

ENERGETICS OF FREE-RANGING MAMMALS, REPTILES, AND BIRDS

K. A. Nagy, I. A. Girard, and T. K. Brown

Department of Organismic Biology, Ecology, and Evolution, University of California, Los Angeles, California 90095-1606; e-mail: kennagy@biology.ucla.edu; igitard@ucla.edu; tracey@ucla.edu

KEY WORDS: allometric scaling, bioenergetics, doubly labeled water, field metabolic rate, food requirement

ABSTRACT

We summarize the recent information on field metabolic rates (FMR) of wild terrestrial vertebrates as determined by the doubly labeled water technique. Allometric (scaling) relationships are calculated for mammals (79 species), reptiles (55 species), and birds (95 species) and for various taxonomic, dietary, and habitat groups within these categories. Exponential equations based on body mass are offered for predicting rates of daily energy expenditure and daily food requirements of free-ranging mammals, reptiles, and birds. Significant scaling differences between various taxa, dietary, and habitat groups (detected by analysis of covariance with $P \leq 0.05$) include the following: (a) The allometric slope for reptiles (0.889) is greater than that for mammals (0.734), which is greater than that for birds (0.681); (b) the slope for eutherian mammals (0.772) is greater than that for marsupial mammals (0.590); (c) among families of birds, slopes do not differ but elevations (intercepts) do, with passerine and procellariid birds having relatively high FMRs and gallinaceous birds having low FMRs; (d) Scleroglossan lizards have a higher slope (0.949) than do Iguanian lizards (0.793); (e) desert mammals have a higher slope (0.785) than do nondesert mammals; (f) marine birds have relatively high FMRs and desert birds have low FMRs; and (g) carnivorous mammals have a relatively high slope and carnivorous, insectivorous, and nectarivorous birds have relatively higher FMRs than do omnivores and granivores. The difference detected between passerine and nonpasserine birds reported in earlier reviews is not evident in the larger data set analyzed here. When the results are adjusted for phylogenetic effects using independent contrasts analysis, the difference between allometric slopes for marsupials and eutherians is no longer significant and the slope difference between Scleroglossan and Iguanian lizards

disappears as well, but other taxonomic differences remain significant. Possible causes of the unexplained variations in FMR that could improve our currently inaccurate FMR prediction capabilities should be evaluated, including many important groups of terrestrial vertebrates that remain under- or unstudied and such factors as reproductive, thermoregulatory, social, and predator-avoidance behavior.

CONTENTS

INTRODUCTION	248
FIELD METABOLIC RATE LITERATURE	249
PREDICTING METABOLIC RATES	259
PREDICTING FOOD REQUIREMENTS	262
WHAT DETERMINES ENERGY REQUIREMENTS?	264
<i>Taxonomic Differences</i>	265
<i>Habitat Effects</i>	267
<i>Effects of Diet</i>	267
<i>Season</i>	267
PHYLOGENETICALLY INDEPENDENT CONTRASTS: AN EXAMPLE	268
CONCLUSIONS AND RECOMMENDATIONS	270

INTRODUCTION

The rate at which a wild animal uses resources in its environment is determined primarily by its metabolic energy requirements. The need for chemical potential energy to fuel energy metabolism is the most influential aspect in determining hunger for food. Thus, daily energy needs largely determine daily feeding rate, a major determinant of the daily intake of other nutrients, including protein, vitamins, and minerals. Diet selection also plays an important role in nutrient and energy intake and feeding activity influences an animal's ecological interactions because it preys on particular plant or animal organisms and must expose itself to specific kinds and durations of predation while feeding.

The ability to measure energy requirements of free-ranging animals is a technological development that is having a major impact on the fields of animal nutrition and ecophysiology. In 1949, it was discovered that oxygen in body water was in isotopic exchange equilibrium with oxygen in exhaled CO₂, mainly because of the carbonic anhydrase present in red blood cells (82). It was realized that the washout rates of purposely-enriched isotopes of oxygen and hydrogen in an animal's body water could be used in measuring its respiratory CO₂ production—and hence energy metabolism—over relatively long periods of time. Application of this doubly labeled water (DLW) method to measure the field metabolic rates (FMR) of wild vertebrate animals has been vigorous and has yielded many insights into the physiology, nutrition,

ecology, and evolution of animals. Many new studies of FMR in terrestrial vertebrates have been published since the last reviews appeared. Here, we (a) summarize the new information, (b) provide new equations for predicting (with 95% confidence intervals) both daily energy expenditure and daily food requirement of free-living birds, mammals, and reptiles, and (c) analyze (with and without adjustments for phylogenetic effects) the allometric relationships for differences that might help explain the factors that determine the energy and food requirements of these animals. Our purposes are to provide updated equations for nutritionists, physiologists, ecologists, and conservationists to predict animal food and energy needs and to explore, through correlation analysis, possible reasons for the large variation (more than 220,000 times from the lowest, 0.23 kJ/day, to the highest, 52500 kJ/day) in the FMRs of active vertebrates.

FIELD METABOLIC RATE LITERATURE

Following the 1966 summary paper on the DLW method (82), many more publications reporting methodological refinements, validation tests, and assumption evaluations have appeared (see summaries in 98, 100, 101, 103, 143). Initial validation studies indicated that the error in the DLW method was approximately 8%, but recent refinements reduced errors in studies of captive animals to approximately 2%. In the field, uncontrolled factors and uncertainties probably increase errors to 4%.

The literature on DLW-determined FMRs has been reviewed for reptiles (99), mammals (102, 104), and birds (102, 118, 172). We summarize and review subsequent research published up to August 1998. Only references for articles not cited in previous reviews are provided here. For older references, please see Table 1, which includes the published information we are aware of on mammals, birds, and reptiles.

When more than one value for FMR and body mass was available for a species, we calculated a single weighted average using a method that reflects the amount of information available for the various cohorts studied. For example, if the mean FMR for spring only was reported in one article, but mean FMRs for the same species studied at a different site during all four seasons appeared in another article, we used the average of all five means. We did not use FMR data for neonate or juvenile reptiles, for young birds and mammals that were not self-supporting (independent of parental feeding, for example juvenile ostriches), or for animals that were seasonally inactive (hibernating mammals, overwintering reptiles). The protocol requiring only one data point per species in allometric analyses necessitates, when measurements for both adults and self-supporting juveniles are available, the use of mean body mass and FMR values that are

Table 1 Summary of field metabolic rates (FMR) in kilojoules per day measured with doubly labeled water in free-living mammals, birds, and reptiles^a

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
Mammals							
<i>Pipistrellus pipistrellus</i>	Pipistrelle	7.3	29.3	Ch	ND	I	104
<i>Plecotus auritus</i>	Brown long-eared bat	8.5	27.6	Ch	ND	I	145
<i>Myotis lucifugus</i>	Little brown bat	9.0	29.9	Ch	ND	I	79
<i>Gerbillus henleyi</i>	Northern pygmy gerbil	9.3	26.5	Ro	D	G	39
<i>Tarsipes rostratus</i>	Honey possum	9.9	34.4	Tr	ND	N	115
<i>Anoura caudifer</i>	Flower-visiting bat	11.5	51.9	Ch	ND	N	63
<i>Macrotus californicus</i>	Big-eared bat	13.0	21.5	Ch	D	I	102
<i>Peromyscus crinitus</i>	Cactus mouse	13.4	39.3	Ro	D	O	102
<i>Mus domesticus</i>	Wild house mouse	15.1	47.1	Ro	D	O	97, 104
<i>Clethrionomys rutilus</i>	Bank vole	16.0	57.6	Ro	ND	H	102
<i>Sminthopsis crassicaudata</i>	Narrow-footed marsup. mouse	16.6	68.6	Da	ND	I	102
<i>Perognathus formosus</i>	Long-tailed pocket mouse	17.9	45.2	Ro	D	G	102
<i>Peromyscus maniculatus</i>	Deer mouse	17.9	53.4	Ro	D	O	61
<i>Peromyscus leucopus</i>	White-footed deer mouse	19.2	41.4	Ro	ND	O	95, 102
<i>Microtus arvalis</i>	Meadow mouse	20.0	90.0	Ro	ND	O	104
<i>Eremitalpa namibensis</i>	Namib Desert golden mole	20.7	12.5	In	D	I	140
<i>Eptesicus fuscus</i>	Big brown bat	20.8	43.6	Ch	ND	I	80
<i>Gerbillus allenbyi</i>	Allenby's gerbil	22.8	35.6	Ro	D	G	104
<i>Clethrionomys glareolus</i>	Bank vole	23.4	88.0	Ro	ND	H	104
<i>Microtus agrestis</i>	Field vole	26.8	77.8	Ro	ND	H	86, 104
<i>Gerbillus pyramidum</i>	Greater Egyptian gerbil	31.8	45.2	Ro	D	G	104
<i>Pseudomys albocinereus</i>	Australian native mouse	32.6	62.2	Ro	ND	O	102
<i>Antechinus stuartii</i>	Brown antechinus	33.0	86.4	Da	ND	I	104
<i>Phascogale calura</i>	Wambenger	33.5	61.9	Da	ND	C	104
<i>Dipodomys merriami</i>	Merriam's kangaroo rat	34.3	47.6	Ro	D	G	102, 104

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Microtus pennsylvanicus</i>	Meadow vole	36.9	115	Ro	ND	H	12
<i>Acomys cahirinus</i>	Common spiny mouse	38.3	51.8	Ro	D	O	102
<i>Sekeetamys calurus</i>	Bushy-tailed jird	41.2	44.0	Ro	D	O	102
<i>Microgale dobsoni</i>	Shrew-tenrec	42.6	77.1	In	ND	I	146
<i>Microgale talazaci</i>	Shrew-tenrec	42.8	66.5	In	ND	I	146
<i>Acomys russatus</i>	Golden spiny mouse	45.0	47.8	Ro	D	O	102
<i>Lemmus trimucronatus</i>	Brown lemming	55.2	201	Ro	ND	H	102
<i>Dipodomys microps</i>	Chisel-tooth kangaroo rat	57.1	84.5	Ro	D	O	102
<i>Praomys natalensis</i>	Multi-mammate mouse	57.3	86.6	Ro	ND	O	102
<i>Antechinus swainsonii</i>	Broad-footed marsup. mouse	62.6	150	Da	ND	I	102
<i>Meriones crassus</i>	Jird	69.2	65.0	Ro	D	G	39
<i>Phyllostomus hastatus</i>	Spear-nosed bat	80.8	146	Ch	ND	I	78
<i>Arvicola terrestris</i>	Water vole	85.8	119	Ro	ND	H	102
<i>Ammospermophilus leucurus</i>	Antelope ground squirrel	87.0	88.0	Ro	D	O	102
<i>Tamias striatus</i>	Eastern chipmunk	96.3	143	Ro	ND	O	102
<i>Thomomys bottae</i>	Botta's pocket gopher	104	130	Ro	ND	H	102
<i>Petaurus breviceps</i>	Sugar glider	124	173	Pt	ND	O	102
<i>Gymnobelideus leadbeateri</i>	Leadbeater's possum	125	226	Pt	ND	O	102
<i>Psammomys obesus</i>	Fat sand rat	170	165	Ro	D	H	104
<i>Spermophilus saturatus</i>	Golden-mantled ground sqrl.	214	226	Ro	ND	H	104
<i>Isodon auratus</i>	Golden bandicoot	333	285	Pe	ND	O	16
<i>Spermophilus parryi</i>	Arctic ground squirrel	630	817	Ro	ND	O	104
<i>Bassariscus astutus</i>	Ring-tailed cat	752	472	Ca	D	C	26
<i>Potorous tridactylus</i>	Long-nosed potoroo	825	517	Ma	ND	H	157
<i>Vulpes cana</i>	Blanford's fox	972	642	Ca	D	C	104
<i>Petauroides volans</i>	Greater glider	995	520	Pt	ND	H	104
<i>Pseudocheirus peregrinus</i>	Ring-tail possum	1,000	615	Pt	ND	H	96

