Annu. Rev. Nutr. 1999. 19:247–77

ENERGETICS OF FREE-RANGING MAMMALS, REPTILES, AND BIRDS

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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

0199-9885/99/0715-0247$08.00

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.

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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 CO_2, 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 CO_2 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							
Pipistrellus pipistrellus	Pipistrelle	7.3	29.3	Ch	ND	I	104
Plecotus auritus	Brown long-eared bat	8.5	27.6	Ch	ND	I	145
Myotis lucifugus	Little brown bat	9.0	29.9	Ch	ND	I	79
Gerbillus henleyi	Northern pygmy gerbil	9.3	26.5	Ro	D	G	39
Tarsipes rostratus	Honey possum	9.9	34.4	Tr	ND	N	115
Anoura caudifer	Flower-visiting bat	11.5	51.9	Ch	ND	N	63
Macrotus californicus	Big-eared bat	13.0	21.5	Ch	D	I	102
Peromyscus crinitus	Cactus mouse	13.4	39.3	Ro	D	O	102
Mus domesticus	Wild house mouse	15.1	47.1	Ro	D	O	97, 104
Cleithrionomys rutilus	Bank vole	16.0	57.6	Ro	ND	H	102
Sminthopsis crassicaudata	Narrow-footed marsup. mouse	16.6	68.6	Da	ND	I	102
Perognathus formosus	Long-tailed pocket mouse	17.9	45.2	Ro	D	G	102
Peromyscus maniculatus	Deer mouse	17.9	53.4	Ro	D	O	61
Peromyscus leucopus	White-footed deer mouse	19.2	41.4	Ro	ND	O	95, 102
Microtus arvalis	Meadow mouse	20.0	90.0	Ro	ND	O	104
Eremitalpa namibensis	Namib Desert golden mole	20.7	12.5	In	D	I	140
Eptesicus fuscus	Big brown bat	20.8	43.6	Ch	ND	I	80
Gerbillus allenbyi	Allenby's gerbil	22.8	35.6	Ro	D	G	104
Cleithrionomys glareolus	Bank vole	23.4	88.0	Ro	ND	H	104
Microtus agrestis	Field vole	26.8	77.8	Ro	ND	H	86, 104
Gerbillus pyramidum	Greater Egyptian gerbil	31.8	45.2	Ro	D	G	104
Pseudomys albocinereus	Australian native mouse	32.6	62.2	Ro	ND	O	102
Antechinus stuartii	Brown antechinus	33.0	86.4	Da	ND	I	104
Phascogale calura	Wambenger	33.5	61.9	Da	ND	C	104
Dipodomys merriami	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
Microtus pennsylvanicus	Meadow vole	36.9	115	Ro	ND	H	12
Acomys cahirinus	Common spiny mouse	38.3	51.8	Ro	D	O	102
Sekeetamys calurus	Bushy-tailed jird	41.2	44.0	Ro	D	O	102
Microgale dobsoni	Shrew-tenrec	42.6	77.1	In	ND	I	146
Microgale talazaci	Shrew-tenrec	42.8	66.5	In	ND	I	146
Acomys russatus	Golden spiny mouse	45.0	47.8	Ro	D	O	102
Lemmus trimucronatus	Brown lemming	55.2	201	Ro	ND	H	102
Dipodomys microps	Chisel-tooth kangaroo rat	57.1	84.5	Ro	D	O	102
Praomys natalensis	Multi-mammate mouse	57.3	86.6	Ro	ND	O	102
Antechinus swainsonii	Broad-footed marsup. mouse	62.6	150	Da	ND	I	102
Meriones crassus	Jird	69.2	65.0	Ro	D	G	39
Phyllostomus hastatus	Spear-nosed bat	80.8	146	Ch	ND	I	78
Arvicola terrestris	Water vole	85.8	119	Ro	ND	H	102
