·062	G	SP												
Alcedinidae	Kingfishers	−0·057	H	A	MF	MF	LV	FW	AQ	F	3	2–4				
Parulidae	Wood warblers	−0·056	H/G/A	A	F	MF	IN	WO/GR/MA	AR	F	4	2–4	PP	M	SP	D
Falconidae	Falcons	−0·053	H/A	SA	F/MF	MF	AN	GR	AE	F	3	1–4	AG/AA	M	SP	D
Casuariidae	Cassowary	−0·052	G	P	M	M	FR	FT	TR	NF	1	4	GG	M	SP	D
Cuculidae	Cuckoos	−0·046	A	A	MF/PA	MF/PA	OM	WO/SC/GR	AR	F	1–5	2–4	GG/PP	M/PR	SP	D
Gruidae	Cranes	−0·041	G	SP	MF	MF	OM	GR/MA	TR	F	4	3	GG	M	SP	D
Dromaiidae	Emu	−0·035	G	P	M	M	FR	GR	TR	NF	3	3	GG	M	SP	D

TABLE 1 (*cont*)

Family	Common name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Pipridae	Manakins	−0·029	A	A	F	F	FR	FT	AR	F	1	4	AA	P	SP	D
Ploceidae	Weavers	−0·028	H/A	A	F/PA	MF/PA	FR	GR	TR	F	1	2–4	GG	M/PR	CL	D
Muscicapidae	Flycatchers/thrushes	−0·017	H/G/A	A	F/MF	MF	IN	FT	AR	F	1–5	1–4	GG/AA/PP	M	SP	D
Laniidae	Shrikes	−0·002	A	A	F	MF	AN	WO	AR	F	4	2–4	PG	M	SP	D
Ardeidae	Herons/bitterns	0·013	G	SA	F/MF	F/MF	LV	MA	TR	F	3	3	PW	M/P	SP	DN
Psittacidae	Parrots	0·019	H	A	F	MF	FR	FT	AR	F	1	4	PP	M	SP	D
Picidae	Woodpeckers	0·022	H	A	MF	MF	IN	WO	AR	F	2	2–4	PP	M	SP	D
Oriolidae	Orioles	0·037	A	A	MF	MF	OM	WO	AR	F	5	2–4	PP	M	SP	D
Procellariidae	Shearwaters	0·047	H	SA	MF	MF	LV	MR	AQ	F	4	2	AW/WW	M	CO	DN
Diomedeidae	Albatrosses	0·050	G	SA	MF	MF	LV	MR	AQ	F	5	2	WW	M	CO	DN
Tyrannidae	Tyrant flycatcher	0·052	H/A	A	F/MF	MF	IN	WO/GR	AR	F	4	2–4	AA	M	SP	D
Emberizidae	Buntings/cardinals	0·055	G/A	A	F	MF	OM	WO/GR	TR	F	1–5	1–4	GG	M	SP	D
Laridae	Gulls	0·057	G	SP	MF	MF	AN	MR/MA	TR/AQ	F	1–5	1–4	GG/AW/AS	M	CO	D
Scolopacidae	Sandpipers/woodcock	0·064	G/A	P/SP	F/MF	F/MF	IN	WO/TU	TR	F	4	1	GG	M/P	SP	N/DN
Hirundinidae	Swallows	0·072	H	A	F/MF	MF	IN	LD	AE	F	1/5	2–4	AA	M	CO	D
Alaudidae	Larks	0·072	G	A	F	MF	OM	GR	TR	F	3	2–4	GG	M	SP	D
Drepanididae	Hawaiian honeycreepers	0·081	A	A	F	MF	FR/IN/NE	FT	AR	F	1	4	PP	M	SP	D
Threskiornithidae	Ibises	0·083	A	SA	MF	MF	IN	MA	TR	F	1	4	PW	M	CO	D
Spheniscidae	Penguins	0·087	G	SA	MF	MF	LV	MR	AQ	NF	3	1	WU	M	CO	D
Aegithalidae	Long-tailed tit	0·089	A	A	F	MF	IN	WO	AR	F	1	2–4	PP	M	SP	D
Hydrobatidae	Petrels	0·092	H	SA	MF	MF	IN	MR	AQ	F	5	3	AS	M	CO	DN
Motacillidae	Wagtails	0·112	G	A	F	MF	IN	GR	TR	F	4	2–4	GG	M	SP	D
Sulidae	Gannets	0·117	G/A	A	MF	MF	LV	MR	AQ	F	2	4	AW	M	CO	D
Meliphagidae	Honeyeaters	0·129	A	A	F	MF	FR/IN/NE	FT	AR	F	1	4	PP	M	SP	D
Pelecanoididae	Diving petrels	0·135	H	SA	MF	MF	IN	MR	AQ	F	2	2	AW	M	CO	N
Formicariidae	Antbirds	0·138	A	A	MF	MF	IN	FT	AR	F	1	4	PP	M	SP	D
Anatidae	Ducks/geese/swans	0·149	G	P	F	MF	OM	FW	AQ	F	4	1–4	WW	M	SP	D
Corvidae	Crows	0·156	H/A	A	F/MF	MF	OM	FT	AR	F	2	1–4	GG/PP	M	SP	D
Phaethontidae	Tropicbirds	0·162	H	SA	MF	MF	LV	MR	AQ	F	4	4	AW	M	CO	D
Sittidae	Nuthatches	0·163	H	A	MF	MF	OM	WO	AR	F	1	2/3	PP	M	SP	D
Ciconiidae	Storks	0·179	A	SA	MF	MF	LV	MA	TR	F	2	3	PW	M	CO	D
Paridae	Tits	0·195	H	A	F	MF	IN	WO	AR	F	2	1–4	PP	M	SP	D
Phoenicopteridae	Flamingoes	0·200	G	SP	MF	MF	IN	FW	AQ	F	3	3	PW	M	CO	DN
Troglodytidae	Wrens	0·213	H	A	F	MF	IN	WO	AR	F	2	2–4	PP	M/P	SP	D
Fringillidae	Finches	0·213	A	A	F	MF	FR	FT	AR	F	3	2–4	GG/PP	M	SP	D
Prunellidae	Accentors	0·215	A	A	F	MF	IN	WO	AR	F	3	2/3	GG	M	SP	D
Trochilidae	Hummingbirds	0·227	A	A	F	F	NE	FT	AR	F	2	4	AA	PR	SP	D
Icteridae	American blackbirds	0·231	A	A	F/PA	MF/PA	OM	WO/GR/MA	AR	F	3	2–4	GG/PP	M/P/PR	SP	D
Sturnidae	Starlings	0·243	H	A	MF	MF	OM	GR	TR	F	3	2–4	GG	M	SP	D
Pelecanidae	Pelicans	0·284	G	A	MF	MF	LV	MR	AQ	F	4	3	AW	M	CO	D
Bombycillidae	Waxwings	0·296	A	A	MF	MF	OM	FT	AR	F	3	2/3	PP	M	SP/CL	D
Phalacrocoracidae	Cormorants	0·352	G	A	MF	MF	LV	MR	AQ	F	3	3	WU	M	CO	D
Stercorariidae	Skuas	0·387	G	SP	MF	MF	LV	TU	TR	F	5	1	AG	M	CO	D
Alcidae	Auks	0·481	G	SP	MF	MF	LV	MR	AQ	F	5	2	WU	M	CO	D

exhibiting most of the variance in RMR and body weight is among families within orders, and the family level was therefore used as the taxonomic level for analysis. The ecological classification for families is shown in Table I. As species within the families shown in **Appendix 2** sometimes differed in these broad categorizations of behaviour and ecology, the usual patterns for the majority of species in the family are shown. In some cases, however, there is considerable variability among species within families and this variation is also shown in Table I. Those families where more than one state is shown for a particular ecological or behavioural category were excluded from the analyses of the correlates of variation in RMR for that particular category. Where species within families differ in ecology according to stage of the annual cycle (e.g. breeding vs. overwintering habitat or diet), the classification given is for typical behaviour during the breeding season. An explanation of these variables and a key to the abbreviations used in Table I follows (partly after Bennett & Harvey, 1985*a, b*; see also Bennett, 1986):

Nest type

H-hole; G-ground (including raised nests in reeds, lakes); A-arboreal (open nests in shrubs, trees)

Development

P-precocial; SP-semi-precocial; SA-semi-altricial; A-altricial

Incubating sex

M-male; F-female; MF-both sexes; PA-brood parasite

Nestling care

M-male; F-female; MF-both sexes; PA-brood parasite

Diet

FO-folivore (leaves and shoots); FR-frugivore (fruit and seeds); IN-invertebrates; LV-lower vertebrates; HV-higher invertebrates (often a combination of fish and marine invertebrates); CA-carrion; OM-omnivore (usually combination of FO, FR and IN); NE-nectar (combination of nectar and invertebrates); AN-animals (combinations of IN, LV and HV)

Habitat

FT-forest; WO-woodland; SC-scrub; TU-tundra or moorland or mountain; GR-grassland or steppe or savannah; MR-marine; MA-marsh; FW-freshwater (streams, rivers, lakes and ponds); LD-land (comprising FT, WO, SC, TU and GR)

Stratification

AR-arboreal; TR-terrestrial; AQ-aquatic; AE-aerial

Locomotion

F-able to fly; NF-flightless

Breeding latitude

Latitude at midpoint of breeding range for species (see Lack, 1968). 1-polar; 2-high; 3-low; 4-tropical

Migration

1-resident; 2-mainly resident in range; 3-partial migrant; 4-mainly migrant; 5-migrant

Mode of prey location and capture

GG-ground to ground; AG-air to ground; AA-air to air; AS-air to water-surface; AW-air to underwater; WW-water to water; WU-water-surface to underwater; PP-perch to perch; PW-perch to underwater; PG-perch to ground

Mating system

M-monogamous (single-male, single-female); P-polygynous (single-male, multi-female); PR-promiscuous (no pair bonds)

Nest dispersion

SP-spaced (territorial); CO-colonial; CL-clumped (small breeding territories, close nest sites)

Activity timing

D-diurnal (active by day); N-nocturnal (active by night); DN-diel (active day and night)

Analysis

It is well established that larger animals have greater metabolic needs, but that metabolic rate does not increase in proportion to body size. Instead, metabolic rate (M) increases with body weight (W) according to an exponential relationship, with the exponent (b) being less than 1·0 (e.g. Schmidt-Nielsen, 1984)

$$M = aW^b$$

After logarithmic transformation M is, therefore, linearly related to W. Metabolic rates and body weights were logarithmically transformed before carrying out bivariate statistical analyses which employed linear models, and all references to data on these 2 variables in the account that follows refer to the log transformed data.

Nested analyses of variance (see Sokal & Rohlf, 1981) on the logarithmically-transformed species data were used to investigate how variation in RMR and body size were distributed at successive taxonomic levels. The taxonomic level used for analyis was that above which no appreciable increase in variance could be detected. This was found to be the family level (see below) and family points were used in subsequent analyses. (Family points were estimated as the mean of constituent generic points, which were themselves the mean of species values.) Analysis at lower taxonomic levels would inflate sample sizes and could result in spurious associations being revealed due to shared descent from a recent common ancestor rather than due to evolutionary convergence (Harvey & Mace, 1982).

Orthogonal deviations from a major axis line, calculated across family points and placed through the log means on both axes, were used to obtain measures of relative metabolic rate for each family. These relative values (which are assumed to correct for size differences) were used to investigate differences between taxa as well as in the analysis of the ecological correlates of variation in RMR. Ecological correlates of variation about the allometric line were examined by 1-way analyses of variance and t-tests (unknown variances not assumed equal). In the t-tests only comparisons between states with 3 or more families could be performed. Where family points were derived from species which differed in state within an ecological category (shown in Table I), those family points were excluded from the comparisons between states for that ecological category. The analysis of ecological correlates was undertaken for all families together, and also with passerines excluded because it is possible that the disproportionate number of passerine families may sometimes give misleading results. For example, all the passerine families are altricial and therefore may bias comparisons within the development category across all families.