(Continued)

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Bettongia penicillata</i>	Short-nosed rat kangaroo	1,100	593	Ma	ND	H	104
<i>Isoodon obesulus</i>	Short-nosed brown bandicoot	1,230	644	Pe	ND	O	106
<i>Vulpes macrotis</i>	Kit fox	1,480	1,180	Ca	D	C	53
<i>Lepus californicus</i>	Black-tailed jackrabbit	1,800	1,300	La	D	H	102
<i>Setonix brachyurus</i>	Quokka	1,900	548	Ma	ND	H	102
<i>Vulpes velox</i>	Swift fox	2,100	1,780	Ca	ND	C	34
<i>Aepyprymnus rufescens</i>	Rufous rat kangaroo	2,860	1,430	Ma	ND	H	104
<i>Tachyglossus aculeatus</i>	Echidna	2,860	875	Ta	ND	I	104
<i>Marmota flaviventris</i>	Yellow-bellied marmot	3,190	2,430	Ro	ND	H	138
<i>Bradypus variegatus</i>	Three-toed sloth	4,150	545	Xe	ND	H	117
<i>Macropus eugenii</i>	Tammar wallaby	4,380	1,150	Ma	ND	H	102
<i>Thylogale billiardieri</i>	Red-bellied wallaby	5,980	1,630	Ma	ND	H	102, 120
<i>Alouatta palliata</i>	Mantled howler monkey	7,330	2,580	Pr	D	H	102
<i>Phascolarctos cinereus</i>	Koala	7,520	1,710	Ph	ND	H	43, 77, 102
<i>Proteles cristatus</i>	Aardwolf	8,540	1,850	Ca	D	I	168
<i>Petrogale xanthopus</i>	Rock wallaby	8,900	2,210	Ma	ND	H	104
<i>Lyacon pictus</i>	African wild dog	25,170	15,300	Ca	D	C	54
<i>Arctocepalus gazella</i>	Antarctic fur seal	34,600	23,000	Pi	M	C	6, 104
<i>Canis lupus</i>	Timber wolf	37,300	17,700	Ca	ND	C	104
<i>Arctocepalus galapagoensis</i>	Galapagos fur seal	37,400	4,780	Pi	M	C	104
<i>Odocoileus hemionus</i>	Mule deer	39,100	18,000	Ar	ND	H	102
<i>Antidorcas marsupialis</i>	Springbok	43,300	24,100	Ar	D	H	113
<i>Macropus giganteus</i>	Eastern grey kangaroo	44,500	8,670	Ma	ND	H	102
<i>Callorhinus ursinus</i>	Northern fur seal	51,100	36,100	Pi	M	C	102

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Zalophus californianus</i>	California sea lion	78,000	38,600	Pi	M	C	104
<i>Neophoca cinerea</i>	Australian sea lion	83,500	39,500	Pi	M	C	104
<i>Phoca vitulina</i>	Common seal	99,000	52,500	Pi	M	C	135
Birds							
<i>Archilochus alexandri</i>	Black-chinned hummingbird	3.7	29.1	Ap	TeF	N	133
<i>Calypte anna</i>	Anna's hummingbird	4.5	31.8	Ap	CS	N	134
<i>Thalurania colombica</i>	Crowned woodnymph	4.9	37.9	Ap	TF	N	162
<i>Auriparus flaviceps</i>	Verdin	6.6	30.0	Pa	D	I	162
<i>Chalybura urochrysia</i>	Bronze-tailed plumeleteer	7.2	57.9	Ap	TF	N	162
<i>Malurus cyaneus</i>	Superb blue wren	8.3	34.2	Pa	TeF	I	160
<i>Lampornis clemenciae</i>	Blue-throated hummingbird	8.8	81.7	Ap	TeF	N	133
<i>Zosterops lateralis</i>	Grey-breasted silvereye	9.5	41.7	Pa	EF	F	102
<i>Parus ater</i>	Coal tit	9.5	47.4	Pa	CF	I	118
<i>Nectarinia violacea</i>	Orange-breasted sunbird	9.5	66.2	Pa	FY	N	167
<i>Acanthorhynchus tenuirostris</i>	Eastern spinebill	9.7	53.0	Pa	TeF	N	161
<i>Troglodytes aedon</i>	House wren	10.6	60.8	Pa	TeF	I	42
<i>Parus cristatus</i>	Crested tit	11.1	40.6	Pa	CF	I	118
<i>Parus montanus</i>	Willow tit	11.4	44.1	Pa	CF	I	23, 118
<i>Parus caeruleus</i>	Blue tit	11.5	64.0	Pa	CF	I	148
<i>Eremiornis carteri</i>	Spinifexbird	12.0	51.5	Pa	D	I	1
<i>Parus cinctus</i>	Siberian tit	12.8	51.4	Pa	CF	I	23
<i>Ficedula hypoleuca</i>	Pied flycatcher	13.5	65.8	Pa	OW	I	91, 93
<i>Riparia riparia</i>	Sand martin	14.3	81.7	Pa	TM	I	102
<i>Muscicapa striata</i>	Pacific swallow	14.4	52.0	Pa	TeF	I	22
<i>Hirundo tahitica</i>	Spotted flycatcher	14.4	64.9	Pa	TF	I	102, 148
<i>Phylidonyris pyrrhoptera</i>	Crescent honeyeater	14.6	75.9	Pa	TeF	N	161
<i>Ficedula albicollis</i>	Collared flycatcher	15.9	78.6	Pa	TeF	I	92
<i>Phylidonyris novaehollandiae</i>	New Holland honeyeater	17.3	77.6	Pa	TeF	N	161
<i>Parus major</i>	Great tit	18.0	97.4	Pa	TeF	O	109, 151

(Continued)

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Erithacus rubecula</i>	Robin	18.7	71.3	Pa	TeF	I	148
<i>Passerculus sandwichensis</i>	Savannah sparrow	18.7	80.4	Pa	SM	O	102, 165, 171
<i>Delichon urbica</i>	House martin	19.0	79.8	Pa	TM	I	102
<i>Junco phaeonotus</i>	Yellow-eyed junco	19.5	73.8	Pa	TM	O	172
<i>Junco hyemalis</i>	Dark-eyed junco	19.6	76.6	Pa	TM	O	163
<i>Tachycineata bicolor</i>	Tree swallow	20.2	209	Pa	TM	I	118
<i>Hirundo rustica</i>	Barn swallow	20.4	95.8	Pa	TM	I	35, 102, 158
<i>Prunella modularis</i>	Dunnock	21.2	86.0	Pa	TeF	I	22
<i>Phainopepla nitens</i>	Phainopepla	22.7	79.1	Pa	D	O	102
<i>Cormobates leucophaeus</i>	White-throated treecreeper	23.7	81.4	Pa	TeF	I	160
<i>Oenanthe oenanthe</i>	Northern wheatear	24.3	91.4	Pa	TM	I	90, 147
<i>Pyrrhula pyrrhula</i>	Bullfinch	25.1	88.0	Pa	TeF	G	22
<i>Philetairus socius</i>	Sociable weaver	25.5	48.7	Pa	D	O	170
<i>Sialia mexicana</i>	Western bluebird	27.4	95.0	Pa	TeF	I	89
<i>Melospittacus undulatus</i>	Budgerigar	27.9	59.1	Ps	D	O	172
<i>Mirafra erythrochlamys</i>	Dune lark	28.5	64.3	Pa	D	O	172
<i>Merops viridis</i>	Blue-throated bee-eater	34.3	85.3	Co	TF	I	102, 148
<i>Oceanites oceanus</i>	Wilson's storm-petrel	42.3	119	Pr	M	C	102
<i>Oceanodroma leucorhoa</i>	Leach's storm-petrel	45.9	118	Pr	M	C	118
<i>Mimus polyglottos</i>	Mockingbird	47.6	121	Pr	DF	O	102
<i>Progne subis</i>	Purple martin	49.0	163	Pa	DF	I	102
<i>Actitis hypoleucos</i>	Common sandpiper	51.6	146	Ch	M	C	148
<i>Calidris alba</i>	Sanderling	52.0	141	Ch	M	C	24
<i>Neophema petrophila</i>	Rock parrot	62.8	106	Ps	D	O	172
<i>Cinclus cinclus</i>	Dipper	63.7	196	Pa	TM	I	18, 118
<i>Charadrius hiaticula</i>	Ringed plover	74.8	302	Ch	M	C	148
<i>Ceryle rudis</i>	Pied kingfisher	76.0	210	Co	TF	C	118
<i>Sturnus vulgaris</i>	Starling	78.7	269	Pa	DF	O	102
<i>Aethia pusilla</i>	Least auklet	80.3	350	Ch	M	C	118, 125

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Melanerpes formicivorus</i>	Acorn woodpecker	82.0	195	Pi	OW	O	172
<i>Geophaps plumifera</i>	Spinifex pigeon	87.0	76.0	Cl	D	G	169
<i>Turdus merula</i>	Blackbird	96.0	179	Pa	TeF	I	22
<i>Sterna paradisaea</i>	Arctic tern	101	335	Ch	M	C	152
<i>Arenaria interpres</i>	Ruddy turnstone	108	352	Ch	M	C	131
<i>Pelecanoides georgicus</i>	South Georgia diving petrel	109	464	Pr	M	C	118
<i>Sterna hirundo</i>	Common tern	127	343	Ch	M	C	72
<i>Pelecanoides urinatrix</i>	Common diving petrel	137	557	Pr	M	C	118
<i>Callipepla gambelii</i>	Gambel's quail	145	90.8	Ga	D	O	102
<i>Barnardius zonarius</i>	Port Lincoln parrot	145	189	Ps	D	O	172
<i>Pachyptila desolata</i>	Antarctic prion	149	391	Pr	M	C	149
<i>Alle alle</i>	Dovkie	164	696	Ch	M	C	172
<i>Ptychoramphus aleuticus</i>	Cassin's auklet	174	413	Ch	M	C	65
<i>Sterna fuscata</i>	Sooty tern	187	241	Ch	M	C	102
<i>Ammoperdix heyi</i>	Sand partridge	190	148	Ga	D	O	102
<i>Anous stolidus</i>	Brown noddy	195	352	Ch	M	C	102
<i>Falco tinnunculus</i>	Eurasian kestrel	211	341	Fa	TM	C	67, 84, 118
<i>Cacatua roseicapilla</i>	Galah	307	349	Ps	D	O	172
<i>Phaethon lepturus</i>	White-tailed tropicbird	370	777	Pe	M	C	127
<i>Cephus grylle</i>	Black guillemot	380	860	Ch	M	C	87, 118
<i>Puffinus pacificus</i>	Wedge-tailed shearwater	384	614	Pr	M	C	102
<i>Rissa tridactyla</i>	Black-legged kittiwake	386	795	Pr	M	C	102
<i>Alectoris chukar</i>	Chukar	395	260	Ga	D	O	102
<i>Uria lomvia</i>	Thick-billed murre	834	1,480	Ch	M	C	118
<i>Uria aalga</i>	Guillemot	940	1,870	Ch	M	C	172
<i>Eudyptula minor</i>	Little penguin	1,050	1,050	Sp	M	C	46, 118
<i>Sula sula</i>	Red-footed booby	1,070	1,220	Pe	M	C	7
<i>Centrocercus urophasianus</i>	Sage grouse	2,500	1,540	Ga	D	G	154
<i>Morus capensis</i>	Cape gannet	2,580	3,380	Pe	M	C	172
<i>Diomedea immutabilis</i>	Laysan albatross	3,070	1,330	Pr	M	C	130
<i>Spheniscus demersus</i>	Jackass penguin	3,170	1,950	Sp	M	C	102

(Continued)