Ammospermophilus leucurus	Antelope ground squirrel	87.0	88.0	Ro	D	O	102
Tamias striatus	Eastern chipmunk	96.3	143	Ro	ND	O	102
Thomomys bottae	Botta's pocket gopher	104	130	Ro	ND	H	102
Petaurus breviceps	Sugar glider	124	173	Pt	ND	O	102
Gymnobelideus leadbeateri	Leadbeater's possum	125	226	Pt	ND	O	102
Psammomys obesus	Fat sand rat	170	165	Ro	D	H	104
Spermophilus saturatus	Golden-mantled ground sqrl.	214	226	Ro	ND	H	104
Isoodon auratus	Golden bandicoot	333	285	Pe	ND	O	16
Spermophilus parryi	Arctic ground squirrel	630	817	Ro	ND	O	104
Bassariscus astutus	Ring-tailed cat	752	472	Ca	D	C	26
Potorous tridactylus	Long-nosed potoroo	825	517	Ma	ND	H	157
Vulpes cana	Blanford's fox	972	642	Ca	D	C	104
Petauroides volans	Greater glider	995	520	Pt	ND	H	104
Pseudocheirus peregrinus	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
Bettongia penicillata	Short-nosed rat kangaroo	1,100	593	Ma	ND	H	104
Isoodon obesulus	Short-nosed brown bandicoot	1,230	644	Pe	ND	O	106
Vulpes macrotis	Kit fox	1,480	1,180	Ca	D	C	53
Lepus californicus	Black-tailed jackrabbit	1,800	1,300	La	D	H	102
Setonix brachyurus	Quokka	1,900	548	Ma	ND	H	102
Vulpes velox	Swift fox	2,100	1,780	Ca	ND	C	34
Aepyrpimnus rufescens	Rufous rat kangaroo	2,860	1,430	Ma	ND	H	104
Tachyglosssus aculeatus	Echidna	2,860	875	Ta	ND	I	104
Marmota flaviventris	Yellow-bellied marmot	3,190	2,430	Ro	ND	H	138
Bradypus variegatus	Three-toed sloth	4,150	545	Xe	ND	H	117
Macropus eugenii	Tammar wallaby	4,380	1,150	Ma	ND	H	102
Thylogale billiardieri	Red-bellied wallaby	5,980	1,630	Ma	ND	H	102, 120
Aloutta palliata	Mantled howler monkey	7,330	2,580	Pr	D	H	102
Phascolarctos cinereus	Koala	7,520	1,710	Ph	ND	H	43, 77, 102
Proteles cristatus	Aardwolf	8,540	1,850	Ca	D	I	168
Petrogale xanthopus	Rock wallaby	8,900	2,210	Ma	ND	H	104
Lyacon pictus	African wild dog	25,170	15,300	Ca	D	C	54
Arctocephalus gazella	Antarctic fur seal	34,600	23,000	Pi	M	C	6, 104
Canis lupus	Timber wolf	37,300	17,700	Ca	ND	C	104
Arctocephalus galapagoensis	Galapagos fur seal	37,400	4,780	Pi	M	C	104
Odocoileus hemionus	Mule deer	39,100	18,000	Ar	ND	H	102
Antidorcas marsupialis	Springbok	43,300	24,100	Ar	D	H	113
Macropus giganteus	Eastern grey kangaroo	44,500	8,670	Ma	ND	H	102
Callorhinus ursinus	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
Zalophus californianus	California sea lion	78,000	38,600	Pi	M	C	104
Neophoca cinerea	Australian sea lion	83,500	39,500	Pi	M	C	104
Phoca vitulina	Common seal	99,000	52,500	Pi	M	C	135
Birds							
Archilochus alexandri	Black-chinned hummingbird	3.7	29.1	Ap	TeF	N	133
Calypte anna	Anna's hummingbird	4.5	31.8	Ap	CS	N	134
Thalurania colombica	Crowned woodnymph	4.9	37.9	Ap	TF	N	162
Auriparus flaviceps	Verdin	6.6	30.0	Pa	D	I	162
Chalybura urochrysia	Bronze-tailed plumeleteer	7.2	57.9	Ap	TF	N	162