Species values were used for analyses of AMR because the aim was to investigate the effect of method and season of measurement on estimates of AMR. As these differed markedly between species, variation in method and season of measurement would be lost by averaging the values at succeeding taxonomic levels. In order to obtain a best-fit line for calculating relative values to correct for size differences, the following procedure was used. A 'common' major axis line (see Harvey & Mace, 1982) was calculated as the mean of the slopes of the logged species points within orders. The possibility that these slopes are statistically heterogeneous was tested by using a maximum likelihood method (Harvey & Mace, 1982). A common slope was calculated because species were unevenly distributed across higher-order categories (e.g. over 1/3 of the species were passerines). Over-representation of particular taxa may bias the value of an allometric exponent calculated across all logged species points regardless of taxonomic affinity. Orthogonal deviations of species points from the common major axis were calculated to obtain estimates of relative AMR. Differences in relative AMR were tested by 1-way analyses of variance and t-tests (unknown variances not assumed equal). Taxonomic differences in these relative values are examined by taking the means of species' values for each order.

Comparisons between the allometric exponents for AMR and RMR were performed by calculating major axes across the 47 species for which estimates of both levels of energy utilization and body weight were available. Unlike previous studies, the ratio between the 2 estimates (AMR/RMR) was not used to examine the extent to which free-living birds operate above resting energy levels because the allometric exponents for the 2 levels of energy expenditure were shown to be significantly different.

Results

Taxonomic level of analysis

The results of the nested analysis of variance of RMR and body weight are shown in Table II. The nested analysis is hierarchical, building from species within genera. For both RMR and body size, the variance among genera within families is less than the variance among species within genera. Since no additional variance is contributed by genera within families, values of zero are given in the Table II. Similarly, the variance among orders within the class is less than among families within orders, and zero values are also given. The procedure for calculating variance components follows Sokal & Rohlf (1981). Only 33% of the variance in RMR and 28% of the variance in body weight is located at the level of species within genera. The highest percentage of variance is located at the level of families within orders (67% for RMR and 72% for body weight), and the family level is therefore used for further analysis. Analysis at a lower taxonomic level would increase sample sizes but might result in spurious associations being revealed due to shared descent from a recent common ancestor rather than due to evolutionary convergence. This result is not surprising because we would expect to find less variance among taxa within lower taxonomic levels because these taxa are more closely related.

TABLE II

Results of the nested analysis of variance to examine the distribution of variation in RMR and body weight at different taxonomic levels. % indicates the additional percentage of variance located at the taxonomic level. Zero figures refer to less variance being found at the stated taxonomic level than at the previous lower taxonomic level (see text)

Taxonomic level	Resting metabolic rate	Body weight
% among orders within classes	0	0
% among families within orders	66·9	71·8
% among genera within families	0	0
% among species within genera	33·1	28·2

Differences between families

The plot of log RMR on log body weight is shown in Fig. 1. The major axis equation across these 78 family points for RMR (kcal/bird/d) on body weight (g) is:

$$\log(\text{RMR}) = 0{\cdot}67.\log(\text{body weight}) - 0{\cdot}25$$

The 95% confidence limits of the allometric exponent are 0·65–0·70 and the correlation coefficient is 0·99. Differences in body size among families accounts for 97·5% of the variation in RMR.

Deviations of family points from this equation enable direct comparison of differences in RMR between families because size differences are corrected for. These family values of relative RMR are ranked in Table I and are given with the ecological classification. They express the extent to which observed RMR differs from that which would be expected for a 'typical' family of the same body size. A positive deviation indicates that a family has a higher RMR than expected for its body size, while a negative deviation indicates that the family has a lower RMR than expected for its size. Differences between families will be discussed below.

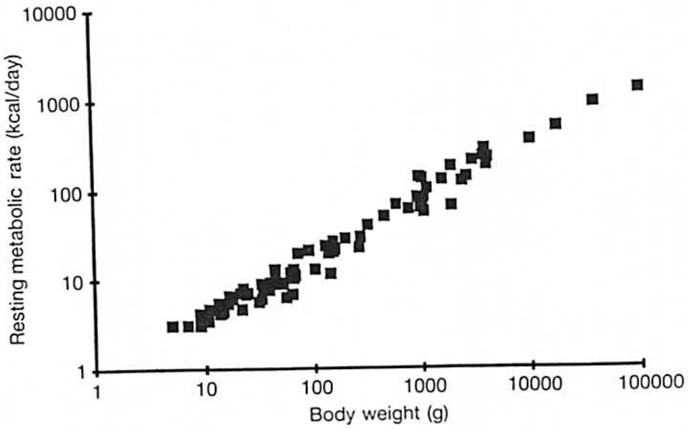

FIG. 1. The plot of resting metabolic rate (kcal/d) against body weight (g) for avian families on logarithmically scaled axes. For details of the best fit line (major axis) through these family points see text. For deviations of family points from this line, see Table I.

Ecological correlates

The scatter of family points about the allometric line for RMR described in Table I is correlated with few broad differences in behaviour and ecology. Thirty of the 78 families listed in Table I are from the order Passeriformes, while the remaining 48 families are distributed across 23 other orders of birds (see **Appendix 2**). Perhaps because the 30 passerine families are more closely related, they show less broad ecological variation than the families from non-passerine orders (e.g. there are no marine or precocial passerine families—see Table I). As the more closely related passerine families are relatively well represented in the sample, we decided to concentrate on the results of the analyses across the 48 non-passerine families. With this procedure, any association between variation in relative RMR and differences in ecology and behaviour would be more likely to result from repeated evolutionary convergence rather than by shared descent from a common ancestor.

The results of the one-way analyses of variance performed across non-passerine families revealed that there are significant differences within the habitat ($F_{8,30}=2{\cdot}63$, $P<0{\cdot}05$), stratification ($F_{3,40}=4{\cdot}97$, $P<0{\cdot}01$), mode of prey capture ($F_{9,30}=3{\cdot}09$, $P<0{\cdot}05$), nest dispersion ($F_{1,45}=15{\cdot}63$, $P<0{\cdot}001$), and activity timing ($F_{2,42}=5{\cdot}54$, $P<0{\cdot}01$) categories. *t*-tests were performed to examine which comparisons within these ecological categories were significantly different. The results are given in Table III. Sample sizes were too small to carry out rigorous tests for confounding variables between the states within the ecological categories (see Clutton-Brock & Harvey, 1984). However, it is evident for some of the differences that there is a confounding association.

One strong association is that marine birds have high relative RMR (see Fig. 2). Ten of the 11 marine families have positive deviations from the allometric line (see Table II), which means that they have higher RMR than expected for their size. The frigatebirds Fregatidae are the one exception. Another finding is that

TABLE III

The significant differences between states within ecological categories for relative RMR among non-passerine families as revealed by t-tests. Only states containing three or more families could be compared. States within categories are described by abbreviations given in the text (see ***Ecological classification****). The sign '>' indicates that families within that state have a significantly higher resting metabolic rate relative to their body size.* ***t****-t statistic;* ***d.f.****—degrees of freedom;* ***P****—probability*

Comparison	*t*	*d.f.*	*P*
Habitat			
MR > GR	3·63	13	< 0·01
MR > FT	2·77	8	< 0·05
MA > GR	2·97	9	< 0·02
Stratification			
AQ > AR	3·75	20	< 0·01
AQ > TR	2·94	24	< 0·01
AQ > AE	3·53	6	< 0·02
Prey capture			
AW > GG	5·14	12	< 0·001
AW > AA	2·70	5	< 0·05
AW > PP	4·16	6	< 0·01
AW > PU	3·39	12	< 0·01
Nest dispersion			
CO > SP	3·88	36	< 0·001

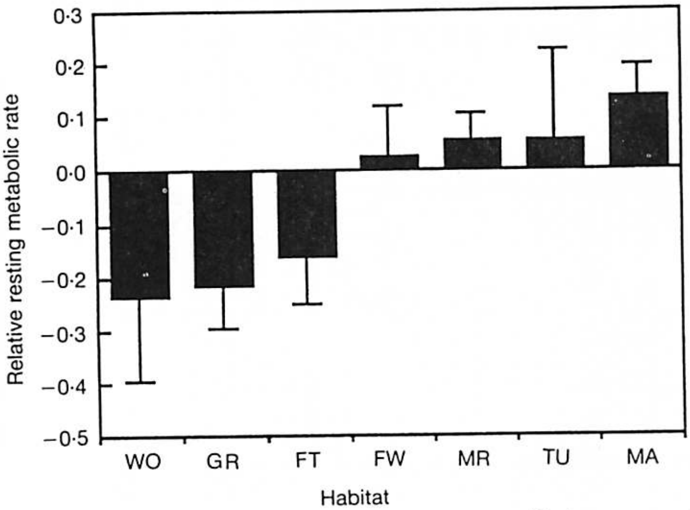

FIG. 2. Histogram of mean relative RMR for states within the habitat category. The bars are standard errors. For sample sizes see Table I. WO woodland, GR grassland/savannah; FT forest; FW freshwater; MR marsh; TU tundra/mountain, MA marine.

aquatic birds have higher relative RMR than other families in the stratification category. However, it is clear that the latter result is confounded by the habitat category because freshwater birds have RMRs which are near to expected for their body size (mean relative RMR $=0{\cdot}027$, $n=4$ families). While flamingoes Phoenicopteridae and wildfowl Anatidae have comparatively high relative RMR, kingfishers Alcedinidae and darters Anhingidae show the reverse and have negative RMR values. All the other non-passerine aquatic families are marine birds which clearly confounds the apparent association between high relative RMR with the aquatic state within the stratification category.

For the mode of prey capture category, birds that catch prey from air to underwater have higher relative RMR than some families that hunt in other ways. However, these four families are all marine, which confounds the association. Likewise, colonially nesting non-passerine families have higher relative RMR than families with nests which are spaced apart. As with the association between high relative RMR and aquatic habits, when marine families are excluded it is found that colonial nesters have either high or low relative RMR. Ibises Threskiornithidae, storks Ciconiidae, flamingoes Phoenicopteridae, and skuas Stercoraiidae, have positive values of relative RMR, whereas bee-eaters Meropidae, darters Anhingidae and swifts Apodidae, also nest colonially but have negative values of relative RMR (see Table I).

One correlation was revealed that does not appear to be confounded by an association with marine habits. For the activity timing category, nocturnal birds have significantly lower relative RMRs than diurnally active or diel birds (see Fig. 3). This is so for frogmouths Podargidae, nightjars Caprimulgidae, kiwis Apterygidae and owls Strigidae, but not for the diving petrels Pelecanoididae which are marine birds.

The possible adaptive significance of high relative RMR being associated with marine life, and low relative RMR being associated with nocturnal activity timing is described below.

Active metabolic rate

The plot of AMR (kcal/bird/d) on body weight (g) across species is shown in Fig. 4. The exponent of the common major axis (i.e. the mean of the slopes across species within the eight orders where $n>3$) is 0·65 and the 95% confidence limits are 0·59 to 0·71. The common correlation coefficient is 0·91. This common slope is

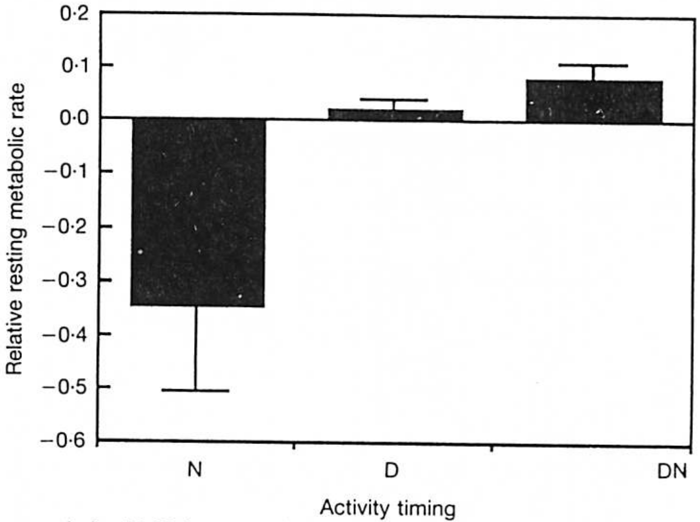

FIG. 3. Histogram of mean relative RMR for states within the activity timing category. The bars are standard errors. For sample sizes see Table I. N nocturnal; D diurnal; DN diel.