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Sula bassanus</i>	Northern gannet	3,210	4,870	Pe	M	C	172
<i>Diomedea chrysostoma</i>	Grey-headed albatross	3,710	2,390	Pr	M	C	118
<i>Pygoscelis antarctica</i>	Chinstrap penguin	3,790	5,600	Sp	M	C	94
<i>Macronectes giganteus</i>	Giant petrel	3,890	4,330	Pr	M	C	124
<i>Pygoscelis adeliae</i>	Adelie penguin	3,990	3,790	Sp	M	C	25, 36, 119
<i>Eudyptes chrysolophus</i>	Macaroni penguin	4,270	2,950	Sp	M	C	172
<i>Pygoscelis papua</i>	Gentoo penguin	6,170	4,650	Sp	M	C	47, 172
<i>Diomedea exulans</i>	Wandering albatross	8,420	3,350	Pr	M	C	102
<i>Aptenodytes patagonicus</i>	King penguin	12,900	7,410	Sp	M	C	75
<i>Struthio camelus</i>	Ostrich	88,300	18,000	St	D	O	172
Reptiles							
<i>Mesalina olivieri</i>	Sand lizard	1.1	0.29	La	SA	I	156
<i>Rhoptropus afer</i>	Namib Desert gecko	2.6	0.23	Ge	D	I	121
<i>Urosaurus nigricaudus</i>	Black-tailed brush lizard	3.2	1.38	Ph	SC	I	60
<i>Uta stansburiana</i>	Side-blotched lizard	3.2	0.67	Ph	D	I	60, 101
<i>Pedioplanis lineocellata</i>	Spotted sand lizard	3.3	0.54	La	D	I	111
<i>Heliobolus lugubris</i>	Bushveld lizard	3.8	0.80	La	D	I	111
<i>Meroles anchietae</i>	Namib Desert dune lizard	4.0	0.60	La	D	O	137
<i>Cnemidophorus hyperythrus</i>	Orangethroat whiptail	4.3	1.13	Te	SC	I	60, 68
<i>Acanthodactylus pardalis</i>	Sand lizard	4.5	0.23	La	SA	I	156
<i>Sceloporus graciosus</i>	Sagebrush lizard	5.0	0.82	Ph	SC	I	33
<i>Sceloporus virgatus</i>	Striped plateau lizard	6.3	1.06	Ph	SC	I	88
<i>Callisaurus draconoides</i>	Zebra-tailed lizard	7.1	1.12	Ph	D	I	69
<i>Podarcis lilfordi</i>	Lacertid lizard	7.4	1.49	La	SC/ME	I	19
<i>Sceloporus variabilis</i>	Rosebelly lizard	7.7	1.92	Ph	TR	I	10

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Chalcides sexlineatus</i>	Gran Canary skink	7.8	0.72	Sc	STR	I	20
<i>Pryodactylus hasselquistii</i>	Negev Desert gecko	9.1	1.2	Ge	D	I	108
<i>Varanus caudolineatus</i>	Goanna/monitor lizard	10.4	3.0	Va	SA/SC	C	150
<i>Galloti atlantica</i>	Agamid lizard	11.9	1.5	La	STR	H	155
<i>Sceloporus occidentalis</i>	Western fence lizard	12.1	1.8	Ph	SC	I	11, 13
<i>Cnemidophorus tigris</i>	Western whiptail	16.5	4.1	Te	D	I	2, 3
<i>Pachydactylus bibronii</i>	Birbon's gecko	16.6	2.2	Ge	D	I	112
<i>Sceloporus jarrovi</i>	Yarrow's spiny lizard	16.6	1.9	Ph	SC	I	10, 83
<i>Mabuya striata</i>	Striped skink	19.5	2.9	Sc	D	I	112
<i>Thamnophis sirtalis</i>	Common garter snake	22.0	5.2	Co	SC	C	129
<i>Phrynosoma platyrhinos</i>	Desert horned lizard	23.0	2.7	Ph	D	I	21
<i>Elgaria multicarinatus</i>	Southern alligator lizard	25.3	2.0	An	SC	I	70
<i>Lacerta viridis</i>	Common lizard	25.5	5.8	La	TE	I	17
<i>Galloti galloti</i>	Agamid lizard	25.6	4.6	La	STR	H	155
<i>Microlophus albemariensis</i>	Lava lizard	28.2	3.3	Tr	IT	I	99
<i>Ctenophorus nuchalis</i>	Central netted dragon	36.8	9.6	Ag	D	I	105
<i>Galloti stehlini</i>	Giant agamid lizard	47.3	7.9	La	STR	H	155
<i>Dipsosaurus dorsalis</i>	Desert iguana	52.5	6.5	Ig	D	H	85
<i>Agama impalearis</i>	Bibron's agama	54.4	16.8	Ag	D	I	173
<i>Angolosaurus skoogi</i>	Skoog's lizard	57.4	3.0	Gr	D	H	107
<i>Varanus acanthurus</i>	Ridge-tailed monitor	60.0	3.7	Va	TE	C	41
<i>Varanus scalaris</i>	Goanna/monitor lizard	66.4	7.8	Va	EW	C	29
<i>Vipera aspis</i>	European viper	67.2	6.3	Vi	TE	C	17
<i>Crotalus lepidus</i>	Mottled rock rattlesnakes	109	4.7	Vi	SC	C	9
<i>Masticophis flagellum</i>	Coachwhip	124	11.7	Co	D	C	139
<i>Crotalus cerastes</i>	Sidewinder	129	5.0	Vi	D	C	139

(Continued)

Table 1 (Continued)

Species	Common name	Mass (g)	FMR (kJ/day)	Taxon ^b	Habitat ^c	Diet ^d	Reference
<i>Coluber constrictor</i>	Racer	132	12.8	Co	W	C	132
<i>Sauromalus obesus</i>	Chuckwalla	167	15.7	Ig	D	H	122
<i>Chlamydosaurus kingii</i>	Frillneck lizard	635	52.4	Ag	W	I	28
<i>Iguana iguana</i>	Green iguana	860	60.1	Ig	SA	H	153
<i>Tupinambis teguixin</i>	Tegu	1,170	214	Te	TR	C	57
<i>Varanus rosenbergi</i>	Goanna/monitor lizard	1,180	100	Va	EW	C	56
<i>Varanus mertensi</i>	Merten's water monitor	1,210	143	Va	M	C	31
<i>Varanus gouldii</i>	Sand monitor	1,320	233	Va	TRW	C	30
<i>Varanus panoptes</i>	Goanna/monitor	1,350	180	Va	TRW/RI	C	30
<i>Amblyrhynchus cristatus</i>	Galapagos marine iguana	1,610	91.2	Ig	M	H	123
<i>Gopherus agassizii</i>	Desert tortoise	2,120	42.9	Ts	D	H	64, 114, 128
<i>Varanus bengalensis</i>	Bengal monitor	2,560	393	Va	TR	C	40
<i>Varanus salvator</i>	Goanna/monitor lizard	7,530	906	Va	SA/TR	C	40
<i>Varanus giganteus</i>	Perenties	7,700	807	Va	DTR	C	40, 59
<i>Varanus komodensis</i>	Komodo dragon	45,200	2,430	Va	TR	C	58

^aBody mass and FMR values are means or weighted means where more than one study per species is available.

^bMarsupial (marsup.) mammals: Squirrel (sqr.); Tr, Tarsipedidae; Da, Dasyuridae; Pt, Petauridae; Pe, Peramelidae; Ma, Macropodidae; Ph, Phascolarctidae. Eutherian mammals: Ch, Chiroptera; Ro, Rodentia; In, Insectivora; Ca, Carnivora; La, Lagomorpha; Xe, Xenarthra; Pr, Primates; Pi, Pinniped; Ar, Artiodactyla. Monotreme: Ta, Tachyglossidae. Birds: Ap, Apodiformes; Pa, Passeriformes; Ps, Psittaciformes; Co, Coraciiformes; Pr, Procellariiformes; Ch, Charadriiformes; Pi, Piciformes; Cl, Columbiformes; Ga, Galliformes; Fa, Falconiformes; Pe, Pelicaniformes; Sp, Sphenisciformes; St, Struthioniformes. Reptiles: Squamata (families): Ag, Agamidae; An, Anguillidae; Co, Colubridae; Ge, Gekkonidae; Gr, Gerrhosauridae; Ig, Iguanidae; La, Lacertidae; Ph, Phrynosomatidae; Sc, Scincidae; Te, Teiidae; Tr, Tropiduridae; Va, Varanidae; Vi, Viperidae. Testudines: Ts, Testudinidae.

^cHabitat: ND, nondesert; D, desert; M, marine; TeF, temperate forest; CS, chaparral scrub; TF, tropical forest; EF, eucalypt forest; CF, coniferous forest; FY, fynbos; OW, oak woodland; TM, temperate meadow; SM, salt marsh; DF, deciduous forest; SA, semi-arid; A, arid; SC, scrub; TR, tropical; STR, subtropical; DTR, dry tropical; TE, temperate; F, forest; EW, eucalypt woodland; TRW, tropical woodland; RI, riparian; W, woodland; IT, inter-tidal; ME, mediterranean.

^dDiet: I, insectivore; G, granivore; N, nectarivore; O, omnivore; H, herbivore; C, carnivore; F, frugivore.

intermediate. Thus, values for some species in Table 1 may seem to be in error, but they are correct for the applications used in this study.

FMR data are given in units of kilojoules per day. When necessary, we converted reported FMR results from CO₂ to kilojoules using the factors 21.7 kJ per liter of CO₂ for herbivores, 20.8 for frugivores, 21.9 for granivores, 25.7 for insectivores, and 25.8 for carnivores (100, 116). We assumed that authors corrected their FMR results to a 24-h average (144). Categorization of habitat and diet for each species was based on information given in the article, or from field guides. Habitats of mammals were determined only as desert, nondesert, or marine, but habitats of reptiles and birds were resolved into more detailed categories. For reptiles, the term desert refers to an area that receives less than 250 mm of rain per year, and semi-arid usually refers to a scrub-type habitat that receives more than 250 mm of rain per year.

PREDICTING METABOLIC RATES

One of the most useful applications of allometric equations (\log_{10} vs \log_{10} regressions) for food and energy requirements of animals is in predicting the needs of species that have not yet been studied by using DLW. Commonly, such predictions are used in (a) hypotheses involving species that are expected to differ from typical (or predicted) animals in a given taxon, (b) community or ecosystem-level studies of ecological energetics, (c) conservation and management efforts to estimate population food needs, and (d) evolutionary studies such as those concerning the food requirements of warm-blooded vs cold-blooded dinosaurs.

Allometric analyses may be done using at least three different methods: linear least-squares regression of \log_{10} -transformed variables, reduced major axis regression, and phylogenetically independent contrasts analysis. For making predictions, we used the linear least-squares regression method, for two main reasons. First, this method yields equations that can be used to predict FMR values directly, and the other methods do not. Second, it yields statistical parameters that allow calculation of confidence intervals for predicted values, and the other methods do not.