Malurus cyaneus	Superb blue wren	8.3	34.2	Pa	TeF	I	160
Lampornis clemenciae	Blue-throated hummingbird	8.8	81.7	Ap	TeF	N	133
Zosterops lateralis	Grey-breasted silvereye	9.5	41.7	Pa	EF	F	102
Parus ater	Coal tit	9.5	47.4	Pa	CF	I	118
Nectarinia violacea	Orange-breasted sunbird	9.5	66.2	Pa	FY	N	167
Acanthorhynchus tenuirostris	Eastern spinebill	9.7	53.0	Pa	TeF	N	161
Troglodytes aedon	House wren	10.6	60.8	Pa	TeF	I	42
Parus cristatus	Crested tit	11.1	40.6	Pa	CF	I	118
Parus montanus	Willow tit	11.4	44.1	Pa	CF	I	23, 118
Parus caeruleus	Blue tit	11.5	64.0	Pa	CF	I	148
Eremiornis carteri	Spinifexbird	12.0	51.5	Pa	D	I	1
Parus cinctus	Siberian tit	12.8	51.4	Pa	CF	I	23
Ficedula hypoleuca	Pied flycatcher	13.5	65.8	Pa	OW	I	91, 93
Riparia riparia	Sand martin	14.3	81.7	Pa	TM	I	102
Muscicapa striata	Pacific swallow	14.4	52.0	Pa	TeF	I	22
Hirundo tahitica	Spotted flycatcher	14.4	64.9	Pa	TF	I	102, 148
Phylidonyris pyrrhoptera	Crescent honeyeater	14.6	75.9	Pa	TeF	N	161
Ficedula albicollis	Collared flytcatcher	15.9	78.6	Pa	TeF	I	92
Phylidonyris novaehollandiae	New Holland honeyeater	17.3	77.6	Pa	TeF	N	161
Parus major	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
Erithacus rubecula	Robin	18.7	71.3	Pa	TeF	I	148
Passerculus sandwichensis	Savannah sparrow	18.7	80.4	Pa	SM	O	102, 165, 171
Delichon urbica	House martin	19.0	79.8	Pa	TM	I	102
Junco phaeonotus	Yellow-eyed junco	19.5	73.8	Pa	TM	O	172
Junco hyemalis	Dark-eyed junco	19.6	76.6	Pa	TM	O	163
Tachycineata bicolor	Tree swallow	20.2	209	Pa	TM	I	118
Hirundo rustica	Barn swallow	20.4	95.8	Pa	TM	I	35, 102, 158
Prunella modularis	Dunnocky	21.2	86.0	Pa	TeF	I	22
Phainopepla nitens	Phainopepla	22.7	79.1	Pa	D	O	102
Cormobates leucophaeus	White-throated treecreeper	23.7	81.4	Pa	TeF	I	160
Oenanthe oenanthe	Northern wheatear	24.3	91.4	Pa	TM	I	90, 147
Pyrrhula pyrrhula	Bullfinch	25.1	88.0	Pa	TeF	G	22
Philetairus socius	Sociable weaver	25.5	48.7	Pa	D	O	170
Sialia mexicana	Western bluebird	27.4	95.0	Pa	TeF	I	89
Melopsittacus undulatus	Budgerigar	27.9	59.1	Ps	D	O	172
Mirafra erythrochlamys	Dune lark	28.5	64.3	Pa	D	O	172
Merops viridis	Blue-throated bee-eater	34.3	85.3	Co	TF	I	102, 148
Oceanites oceanus	Wilson's storm-petrel	42.3	119	Pr	M	C	102
Oceanodroma leucorhoa	Leach's storm-petrel	45.9	118	Pr	M	C	118
Mimus polyglottos	Mockingbird	47.6	121	Pr	DF	O	102
Progne subis	Purple martin	49.0	163	Pa	DF	I	102
Actitis hypoleucos	Common sandpiper	51.6	146	Ch	M	C	148
Calidris alba	Sanderling	52.0	141	Ch	M	C	24
Neophema petrophila	Rock parrot	62.8	106	Ps	D	O	172
Cinclus cinclus	Dipper	63.7	196	Pa	TM	I	18, 118
Charadrius hiaticula	Ringed plover	74.8	302	Ch	M	C	148
Ceryle rudis	Pied kingfisher	76.0	210	Co	TF	C	118
Sturnus vulgaris	Starling	78.7	269	Pa	DF	O	102
Aethia pusilla	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