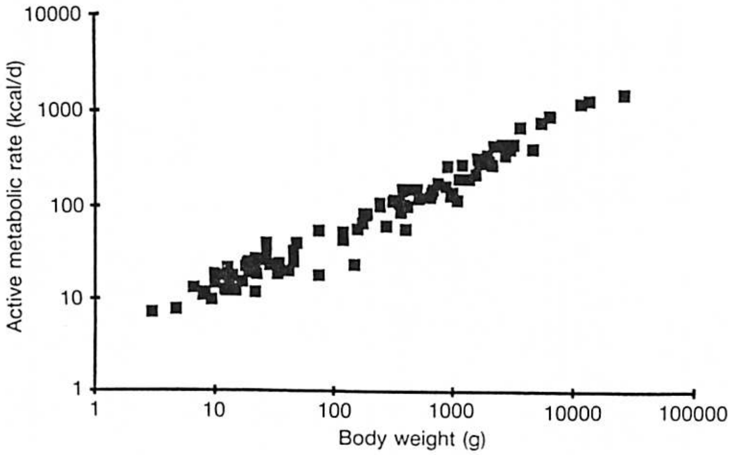

FIG. 4. The plot of active metabolic rate (kcal/d) against body weight (g) for avian species on logarithmically scaled axes. For details of the common major axis among the slopes for species within each order see text. For deviations of species points from the common slope, see **Appendix 3**.

estimated from statistically homogeneous slopes for species within the eight orders (heterogeneity tests $\chi^2 = 12{\cdot}5$, $d.f. = 7$, $P > 0{\cdot}05$).

The deviations of species values from this common major axis are given in **Appendix 3**. No significant differences between the methods used to estimate AMR were detected by analysis of variance across all species' deviations ($F_{9,84} = 1{\cdot}04$). When the species deviations were compared (using analysis of variance) by the stage in the annual cycle during which the estimates were obtained, it was found that those species undertaking breeding activities had significantly higher AMR for their size than birds at other stages of the annual cycle ($F_{1,93}=7{\cdot}55$, $P<0{\cdot}01$). This result confounds comparisons between taxonomic groups, however significant variation was found between orders ($F_{12,83}=3{\cdot}98$, $P<0{\cdot}001$). Species of penguins Sphenisciformes, hummingbirds Apodiformes, waders and gulls Charadriiformes, and passerines Passeriformes, have higher AMR relative to body size than species of herons Ciconiiformes, waterfowl Anseriformes, gamebirds Galliformes, raptors Falconiformes and owls Strigiformes. The means, standard errors, and sample sizes, for the estimates of relative AMR for breeding and non-breeding species are shown in Table IV, and those for the different orders are given in Table V.

The 47 species for which estimates of both AMR and RMR were available enable a direct comparison of allometric exponents for the differing levels of energy utilization (in kcal/bird/day). The major axes across species points using the body weights given in the studies of AMR are:

$$\log(\mathrm{RMR})=0{\cdot}68.\log(\text{body weight})-0{\cdot}28; \qquad 95\%\ \mathrm{C.I.}=0{\cdot}65-0{\cdot}72;\ r=0{\cdot}98;\ n=47$$
$$\log(\mathrm{AMR})=0{\cdot}61.\log(\text{body weight})+1{\cdot}18; \qquad 95\%\ \mathrm{C.I.}=0{\cdot}57-0{\cdot}64;\ r=0{\cdot}98;\ n=47$$

These equations are plotted in Fig. 5. The slope for AMR is significantly shallower than that for RMR. This result indicates that active small-bodied species expend greater amounts of energy above resting levels than active large-bodied species. In addition, it indicates that the common practice of assuming a constant ratio between AMR and RMR is invalid. The two slopes are not parallel. Consequently, the commonly used

TABLE IV

*The means, standard errors (S.E.), and sample sizes (n), of species values of relative AMR (see **Appendix 3**) according to whether AMR was estimated while species were breeding or not*

Annual cycle	Mean	S.E.	*n*
Breeding activities	0·061	0·03	43
Non-breeding activities	−0·076	0·04	52

TABLE V

*The means, standard errors (S.E.), and sample sizes (n), of species values of relative AMR (see **Appendix 3**) according to their representation among orders*

Order	Mean	S.E.	*n*
Sphenisciformes	0·067	0·07	5
Procellariiformes	0·161	—	1
Pelecaniformes	−0·083	0·13	6
Ciconiiformes	−0·084	0·05	9
Anseriformes	−0·197	0·08	7
Falconiformes	−0·152	0·07	10
Galliformes	−0·279	0·20	4
Charadriiformes	0·062	0·07	10
Columbiformes	−0·062	—	1
Strigiformes	−0·324	0·08	2
Apodiformes	0·163	0·05	4
Coraciiformes	−0·484	0·23	2
Passeriformes	0·105	0·03	35

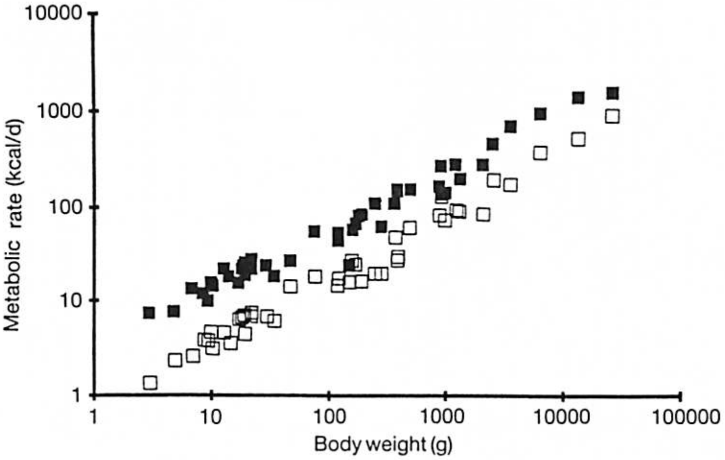

FIG. 5. The plot of AMR (■) and RMR (□) in kcal/d against body weight (g) on logarithmically scaled axes for the 47 species for which both estimates were available.

indirect method of estimating AMR by using this ratio established for species of differing body size is incorrect. The ratio is negatively correlated with body size, and its use will result in bias in these estimates if the body size of the species on which the measurements of AMR and RMR are taken differs from that of the species for which the ratio is used to estimate AMR from RMR.

Twelve of the measurements of AMR used in the above analysis were actually based on method 5. In order to remove this possible source of bias, we repeated the analysis omitting those measures. The results are not affected (major axis slope = 0·61, $n = 35$, $r = 0{\cdot}98$).

Discussion

The empirical testing of allometric exponents in comparative studies is complicated by a number of theoretical and methodological issues (see Harvey & Mace, 1982; Clutton-Brock & Harvey, 1984; Pagel & Harvey, 1987). Many authors who make functional arguments about the reasons for differences in scaling between different variables or taxonomic groups fail to consider these problems (e.g. Calder, 1984). This is particularly the case in studies of the allometry of metabolic rate. Uncritical acceptance of allometric exponents which have been generated using weak data bases and poor analytical techniques are prevalent in the literature (see review of literature on birds in **Appendix 1**). Only recently have the early results of Kleiber (1932) and Brody (1945) been critically evaluated and then only for mammals (Bartels, 1982; Heusner, 1982; Prothero, 1984; Hayssen & Lacy, 1985). We examined how the exponent scaling RMR to body weight in birds changes according to the taxonomic level of analysis (as described in **Appendix 1**). The results suggest that we should be wary of making functional interpretations of differences in allometric exponents because differences are taxon dependent and may be an artefact of statistical technique.

Our analyses reveal a strong correlation between log RMR and log body size across family points (see Fig. 1). The family level was used for analysis because, under a hierarchical taxonomic model, the highest proportion of variance in RMR and body weight for the sample was located at that level. If we had used species as the unit of analysis, any associations that were found would be less likely to result from independent evolutionary events (see Ridley, 1984) and be more likely to result from phylogenetic relationship. In addition, analyses at high taxonomic levels result in fewer degrees of freedom for statistical tests, so only robust associations are revealed. Not only are statistical tests more conservative, but analysis across families from a wide

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The strong correlation between log RMR and log body weight (0·99) means that there are few extreme deviations (outliers) from the allometric line (see Table I). Deviations (which we refer to as measures of 'relative RMR') range from the lowest value for frogmouths Podargidae (−0·523) to the highest among the auks Alcidae (0·481). Nevertheless, the results demonstrate that some of this scatter about the allometric line may be adaptive because it is correlated with differences in ecology. Before discussing ecological correlates, the taxonomic differences will be reviewed in relation to previous studies.

Lasiewski & Dawson's (1967) finding that passerine species have higher metabolic rates when corrected for size differences than species from other orders is confirmed in this study across families. When the deviations of passerine families are compared with an artificial 'lumped' category of all non-passerine families by analysis of variance, the difference is significant ($F_{1,76}=4{\cdot}80$, $P<0{\cdot}05$). However, Lasiewski & Dawson's procedure of including intra- and interspecific data on the same plot is questionable (see **Appendix 1**). Moreover, the common practice of amalgamating non-passerine species in studies of RMR, and then using the derived allometric equation to obtain expected values for examining taxonomic differences and constructing adaptive scenarios is inappropriate. This is because there is strong evidence for differences in relative RMR across non-passerine taxa (see Table I, which also shows that there is considerable variation among passerine families). Table I is the first systematic description of variation in relative RMR among birds, and only some of Zar's (1969) results based on small samples are confirmed (e.g. pigeons Columbidae have low relative RMR). Rather than re-describing the results for each family, the reader is referred to the details given in Table I for the taxonomic differences in relative RMR.

Despite methodological inadequacies in previous studies, there is evidence in the literature for factors other than body size being associated with variation in RMR among birds. Interspecific studies have provided evidence that tropical birds have lower relative metabolic rates than birds from higher latitudes (Weathers, 1979; Hails, 1983; Ellis, 1984). In addition, relative RMR is related to plumage colour and to foraging behaviour among tropical birds, with dark birds and those that forage in the open having lower relative RMR than light coloured birds and birds that forage in shade (Weathers, 1979; Hails, 1983; Ellis, 1980, 1984). Ellis (1984) has also shown that metabolic rate is correlated with mode of prey capture among a sample of seabirds. However, there has been no previous attempt to determine whether differences in habitat and diet are correlated with variation in relative RMR among birds, although such correlates have been demonstrated among species of mammals (McNab, 1983, 1986; but see Elgar & Harvey, 1987). Moreover, there have been no previous analyses which examine whether ecological correlates can be consistently demonstrated when both a wide variety of taxa are examined and when attempts are made to eliminate similarities that might be attributed to shared descent from a common ancestor (which are commonly found in interspecific studies).

Our analyses searched for broad ecological associations that were consistent across a range of avian families. After considering possible confounding associations between ecological categories, the results show that high relative RMR is significantly correlated with marine life, while low relative RMR is associated with nocturnal activity. How can these results be explained?

The finding that nocturnally active birds have low relative RMR might be the result of an adaptive response to the higher ambient temperatures encountered during the day when the birds are resting. Low relative RMR is likely to be advantageous when there are food shortages, or when it is necessary to build up energy stores for breeding (Calder, 1984). Thus, adaptive lowering of relative RMR in response to higher ambient temperatures might increase the chances of both survival and reproduction. We might predict, therefore, that birds at low latitudes would have lower relative RMR than those that live at high latitudes. This prediction is supported by interspecific studies (Weathers, 1979; Hails, 1983; Ellis, 1984). Although we could establish a trend in the right direction (see Fig. 6), no significant differences in breeding latitude between families were detected using analysis of variance. This could be because many families contain species which differ in breeding latitude (see Table I), and these families were therefore excluded from the analysis. In addition, our classification for latitude is qualitative and may be too broad to detect detailed differences in relative RMR.