We calculated allometric regressions for all mammals, all birds, and all reptiles listed in Table 1, and then for groups within each of these taxonomic classes, based either on smaller taxonomic categories, habitat, or diet. The equation (in power form) for every regression that was statistically significant ($P < 0.05$ via an F test for significance of the regression) is shown in Table 2, along with the regression statistics r^2 (coefficient of determination) and P (probability value from an F test) for that equation. Also shown are the values needed to calculate the 95% confidence interval (CI) of any FMR predicted by solving that

Table 2 Summary of allometric equations for field metabolic rates (FMR) of free-living mammals, birds, and reptiles^a

Group	<i>a</i>	<i>b</i>	<i>n</i>	<i>r</i> ²	<i>P</i>	Statistics for 95% CI of prediction				Equation
						Mean log <i>x</i>	<i>c</i>	<i>d</i>	<i>e</i>	
Mammals										
All mammals	4.82	0.734	79	0.950	<0.0001	2.481	0.422	1.013	0.008	1
Eutherians	4.21	0.772	58	0.959	<0.0001	2.364	0.423	1.017	0.010	2
Marsupials	10.1	0.59	20	0.977	<0.0001	2.772	0.200	1.050	0.051	3
Chiroptera	6.49	0.681	7	0.781	0.008	1.164	0.365	1.143	1.286	4
Carnivora	1.67	0.869	7	0.918	0.001	3.609	0.504	1.143	0.350	5
Rodentia	5.48	0.712	30	0.848	<0.0001	1.684	0.332	1.003	0.125	6
Diprotodont marsupials	8.67	0.609	14	0.973	<0.0001	3.126	0.216	1.071	0.090	7
Desert mammals	3.18	0.785	25	0.963	<0.0001	2.174	0.366	1.040	0.033	8
Terrestrial mesic mammals	8.18	0.639	48	0.947	<0.0001	2.355	0.336	1.021	0.018	9
Desert rodents	9.68	0.487	15	0.763	<0.0001	1.519	0.207	1.067	0.618	10
Mesic rodents	7.38	0.694	15	0.912	<0.0001	1.849	0.305	1.067	0.179	11
Carnivores	2.23	0.85	13	0.956	<0.0001	3.960	0.448	1.077	0.073	12
Granivores	11.1	0.414	6	0.860	0.008	1.409	0.153	1.167	2.314	13
Herbivores	7.94	0.646	26	0.914	<0.0001	2.995	0.435	1.038	0.036	14
Insectivores	6.98	0.622	14	0.890	<0.0001	1.685	0.453	1.071	0.092	15
Omnivores	6.03	0.678	18	0.876	<0.0001	1.808	0.310	1.056	0.190	16
Birds										
All birds	10.5	0.681	95	0.938	<0.0001	1.950	0.328	1.011	0.012	17
Passerines	10.4	0.68	40	0.724	<0.0001	1.268	0.225	1.025	0.375	18
Charadriiformes	8.13	0.77	13	0.878	<0.0001	2.202	0.270	1.077	0.496	19
Procellariiformes	18.4	0.599	11	0.907	<0.0001	2.671	0.381	1.091	0.144	20

Sphenisciformes	4.53	0.795	7	0.808	<0.01	3.605	0.357	1.143	1.555	21
Galliformes	0.851	0.959	4	0.994	<0.005	2.609	0.216	1.250	1.073	22
Pelecaniformes	4.54	0.844	4	0.939	<0.05	3.129	0.484	1.250	1.829	23
Psittaciformes	5.05	0.735	4	0.999	<0.001	1.973	0.061	1.250	1.643	24
Apodiformes	5.54	1.212	5	0.979	<0.003	0.742	0.102	1.200	10.520	25
Marine birds	14.25	0.659	36	0.923	<0.0001	2.721	0.298	1.028	0.050	26
Temperate forest birds	15.9	0.543	16	0.801	<0.001	1.203	0.183	1.063	0.718	27
Desert birds	6.35	0.671	15	0.957	<0.0001	2.089	0.330	1.067	0.067	28
Temperate meadow birds	18.7	0.548	9	0.697	0.005	1.461	0.339	1.111	0.909	29
Insectivores	9.70	0.705	26	0.754	<0.0001	1.254	0.229	1.038	0.547	30
Omnivores	9.36	0.628	18	0.911	<0.0001	1.927	0.373	1.056	0.077	31
Reptiles										
All reptiles	0.196	0.889	55	0.945	<0.0001	1.726	0.459	1.018	1.017	32
All lizards	0.190	0.916	48	0.963	<0.0001	1.668	0.400	1.021	0.018	33
Iguanians	0.301	0.793	17	0.948	<0.0001	1.502	0.344	1.059	0.087	34
Scleroglossans	0.163	0.949	31	0.971	<0.0001	1.760	0.415	1.032	0.022	35
Varanidae	0.208	0.915	11	0.966	<0.0001	2.986	0.433	1.091	0.089	36
Lacertidae	0.158	1.009	10	0.870	<0.0001	0.884	0.477	1.100	0.444	37
Iguanidae	0.291	0.782	4	0.999	0.0003	2.521	0.074	1.250	0.729	38
Phrynosomatidae	0.454	0.542	9	0.666	0.007	0.877	0.289	1.111	1.417	39
Desert lizards	0.177	0.935	16	0.876	<0.0001	1.157	0.428	1.062	0.220	40
Herbivores	0.232	0.813	8	0.939	<0.0001	2.000	0.406	1.125	0.261	41

^aThe equations are in the power form: $\text{kJ/day} = a(g \text{ body mass})^b$; n , number of species; r^2 , coefficient of determination; P , probability of a statistically significant regression (via F-test); and mean $\log x$, c , d , and e are values for use in the following equation for calculation of 95% confidence intervals of the prediction:

$$95\% \text{ CI}_{\log(\text{predicted kJ/day})} = \log(\text{predicted kJ/day}) \pm c\{d + e[\log(g \text{ body mass}) - (\text{mean log } x)]^2\}^{0.5}.$$

equation for a given body mass. The equation for 95% CI of the prediction is $95\% \text{ CI}_{\log(\text{FMR})} = \log(\text{FMR}) \pm c\{d + e[\log(\text{mass}) - \text{mean } \log(\text{mass})]^2\}^{0.5}$.

As an example of how to use these equations, we show the results of predicting the FMR \pm 95% CI of the prediction for a spotted hyena weighing 62 kg. Using Equation 1 in Table 2, we get $4.82 (62,000)^{0.734} = 15,873 \approx 15,900$ kJ/day as the predicted FMR. For the 95% CI, we get $\log(15,900) \pm 0.422\{1.013 + 0.008[\log(62,000) - 2.481]^2\}^{0.5}$, or $4.201 \pm 0.422[1.013 + 0.008(5.343)]^{0.5}$, or $4.201 \pm 0.422(1.027)$, or $4.201 + 0.434 = 4.635$, and $4.201 - 0.434 = 3.767$. The anti-logs of these values are 43,100 kJ/day and 5,850 kJ/day, which are 271% and 37%, respectively, of the predicted FMR. If these equations are used to predict FMRs for animals with body masses that fall outside the range of masses used to derive the equations (see Table 1), 95% CI will be larger (extrapolation vs interpolation). The relatively large CIs of the predicted values are due to the amount of residual variation around the allometric regression lines (Figure 1), despite the high r^2 values (Table 2). We recommend that colleagues calculate predicted FMR and 95% CI values using the equation that applies most specifically to their animal of interest.

The literature contains additional allometric equations for predicting FMR for a variety of bird subgroups not addressed here. These include small birds (58 species), $\text{kJ/day} = 15.94(\text{g})^{0.53}$ (22); aerially foraging birds with nestlings (seven species of Hirundines), $\text{kJ/day} = 21.9(\text{g})^{0.53}$ (166); ground-foraging, fly-catching, and piscivorous birds with nestlings (11 species), $\text{kJ/day} = 7.76(\text{g})^{0.75}$ (166); incubating birds (17 species), $\text{kJ/day} = 12.93(\text{g})^{0.61}$ (148); seabirds (23 species), $\text{kJ/day} = 12.0(\text{g})^{0.667}$ (15); cold-water seabirds (5 species), $\text{kJ/day} = 15.6(\text{g})^{0.646}$ (15); warm-water seabirds (16 species), $\text{kJ/day} = 9.16(\text{g})^{0.646}$ (15); seabirds using flapping flight (10 species), $10.3(\text{g})^{0.726}$ (15); seabirds not using flapping flight (13 species), $\text{kJ/day} = 6.63(\text{g})^{0.726}$ (15); cold-water seabirds using flapping flight (8 species), $\text{kJ/day} = 11.5(\text{g})^{0.727}$ (15); hovering nectarivores (five species of hummingbirds), $\text{kJ/day} = 5.61(\text{g})^{1.21}$ (161); perching nectarivores (three species of honeyeaters), $\text{kJ/day} = 11.0(\text{g})^{0.697}$ (161); birds during parental care (30 species), $\text{kJ/day} = 13.8(\text{g})^{0.65}$ (84); and fledgling birds (11 species), $\text{kJ/day} = 4.58(\text{g})^{0.76}$ (136).

PREDICTING FOOD REQUIREMENTS

The ration of food, in dry matter units (grams/day), that an animal must consume to supply the metabolizable energy it uses in a day can be estimated from its FMR. This calculation requires a factor indicating the metabolizable energy available from a gram of dry matter (DM) in the animal's diet. Fortunately, different kinds of vertebrate animals that eat a given diet have similar digestive efficiencies. For example, nectarivorous bats and birds both assimilate essentially 100% of the dry matter (sugar) in their diet. Thus, for these animals,

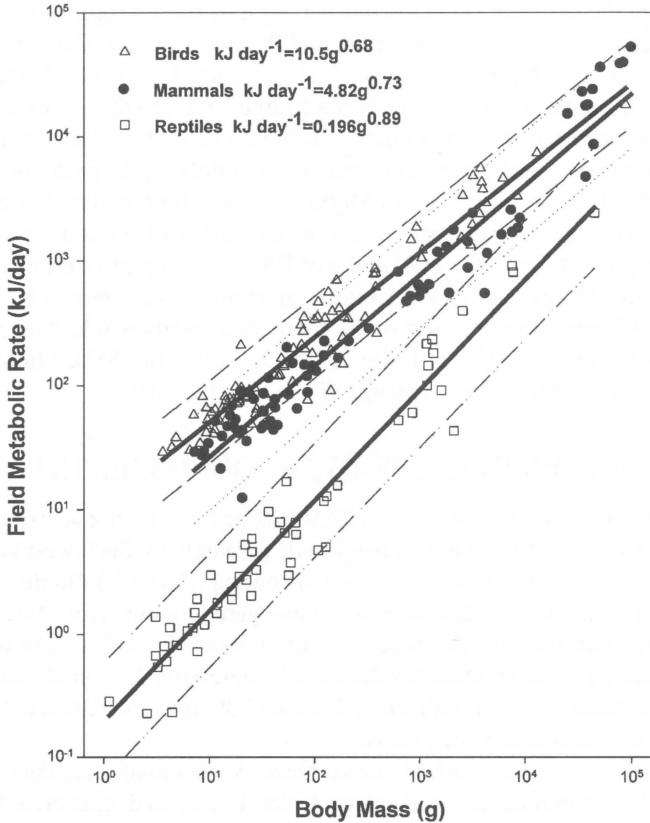


Figure 1 Allometry of field metabolic rate in terrestrial vertebrates. (Solid lines) least-squares linear regression lines for birds, mammals, and reptiles (see Equations 1, 17, and 32 in Table 2); (dashed or dotted lines) 95% confidence intervals of the prediction for each line.

daily food requirements may be estimated as their FMR, in kJ/day, divided by 16.0 kJ/g of DM, the gross energy content of mixed sugars. Energy digestibility studies done on a variety of wild vertebrates suggest the following conversion factors: mammalian insectivores, 18.7 kJ/g of DM, and bird and reptile insectivores, 18.0 kJ/g of DM (lower than mammals due to greater energy loss in uric acid); fish-eating mammals, 18.7 kJ/g of DM, and fish-eating birds, 16.2 kJ/g of DM; mammalian carnivores, 16.8 kJ/g of DM; mammalian frugivores, 6.6 kJ/g of DM; mammalian granivores, 16.9 kJ/g of DM; herbivores, 10.0 kJ/g of DM for monogastric digesters and 11.5 kJ/g of DM for ruminants and other fermentative digesters; and an estimated intermediate value of 14 kJ/g of DM for omnivores (100, 102, 110). Daily feeding rates necessary to maintain energy balance, in grams of DM consumed per day, may be estimated easily by

dividing predicted FMR (in kilojoules per day), by the appropriate dietary factor (in metabolizable kilojoules per day of DM, given above). For example, the hyena mentioned above (a carnivore) had a predicted FMR of 15,900 kJ/day, and its diet contains about 16.8 metabolizable kJ/g of DM, so its estimated food consumption is $(15,900 \text{ kJ/day} \div 16.8 \text{ kJ/g of DM}) \Rightarrow 946 \text{ g of DM/day}$. Fresh matter (FM) intake can be estimated by multiplying the grams of DM/day estimate by the ratio of grams of FM/grams of DM for the diet. For example, animal foods (insects, fish, rodents) are usually about 70% water, or 30% DM, so their ratio is about $1 \text{ g of FM}/0.30 \text{ g of DM} = 3.33 \text{ g of FM/g of DM}$, and their rate of FM intake will be 3.33 times greater than their rate of DM intake, with the difference being water in the food. Our hyena would thus consume $(946 \text{ g of DM/day} \times 3.33 \text{ g of FM/g of DM}) \Rightarrow 3150 \text{ g of FM/day}$ (a little over 3 g/kg daily) to achieve energy balance in its natural habitat.