Melanerpes formicivorous	Acorn woodpecker	82.0	195	Pi	OW	O	172
Geophaps plumifera	Spinifex pigeon	87.0	76.0	Cl	D	G	169
Turdus merula	Blackbird	96.0	179	Pa	TeF	I	22
Sterna paradisaea	Arctic tern	101	335	Ch	M	C	152
Arenaria interpres	Ruddy turnstone	108	352	Ch	M	C	131
Pelecanoides georgicus	South Georgia diving petrel	109	464	Pr	M	C	118
Sterna hirundo	Common tern	127	343	Ch	M	C	72
Pelecanoides urinatrix	Common diving petrel	137	557	Pr	M	C	118
Callipepla gambelii	Gambel’s quail	145	90.8	Ga	D	O	102
Barnardius zonarius	Port Lincoln parrot	145	189	Ps	D	O	172
Pachyptila desolata	Antarctic prion	149	391	Pr	M	C	149
Alle alle	Dovkie	164	696	Ch	M	C	172
Ptychoramphus aleuticus	Cassin’s auklet	174	413	Ch	M	C	65
Sterna fuscata	Sooty tern	187	241	Ch	M	C	102
Ammoperdix heyi	Sand partridge	190	148	Ga	D	O	102
Anous stolidus	Brown noddy	195	352	Ch	M	C	102
Falco tinnunculus	Eurasian kestrel	211	341	Fa	TM	C	67, 84, 118
Cacatua roseicapilla	Galah	307	349	Ps	D	O	172
Phaethon lepturus	White-tailed tropicbird	370	777	Pe	M	C	127
Cepphus grylle	Black guillemot	380	860	Ch	M	C	87, 118
Puffinus pacificus	Wedge-tailed shearwater	384	614	Pr	M	C	102
Rissa tridactyla	Black-legged kittiwake	386	795	Pr	M	C	102
Alectoris chukar	Chukar	395	260	Ga	D	O	102
Uria lomvia	Thick-billed murre	834	1,480	Ch	M	C	118
Uria aalga	Guillemot	940	1,870	Ch	M	C	172
Eudyptula minor	Little penguin	1,050	1,050	Sp	M	C	46, 118
Sula sula	Red-footed booby	1,070	1,220	Pe	M	C	7
Centrocercus urophasianus	Sage grouse	2,500	1,540	Ga	D	G	154
Morus capensis	Cape gannet	2,580	3,380	Pe	M	C	172
Diomedea immutabilis	Laysan albatross	3,070	1,330	Pr	M	C	130
Spheniscus demersus	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
Sula bassanus	Northern gannet	3,210	4,870	Pe	M	C	172
Diomedea chrysostoma	Grey-headed albatross	3,710	2,390	Pr	M	C	118
Pygoscelis antarctica	Chinstrap penguin	3,790	5,600	Sp	M	C	94
Macronectes giganteus	Giant petrel	3,890	4,330	Pr	M	C	124
Pygoscelis adeliae	Adelie penguin	3,990	3,790	Sp	M	C	25, 36, 119
Eudyptes chrysolophus	Macaroni penguin	4,270	2,950	Sp	M	C	172
Pygoscelis papua	Gentoo penguin	6,170	4,650	Sp	M	C	47, 172
Diomedea exulans	Wandering albatross	8,420	3,350	Pr	M	C	102
Aptenodytes patagonicus	King penguin	12,900	7,410	Sp	M	C	75
Struthio camelus	Ostrich	88,300	18,000	St	D	O	172
Reptiles							
Mesalina olivieri	Sand lizard	1.1	0.29	La	SA	I	156
Rhoptropus afer	Namib Desert gecko	2.6	0.23	Ge	D	I	121
Urosaurus nigricaudus	Black-tailed brush lizard	3.2	1.38	Ph	SC	I	60
Uta stansburiana	Side-blotched lizard	3.2	0.67	Ph	D	I	60, 101
Pedioplanis lineoocellata	Spotted sand lizard	3.3	0.54	La	D	I	111
Heliobolus lugubris	Bushveld lizard	3.8	0.80	La	D	I	111
Meroles anchietae	Namib Desert dune lizard	4.0	0.60	La	D	O	137
Cnemidophorus hyperythrus	Orangethroat whiptail	4.3	1.13	Te	SC	I	60, 68