The result that seabirds tend to have high relative RMR has been noted but not explained by Rahn &

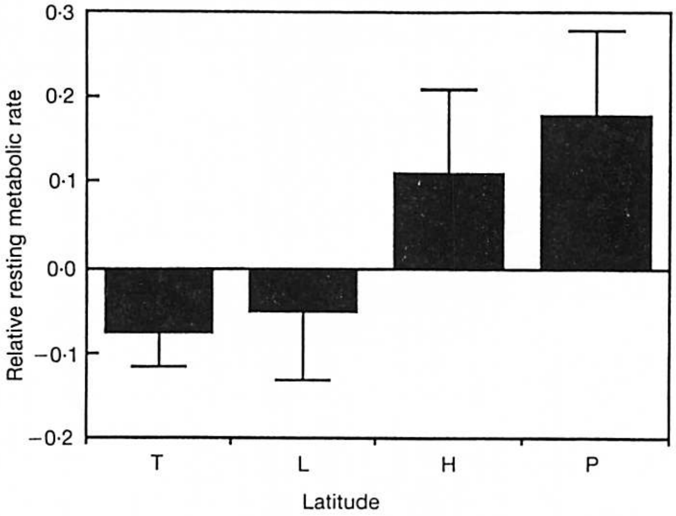

FIG. 6. Histogram of mean relative RMR for states within the latitude category. The bars are standard errors. For sample sizes see Table I. T tropical; L low; H high; P polar.

Whittow (1984) and Ellis (1984) who compared the observed values for species to those expected from the non-passerine equation of Lasiewski & Dawson (1967). Ellis (1984) showed that there is a correlation among species of seabirds between relative RMR and latitude. This fact makes it difficult to explain, in terms of a climatic gradient associated with differences in latitude, why seabird families as a group have significantly higher relative RMR than bird families which exploit other habitats. While birds from some marine families breed at high latitude (e.g. penguins, Spheniscidae and auks, Alcidae), many others are tropical in distribution. McNab (1986) argues that sea mammals (Cetacea and Pinnipedia) have relatively high metabolic rates because of greater heat loss to the environment. We are wary of making functional explanations for the high relative RMR of seabirds because the result may be complicated by the fact that the thermoneutral zone was not established in RMR measurements for some seabird species, so the estimates given in **Appendix 2** may include some costs of thermoregulation. Thus, we cannot exclude the possibility that the association between high relative RMR and marine life may to some extent be an artefact of experimental technique. Nevertheless, detailed examination of the data for birds and mammals to exclude this possibility, as well as experimental work, may establish whether some common problem shared by marine birds and mammals (e.g. salt intake) is involved in their tendency to have elevated relative RMR.

We could detect no significant associations between variation in relative RMR and differences in diet across families of birds. McNab (1983, 1986) has found dietary correlates of relative RMR among species of mammals. Species that eat vertebrates, herbs or nuts have higher relative RMR than species that eat leaves, fruit or invertebrates. Elgar & Harvey (1987) have confirmed these correlates but point out that they are for the most part also taxonomic correlates. For example, the nut-feeding vertebrates in the samples are all rodents, and rodent species have relatively high metabolic rates, whatever the diet. After controlling for such taxonomic associations, Elgar & Harvey (1987) found that high relative RMR was associated with a vertebrate diet only, and that two marine orders (Cetacea and Pinnipedia) were largely responsible for this association. It is probable that if we had conducted our analysis across species, we would have found dietary correlates of relative RMR for birds. However, as this study and the results presented by Elgar & Harvey (1987) show, it is important to attempt to establish whether associations found in interspecific studies arise due to repeated convergent evolution rather than phylogenetic relationship. Otherwise, broad interspecific studies may reveal spurious associations because of unequal representation of species among higher taxonomic units (for other examples see Clutton-Brock & Harvey, 1984).

The comparison made in this study reveals a significant difference between the allometric exponents of AMR and RMR for the 47 species where estimates of both levels of energy utilization were available. The form of the relationship between AMR and body weight across species of birds was first examined by King (1974). Using AMR data for 12 species, estimated using widely differing methods, he found the allometric exponent to be 0·71. Walsberg (1980) collected estimates for 30 species and found an exponent of 0·61, and later reanalysed the relationship for 42 species and again found an exponent of 0·61 (Walsberg, 1983). Mace & Harvey (1983) analysed the data for a mixture of 15 passerine and hummingbird genera and found an exponent of 0·69.

The estimates used in the above studies were derived using at least 10 different methods and during different phases of the annual cycle. The effects of these varying techniques on results has not been examined previously. We could detect no consistent effect of difference in technique on values of relative AMR. However, we found that relative AMR is significantly higher among species undertaking breeding activities at the time of measurement, which confirms the result of single species studies (reviewed in Walsberg, 1983). But, because of its size dependence, we caution against the use of the ratio AMR/RMR to investigate differences in energy utilization of birds undertaking different activities. Our results agree with Walsberg (1980, 1983), who also argued that AMR and RMR scale differently with body size. The lower exponent for AMR indicates that active small-bodied birds require disproportionately more energy per unit time above resting levels. As Walsberg (1983) argues, this may be a consequence of the tendency for smaller birds to spend a greater proportion of their day flying.

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REFERENCES

Adams, N. J. & Brown, C. R. (1984). Metabolic rates of sub-Antarctic *Procellariiformes*: a comparative study. *Comp. Biochem. Physiol.* (*A*) **77:** 169–173.

Aschoff, J. & Pohl, H. (1970*a*). Rhythmic variations in energy metabolism. *Fedn Proc. Fedn Am. Socs exp. Biol.* **29:** 1541–1552.

Aschoff, J. & Pohl, H. (1970*b*). Der Ruheumsatz von Vogeln als Funktion der Tageszeit und der Korpergrosse. *J. Orn., Berl.* **111:** 38–47.

Bartels, H. (1982). Metabolic rate of mammals equals the 0·75 power of their body weight. *Exp. Biol. Med.* **7:** 1–11.

Bennett, P. M. (1986). *Comparative studies of morphology, life history and ecology among birds*. D.Phil. thesis, University of Sussex.

Bennett, P. M. & Harvey, P. H. (1985*a*). Relative brain size and ecology in birds. *J. Zool., Lond.* (*A*) **207:** 151–169.

Bennett, P. M. & Harvey, P. H. (1985*b*). Brain size, development and metabolism in birds and mammals. *J. Zool., Lond.* (*A*) **207:** 491–509.

Brody, S. (1945). *Bioenergetics and growth*. New York: Reinhold.

Brody, S. & Proctor, T. C. (1932). Growth and development with special reference to domestic animals-XXIII. Relation between basal metabolism and mature body weight in different species of birds and mammals. *Univ. Miss. Agr. Exp. Sta. Res. Bull.* **166:** 89–101.

Brown, C. R. (1984). Resting metabolic rate and energetic cost of incubation in macaroni penguins (*Eudyptes chrysolophus*) and rockhopper penguins (*E. chrysocome*). *Comp. Biochem. Physiol.* (*A*) **77:** 345–350.

Calder, W. A. (1984). *Size, function and life history*. Cambridge, Mass.: Harvard University Press.

Clutton-Brock, T. H. & Harvey, P. H. (1984). Comparative approaches to investigating adaptation. In *Behavioural ecology*: 7–29. Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell Scientific Publications.

Elgar, M. A. & Harvey, P. H. (1987). Basal metabolic rates in mammals: allometry, phylogeny and ecology. *J. Funct. Ecol.* **1:** 25–36.

Ellis, H. I. (1980). Metabolism and solar radiation in dark and white herons in hot climates. *Physiol. Zool.* **53:** 358–372.

Ellis, H. I. (1984). Energetics of free-ranging seabirds. In *Seabird energetics*: 203–234. Whittow, G. C. & Rahn, H. (Eds).

New York: Plenum Press.

Graber, R. C. (1962). Food and oxygen consumption in three species of owls (Strigidae). *Condor* **64:** 473–487.

Hails, C. J. (1983). The metabolic rate of tropical birds. *Condor* **85:** 61–65.

Harvey, P. H. & Clutton-Brock, T. H. (1985). Life history variation in primates. *Evolution, Lawrence, Kans.* **39:** 559–581.

Harvey, P. H. & Mace, G. M. (1982). Comparisons between taxa and adaptive trends: problems of methodology. In *Current problems in sociobiology*: 346–361. King's College Sociobiology Group (Eds). Cambridge: Cambridge University Press.

Hayssen, V. & Lacy, R. C. (1985). Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.* **4:** 741–754.

Hemmingsen, A. M. (1960). Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno. meml Hosp.* **9:** 1–110.

Heusner, A. A. (1982). Energy metabolism and body size. I. Is the 0·75 mass exponent of Kleiber's equation a statistical artifact? *Resp. Physiol.* **48:** 1–12.

Kendeigh, S. C., Dol'nik, V. R. & Gavrilov, V. M. (1977). Avian energetics. In *Granivorous birds in ecosystems*: 129–204, 363–373. Pinowski, J. & Kendeigh, S. C. (Eds). Cambridge: Cambridge University Press.

King, J. R. (1974). Seasonal allocation of time and energy resources in birds. Publs Nuttall orn. Club. No. 15: 4–85.

King, J. R. & Farner, D. S. (1961). Energy metabolism, thermoregulation, and body temperature. In *Biology and comparative physiology of birds*: 215–288. Marshall, A. J. (Ed.). New York: Academic Press.

Kleiber, M. (1932). Body size and metabolism. *Hilgardia* **6:** 315–353.

Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.

Lasiewski, R. C. & Dawson, W. R. (1967). A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **69:** 13–23.

Mace, G. M. & Harvey, P. H. (1983). Energetic constraints on home-range size. *Am. Nat.* **121:** 120–132.

Martin, R. D. & Harvey, P. H. (1984). Brain size allometry: ontogeny and phylogeny. In *Size and scaling in primate biology*: 147–173. Jungers, W. L. (Ed.). New York: Plenum Press.

McMahon, T. (1973). Size and shape in biology. *Science, Wash.* **179:** 1201–1204.

McMahon, T. (1975). Allometry and biomechanics: limb bones in adult ungulates. *Am. Nat.* **109:** 547–563.

McNab, B. K. (1983). Energetics, body size, and the limits to endothermy. *J. Zool., Lond.* **199:** 1–29.

McNab, B. K. (1986). The influence of food habits on the energetics of eutherian mammals. *Ecol. Monogr.* **56:** 1–19.

Morony, J. J., Jr, Bock, W. J. & Farrand, J., Jr (1975). *Reference list of the birds of the world*. New York: American Museum of Natural History.

Pagel, M. & Harvey, P. H. (1987). The taxon level problem in mammalian brain size evolution: facts and artefacts. *Am. Nat.* (In press).

Prinzinger, R. & Hänssler, I. (1980). Metabolism-weight relationship in some small nonpasserine birds. *Experientia* **36:** 1299–1300.

Prinzinger, R., Kruger, K. & Schuchmann, K. L. (1981). Metabolism-weight relationship in 17 humming-bird species at different temperatures during day and night. *Experientia* **37:** 1307–1309.

Prothero, J. (1984). Scaling of standard energy metabolism in mammals. 1. Neglect of circadian rhythms. *J. theor. Biol.* **106:** 1–8.

Rahn, H. & Whittow, G. C. (1984). Comparison of embryonic development in birds and mammals: birth weight, time, and cost. In *A companion to animal physiology*: 124–137. Taylor, C. R., Johansen, K. & Bolis, L. (Eds). Cambridge: Cambridge University Press.

Ridley, M. (1984). *The explanation of organic diversity*. Oxford: Oxford University Press.

Schmidt-Nielsen, K. (1984). *Scaling: why is animal size so important*? Cambridge: Cambridge University Press.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. 2nd edn. San Francisco: W. H. Freeman & Co.

Walsberg, G. E. (1980). Energy expenditure in free-living birds: patterns and diversity. *Acta Congr. int. orn.* **1:** 300–305.

Walsberg, G. E. (1983). Avian ecological energetics. In *Avian biology* **7:** 161–220. Farner, D. S. & King, J. R. (Eds). New York: Academic Press.

Weathers, W. W. (1979). Climatic adaptation in avian standard metabolic rate. *Oecologia* **42:** 81–89.

Whittow, G. C. & Rahn, H. (Eds) (1984). *Seabird energetics*. New York: Plenum Press.