WHAT DETERMINES ENERGY REQUIREMENTS?

The highest measured FMR to date (52,500 kJ/day in a harbor seal) is 228,000 times, or more than five orders of magnitude greater than, the lowest vertebrate FMR measured (0.23 kJ/day in two small species of lizards) (Table 1). What accounts for this huge difference in the energetic cost of living through one day? Body size (mass) differences explain most of the variation in the FMR data in Table 1. The r^2 value for the overall regression (mammals, birds, and reptiles combined) is 0.71, indicating that over 70% of the variation in log FMR is due to variation in log body mass.

After accounting only for body mass effects, variation of more than 20 times between lowest and highest still exists. A simple way to demonstrate this is to calculate predicted FMRs for a 100-g mammal, bird, and reptile using the equations in Table 2. The results are 142 kJ/day for a 100-g mammal, 242 kJ/day for a 100-g bird, and 11.8 kJ/day for a 100-g reptile (see Table 2). The bird has to use 20 times more energy to live each day than does the lizard, and the mammal pays 12 times more than the lizard. Thus, there are large differences between these three taxonomic classes of animals. The slopes (b) of the regressions for mammals ($b = 0.734$, 95% CI = 0.696–0.772), birds (0.681, 0.645–0.717), and reptiles (0.889, 0.830–0.948) all differ significantly from each other, judging by nonoverlap of 95% CIs and confirmed by analysis of covariance (ANCOVA). However, within these classes, the r^2 values in Table 2 indicate that from 93% to 95% of the variation in log FMR is explained by variation in log body mass. Thus, the second most important determinant of FMR is taxonomic class.

The higher FMRs of birds may reflect a higher cost of living than for mammals in general, which would be in accord with the significantly higher basal metabolic rates of birds (8). Or it may reflect the fact that nearly all of the bird

FMR data were gathered during the birds' breeding season, when birds can be reliably recaptured for DLW sampling. This interpretation, however, assumes that birds have higher FMRs during breeding than in other seasons. No such significant elevation of FMR during the breeding season is found in mammals studied throughout the year with DLW (see below).

Even after accounting for body mass and taxonomic class effects, variation in FMRs is still more than about six times (see scatter about the regression lines in Figure 1). Can lower taxonomic categories, or habitat effects, or diet effects account for this variation? If so, then allometric regressions calculated for these subgroups should contain less scatter and have higher r^2 values and perhaps significantly different slopes or intercepts. We use analysis of covariance (ANCOVA, using Prophet 5.0 software, copyright 1997 BBN Systems and Technologies) to test for significant differences (where $P < 0.05$) between slopes and intercepts of regression lines.

Taxonomic Differences

The FMRs of eutherian and marsupial mammals scale differently (Table 2). The slope of the log-log regression for eutherians is 0.772 (95% CI = 0.730–0.815), which is significantly higher than the value of 0.696 reported by Hayssen & Lacey (62) for basal metabolic rate (BMR) in eutherians ($P = 0.0015$) but does not differ from the reported (and theoretical) value of 0.75 (73). For marsupial mammals, the slope is 0.590 (0.545–0.635), which is significantly lower than the eutherian slope (ANCOVA $F_{1,74} = 15.1$, $P = 0.0002$) and is significantly lower ($P < 0.0001$) than the BMR slope values of 0.747 reported by Dawson & Hulbert (37) and of 0.747 reported by Hayssen & Lacey (62). The slope of marsupial FMR is also significantly different ($P < 0.001$) from both of the theoretical slopes of 0.75 and 0.67. The intercept for the eutherian regression (0.624) is lower than that of the marsupial regression (1.00), such that small eutherians (<125 g) have a relatively lower FMR, whereas larger eutherians tend to have a relatively higher FMR, than do similarly sized marsupials. The single monotreme, the echidna (*Tachyglossus aculeatus*), had a field metabolic rate within the 95% CI of the predictions for both eutherians and marsupials and was 89.3% and 96.6% of the FMR predicted for its body mass by the eutherian and marsupial equations, respectively. Although significant regressions existed for Carnivora, Chiroptera, Rodentia, and Diprodontia, there were no significant differences in scaling among any of the lower taxonomic categories (eutherian orders Carnivora, Chiroptera, Pinnipedia, Rodentia, and the marsupial superorders Dasyuromorphia and Diprodontia contained sufficient sample sizes for comparison) (ANCOVA $F_{5,56} = 2.02$, $P = 0.0895$). Regressions for Artiodactyla ($n = 2$), Insectivora ($n = 3$), Pinnipedia ($n = 6$), and Dasyuromorphia ($n = 4$) were not significant.

For all birds studied, the slope of the regression (0.681, 95% CI = 0.645–0.71) is different from the theoretical slope of 0.75 but is not different from the theoretical slope of 0.67 or the slope of 0.668 for BMR of all birds (81). The scaling of FMR among passerine birds does not differ from that of non-passerine species taken together, in contrast to the earlier finding based on fewer data (102). However, an ANCOVA on all taxonomic orders for which adequate data exist indicates no significant differences in slopes, but in pairwise comparisons, intercepts of regressions for Passeriformes and Procellariiformes are relatively high, and the intercept for Galliformes is relatively low, compared with other families.

The 55 species of reptiles used in the analyses included 48 lizards, 6 snakes and 1 tortoise (Table 1). The allometric slope for all reptiles is 0.889 (95% CI = 0.830–0.948), which is higher than both theoretical slopes of 0.67 or 0.75. Among lizards, the slope is even higher, at 0.916, and has smaller relative CIs (0.863–0.969). The regression for snakes is not significant. The measured FMR of the two *Crotalus* snakes and the desert tortoise (*Gopherus agassizii*) fall below the 95% CI of the prediction, indicating that they have significantly lower FMRs than would lizards of comparable size. For all subsequent analyses (see below), only lizard data are used. No significant differences are found in the scaling of four lizard families (Iguanidae, Phrynosomatidae, Varanidae, and Lacertidae). When each family is compared with all other lizards (i.e. phrynosomatids versus nonphrynosomatids), there are also no significant differences. It is interesting to note that excluding the varanids does not lower the slope or the intercept of the lizard regression (slope for all lizards 0.916, nonvaranid lizards slope is 0.88, $P = 0.659$). Thus, varanids, despite their generally large body size and highly active lifestyle, do not appear to have higher energy expenditures than do nonvaranid lizards of the same body mass. Are there differences at higher taxonomic levels of reptiles? Within the order Squamata, there are two major clades, Iguania and Scleroglossa (Gekkota plus Autarchoglossa), that diverged about 200 million years ago. Our data include species from the Iguania clade (Iguanidae, Phrynosomatidae, Tropicuridae, and Agamidae) as well as the Scleroglossa clade (Teiidae, Lacertidae, Scincidae, Gerrhosauridae, Anguidae, and Varanidae). ANCOVA indicates that Iguanians ($n = 17$) and Scleroglossans ($n = 31$) have significantly different slopes (Iguanian 0.793; Scleroglossan 0.949; $P = 0.017$). Even if varanids are excluded, there is still a significant scaling difference between the two clades ($F_{1,33} = 4.422$; $P = 0.043$).

To summarize, taxonomic differences in FMR of vertebrates are substantial between classes (mammals vs birds vs reptiles). Scaling differences apparently extend down only to the infraclass level in mammals (eutherians, marsupials), to just below the order level in reptiles, and to the family level in birds. A lack of information about many taxonomic groups precludes a more robust conclusion about taxonomic effects on FMR, at present.

Habitat Effects

The allometric slope for desert mammals (0.785) is significantly higher ($P = 0.0007$) than that for nondesert, nonmarine mammals (0.639), although marine mammals (1.438) do not differ from either desert or nondesert groups. Among rodents, there is no significant difference in scaling between desert ($n = 15$) and nondesert species ($n = 15$). Among birds, the allometric slopes of marine, desert, temperate forest, and temperate meadow species do not differ, but significant differences exist in the intercepts, which indicate that marine birds have FMRs averaging 60% higher than those of nonmarine birds, and desert birds have FMRs averaging 48% lower than those of nondesert birds. In reptiles, no significant scaling differences in FMR are found between desert and nondesert species, even among nonherbivores. Thus, demonstrated habitat effects on FMR of vertebrates are restricted to an increased allometric slope in desert mammals, a lower intercept (reduced FMR) in desert birds, and a higher intercept (elevated FMR) in marine birds.

Effects of Diet

There are significant differences in the scaling of FMR among the five mammalian dietary categories we compared (carnivores, granivores, herbivores, insectivores, and omnivores): Carnivores have a higher slope than both insectivores and herbivores. However, these results must be interpreted with caution, because the analysis of dietary effects is confounded by taxonomic affiliation. For example, most of the mammalian carnivores are canids and pinnipeds, which have relatively higher slopes, and many of the herbivores are marsupials, which have a relatively lower slope. If dietary categories are compared within eutherians and marsupials separately, no differences in scaling of FMR between dietary types remain. For birds, there are no significant differences in slopes of dietary categories, but carnivores, nectarivores, and insectivores have relatively high FMRs whereas granivores are lowest. Among lizards, there are no significant differences in the slopes or intercepts among insectivores, carnivores, and herbivores, or between insectivores and carnivores combined vs herbivores.

Season

The data for mammals are complete enough, including summer and winter measurements in 19 species of mammals (4 marsupials, 1 monotreme, 12 rodents, and 2 canids), to test for effects of season on FMR. There is no difference between summer and winter values in FMR (kJ/day), in mass-adjusted FMR ($\text{kJ g}^{-0.772} \text{d}^{-1}$ for eutherians or $\text{kJ g}^{-0.590} \text{d}^{-1}$ for marsupials and the monotreme), or in body mass (t -test, $P > 0.05$). Seven of these species were studied in spring, summer, autumn, and winter, and ANCOVA indicated no significant seasonal effects on body mass, FMR, or mass-adjusted FMR. These findings

challenge the assumption that mammals increase energy expenditure in winter when thermoregulatory costs presumably increase.

PHYLOGENETICALLY INDEPENDENT CONTRASTS: AN EXAMPLE

Because mean values for two or more closely related species cannot truly be considered to be completely independent in statistical analyses, it is becoming common practice to adjust results for phylogenetic relatedness (48, 50). We use Felsenstein's (45) method of phylogenetically independent contrasts to investigate the effects of phylogeny on the relationships revealed by the conventional log-linear methods used above. We used the program PDTREE [version 5.0, described in Garland et al (51)] to generate statistically independent observations, using Grafen's (55) arbitrary branch lengths (49). This method minimizes bias due to relatedness at the subspecific level as well as at higher levels, so published mean FMR and body mass values for different populations within species for which we have data (details not shown in Table 1) are used in the analyses for mammals and reptiles. Standardized contrasts for FMR are analyzed by least-squares regression through the origin on the positivized body mass contrasts. The intercept of the regression is then generated by PDTREE by mapping the slope of the standardized regression back onto the original data space (50).