Acanthodactylus pardalis	Sand lizard	4.5	0.23	La	SA	I	156
Sceloporus graciosus	Sagebrush lizard	5.0	0.82	Ph	SC	I	33
Sceloporus virgatus	Striped plateau lizard	6.3	1.06	Ph	SC	I	88
Callisaurus draconoides	Zebra-tailed lizard	7.1	1.12	Ph	D	I	69
Podarcis lilfordi	Lacertid lizard	7.4	1.49	La	SC/ME	I	19
Sceloporus variabilis	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
Chalcides sexlineatus	Gran Canarian skink	7.8	0.72	Sc	STR	I	20
Ptyodactylus hasselquistii	Negev Desert gecko	9.1	1.2	Ge	D	I	108
Varanus caudolineatus	Goanna/monitor lizard	10.4	3.0	Va	SA/SC	C	150
Galloti altantica	Agamid lizard	11.9	1.5	La	STR	H	155
Sceloporus occidentalis	Western fence lizard	12.1	1.8	Ph	SC	I	11, 13
Cnemidophorus tigris	Western whiptail	16.5	4.1	Te	D	I	2, 3
Pachydactylus bibronii	Birbon's gecko	16.6	2.2	Ge	D	I	112
Sceloporus jarrovi	Yarrow's spiny lizard	16.6	1.9	Ph	SC	I	10, 83
Mabuya striata	Stiped skink	19.5	2.9	Sc	D	I	112
Thamnophis sirtalis	Common garter snake	22.0	5.2	Co	SC	C	129
Phrynosoma platyrhinos	Desert horned lizard	23.0	2.7	Ph	D	I	21
Elgaria multicarinatus	Southern alligator lizard	25.3	2.0	An	SC	I	70
Lacerta viridis	Common lizard	25.5	5.8	La	TE	I	17
Galloti galloti	Agamid lizard	25.6	4.6	La	STR	H	155
Microlophus albemariensis	Lava lizard	28.2	3.3	Tr	IT	I	99
Ctenophorus nuchalis	Central netted dragon	36.8	9.6	Ag	D	I	105
Galloti stehlini	Giant agamid lizard	47.3	7.9	La	STR	H	155
Dipsosaurus dorsalis	Desert iguana	52.5	6.5	Ig	D	H	85
Agama impalearis	Bibron's agama	54.4	16.8	Ag	D	I	173
Angolosaurus skoogi	Skoog's lizard	57.4	3.0	Gr	D	H	107
Varanus acanthurus	Ridge-tailed monitor	60.0	3.7	Va	TE	C	41
Varanus scalaris	Goanna/monitor lizard	66.4	7.8	Va	EW	C	29
Vipera aspis	European viper	67.2	6.3	Vi	TE	C	17
Crotalus lepidus	Mottled rock rattlesnakes	109	4.7	Vi	SC	C	9
Masticophus flagellum	Coachwhip	124	11.7	Co	D	C	139
Crotalus cerastes	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
Coluber constrictor	Racer	132	12.8	Co	W	C	132
Sauromalus obesus	Chuckwalla	167	15.7	Ig	D	H	122
Chlamydosaurus kingii	Frillneck lizard	635	52.4	Ag	W	I	28
Iguana iguana	Green iguana	860	60.1	Ig	SA	H	153
Tupinambis teguixin	Tegu	1,170	214	Te	TR	C	57
Varanus rosenbergi	Goanna/monitor lizard	1,180	100	Va	EW	C	56
Varanus mertensi	Merten's water monitor	1,210	143	Va	M	C	31
Varanus gouldii	Sand monitor	1,320	233	Va	TRW	C	30
Varanus panoptes	Goanna/monitor	1,350	180	Va	TRW/RI	C	30
Amblyrhynchus cristatus	Galapagos marine iguana	1,610	91.2	Ig	M	H	123
Gopherus agassizzi	Desert tortoise	2,120	42.9	Ts	D	H	64, 114, 128
Varanus bengalensis	Bengal monitor	2,560	393	Va	TR	C	40
Varanus salvator	Goanna/monitor lizard	7,530	906	Va	SA/TR	C	40
Varanus giganteus	Perenties	7,700	807	Va	DTR	C	40, 59
Varanus komodensis	Komodo dragon	45,200	2,430	Va	TR	C	58