Wijnandts, H. (1984). Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* **72:** 1–92.

Zar, J. H. (1969). The use of the allometric model for avian standard metabolism-body weight relationships. *Comp. Biochem. Physiol.* **29:** 227–234.

Appendix 1

Allometry of resting metabolic rate

How does resting metabolic rate (RMR) scale with body size among different avian taxa? There has been considerable debate about whether the metabolic rates of vertebrates follow the 'surface rule' with a 0·67 exponent, or 'Kleiber's rule' with a 0·75 exponent (for a review see Schmidt-Nielsen, 1984). A 0·67 exponent suggests an increase in metabolic rate with body surface area, resulting from the greater mass-specific heat loss from the surfaces of small bodied animals which necessitates a higher mass-specific RMR to maintain heat balance. The apparent 0·75 exponent found across a sample of mammal species by Kleiber (1932) has encouraged a variety of other explanations of metabolic scaling. These range from attempts to explain the 0·75 exponent as a compromise (e.g. Hemmingsen, 1960) between heat loss from body surfaces (0·67 exponent) and maintenance of metabolic rates in direct proportion to mass (1·0 exponent), to precise algebraic manipulations of exponents to derive the 0·75 power (McMahon, 1973, 1975).

Brody & Proctor (1932) calculated an allometric exponent of 0·64 scaling RMR to body weight for a sample of birds. King & Farner (1961) reanalysed the relationship and found that the exponent for birds greater than 125 g was 0·74, compared with 0·66 for all birds in their sample. Using a larger sample, Lasiewski & Dawson (1967) distinguished between passerine species ($n = 35$) and non-passerines ($n = 58$). They found that while both groups had a scaling exponent of 0·72, the allometric coefficients differed, with passerines having higher RMRs for their body sizes; the exponent was 0·67 when all species were combined in a single analysis. Zar (1969) used the same data to determine exponents ranging from 0·63 to 0·87 within orders. Aschoff & Pohl (1970*b*) established that estimates of RMR taken during the active phase of the daily cycle were around 25% greater than those taken during the rest phase for a small sample of birds. When measurements for the two phases were separated, they found exponents ranging between 0·61 and 0·76.

The most recent comprehensive study was by Kendeigh *et al.* (1977) who, using data from 172 species, established exponents between 0·66 and 0·73 across passerine and 'non-passerine' groups of species. Kendeigh *et al.* (1977) found that segregating the estimates of RMR into measurements taken during the active and rest phases of the daily cycle resulted in exponents of 0·67 for passerines, but combining the data for all species led to an exponent around 0·72. Since then, various other estimates of the allometric exponents for different groups of birds with small sample sizes and varying taxonomic status have been made, with the exponents ranging between 0·62 and 0·74 (Prinzinger & Hänssler, 1980; Prinzinger, Kruger & Schuchmann, 1981; Hails, 1983; Adams & Brown, 1984; Brown, 1984; Ellis, 1984).

The above review shows that there has not been good evidence enabling an evaluation of whether RMR scales with the 0·67, 0·75 or, indeed, some other exponent among birds. The confidence limits on the exponents often embrace both values, the exponent differs according to how many species from particular taxonomic groups are included, and inter- and intraspecific data have often been included on the same graph (e.g. Lasiewski & Dawson, 1967). Despite these problems, the 0·72 exponent found by Lasiewski & Dawson (1967) and Aschoff & Pohl (1970*b*) across passerine species and an artificial grouping of 'non-passerine' species has enjoyed general acceptance in the literature. But does the exponent change with the taxonomic level of analysis?

We used the estimates of RMR and body weight detailed in **Appendix 2**. All species where measurements were described as being taken during the active phase of the daily cycle were excluded. Data were therefore available for 356 species. Both RMR and body weight were logarithmically transformed before analysis. Average values of both variables were calculated for successive taxonomic levels. For example, tribe values are the means of constituent generic values. Major axis slopes were then calculated within taxa (where the number of points was more than two) at each taxonomic level. For example, a major axis slope was calculated for each tribe that had three or more generic values. A 'common' major axis was then estimated as the sample size weighted mean of all the slopes at each taxonomic level. The taxonomic levels used were determined by the distribution of taxa (see **Appendix 2**). For example, there were few subfamily divisions within families, so the subfamily level was excluded and the common slope value for tribes within families was calculated instead. Heterogeneity of slopes was tested for using a maximum likelihood method (see Harvey & Mace, 1982). All the above tests were also performed using analysis of covariance based on Model 1 regression (Sokal & Rohlf, 1981).

The results are given in Table I and Fig. 1. Common major axes could be calculated for each taxonomic level because no significant heterogeneity among taxa at any level was detected. There is a significant decrease in slope with increasing taxonomic level. The exponent among species within genera is not significantly different from 1·0, but is significantly greater than slopes at higher taxonomic levels. The common slopes at lower taxonomic levels are significantly greater than the usually accepted value of 0·72 for passerine and 'non-passerine' groups of bird species (see above), while at higher taxonomic levels they approximate the 0·67 exponent. Similar results were obtained using Model 1 regression (see Table I).

This pattern of increase in slope with decreasing taxonomic level requires explanation. We caution that these apparent differences in allometric exponent with taxonomic level may be a statistical artefact arising from error variability in RMR and body weight. Pagel & Harvey (1987)

APPENDIX 1 TABLE I

Results of the statistical analyses used to test for changes in allometric exponent with taxonomic level for resting metabolic rate (RMR)

Taxonomic level	Number of taxa	Number of subtaxa	Common major axis	95% c.l.	Common correlation	Common regression	Heterogeneity test χ^2	Heterogeneity test *d.f.*	Heterogeneity test *P*
Genus	28	111	0·92	0·83–1·02	0·88	0·82	26·8	27	NS
Tribe	23	131	0·81	0·74–0·88	0·90	0·75	15·5	22	NS
Family	5	20	0·72	0·63–0·81	0·97	0·70	0·2	4	NS
Suborder	7	53	0·72	0·66–0·77	0·96	0·70	7·2	6	NS
Class	1	24	0·68	0·63–0·74	0·99	0·68	—	—	—

The column headings refer to:

Taxonomic level—When, for example, the family is the taxonomic level of analysis then tribe points were used to calculate best fit lines using logarithmically transformed data. Thus, 'genus' indicates that slopes were calculated for species points within genera, 'tribe' indicates that slopes were calculated for generic points within tribes, and so on.

Number of taxa—The number of major axes used to estimate the common major axis at each taxonomic level. For example, 28 genera contained more than two species for which estimates of resting metabolic rate and body weight were available. As a result, 28 major axis slopes were used to estimate the common major axis at this taxonomic level.

Number of subtaxa—The total number of taxonomic points at each level across which the major axes used to derive the common major axis were calculated. For example, 111 species values were used to derive the 28 major axes for species within genera from which the common major axis for the generic level was estimated.

95% c.l.—The 95% confidence limits of the common major axis.

Heterogeneity test—The results of the statistical tests to examine whether the major axes used to calculate the common major axis at each taxonomic level were parallel. *d.f.*—degrees of freedom, *P*—probability, NS—not significant.

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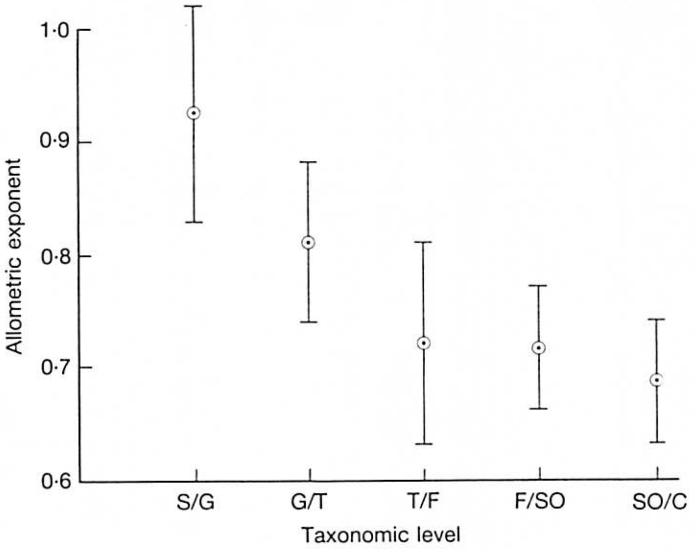

APPENDIX 1 FIGURE 1. Changes in the allometric exponent scaling resting metabolic rate to body weight at different taxonomic levels among birds. The bars are 95% confidence limits of the common major axes at the different taxonomic levels. The labels on the taxonomic level axis refer to: species within genera (S/G), genera within tribes (G/T), tribes within families (T/F), families within suborders (F/SO), and suborders within the class (SO/C).

present evidence suggesting that patterns of change in allometric exponent with taxonomic level for brain size in mammals (see Martin & Harvey, 1984, and references therein) may arise because the assumptions of the different 'best fit' line fitting procedures are violated when the variables are measured with different amounts of error (see Harvey & Mace, 1982). There are many possible sources of error in the estimates of both RMR and body weight given in **Appendix 2**. The potential sources of experimental error arising from the way body weight and RMR are measured is discussed in the **Material and methods** section of this paper. These factors suggest that error variance in RMR is probably greater than that for body weight. Potential sources of sampling error, where the species values may not represent the true population mean, may also be large because sample sizes per species are usually small. Inspection of **Appendix 2** shows that, when a species has been measured a number of times (e.g. *Passer domesticus*, *Parus major*), there is considerable variability in the measurements, and both experimental and sampling error must contribute to this intraspecific variability. Without detailed intraspecific analyses on a range of species, we cannot assess the importance of error variability as a possible cause of misleading results. We will therefore not attempt to provide an evolutionary explanation for the differences in allometric exponent for RMR among different avian taxa. The differences may be an artefact of commonly used statistical techniques.

All previous allometric studies of RMR in birds have used a subset of the data presented in **Appendix 2**. Therefore, the empirical demonstration that there are significant differences in allometric exponents (whether a biologically real phenomenon or a statistical artefact) has important implications for the large literature on metabolic scaling and its interpretation among birds (see above references). There is no firm basis for accepting any particular exponent as 'correct'. Most discussions distinguish between the 0·67 and 0·75 exponents. However, this study shows that, for species within genera, we cannot reject the hypothesis that there is proportionality between RMR and body size (1·0 slope). In such situations, where the pattern of variation differs among taxonomic groups, and indeed where we are not certain whether these differences are an artefact, it has been argued that one solution is to evaluate questions at the taxonomic level at which the highest proportion of variance is located (Harvey & Mace, 1982; Harvey & Clutton-Brock, 1985; Pagel & Harvey, 1987). The exponent across all family points was shown to be 0·67 (see **Results**) and the 95% confidence limits do not overlap either the 0·72 exponent usually quoted for birds, or the 0·75 exponent often quoted for mammals. This 0·67 exponent conforms with the surface area-to-volume interpretation of metabolic scaling based on consideration of heat loss.