The mammalian phylogenetic tree (figures and legends from this review for the phylogenetic trees for mammals, birds, and reptiles can be accessed at Annual Review's Website: <http://www.annualreviews.org> under Supplementary Materials, Nutrition) has been constructed from a number of published sources, including Wayne et al (159) (Carnivora), Degen et al (38) (Rodentia), Kirsch et al (71) (Marsupialia), Bininda-Emonds & Russell (14) (Pinnipeds), Onuma et al (126) (Insectivora), Hutcheon et al (66) (Chiroptera), Simmons & Geisler (142) (Chiroptera), Arnason et al (4), and Geffen et al (52). The avian phylogenetic tree is based mainly on Sibley & Ahlquist (141). Because of the small number of FMR studies done on snakes and tortoises, and their unresolved phylogenetic positions, only lizards are included in the phylogenetically independent contrast analysis of reptiles. The lizard phylogenetic tree is based largely on Appendix II of Clobert et al (32), combined with trees from Estes & Pregill (44), Christian & Garland (27), Wiens & Reeder (164), Kluge (74), and Arnold (5).

Analyses of independent contrasts (ICA) yields estimates of slope for all mammals, and for eutherians, which were similar to the slopes from the nonphylogenetic (conventional) analyses. The ICA slope for all mammals (including multiple populations for some species) is 0.772 (SE = 0.390, $n = 85$ independent contrasts), which is not significantly different from the conventional slope of 0.734 (t -test, $P = 0.38$). The ICA intercept (in \log_{10} format) of 0.460

(SE = 0.0394) is significantly lower than that of the conventional intercept (in \log_{10} format) of 0.683 ($P < 0.001$). For eutherian mammals, the ICA slope of 0.820 (SE = 0.558, $n = 62$) does not differ from the conventional slope of 0.772, but the ICA intercept is lower than the conventional intercept (0.391 vs 0.624, $P = 0.0014$). For marsupials, the method of independent contrasts yields a significantly higher scaling coefficient than does the nonphylogenetic regression [0.706 (SE = 0.0412, $n = 21$) vs 0.590 ($P = 0.018$)] and is more similar to the marsupial BMR slope of 0.747 (62) and the marsupial BMR-FMR slope of 0.723 (76). The marsupial ICA (0.682) and conventional (1.005) intercepts do not differ. With the phylogenetic analysis, there is no difference in slope or intercept between eutherians and marsupials (t-test, $P > 0.1$), in contrast to the results of the conventional analysis above and of previous studies (102, 104).

In birds, the ICA slopes and intercepts (\log_{10} format) for all birds ($b = 0.746$, $a = 0.807$, $n = 94$) and for passerine birds ($b = 0.650$, $a = 1.063$, $n = 39$) do not differ significantly from those derived conventionally. The ICA slopes and intercepts of passerine and nonpasserine birds are not different from each other, as is the case for conventionally derived regression parameters.

For reptiles, the ICA regressions tend to have lower slopes and higher intercepts than do the conventional regression results. For all lizards (including multiple populations), the ICA slope (0.787; 95% CI = 0.695–0.879) and \log_{10} format intercept (0.281; 0.043–1.85) are not significantly different from the conventional results. Even when the ICA data were limited to only species means (no multiple populations), no significant differences were detected from the conventional regressions. Clobert et al (32) compared several demographic parameters between Iguanians and Scleroglossans using ICA and found some significant differences, including the rate of evolution of mortality (corrected for body mass). Within the two lizard clades (Iguania and Scleroglossa), the ICA slope and intercept estimates of FMR are not significantly different from conventional results (ICA iguanian $b = 0.701$, $a = 0.426$; ICA scleroglossan $b = 0.822$, $a = 0.233$). Furthermore, in contrast to the conventional clade comparison, no significant difference exists between the clades, even if the ICA data are limited to species means.

As demonstrated, use of ICA can produce different results than conventional linear regression comparisons. For both mammals and reptiles, conventional comparisons indicate significant differences in the scaling of FMR to body mass between major taxonomic groups (marsupials vs eutherians; iguanians vs scleroglossans). When using ICA to lessen phylogenetic bias, these differences disappear. ICA does not identify new differences that are not found by conventional regression. It is clear from the obvious differences in FMR allometry between mammals, birds, and reptiles identified early in this article (Figure 1), and from the above phylogenetically independent analysis, that phylogenetic relationships are an important component influencing energy

expenditure in wild animals. As more robust phylogenetic trees and improved statistical methods become available, incorporation of phylogeny into analyses of field metabolism will improve understanding of the determinants of FMR in free-living animals.

CONCLUSIONS AND RECOMMENDATIONS

Doubly labeled water (DLW) studies of the field metabolic rates of free-living mammals, birds, and reptiles reveal that body mass is the primary determinant of energy and food requirements (accounting for 71% of the variation in log FMR), followed by phylogeny, which together account for 93–95% of the variation in log FMR. Nevertheless, the residual variation remaining (after anti-log transformation) is large (more than six times, lowest to highest) and is poorly explained by taxonomic affiliations below the order level, or by habitat or dietary considerations. Thus, the 95% CI around FMRs predicted from body masses of unstudied animals are large (ca 50–200% of the predicted value). Our experience with DLW results for single species indicates that variation in FMR among individuals within a study is typically only about 20% for endotherms and 35% for ectotherms, so it should be possible to predict FMRs more accurately than we can now. One of the reasons for this is that there are insufficient data available for lower taxons (e.g. families) to evaluate whether these categories can improve explanatory and predictive capabilities. Major taxa of vertebrates [e.g. turtles, raptors, cetaceans, skinks, owls, insectivores (moles and shrews), etc] remain poorly or unstudied. Another reason is that DLW studies are relatively short-term, and one-time FMR measurements may reflect unusually energetic or unusually slothful phases of an animal's life, rather than being a representative year-round FMR. A third, and perhaps most important, reason is that we are probably missing the factors that cause variation in the existing FMR data. Habitat and dietary considerations may be much less influential regarding daily energy expenditure than are reproductive activities, responses to immediate social or predator pressures, and adjustments to that day's or week's vagaries of weather conditions. We recommend increased attention to evaluating these sources of variation in vertebrate FMR.

ACKNOWLEDGMENTS

We thank Theodore J Garland for advice on phylogenetically independent contrasts, and Rebecca Verity for help in searching the literature.

Visit the *Annual Reviews* home page at
<http://www.AnnualReviews.org>

Literature Cited

1. Ambrose SJ, Bradshaw SD, Withers PC, Murphy DP. 1996. Water and energy balance of captive and free-ranging spinifexbirds (*Eremiornis carteri*) North (Aves: Sylviidae) on Barrow Island, Western Australia. *Aust. J. Zool.* 44:107-17
2. Anderson RA, Karasov WH. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* 49:67-72
3. Anderson RA, Karasov WH. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecol. Monogr.* 58:79-110
4. Arnason U, Bodin K, Gullberg A, Ledje C, Mouchaty S. 1995. A molecular view of pinniped relationships with particular emphasis on the true seals. *J. Mol. Evol.* 40:78-85
5. Arnold EN. 1989. Towards a phylogeny and biogeography of the *Lacertidae*: relationships within an old-world family of lizards derived from morphology. *Bull. Br. Mus. Nat. Hist. Zool.* 55:209-57
6. Arnould JPY, Boyd IL, Speakman JR. 1996. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J. Zool.* 239:769-82
7. Balance LT. 1995. Flight energetics of free-ranging red-footed boobies (*Sula sula*). *Physiol. Zool.* 68:887-914
8. Bartholomew GA. 1982. Energy metabolism. In *Animal Physiology: Principles and Adaptations*, ed. MS Gordon, GA Bartholomew, AD Grinnell, CB Jorgensen, FN White, pp. 46-93. New York: Macmillan. 4th ed. 635 pp.
9. Beaupre SJ. 1996. Field metabolic rate, water flux, and energy budgets of mottled rock rattlesnakes, *Crotalus lepidus*, from two populations. *Copeia*, pp. 319-29
10. Benabib M, Congdon JD. 1992. Metabolic and water-flux rates of free-ranging tropical lizards *Sceloporus variabilis*. *Physiol. Zool.* 65:788-802
11. Bennett AF, Nagy KA. 1977. Energy expenditure in free-ranging lizards. *Ecology* 58:697-700
12. Berteaux D, Thomas DW, Bergeron JM, Lapierre HL. 1996. Repeatability of daily field metabolic rate in female meadow voles (*Microtus pennsylvanicus*). *Funct. Ecol.* 10:751-59
13. Bickler PE, Nagy KA. 1980. Effect of parietectomy on energy expenditure in free-ranging lizards. *Copeia*, pp. 923-25
14. Bininda-Edmonds ORP, Russell AP. 1996. A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonn. Zool. Monogr.* 1996:5-256
15. Birt-Friesen VL, Montevecchi WA, Cairns DK, Macko SA. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70:357-67
16. Bradshaw SD, Morris KD, Dickman CR, Withers PC, Murphy D. 1994. Field metabolism and turnover in the golden bandicoot (*Isodan auratus*) and other small mammals from Barrow Island, Western Australia. *Aust. J. Zool.* 42:29-41
17. Bradshaw SD, Saint Girons H, Naulleau G, Nagy KA. 1987. Metabolic and energy balance of some captive and free-ranging reptiles in western France. *Amphib. Reptil.* 8:129-42
18. Brown CR, Bryant DM. 1996. Energy expenditure during molt in dippers (*Cinclus cinclus*): no evidence of elevated costs. *Physiol. Zool.* 69:1036-56
19. Brown RP, Perez-Mellado V. 1994. Ecological energetics and food acquisition in dense Menorcan islet populations of the lizard *Podarcis lilfordi*. *Funct. Ecol.* 8:427-34
20. Brown RP, Thorpe RS, Speakman JR. 1992. Comparisons of body size, field energetics, and water flux among populations of the skink *Chalcides sexlineatus*. *Can. J. Zool.* 70:1001-6
21. Brown TK. 1999. *The physiological ecology of desert horned lizards (Phrynosoma platyrhinos) in the Mojave Desert*. PhD thesis. Univ. Calif., Los Angeles. 107 pp.
22. Bryant DM. 1997. Energy expenditure in wild birds. *Proc. Nutr. Soc.* 56:1025-39
23. Carlson A, Moreno J, Alatalo RV. 1993. Winter metabolism of coniferous forest tits *Paridae* under arctic conditions: a study with doubly labeled water. *Ornis Scand.* 24:161-64
24. Castro G, Myers JP, Ricklefs RE. 1992. Ecology and energetics of Sanderlings migrating to four latitudes. *Ecology* 73: 833-44
25. Chappell MA, Shoemaker VH, Janes DN, Maloney SK, Bucher TL. 1993. Energetics of foraging in breeding Adelie penguins. *Ecology* 74:2450-61
26. Chevalier CD. 1989. Field energetics and water balance of desert-dwelling ringtail