[a] Body mass and FMR values are means or weighted means where more than one study per species is available.

[b] Marsupial (marsup.) mammals: Squirrel (sqrl.); 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, Procellariformes; Ch, Charadriiformes; Pi, Piciformes; Cl, Columbiformes; Ga, Galliformes; Fa, Falconiformes; Pe, Pelicaniformes; Sp, Sphenisciformes; St, Struthioniformes. Reptiles: Squamata (families): Ag, Agamidae; An, Anguidae; Co, Colubridae; Ge, Gekkonidae; Gr, Gerrhosauride; Ig, Iguanidae; La, Lacertidae; Ph, Phrynosomatidae; Sc, Scincidae; Te, Teiidae; Tr, Tropiduridae; Va, Varanidae; Vi, Viperidae. Testudines: Ts, Testudinidae.

[c] Habitat: 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, semiarid; 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.

[d] Diet: 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 CO_2 to kilojoules using the factors 21.7 kJ per liter of CO_2 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]

						Statistics for 95% CI of prediction				
Group	*a*	*b*	*n*	r^2	*P*	Mean log x	c	d	e	Equation
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

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[a] The equations are in the power form: 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:

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

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

As an example of how to use these equations, we show the results of predicting the FMR ± 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), kJ/day $= 15.94(\mathrm{g})^{0.53}$ (22); aerially foraging birds with nestlings (seven species of Hirundines), kJ/day $= 21.9(\mathrm{g})^{0.53}$ (166); ground-foraging, flycatching, and piscivorous birds with nestlings (11 species), kJ/day $= 7.76(\mathrm{g})^{0.75}$ (166); incubating birds (17 species), kJ/day $= 12.93(\mathrm{g})^{0.61}$ (148); seabirds (23 species), kJ/day $= 12.0(\mathrm{g})^{0.667}$ (15); cold-water seabirds (5 species), kJ/day $= 15.6(\mathrm{g})^{0.646}$ (15); warm-water seabirds (16 species), kJ/day $= 9.16(\mathrm{g})^{0.646}$ (15); seabirds using flapping flight (10 species), $10.3(\mathrm{g})^{0.726}$ (15); seabirds not using flapping flight (13 species), kJ/day $= 6.63(\mathrm{g})^{0.726}$ (15); cold-water seabirds using flapping flight (8 species), kJ/day $= 11.5(\mathrm{g})^{0.727}$ (15); hovering nectarivores (five species of hummingbirds), kJ/day $= 5.61(\mathrm{g})^{1.21}$ (161); perching nectarivores (three species of honeyeaters), kJ/day $= 11.0(\mathrm{g})^{0.697}$ (161); birds during parental care (30 species), kJ/day $= 13.8(\mathrm{g})^{0.65}$ (84); and fledgling birds (11 species), kJ/day $= 4.58(\mathrm{g})^{0.76}$ (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,

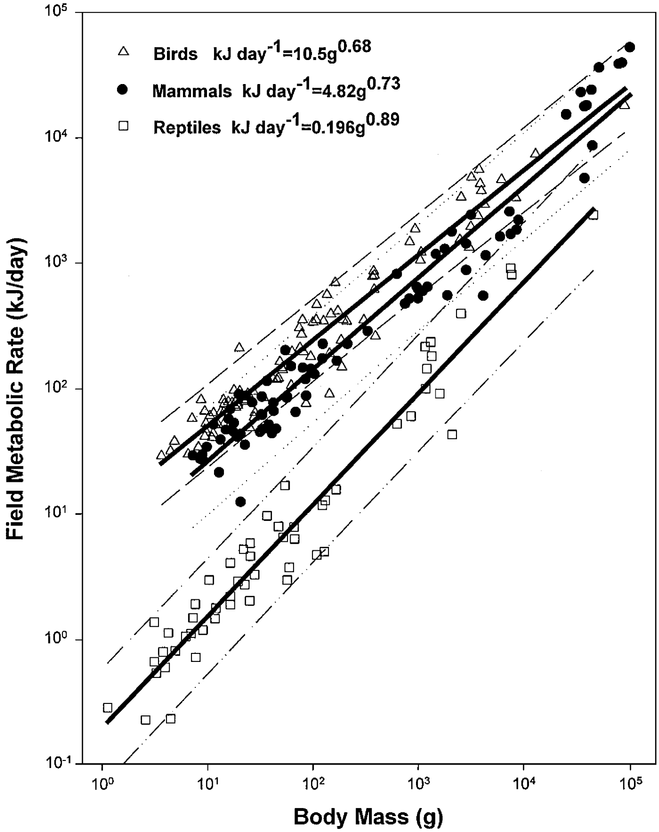

Figure 1 Allometry of field metabolic rate in terrestrial vertebrates. (*Solid lines*) least-squares linear regression lines for birds, mammals, and reptiles (see Equations 1, 17, and 32 in Table 2); (*dashed or dotted lines*) 95% confidence intervals of the prediction for each line.

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 kJ/day ÷ 16.8 kJ/g of DM ⇒) 946 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 g of FM/0.30 g of DM = 3.33 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 g of DM/day × 3.33 g of FM/g of DM ⇒) 3150 g of FM/day (a little over 3 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 montreme, 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 nonpasserine 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 Procellariformes 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, Tropiduridae, 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-Edmonds & 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.

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