Appendix 2

APPENDIX 2 TABLE I

The estimates of RMR and body weight for species of birds. Sources are given in Bennett (1986). The classification used was Morony, Bock & Farrand (1975)

✓ = in Heusner

X = ~~out~~ not in heusner

Order	Family	Species	WT	RMR	C
Struthioniformes	Struthionidae	*Struthio camelus*	100000	2350	
			100000	1302	*
Rheiformes	Rheidae	*Rhea americana*	21700	800	A ✓
Casuariiformes	Casuariidae	*Casuarius bennetti*	17600	516	*
	Dromaiidae	*Dromaius novaehollandiae*	38925	896·2	*
Apterygiformes	Apterygidae	*Apteryx australis*	2380	83·2	*
		A. owenii	1095·5	42·7	*
		A. haasti	2540	86·3	*
Sphenisciformes	Spheniscidae	*Aptenodytes patagonica*	13270	534·6	*
			12662	687·6	
			11080	451·2	
		A. forsteri	31750	1384	
			24800	1013	
			23370	885·3	*
			20790	790·4	
		Pygoscelis papua	6290	383·6	*
		P. adeliae	3500	377·9	
			3970	252·6	*
			4500	373·3	
		Eudyptes pachyrhynchus	2600	142·9	*
		E. chrysolophus	3779	277·4	
			3870	178·5	*
		E. crestatus	2506	206·2	
			2330	120·5	*
		Megadyptes antipodes	4800	238	*
		Eudyptula minor	960	86·2	A ✗
			960	77·1	*
		E. albosignata	1150	136·5	*
		Spheniscus humboldti	3870	196	*
Procellariiformes	Diomedeidae	*Diomedea exulans*	8130	419·4	*
		D. immutabilis	2522	154·1	A ✓
		D. chrysostoma	3753	175·7	*
		Phoebetria fusca	2875	170·9	*
	Procellariidae	*Macronectes giganteus*	4780	275·8	*
			3630	357·1	
		Pterodroma hypoleuca	180	21·5	
			167	17·3	*
		P. brevirostris	315	36·6	*
		P. mollis	274	36·1	*
		P. phaeopygia	425	108·4	*
		Pachyptila salvini	165	32	*
		Bulweria bulwerii	87	10·5	*
		Procellaria cinerea	1014	103·5	*
		P. aequinoctialis	1287	130·3	*
		Puffinus pacificus	337·8	30·7	*
		P. griseus	740	59·6	*
		P. nativitatis	307·6	30·4	*
	Hydrobatidae	*Oceanodroma leucorhoa*	42	13·2	
			45	13·4	*
		O. furcata	49	13·1	
			44·6	9·3	*
	Pelecanoididae	*Pelecanoides georgicus*	127	20·3	*

swap.

Appendix 2 Table I (*cont.*)

Order	Family	Species	WT	RMR	C
		P. urinatrix	136	28·8	*
Pelecaniformes	Phaethontidae	*Phaethon rubricauda*	593·2	68·7	*
	Pelecanidae	*Pelecanus occidentalis*	3510	264	
			3038	214	*
		P. conspicillatus	5090	374	*
	Sulidae	*Sula dactylatra*	1289	113·7	*
		S. sula	1017	89·9	*
	Phalacrocoracidae	*Phalacrocorax auritus*	1330	130·2	A ✗
			1330	113·4	*
		P. atriceps	2660	308·7	*
	Anhingidae	*Anhinga anhinga*	1120	76·1	A ✗
			1040	65·9	*
	Fregatidae	*Fregata magnificens*	1078	57·3	*
Ciconiiformes	Ardeidae	*Botaurus lentiginosus*	600	56	*
		Ardea herodias	1870	128	*
		Hydranassa tricolor	309·9	35·3	A ✓
		H. caerulea	290·3	20·7	A ✓
		Egretta thula	314	28·2	A ✓
		Ardeola ibis	299·2	27·3	A ✓
	Threskiornithidae	*Eudocimus albus*	940	85	*
	Ciconiidae	*Mycteria americana*	2500	201	*
		Jabiru mycteria	5470	272	*
		Leptoptilos javanicus	5710	307	*
	Phoenicopteridae	*Phoenicopterus ruber*	2210	262·2	
			3040	215	*
Anseriformes	Anatidae	*Cygnus olor*	8300	625	A ✓
		C. buccinator	8880	418	*
		Anser anser	3250	224	*
			3300	219	
			5000	280	
			5890	271	
		Branta bernicla	1130	108·5	
			1168	93·4	*
		Aix sponsa	448	46·4	*
			469	49·1	
			485	65	
		Anas platyrhynchos	1166	110·2	A ✗
			1020	84	*
			1132	104	
			1263	104·5	A ✗
			1081	115·8	
		A. penelope	718	62·2	
			723	58·3	*
			539	64·8	
		A. rubripes	904	73·7	*
			1026	125·1	
			1066	96·7	
		A. crecca	250	34·4	*
		A. querquedula	289	46·1	*
		A. clypeata	554	80·1	*
		A. acuta	721	90·1	*
		A. strepera	791	128·1	*
		Netta rufina	1237	146·6	*
		Aythya nyroca	440	67·6	*
			436	48·8	A ✓
			780	57·6	*
			754	90·1	

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
Charadriiformes	Charadriidae	*Charadrius dubius*	36	8·6	*
		Pluvialis dominica	118	13·3	*
	Thinocoridae	*Thinocorus rumicivorus*	55·5	6·4	*
	Scolopacidae	*Tringa ochropus*	90	19	*
		Scolopax rusticola	430	44·6	*
	Stercoraiidae	*Catharacta skua*	970	98	*
		C. maccormicki	1130	177·4	*
	Laridae	*Gabianus pacificus*	1210	127	*
		Larus delawarensis	439	59·6	*
		L. canus	428	48	
			431	46·6	*
		L. argentatus	1000	99·2	*
		L. occidentalis	761	70·2	*
		L. hyperboreus	1210	180·1	*
		L. atricilla	275·6	38·7	*
		L. ridibundus	252	44·8	
			289	42·8	
			285	41·4	
			306	38·4	*
		Sterna lunata	131·7	14·5	*
		S. fuscata	148	16·4	*
		S. maxima	373	51·9	*
		Anous stolidus	138·7	16·1	*
		A. tenuirostris	90·2	13·1	*
		Gygis alba	98·1	16·8	*
	Alcidae	*Uria lomvia*	989	140·5	*
		U. aalge	956	140·5	*
Columbiformes	Columbidae	*Columba palumbus*	150	17	*
		C. unicincta	318	35·4	*
		C. livia	314	34·8	A
			315	35·9	
			353	38·3	
			266	33·7	
			300	30	
			311	32·9	
			372	35·5	*
		Streptopelia senegalensis	108	17·5	*
		S. turtur	154	23·5	*
		S. decaocto	187	26·3	
			152	21·8	
			155	18·3	*
		Zenaida macroura	91·4	13·4	
			123	15·2	*
		Scardafella inca	40·5	5·2	*
		Petrophassa ferruginea	81	8·2	*
		Leptotila verreauxi	131	18·3	*
		Turtur tympanistra	68	12·8	*
	Cacatuidae	*Eolophus roseicapillus*	271	29	*
			321	62·9	
		Nymphicus hollandicus	85·6	14·2	*
		Aythya fuligula	574	55·8	*
		A. ferina	816	120·1	*
	Anhimidae	*Chauna chavaria*	2620	142	*
Falconiformes	Cathartidae	*Vultur gryphus*	10320	351	*
	Falconidae	*Falco tinnunculus*	108	17	*
		F. subbuteo	208	26·8	*

Appendix 2 Table I (*cont.*)

Order	Family	Species	WT	RMR	C
		F. sparverius	117	17·4	*
	Accipitridae	*Pernis apivorus*	652	48·3	*
		Accipiter nisus	135	19·6	*
		Buteo buteo	1012	77·6	*
		Aquila chrysaetos	3000	102	*
		Gypaetus barbatus	5070	228	*
		Geranoaetus melanoleucus	2860	106	*
		Haliaeetus leucocephalus	4096	272·4	A✓
Galliformes	Phasianidae	*Meleagris gallopavo*	3700	184	*
		Lagopus lagopus	524	64·2	
			567	59·3	*
			539	78·8	
			590	70·5	A✗
		L. mutus	432	77·8	A✗
		L. leucurus	326	48·8	*
		Tetrao urogallus	3900	246	
			4010	244	*
		T. tetrix	1079	144·5	*
			931	157·3	
		Bonasa umbellus	644	49·2	*
		Lophortyx californica	138	15·7	*
		L. gambelii	126·1	15·6	*
		Colinus virginianus	194	23	*
		Excalfactoria chinensis	42·7	6	*
			49	13	
		Coturnix coturnix	97	18·4	*
			97	23	
			97·5	21·3	A✗
		C. japonica	115	20·2	*
		Perdix perdix	483	49·5	
			501	44·5	*
		Alectoris graeca	620	58·9	
			633	52·3	*
		A. chukar	475	40·5	*
		Gallus gallus	2430	160·4	A✗
			2000	97·5	
			2000	137	
			2000	115	
			2006	130·7	
			2710	124	*
	Cracidae	*Penelope purpurescens*	2040	112	*
		Crax alberti	2800	136	*
		C. daubentoni	2800	148·4	*
Gruiformes	Gruidae	*Grus canadensis*	3890	168	*
		Anthropoides paradisea	4030	220	*
	Rallidae	*Crex crex*	96	16·3	*
		Fulica atra	412	42·1	
Psittaciformes	Psittacidae	*Melopsittacus undulatus*	39	12·8	
			25·2	6·2	*
			33·7	9·9	A✗
		Agarpornis roseicollis	48·1	9·6	*
		Myiopsitta monachus	81·5	16·2	
			83·1	16·3	A✗
			83·1	14·1	
			80·4	15·5	A✗
			80·4	10·6	*

Appendix 2 Table I (*cont.*)

Order	Family	Species	WT	RMR	C
		Bolborhynchus lineola	55·7	12·5	A ✓
		Loriculus galgulus	27	10·7	*
		Neophema pulchella	40	12	*
		N. bourkii	40	11·1	*
		Amazona viridigenalis	337·8	43·9	A ✓
Cuculiformes	Cuculidae	*Cuculus canorus*	111·6	17·3	*
			128	25·9	
		Eudyramys scolopacea	188	34	*
		Cacomantis variolosus	23·8	3·9	A ✗
			23·8	2·5	*
		Geococcyx californica	284·7	30·2	*
		Centropus senegalensis	175	31·1	*
Strigiformes	Strigidae	*Micrathene whitneyi*	45·9	5·3	*
		Nyctea scandiaca	2026	87	*
		Bubo virginianus	1450	108	*
		Speotyto cunicularia	132·4	16	
			142·7	14	*
		Otus asio	151	14·6	
			166	12·1	*
		O. scops	63·9	7·3	*
		O. trichopsis	120	9·2	*
		Glaucidium gnoma	54	9·1	*
		G. cuculoides	163	17·9	*
		Surnia ulula	333	35·1	*
		Strix aluco	520	43	*
		Aegolius acadicus	124	13·5	*
			105·9	16·2	
			83	10·5	
			85·5	14·5	
		Asio flammeus	406	26·6	*
		A. otus	252	19·7	*
			236	27	A ✗
			243	29·2	
			240·5	26·4	
Caprimulgiformes	Podargidae	*Podargus ocellatus*	145	11·7	*
	Caprimulgidae	*Chordeiles minor*	72	9·1	*
		Caprimulgus europaeus	77·4	13·3	A ✓
		Phalaenoptilus nuttalli	40	3·7	
			35	3·2	*
		Nyctidromus albicollis	43	7·7	A ✓
		Eurostopodus guttatus	88	8·4	*
Apodiformes	Apodidae	*Apus apus*	44·9	9	*
	Trochilidae	*Calypte costae*	3·2	1·1	*
		C. anna	4	2·2	
			4·8	2·4	*
		Stellula calliope	3	1·4	*
		Archilochus colubris	3·2	1·6	*
		A. alexandri	3·3	1·3	*
			3·1	3·9	
			3·1	8·4	A ✗
		Selasphorus rufus	3·8	1·4	*
		S. sassin	3·7	1·4	*
		Eugenes fulgens	6·6	2·1	*
			7·9	12·9	A ✗
			7·9	5·3	
		Lampornis clemenciae	7·9	2·1	*

Appendix 2 Table I (*cont.*)