- cats *Bassariscus astutus* (Carnivora Procyonidae). *Am. Zool.* 29:A8
27. Christian A, Garland TJ. 1996. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). *J. Herpetol.* 30: 219–30
 28. Christian K, Green B. 1994. Seasonal energetics and water turnover of the frill-neck lizard, *Chlamydosaurus kingii*, in the wet-dry tropics of Australia. *Herpetologica* 50:274–81
 29. Christian K, Green B, Bedford G, Newgrain K. 1996. Seasonal metabolism of a small, arboreal monitor lizard, *Varanus scalaris*, in tropical Australia. *J. Zool.* 240:383–96
 30. Christian KA, Corbett LK, Green B, Weavers BW. 1995. Seasonal activity and energetics of two species of varanid lizards in tropical Australia. *Oecologia* 103:349–57
 31. Christian KA, Weavers BW, Green B, Bedford GS. 1996. Energetics and water flux in a semiaquatic lizard, *Varanus mertensi*. *Copeia*, pp. 354–62
 32. Clobert J, Garland TJ, Barbault R. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *J. Evol. Biol.* 11:329–64
 33. Congdon JD, Tinkle DW. 1982. Energy expenditure in free-ranging sagebrush lizards (*Sceloporus graciosus*). *Can. J. Zool.* 60:1412–16
 34. Covell DF, Miller DS, Karasov WH. 1996. Cost of locomotion and daily energy expenditure by free-living swift foxes (*Vulpes velox*): a seasonal comparison. *Can. J. Zool.* 74:283–90
 35. Cuervo JJ, De Lope F, Moller AP, Moreno J. 1996. Energetic cost of tail streamers in the barn swallow (*Hirundo rustica*). *Oecologia* 108:252–58
 36. Culik BM, Wilson RP. 1992. Field metabolic rates of instrumented Adie penguins using double-labelled water. *J. Comp. Physiol. B* 162:567–73
 37. Dawson TJ, Hulbert AJ. 1970. Standard metabolism, body temperature and surface areas of Australian marsupials. *Am. J. Physiol.* 218:1233–38
 38. Degen AA, Kam M, Khokhlova IS, Krasnov BR, Barraclough TG. 1998. Average daily metabolic rate of rodents: habitat and dietary comparisons. *Funct. Ecol.* 12:63–73
 39. Degen AA, Khokhlova IS, Kam M, Nagy KA. 1997. Body size, granivory and seasonal dietary shifts in desert gerbilline rodents. *Funct. Ecol.* 11:53–59
 40. Dryden G, Green B, King D, Losos J. 1990. Water and energy turnover in a small monitor lizard, *Varanus acanthurus*. *Aust. Wild. Res.* 17:641–46
 41. Dryden GL, Green B, Wikramanayake ED, Drysen KG. 1992. Energy and water turnover in two tropical energy lizards, *Varanus bengalensis* and *V. salvator*. *Copeia*, pp. 102–7
 42. Dykstra CR, Karasov WH. 1993. Daily energy expenditure by nestling house wrens. *Condor* 95:1028–30
 43. Ellis WAH, Melzer A, Green B, Newgrain K, Hindell MA, Carrick FN. 1995. Seasonal variation in water flux, field metabolic rate and food consumption of free-ranging koalas (*Phascolarctos cinereus*). *Aust. J. Zool.* 43:59–68
 44. Estes R, Pregill GK. 1988. *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*. Stanford, CA: Stanford Univ. Press. 631 pp.
 45. Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15
 46. Gales R, Green B. 1990. The annual energetics cycle of little penguins (*Eudyptula minor*). *Ecology* 71:2297–312
 47. Gales R, Green B, Libke J, Newgrain K, Pemberton D. 1993. Breeding energetics and food requirements of Gentoo penguins *Pygoscelis*-Papua at Heard and Macquarie Islands. *J. Zool.* 231:125–39
 48. Garland TJ, Dickerman AW, Janis CM, Jones JA. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* 42:265–92
 49. Garland TJ, Harvey PH, Ives AR. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41:18–32
 50. Deleted in Proof
 51. Garland TJ, Jones JA, Midford PE. 1998. *Phenotypic diversity analysis program—PDTree Module*. Version 5.0, Madison, WI: Univ. Wisconsin
 52. Geffen E, Mercure A, Girman DJ, Macdonald DW, Wayne RK. 1992. Phylogenetic relationships of the fox-like canids mitochondrial DNA restriction fragment site and cytochrome beta sequence analyses. *J. Zool.* 228:27–39
 53. Girard I. 1998. *The physiological ecology of a small canid, the kit fox (Vulpes macrotis), in the Mojave Desert*. PhD thesis. Univ. Calif., Los Angeles. 112 pp.
 54. Gorman ML, Mills MG, Raath JP, Speakman JR. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* 391: 479–81

55. Grafen A. 1989. The phylogenetic regression. *Philos. Trans. R. Soc. London Ser. B* 326:119–57
56. Green B, Dryden G, Dryden K. 1991. Field energetics of a large carnivorous lizard, *Varanus rosenbergi*. *Oecologia* 88: 547–51
57. Green B, Herrera E, King D, Mooney N. 1997. Water and energy use in a free-living tropical, carnivorous lizard, *Tupinambis teguixin*. *Copeia*, pp. 200–3
58. Green B, King D, Braysher M, Saim A. 1991. Thermoregulation, water turnover and energetics of free-living komodo dragons, *Varanus komodoensis*. *Comp. Biochem. Physiol. A* 99:97–102
59. Green B, King D, Butler H. 1986. Water, sodium and energy turnover in free-living perenties, *Varanus giganteus*. *Aust. Wild. Res.* 13:589–96
60. Grenot CJ, Galina-Tessaró P, Alvarez-Cardenas S. 1995. Field metabolism of lizards from lower altitude regions of Baja California sur (Mexico). *Amphib. Reptil.* 16:11–23
61. Hayes JP. 1989. Field and maximal metabolic rates of deer mice (*Peromyscus maniculatus*) at low and high altitudes. *Physiol. Zool.* 62:732–44
62. Hayssen V, Lacy RC. 1985. Basal metabolic rates in mammals' taxonomic differences in the allometry of basal metabolic rate and body mass. *Comp. Biochem. Physiol. A* 81:741–54
63. Helversen OV, Reyer HU. 1984. Nectar intake and energy expenditure in a flower visiting bat [*Anoura caudifer*]. *Oecologia* 63:178–84
64. Henen BT. 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). *Ecology* 78:283–96
65. Hodum PJ, Sydeman WJ, Visser GH, Weathers WW. 1998. Energy expenditure and food requirement of Cassin's Auklets provisioning nestlings. *Condor* 100:546–50
66. Hutcheon JM, Kirsch JAW, Pettigrew JD. 1998. Base-compositional biases and the bat problem. III. The question of microchiropteran monophyly. *Philos. Trans. R. Soc. London Ser. A* 353:607–17
67. Jonsson KI, Korpimäki E, Pen I, Tolonen P. 1996. Daily energy expenditure and short-term reproductive costs in free-ranging Eurasian kestrels (*Falco tinnunculus*). *Funct. Ecol.* 10:475–82
68. Karasov WH, Anderson RA. 1984. Interhabitat differences in energy acquisition and expenditure in a lizard. *Ecology* 65:235–47
69. Karasov WH, Anderson RA. 1998. Correlates of average daily metabolism of field-active zebra-tailed lizards (*Callisaurus draconoides*). *Physiol. Zool.* 71:93–105
70. Kingsbury BA. 1995. Field metabolic rates of a eurythermic lizard. *Herpetologica* 51:155–59
71. Kirsch JAW, Lapointe FJ, Springer MS. 1997. DNA-hybridisation studies of marsupials and their implications for metatherian classification. *Aust. J. Zool.* 45:211–80
72. Klaassen M, Becker PH, Wagener M. 1992. Transmitter loads do not affect the daily energy expenditure of nesting common terns. *J. Field Ornithol.* 63:181–85
73. Kleiber M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. Melbourne, FL: Kreiger. 453 pp. 2nd ed.
74. Kluge AG. 1987. Cladistic relationships in the Gekkonoidea (Squamata, Sauria). *Misc. Publ. Mus. Zool. Univ. Mich.* 54 pp.
75. Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, et al. 1992. Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* 62:143–63
76. Koteja P. 1991. On the relation between basal and field metabolic rates in birds and mammals. *Funct. Ecol.* 5:56–64
77. Krockenberger AK, Hume ID, Cork SJ. 1998. Production of milk and nutrition of the dependent young of free-ranging koalas (*Phascolarctos cinereus*). *Physiol. Zool.* 71:45–56
78. Kunz TH, Robson SK, Nagy KA. 1998. Economy of harem maintenance in the greater spear-nosed bat, *Phyllostomus hastatus*. *J. Mammal.* 79:631–42
79. Kurta A, Johnson KA, Kunz TH. 1987. Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. *Physiol. Zool.* 60:386–97
80. Kurta A, Kunz TH, Nagy KA. 1990. Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *J. Mammal.* 71:59–65
81. Lasiewski RC, Dawson WR. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23
82. Lifson N, McClintock R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* 12:46–74
83. Marler CA, Walsberg G, White ML, Moore M. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behav. Ecol. Sociol.* 37:225–31

84. Masman D, Dijkstra C, Daan S, Bult A. 1989. Energetic limitation of avian parental effort: field experiments in the kestrel (*Falco tinnunculus*). *J. Evol. Biol.* 2:435–56
85. Mautz WJ, Nagy KA. 1987. Ontogenetic changes in diet field metabolic rate and water flux in the herbivorous lizard *Dipsosaurus dorsalis*. *Physiol. Zool.* 60:640–58
86. Meerlo P, Bolle L, Visser GH, Masman D, Daan S. 1997. Basal metabolic rate in relation to body composition and daily energy expenditure in the field vole, *Microtus agrestis*. *Physiol. Zool.* 70:362–69
87. Mehlum F, Gabrielsen GW, Nagy KA. 1993. Energy expenditure by black guillemots *Cephus grylle* during chick-rearing. *Colon Waterbird* 16:45–52
88. Merker GP, Nagy KA. 1984. Energy utilization by free-ranging *Sceloporus virgatus* lizards. *Ecology* 65:575–81
89. Mock PJ. 1991. Daily allocation of time and energy of western bluebirds feeding nestlings. *Condor* 93:598–611
90. Moreno J. 1989. Variation in daily energy expenditure in nesting northern wheatears (*Oenanthe oenanthe*). *Auk* 106:18–25
91. Moreno J, Cowie RJ, Sanz JJ, Williams RSR. 1995. Differential response by males and females to brood manipulations in the pied flycatcher: energy expenditure and nestling diet. *J. Anim. Ecol.* 64:721–32
92. Moreno J, Gustafsson L, Carlson A, Part T. 1991. The cost of incubation in relation to clutch-size in the collared flycatcher *Ficedula albicollis*. *Ibis* 133:186–92
93. Moreno J, Sanz JJ. 1994. The relationship between the energy expenditure during incubation and clutch size in the pied flycatcher *Ficedula hypoleuca*. *J. Avian Biol.* 25:125–30
94. Moreno J, Sanz JJ. 1996. Field metabolic rates of breeding chinstrap penguins (*Pygoscelis antarctica*) in the South Shetlands. *Physiol. Zool.* 69:586–98
95. Munger JC, Karasov WH. 1994. Costs of bot fly infection in white-footed mice: energy and mass flow. *Can. J. Zool.* 72:166–73
96. Munks SA, Green B. 1995. Energy allocation for reproduction in a marsupial arboreal folivore, the common ringtail possum (*Pseudocheirus peregrinus*). *Oecologia* 101:94–104
97. Mutze GJ, Green B, Newgrain K. 1991. Water flux and energy use in wild house mice (*Mus domesticus*) and the impact of seasonal aridity on breeding and population levels. *Oecologia* 88:529–38
98. Nagy KA. 1980. CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* 238:R466–73
99. Nagy KA. 1982. Energy requirements of free-living iguanid lizards. In *Iguanas of the World: Their Behavior, Ecology and Conservation*, ed. GM Burghardt, AS Rand, pp. 49–59. Park Ridge, NJ: Noyes. 472 pp.
100. Nagy KA. 1983. *The Doubly Labeled Water (³HH¹⁸O) Method: A Guide to Its Use*. Los Angeles: Univ. Calif. Publ. No. 12-1417
101. Nagy KA. 1983. Ecological energetics. In *Lizard Ecology: Studies of a Model Organism*, ed. RB Huey, ER Pianka, TW Schoener, pp. 24–54. Cambridge, MA: Harvard Univ. Press. 501 pp. 2nd ed.
102. Nagy KA. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57:111–28
103. Nagy KA. 1989. Doubly-labeled water studies of vertebrate physiological ecology. In *Stable Isotopes in Ecological Research*, ed. PW Rundel, JR Ehleringer, KA Nagy, pp. 270–87. New York: Springer-Verlag. 525 pp.
104. Nagy KA. 1994. Field bioenergetics of mammals: What determines field metabolic rates? *Aust. J. Zool.* 42:43–53
105. Nagy KA, Bradshaw SD. 1995. Energetics, osmoregulation, and food consumption by free-living desert lizards, *Ctenophorus* (= *Amphibolurus*) *nuchalis*. *Amphib. Reptil.* 16:25–35
106. Nagy KA, Bradshaw SD, Clay BT. 1991. Field metabolic rate, water flux, and food requirements of short-nosed bandicoots, *Isodon obesulus* (Marsupialia: Peramelidae). *Aust. J. Zool.* 39:299–306
107. Nagy KA, Clarke BC, Seely MK, Mitchell D, Lighton JRB. 1991. Water and energy balance in Namibian Desert sand-dune lizards *Angolosaurus skoogi* (Andersson, 1916). *Funct. Ecol.* 5:731–39
108. Nagy KA, Degen AA. 1988. Do desert geckos conserve energy and water by being nocturnal? *Physiol. Zool.* 61:495–99
109. Nagy KA, Gavrilov VM, Kerimov AB, Ivankina EV. 1999. Relationships between field metabolic rate and territoriality in passerines. *Acta XXII Congr. Int. Ornithol.* Greenside, So. Africa: Birdlife So. Africa
110. Nagy KA, Gruchacz MJ. 1994. Seasonal water and energy metabolism of the desert dwelling kangaroo rat (*Dipodomys merriami*). *Physiol. Zool.* 67:1461–78
111. Nagy KA, Huey RB, Bennett AF. 1984. Field energetics and foraging mode of