Order	Family	Species	WT	RMR	C
			8·15	13	A ✗
			8·15	5	
		Eulampis jugularis	8·4	3·2	*
			9·5	11·1	A ✗
			9·5	5·9	
		Patagona gigas	19·1	5·9	*
			17·5	19·8	A ✗
			17·5	9·4	
		Oreotrochilus estella	8·4	4	*
			8·7	12·6	A ✗
			8·7	6·9	
		Ocreatus underwoodii	2·7	7·6	A ✗
			2·7	3·1	*
		Chlorostilbon mellisugus	2·9	7·1	A ✗
			2·9	3	*
		Orthorhynchus cristatus	2·9	6·7	A ✗
			2·9	1·9	*
		Acestrura mulsant	3·3	8·4	A ✗
			3·3	1·6	*
		Urosticte benjamini	3·9	6·1	A ✗
			3·9	2·7	*
		Chrysuronia oenone	5	12·4	A ✗
			5	5	*
		Florisuga mellivora	6·9	16	A ✗
			6·9	8	*
		Agleactis cupripennis	7·2	10·2	A ✗
			7·2	5·2	*
		Boissonneaua matthewsii	7·2	11·4	A ✗
			7·2	6·7	*
		Anthracothorax nigricollis	7·7	11·8	A ✗
			7·7	6·3	*
		Trochilus scitulus	4	11·8	A ✗
			4	5·4	*
			4·9	6·8	A ✗ ✓
		T. polytmus	6·3	8·4	A ✓
Coliiformes	Coliidae	*Colius striatus*	52·5	7·3	A ✓
			51·2	11·2	A ✗
		C. castanotus	69	31·3	A
			69	21·4	
			57·7	15·8	A ✓
		C. macrourus	48·5	15·2	A ✗ ✓
		Colius indicus	53·5	14·8	A ✓
Trogoniformes	Trogonidae	*Trogon rufus*	53	8·9	*
Coraciiformes	Alcedinidae	*Alcedo atthis*	34·3	7·8	*
	Upupidae	*Upupa epops*	67	11·4	*
	Meropidae	*Merops viridis*	33·8	6·1	*
			33·8	8·1	A ✗
Piciformes	Picidae	*Jynx torquilla*	31·8	7·4	*
		Picoides major	98	18·5	
			117	21·5	*
Passeriformes	Dendrocolaptidae	*Xiphorhynchus guttatus*	45·2	9·2	*
	Formicariidae	*Thamnophilus punctatus*	21	7·1	*
	Pipridae	*Pipra mentalis*	12	6·6	A ✗
			12·3	4	*
			12·4	5·3	A ✗
			14·5	6·1	

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
		Manacus vitellinus	15·8	4·9	A ✗
			15·5	4·8	*
			15·6	5·7	
	Tyrannidae	*Sayornis phoebe*	21·6	7·1	*
		Empidonax virescens	12·3	3·7	*
		E. minimus	10	4·9	A ✓
		Myiarchus crinitus	33·9	7·9	*
		Contopus virens	13·9	5·3	*
		Tyrannus tyrannus	35·7	9	*
	Alaudidae	*Eremophila alpestris*	26	6·4	*
			26	6·8	
		Lullula arborea	33·2	10·1	*
		Alauda arvensis	46·1	11·6	*
	Hirundinidae	*Riparia riparia*	13·6	4·8	*
		Hirundo rustica	18	6·5	*
		H. tahitica	14·1	3·7	*
			14·1	4·8	A ✗
		Delichon urbica	20·5	7·3	*
	Motacillidae	*Motacilla flava*	14·7	5·3	*
		M. alba	18	6·2	*
			18·2	5·8	*
		Anthus pratensis	18·9	6·2	*
		A. trivialis	19·7	7	*
		A. campestris	21·8	7·9	*
	Pycnonotidae	*Pycnonotus goiavier*	28·6	5·1	*
			28·6	7	A ✗
		P. finlaysoni	26·3	4·6	*
			26·3	6·5	A ✗
		Criniger bres	35	7·3	*
			35	9·6	A ✗
	Irenidae	*Chloropsis sonnerati*	39·7	7·8	*
	Laniidae	*Lanius collurio*	27	7·9	*
		L. excubitor	72·4	16·8	*
		L. cristatus	26·9	5·2	*
			26·9	6·3	A ✗
	Bombycillidae	*Bombycilla garrulus*	72·5	19·7	*
	Cinclidae	*Cinclus mexicanus*	50·2	9·5	*
	Troglodytidae	*Troglodytes troglodytes*	9	4·4	*
			9·2	5	
		T. aedon	9·7	6	A ✓
	Prunellidae	*Prunella modularis*	16·8	6·7	*
	Muscicapidae	*Erithacus rubecula*	17·6	6·2	
			17·6	5·8	*
			16·7	10	
			14	10·5	
			15·4	9·2	
		E. cyane	13·4	5·5	A ✗
			13·4	3·6	*
		E. luscinia	30	8·4	*
		E. svecicus	20·8	7·4	*
		Saxicola rubetra	14·3	5	*
		Phoenicurus phoenicurus	13	4·8	*
			14·1	6·7	
			18·1	6·9	
		P. ochruros	13·9	5	*

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
		Turdus iliacus	58	14·9	*
		T. philomelos	62·8	15	*
			64	15·6	
			67·9	27·4	
		T. merula	82·6	19·2	*
			83	21·4	
		T. viscivorus	108·2	22·8	*
		Hylocichla mustelina	43·3	12·5	A✓
		Catharus fuscescens	28·8	10·1	A✓
		C. guttatus	27·8	9·7	A✓
		C. ustulatus	27·9	9·8	A✓
		C. minimus	24·8	9·3	A✓
		Copsychus saularis	33·5	6·9	A✗
			33·5	4·8	*
		Ficedula hypoleuca	11·7	4·8	*
		Muscicapa striata	14·4	5·1	*
		Sylvia borin	24·8	8·6	*
			23·2	10·7	
			23·4	9·9	
		S. curruca	10·6	4·1	*
			16·8	10·7	
			10·4	7·2	
		S. nisoria	21·3	7·9	*
		S. atricapilla	21·9	8·6	*
			22·9	10·8	
			18·1	9·2	
			19·1	9·2	
		S. communis	20·8	10·2	
			14·6	7·3	*?
		Acrocephalus palustris	10·8	4·2	*
		A. schoenobaenus	11·5	4·5	*
		A. dumetorum	12·6	5·6	*
		A. arundinaceus	21·9	6·2	A✗
			21·9	5·3	*
		A. bistrigiceps	7·9	2·7	*
		Phylloscopus collybita	8·2	3·4	*
		P. sibilatrix	9·2	3·6	*
			8·6	5·2	
		P. trochilus	10·7	4·3	*
		Regulus regulus	5·5	3·8	*
		Hippolais icterina	12·5	5·2	*
		Hypothymis azurea	10·8	3·7	A ✗
			10·8	2·9	*
		Malacopteron cinereum	15·8	6·5	A ✗
			15·8	4·4	*
		Epithianura albifrons	13	3·9	A✓
			12·9	4·1	A✗
		E. tricolor	11·9	3·3	A✓
			11·2	3·6	A✗
		E. aurifrons	11·5	3·2	A✓
			11·8	3·8	A✗
	Aegithalidae	*Aegithalos caudatus*	8·9	4·1	*✓
			8·8	5·2	
			8·2	5·4	
			7·6	6·6	

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
		Psaltriparus minimus	5·5	2·5	*
	Remizidae	*Auriparus flaviceps*	6·8	3·4	*
	Paridae	*Parus major*	18·5	8·4	
			16·4	6·8	
			17·1	7·7	
			18·4	7·8	
			19	7·6	
			18	6·7	*
			16·9	12·4	
			15·5	11·7	
			16·7	11·6	
			17·1	9·6	
		P. ater	10·8	4·9	*
			11	5·6	
			10·9	7·5	
			8·9	8·2	
		P. atricapillus	10·3	5·2	*
			12	5·3	
			10·8	6·7	
			9·1	10·1	
			11·1	9·1	
		P. coeruleus	11·7	9	
			11·7	11·3	
		P. cristatus	11·5	8·5	
	Sittidae	*Sitta canadensis*	11·2	4·8	*
		S. europaea	22·9	13·5	
			19·6	11·8	← or
	Nectariniidae	*Arachnothera longirostra*	13	3·9	*
			13	5	A ×
		A. flavigaster	36·3	6·2	*
			36·3	8·4	A ×
	Meliphagidae	*Meliphaga virescens*	25	7·3	*
		Lichmera indistincta	9	4·3	*
	Emberizidae	*Emberiza schoeniclus*	17·6	6·2	*
		E. hortulana	22	8·7	
			24·3	8·6	
			27	8·4	*
		E. citrinella	26·4	9·1	
			26·8	9	*
			27·4	10·3	
			26·5	16·5	
		Zonotricha leucophrys	26·1	7	*
			28·6	8	
		Z. albicollis	22·5	7·1	
			23·6	9·5	
			20·2	5·8	*
		Z. melodia	19·1	5·2	*
			18·6	7·8	
		Z. georgiana	14·9	4·4	*
		Z. iliaca	31·7	11·3	
			30·7	7·7	*
		Z. querula	33·3	9·3	*
			33	13·3	
		Ammodramus sandwichensis	15·9	4·6	*
			16·7	5·9	
		A. savannarum	13·8	3·7	*

Appendix 2 Table I (*cont.*)

Order	Family	Species	WT	RMR	C
		Junco hyemalis	18	6·1	*
		Spizella passerina	11·9	4	*
		S. arborea	16·6	6·8	*
		Pooecetes gramineus	21·5	5·6	*
		Plectrophenax nivalis	41·8	11·4	A ✓
		Tiaris canora	7	3·2	*
		Pipilo fuscus	43·7	13·7	*
		P. alberti	46·6	15	*
		Amphispiza bilineata	11·6	4·1	*
		Calamospiza melanocorys	32·6	9·4	A ✓
		Cardinalis cardinalis	41	12·2	
			41	10·4	*
		C. sinuata	32	8·1	*
	Parulidae	*Parula americana*	7	2·5	*
		Dendroica dominica	9·8	3·3	*
		D. palmarum	9·8	3·2	*
		D. coronata	11·5	3·9	*
		D. pinus	12	3·7	*
		D. caerulescens	9·4	3·8	*
		Seiurus noveboracensis	18·7	5·8	*
		S. aurocapillus	19	5	*
		Wilsonia citrina	12	4·4	*
		Protonotaria citrea	12·8	4·1	*
		Mniotilta varia	8·2	2·6	*
		Vermivora pinus	7·8	3·1	*
		V. celata	9·3	3·1	*
		Geothlypis trichas	10·6	3·6	*
	Drepanididae	*Psittirostra cantans*	31	9·7	A ✗
			31·6	8·8	*
		P. bailleui	34·8	9·2	*
		Loxops parva	7·9	2·9	A ✓
		L. virens	15·3	6·1	A ✗
			10·7	4·3	A ✓
		Vestiaria coccinea	15	6·4	A ✓
		Himatione sanguinea	12·9	5·1	A
			13·5	6·2	
	Vireonidae	*Vireo olivaceus*	17	6·6	A ✓
	Icteridae	*Molothrus ater*	42·5	12·9	*
			33·7	11	
		Agelaius phoeniceus	56·7	17·2	*
		Icterus galbula	37·5	10·4	*
	Fringillidae	*Serinus canaria*	13·3	4·7	*
		Carduelis spinus	13	5·8	*
			13·7	7·5	
			13·7	7·3	
			10·4	9·5	
		C. pinus	14	6	*
			13·8	7·2	
			14·2	6·8	
		C. chloris	24·5	11·1	
			31·1	11·2	
			28·2	9·8	*
			29	11·5	
			26·5	13·7	
			25·6	16·4	
			26·1	13·7	

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
			29·2	13·6	
		C. carduelis	16·5	7·2	*
			19·8	12·4	
			17·9	12·5	
			14·8	10·1	
		C. tristis	13·5	17·3	
			13·6	6·9	*
			13·5	15	
		Acanthis flammea	11·2	5·8	
			12·8	5·4	
			13·2	5·9	A
			13·8	9·7	A
			14	5·9	*
			14·3	7	
			15·6	8·3	
			16	10·5	
			17·3	11·3	
		A. cannabina	15·5	7·3	
			16·9	7	*
			20·2	11·5	
			20·6	13·9	
		Carpodacus erythrinus	21·2	7·6	
			21·6	7·4	*
		C. cassinii	28·1	7·6	
			27·4	7	*
		C. mexicanus	20·4	6·4	*
		Loxia curvirostra	29·4	10·5	
			39·4	12·4	*
			42·7	13·9	
			42·5	16·8	
			43·3	18·5	
		L. leucoptera	29·8	9·6	*
		L. pytyopsittacus	53·7	16·5	*
		Pyrrhula pyrrhula	30·4	11·4	*
			31·1	16·4	
			30·8	15·9	
			27·6	14·8	
			31	15·4	
		Coccothraustes coccothraustes	48·3	14·4	*
		C. vespertinus	54·5	14·9	*
			55·3	15·6	
		Rhodopechys obsoleta	21·1	8·1	*
		Fringilla coelebs	20·8	9·1	
			21	7·7	*
			20·9	12·8	
			17·4	12·3	
			19·6	9·4	
		F. montifringilla	24·8	9·5	
			21	7·9	*
	Estrildidae	*Estrilda troglodytes*	6·7	3·6	A
			6·4	2·7	A
			6·5	2·6	*
			7·7	3·2	
		Uraeginthus bengalus	8·1	2·8	*
			9·2	3·4	
		Poephila guttata	11·5	4·9	A

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
			11·7	4·4	*
			11·8	4·8	
		Lonchura striata	10·3	4·4	*
		L. fuscans	9·5	2	*
		L. malacca	11·8	2·9	*
			11·8	4·6	A ✗
		L. maja	12·8	3·1	*
			12·8	5·6	A ✗
	Ploceidae	*Vidua paradisaea*	10·5	4	*
		Passer montanus	22	8·5	
			17·5	6·8	A ✗
			17·5	4·1	*
			22·3	8·4	
			22·2	13	
			21·3	12·7	
		P. domesticus	22·4	9·5	
			23·5	11	
			23·7	10·1	
			25	6·9	
			26	9·4	
			27·3	8·5	
			23	7·6	
			23·2	7·6	
			25·1	9·3	A ✗
			25·3	8·4	
			25·5	6·9	* △
			26·5	9·8	
			26·4	10·1	
			26·5	7·9	
			22·5	11·2	
	Sturnidae	*Sturnus vulgaris*	67	18·1	
			75	18·5	*
		Acridotheres cristatellus	109·4	24·9	*
	Oriolidae	*Oriolus oriolus*	64·9	13·4	*
	Corvidae	*Perisoreus canadensis*	71·2	14	*
			64·5	20	A ✗
		Cyanocitta cristata	80·8	17·2	*
		C. stelleri	99·1	20·6	A ✓
		Pica pica	202	35·5	
			158·9	24·7	*
			208	32·4	
		P. nuttalli	151·9	30·3	*
		Garrulus glandarius	153	28·6	*
		Pyrrhocorax graculus	206·4	35·4	*
		Nucifraga caryocatactes	147	27·8	*
		Aphelocoma coerulescens	78·7	20	A ✓
		Corvus monedula	215	38·6	
			193	34·5	*
		C. cryptoleucus	640	79	*
		C. ruficollis	660	70·1	*
		C. frugilegus	390	54	*
		C. brachyrhynchos	384·8	67·8	*
		C. corone	518	68·5	*
			540	79	
			360	51·9	
		C. caurinus	282	74·7	A ✓

APPENDIX 2 TABLE I (*cont.*)

Order	Family	Species	WT	RMR	C
			306	98·7	A
		C. corax	1203	113·7	*
			1208	123·8	
			850	92	
			866	94·9	
			1079	201·6	

The column headings are:

WT—body weight (g)

RMR—resting metabolic rate (kcal/d)

C—the phase of the daily cycle in which estimates of RMR were taken. 'A' indicates that RMR was estimated in the active phase of the daily cycle and therefore it was not used in the analyses. An asterisk '*' indicates that this estimate for a species was used in the analyses (the criteria used for selection are given in the text). Estimates that do not have an asterisk were not used in the analysis.

Appendix 3

Appendix 3 Table I

The estimates of AMR and body weight for species of birds. Sources are given in Bennett (1986)

Order	Family	Species	WT	AMR	DEV	M	Cycle
Sphenisciformes	Spheniscidae	*Aptenodytes patagonica*	13000	1340	0·100	3	breeding
		A. forsteri	25090	1522	−0·151	10	incubating
		Pygoscelis papua	6200	908	0·176	3	breeding
		Eudyptes chrysolophus	3600	676	0·224	3	breeding
		Spheniscus demersus	3130	465	−0·014	4	breeding
Procellariiformes	Procellariidae	*Puffinus pacificus*	384	147	0·161	4	breeding
Pelecaniformes	Pelecanidae	*Pelecanus onocrotalus*	11300	1201	0·084	9	non-breeding
		P. rufescens	5400	776	0·119	9	non-breeding
	Sulidae	*Morus capensis*	2672	350	−0·166	9	non-breeding
	Phalacrocoracidae	*Phalacrocorax carbo*	2178	433	0·124	9	non-breeding
		P. lucidus	1933	350	0·010	9	non-breeding
		Halietor africanus	400	56	−0·671	9	non-breeding
Ciconiiformes	Ardeidae	*Nycticorax nycticorax*	670	140	−0·182	9	non-breeding
		Ardeola ibis	383	150	0·180	9	non-breeding
		Egretta garzetta	515	120	−0·169	9	non-breeding
		E. alba	1640	285	−0·073	9	non-breeding
		Ardea cinerea	1800	325	−0·013	9	non-breeding
		Mycteria americana	2500	450	0·081	6	breeding
		Eudocimus albus	881	164·6	−0·195	9	nestlings
		Plegadis falcinellus	650	125	−0·261	9	non-breeding
		P. leucorodia	1950	300	−0·124	9	non-breeding
Anseriformes	Anatidae	*Anser caerulescens*	2993	403·7	−0·108	5	spring-fattening
		Branta bernicla	1350	201	−0·260	9	non-breeding
		B. leucopsis	1550	222	−0·252	9	non-breeding/winter
		Anas strepera	955	131·8	−0·426	5	laying
		A. rubripes	1000	138	−0·412	5	non-breeding/summe
		Somateria mollissima	2200	442	0·135	9	non-breeding
		Oxyura maccoa	761	176·4	−0·058	5	breeding
Falconiformes	Accipitridae	*Elanus leucurus*	331	113·1	0·022	9	non-breeding/winter
		E. caeruleus	243	98·3	0·073	5	non-breeding
		Rostrhamus sociabilis	367·6	85·7	−0·268	5	non-breeding
		Haliaeetus leucocephalus	4500	407	−0·323	5	non-breeding/winter
		Accipiter gentilis	1115	200	−0·160	6	non-breeding/winter
		A. nisus	246	105	0·121	9	non-breeding
		Buteo platypterus	397	103	−0·155	9	incubating
		B. jamaicensis	1104	114·5	−0·623	5	nestlings
		B. regalis	1610	316·5	0·025	5	nestlings
	Falconidae	*Falco sparverius*	119	42·9	−0·235	9	non-breeding/winter
Galliformes	Phasianidae	*Lagopus lagopus*	605	206	—	8	laying spring
			500	150	0·035	8	non-breeding/winter
		L. mutus	420	100	−0·211	8	non-breeding/winter
		L. leucurus	360	105	−0·086	8	non-breeding/winter
		Lophortyx gambelii	150	23·8	−0·855	4	non-breeding/summ
Charadriiformes	Haematopodidae	*Haematopus moquini*	694	150·3	−0·142	5	non-breeding
	Recurvirostridae	*Recurvirostra americana*	316	110·9	0·031	5	nestlings
	Scolopacidae	*Tringa totanus*	183	83	0·085	9	non-breeding
		Actitis macularia	42·5	20·4	−0·298	5	laying
		Calidris pusilla	27·1	39·6	0·503	5	nestlings
	Chionidae	*Chionis minor*	479	151·8	0·068	5	nestlings
	Laridae	*Larus argentatus*	1200	275	0·067	9	non-breeding
		Sterna fuscata	184	81·4	0·066	4	breeding
		Anous stolidus	195	84	0·061	4	breeding
	Alcidae	*Uria aalge*	912	262	0·176	9	non-breeding
Columbiformes	Columbidae	*Zenaida macroura*	120	53	−0·062	2	non-breeding/autu
Strigiformes	Strigidae	*Nyctea scandiaca*	2086	272·2	−0·242	9	non-breeding
		Asio otus	280	60·9	−0·406	1	non-breeding

Appendix 3 Table I (*cont.*)

Order	Family	Species	WT	AMR	DEV	M	Cycle
Apodiformes	Trochilidae	*Colibri coruscans*	8·2	11·4	0·109	5	fledglings
		Stellula calliope	3	7·4	0·293	5	incubating
		Oreotrochilus estella	8·4	12·4	0·166	5	non-breeding/winter
		Calypte anna	4·8	7·8	0·082	5	breeding
Coraciiformes	Alcedinidae	*Ceryle rudis*	75	18	−0·712	9	non-breeding
	Meropidae	*Merops viridis*	33·8	18·5	−0·256	4	breeding
Passeriformes	Tyrannidae	*Empidonax traillii*	12·6	12·7	−0·034	5	nestlings
		E. minimus	10	15·9	0·280	5	nestlings
	Hirundinidae	*Progne subis*	49	39	0·168	4	breeding
		Riparia riparia	12·9	22	0·414	4	breeding
		Hirundo rustica	19·1	26·2	0·347	4	breeding
		H. tahitica	14·1	18·3	0·211	4	breeding
		Petrochelidon pyrrhonota	24·6	26·4	0·216	5	nestlings
		Delichon urbica	18·5	24·5	0·308	4	breeding
	Motacillidae	*Anthus spinoletta*	22	12	−0·385	8	non-breeding/winter
	Laniidae	*Lanius ludovicianus*	45·5	25·3	−0·155	4	non-breeding/autumn
	Bombycillidae	*Phainopepla nitens*	22·7	18·9	−0·021	4	breeding
	Mimidae	*Mimus polyglottus*	46·8	33·3	0·061	4	breeding
	Paridae	*Parus major*	19·4	22·5	0·211	7	non-breeding/winter
	Nectariniidae	*Nectarina olivacea*	12·1	13·2	0·020	5	non-breeding
		N. reichenowi	15	12·7	−0·129	5	non-breeding
		N. famosa	13·5	17	0·173	5	breeding
	Emberizidae	*Calcarius lapponicus*	27·5	32·3	0·324	5	breeding
		Zonotrichia leucophrys	21·8	22·3	0·140	—	nestlings
		Ammodramus sandwichensis	19·1	19·2	0·086	4	breeding
		Spizella arborea	18	22·6	0·255	6	breeding
		Pipilo alberti	46·8	26·7	−0·125	5	breeding
		Spiza americana	35	24·4	−0·042	5	breeding
	Parulidae	*Vermivora peregrina*	10	18·8	0·421	9	non-breeding/migration
		Dendroica caerulescens	9·4	10·1	−0·067	5	nestlings
		D. palmarum	10·2	14·9	0·215	9	non-breeding/migration
		D. striata	12·6	17·9	0·254	9	non-breeding/migration
	Drepanididae	*Vestiaria coccinea*	16·9	15·7	−0·016	5	non-breeding
	Vireonidae	*Vireo olivaceus*	17	15·5	−0·030	5	nestlings
	Fringillidae	*Fringilla montifringilla*	21·7	28·3	0·342	5	non-breeding/winter
	Estrildidae	*Estrilda troglodytes*	6·7	13·7	0·373	4	non-breeding/spring
	Ploceidae	*Passer domesticus*	29	23·9	0·043	6	non-breeding
	Sturnidae	*Sturnus vulgaris*	76	54	0·202	4	nestlings
	Corvidae	*Pica pica*	173	65·7	−0·080	5	nestlings
		Nucifraga caryocatactes	158	56·9	−0·152	—	—
		Corvus caurinus	386	101·5	−0·152	6	non-breeding/winter

The columns headings refer to the following:

WT—body weight (g)

AMR—active metabolic rate (kcal/d). When studies gave multiple estimates for birds using the same method and undertaking the same activities the median value is shown in the table (or if only the range of values was given then the mean of the extreme values).

DEV—the value of relative AMR for each species. This is the deviation of each species point from the estimate of the common major axis derived from the eight major axes calculated across species points within each order.

M—these numbers refer to the different methods used for estimating AMR. For an explanation of these codes see text.

CYCLE—activities of the birds at the time estimates of AMR were made. 'Breeding', 'laying', 'incubating', 'nestlings' and 'fledglings' were included in the analyses as estimates taken when the birds were breeding. 'Non-breeding' and 'spring-fattening' were used as estimates taken when the birds were not breeding.