- Kalahari lacertid lizards [*Eremias* spp.]. *Ecology* 65:588-96
112. Nagy KA, Knight MH. 1989. Comparative field energetics of a Kalahari skink (*Mabuya striata*) and gecko (*Pachydactylus bibroni*). *Copeia*, pp. 13-7
 113. Nagy KA, Knight MH. 1994. Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *J. Mammal.* 75:860-72
 114. Nagy KA, Medica PA. 1986. Physiological ecology of desert tortoises in southern Nevada. *Herpetologica* 42:73-92
 115. Nagy KA, Meienberger C, Bradshaw SD, Wooller RD. 1995. Field metabolic rate of a small marsupial mammal, the honey possum (*Tarsipes rostratus*). *J. Mammal.* 76:862-66
 116. Nagy KA, Milton K. 1979. Energy metabolism and food consumption by wild howler monkeys (*Alouatta palliata*). *Ecology* 60:475-80
 117. Nagy KA, Montgomery GG. 1980. Field metabolic rate, water flux and food consumption in three-toed sloths (*Bradypus variegatus*). *J. Mammal.* 61:465-72
 118. Nagy KA, Obst BS. 1991. Body size effects on field energy requirements of birds: What determines their metabolic rates? *Acta XX Congr. Int. Ornithol.* pp. 793-99. Wellington, New Zealand: New Zealand Ornitho. Congr. Trust Board. 2568 pp.
 119. Nagy KA, Obst BS. 1992. Food and energy requirements of Adelie penguins *Pygoscelis adeliae* on the Antarctic Peninsula. *Physiol. Zool.* 65:1271-84
 120. Nagy KA, Sanson GD, Jacobsen NK. 1990. Comparative field energetics of two macropod marsupials and a ruminant. *Aust. Wild. Res.* 17:591-600
 121. Nagy KA, Seely MK, Buffenstein R. 1993. Surprisingly low field metabolic rate of a diurnal desert gecko *Rhoptropus afer*. *Copeia*, pp. 216-19
 122. Nagy KA, Shoemaker VH. 1975. Energy and nitrogen budgets of the free-living desert lizard *Sauromalus obesus*. *Physiol. Zool.* 48:252-62
 123. Nagy KA, Shoemaker VH. 1984. Field energetics and food consumption of the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiol. Zool.* 57:281-90
 124. Obst BS, Nagy KA. 1992. Field energy expenditures of the southern Giant-Petrel. *Condor* 94:801-10
 125. Obst BS, Russell RW, Hunt GLJ, Eppley ZA, Harrison NM. 1995. Foraging radii and energetics of least auklets (*Aethia pusilla*) breeding on three Bering Sea Islands. *Physiol. Zool.* 68:647-72
 126. Onuma M, Kusakabe T, Kusakabe S. 1997. Phylogenetic positions of insectivora in eutheria inferred from mitochondrial genes. *Zool. Sci.* 14:1-39
 127. Pennycuik CJ, Schaffner FC, Fuller MR, Obrecht HHI, Sternberg L. 1990. Foraging flights of the white-tailed tropicbird (*Phaethon lepturus*): radiotracking and doubly-labelled water. *Colon Waterbird* 13:96-102
 128. Peterson CC. 1996. Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. *Ecology* 77:1831-44
 129. Peterson CC, Walton BM, Bennett AF. 1998. Intrapopulation variation in ecological energetics of the garter snake *Thamnophis sirtalis*, with analysis of the precision of doubly labeled water measurements. *Physiol. Zool.* 71:333-49
 130. Pettit TN, Nagy KA, Ellis HI, Whitton GC. 1988. Incubation energetics of the Laysan albatross. *Oecologia* 74:546-50
 131. Piersma T, Morrisson RIG. 1994. Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high Arctic climatic conditions. *Auk* 111:366-76
 132. Plummer MV, Congdon JD. 1996. Rates of metabolism and water flux in free-ranging racers, *Coluber constrictor*. *Copeia*, pp. 8-14
 133. Powers DR, Conley TM. 1994. Field metabolic rate and food consumption of two sympatric hummingbird species in southeastern Arizona. *Condor* 96:141-50
 134. Powers DR, Nagy KA. 1988. Field metabolic rate and food consumption by free-living Anna's hummingbirds (*Calypte anna*). *Physiol. Zool.* 61:500-6
 135. Reilly JJ, Fedak MA. 1991. Rates of water turnover and energy expenditure of free-living male common seals (*Phoca vitulina*). *J. Zool.* 223:461-68
 136. Riedstra B, Dijkstra C, Daan S. 1998. Daily energy expenditure of male and female Marsh Harrier nestlings. *Auk* 115: 635-41
 137. Robinson MD. 1990. Summer field energetics of the Namib Desert dune lizard *Aporosaura anchietae* (Lacertidae), and its relation to reproduction. *J. Arid Environ.* 18:207-16
 138. Salsbury CM, Armitage KB. 1994. Home-range size and exploratory excursions of adult, male yellow-bellied marmots. *J. Mammal.* 75:648-56
 139. Secor SM, Nagy KA. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75:1600-14

140. Seymour RS, Withers PC, Weathers WW. 1998. Energetics of burrowing, running, and free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). *J. Zool.* 244:107–17
141. Sibley CG, Ahlquist JE. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. New Haven: Yale Univ. Press. 976 pp.
142. Simmons NB, Geisler JH. 1998. Phylogenetic relationships of Icaronycteris, Archaeonycteris, Hassianycteris, and Palaeochiropteryx to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in microchiroptera. *Bull. Am. Nat. Hist. Mus.*, pp. 1–182
143. Speakman JR. 1997. *Doubly Labelled Water: Theory and Practice*. London: Chapman & Hall. 399 pp.
144. Speakman JR. 1997. Factors influencing the daily energy expenditure of small mammals. *Proc. Nutr. Soc.* 56:1119–36
145. Speakman JR, Racey PA. 1987. The equilibrium concentration of oxygen-18 in body water: implications for the accuracy of the doubly-labelled water technique and a potential new method of measuring RQ in free-living animals. *J. Theor. Biol.* 127:79–96
146. Stephenson PJ, Speakman JR, Racey PA. 1994. Field metabolic rate in two species of shrew-tenrec, *Microgale dobsoni* and *M. talazaci*. *Comp. Biochem. Physiol. A* 107:283–87
147. Tatner P. 1990. Energetic demands during brood rearing in the wheatear *Oenanthe oenanthe*. *Ibis* 132:423–35
148. Tatner P, Bryant DM. 1993. Interspecific variation in daily energy expenditure during avian incubation. *J. Zool.* 231:215–32
149. Taylor JRE, Place AR, Roby DD. 1997. Stomach oil and reproductive energetics in Antarctic prions, *Pachyptila desolata*. *Can. J. Zool.* 75:490–500
150. Thompson GG, Bradshaw SD, Withers PC. 1997. Energy and water turnover rates of a free-living and captive goanna, *Varanus caudolineatus* (Lacertilia: Varanidae). *Comp. Biochem. Physiol. A* 116:105–11
151. Tinbergen JM, Dietz MW. 1994. Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* 8:563–72
152. Uttley J, Tatner P, Monaghan PT. 1994. Measuring the daily energy expenditure of free-living arctic terns (*Sterna paradisaea*). *Auk* 111:453–59
153. Van Marken Lichtenbelt WD, Wesseling RA, Vogel JT, Albers KBM. 1993. Energy budgets in free-living green iguanas in a seasonal environment. *Ecology* 74:1157–72
154. Vehrencamp SL, Bradbury JW, Gibson RM. 1989. The energetic cost of display in male sage grouse. *Anim. Behav.* 38:885–96
155. Vernet R, Castanet J, Baez M. 1995. Comparative water flux and daily energy expenditure of lizards of the genus *Gallotia* (Lacertidae) from the Canary islands. *Amphib. Reptil.* 16:55–66
156. Vernet R, Grenot C, Nouira S. 1988. Water flux and energy metabolism in a population of Lacertidae from the Kerkenna islands (Tunisia). *Can. J. Zool.* 66:555–61
157. Wallis IR, Green B, Newgrain K. 1997. Seasonal field energetics and water fluxes of the long-nosed potoroo (*Potorous tridactylus*) in southern Victoria. *Aust. J. Zool.* 45:1–11
158. Ward S. 1996. Energy expenditure of female barn swallows *Hirundo rustica* during egg formation. *Physiol. Zool.* 69:930–51
159. Wayne RK, Van Valkenburgh B, O'Brien SJ. 1991. Molecular distance and divergence time in carnivores and primates. *Mol. Biol. Evol.* 8:297–319
160. Weathers WW, Paton DC. 1997. Summer field metabolic rate and water intake rate in superb fairy-wrens and a white-throated treecreeper. *Emu* 97:324–25
161. Weathers WW, Paton DC, Seymour RS. 1996. Field metabolic rate and water flux of nectarivorous honeyeaters. *Aust. J. Zool.* 44:445–60
162. Weathers WW, Stiles FG. 1989. Energetics and water balance in free-living tropical hummingbirds. *Condor* 91:324–31
163. Weathers WW, Sullivan KA. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66:511–36
164. Wiens JJ, Reeder TW. 1997. Phylogeny of the spiny lizards (*Sceloporus*) based on molecular and morphological evidence. *Herpetol. Monogr.* pp. 1–101
165. Williams JB. 1987. Field metabolism and food consumption of savannah sparrows during the breeding season. *Auk* 104:277–89
166. Williams JB. 1988. Field metabolism of tree swallows during the breeding season. *Auk* 105:706–14
167. Williams JB. 1993. Energetics of incubation in free-living orange-breasted sunbirds in South Africa. *Condor* 95:115–26
168. Williams JB, Anderson MD, Richardson

- PRK. 1997. Seasonal differences in field metabolism, water requirements, and foraging behavior of free-living aardwolves. *Ecology* 78:2588-602
169. Williams JB, Bradshaw D, Schmidt L. 1995. Field metabolism and water requirements of spinifex pigeons (*Geophaps plumifera*) in Western Australia. *Aust. J. Zool.* 43:1-15
170. Williams JB, Du Plessis MA. 1996. Field metabolism and water flux of sociable weaver *Philetairus socius* in the Kalahari Desert. *Ibis* 138:168-71
171. Williams JB, Dwinell B. 1990. Field metabolism of free-living female savannah sparrows during incubation: a study using doubly labeled water. *Physiol. Zool.* 63:353-72
172. Williams JB, Siegfried WR, Milton SJ, Adams NJ, Dean WRJ, et al. 1993. Field metabolism water requirements and foraging behavior of wild ostriches in the Namib. *Ecology* 74:390-404
173. Znari M, Nagy KA. 1997. Field metabolic rate and water flux in free-living bibron's agama (*Agama impalearis*, boettger, 1874) in Morocco. *Herpetologica* 53:81-88