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Food requirements of wild animals: Predictive equations for free-living mammals, reptiles, and birds

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Abstract

Feeding rates (intake of both dry matter and fresh matter) by 79 species of mammals, 95 species of birds and 55 species of reptiles were estimated from doubly labeled water-based measurements of field metabolic rate on each species. Allometric (scaling) regression analyses of $\log_{10}$-transformed feeding rates vs. body mass yielded statistically significant relationships for 90 different taxonomic, dietary and habitat groupings of species. The resulting exponential equations can be used to predict the daily food requirements needed to maintain energy balance for free-living mammals, birds, and reptiles with an average error of about 5% to 60%, depending on the group. The ability to predict feeding rates of terrestrial vertebrates should be useful to zoo keepers, animal nutritionists, veterinarians, pet hobbyists, wildlife zoologists, game managers, range biologists, preserve directors and planners, conservationists, paleontologists and ecosystem modelers. These equations should underestimate somewhat the feeding rates of free-living animals that are growing, reproducing or storing up fat. The equations probably overestimate the feeding rates of captive wild animals (e.g. in zoos) and of free-ranging animals during some phases of their lives when they either do not or cannot feed normally.

Key words

allometry, bioenergetics, diet effect, dry matter intake, feeding rate, fresh matter intake, habitat effect, scaling

Introduction

One of the first questions people ask about a wild animal is "What does it eat?" Those who work with animals also want to know "How much does it eat each day?" Zoo keepers, animal nutritionists, veterinarians, pet hobbyists, wildlife zoologists, game managers, range biologists, preserve managers, conservationists, paleontologists and ecosystem modelers are among the people that are concerned about the daily food needs of different species of living and extinct mammals, birds and reptiles. The utility of such information ranges from practical applications to theoretical evaluation of the role of vertebrate consumers in models of the biosphere.

Early estimates of the food needs of wild animals were based on laboratory measurements of rates of oxygen consumption or carbon dioxide production (indirect calorimetry). Corrections to account for the differences between metabolic rates measured in captivity and those in the field were problematic, and largely conjectural. Fortunately, the advent of the doubly labeled water method (Lifson and McClintock, 1966) has made it possible to measure carbon dioxide production in free-living, air-breathing vertebrates in their natural habitats. The field metabolic rates (FMRs) of over 229 species of terrestrial vertebrates have now been determined with this technique. The size of the animal, expressed as body mass, explains most of the difference in whole-animal FMR between species, with larger animals generally (but not always) using more total energy each day than do smaller ones. Taxonomic Class (mammal, bird, reptile) explains much of the remaining difference between species. Thus, allometric or scaling analyses ($\log_{10}$ FMR in kilojoules metabolized per day versus $\log_{10}$ body mass in grams) indicate that, within each Class, log body mass explains about 94% of the variation in log FMR between species (Nagy *et al.*, 1999). The equations describing these allometric relationships can be used to predict the FMRs of species that have not yet been studied.

The food requirement of an animal can be estimated from its energy requirement by calculating the amount of food needed to provide that amount of metabolisable energy. This review includes allometric equations for predicting both dry matter and fresh matter intake rates for wild reptiles, birds, and mammals living in their natural habitats, as derived from FMR measurements along with information about dietary energy content. Animals that are held captive, as in zoos, corrals or cages, will probably but not necessarily have lower daily food needs than those estimated from the equations herein, due to lower activity levels and more benign microclimates than those they experience in nature.

Methods

Field feeding rates were estimated from field metabolic rates, as measured using the doubly labeled water method (Lifson and McClintock, 1966; Nagy, 1983; Speakman, 1997) for the 229 species of terrestrial vertebrates summarized in the recent review by Nagy *et al.* (1999; see link *http://nutr.AnnualReviews.org/cgi/content/full/19/1/247* for references to individual studies). The FMR for a species, in units of kJ/d, was divided by the metabolisable energy content of its diet, either in units of metabolisable kJ/g dry matter or in units of metabolisable kJ/g fresh matter, to calculate feeding rates in units of g dry matter intake (DMI)/d or in units of g fresh matter intake (FMI)/d. Metabolisable energy, as used in this review, is defined as gross food energy minus energy excreted as feces and urine, and values based on dry matter for the various diets were taken from Nagy *et al.* (1999). These values were converted to units of fresh matter using average dietary water content values of 66% for insects, 70% for a carnivore's diet, 67% for green plant matter, 68% for an omnivore's diet, 10% for dry seeds, 76% for nectar, 73% for fruit, and 73% for fish (from Nagy and Peterson, 1988).

The conversion factors used were: mammalian insectivore (having urea excretion), 18.7 kJ/g DMI and 6.17 kJ/g FMI; bird and reptile insectivore (having uric acid excretion), 18.0 kJ/g DMI and 5.94 kJ/g FMI; mammalian carnivore (excluding fish eating), 16.8 kJ/g DMI and 5.04 kJ/g FMI; avian and reptilian carnivore (not fish), 15.4kJ/g DMI and 4.61 kJ/g FMI; mammal eating a fish diet (piscivore), 18.7 kJ/g DMI and 5.11 kJ/g FMI; avian piscivore, 16.2 kJ/g DMI and 4.43 kJ/g FMI; herbivore (fermenter), 11.5 kJ/g DMI and 3.80 kJ/g FMI; herbivore (nonfermenter), 10.0 kJ/g DMI and 3.30 kJ/g FMI; omnivore, 14.0 kJ/g DMI and 4.48 kJ/g FMI; granivore, 16.9 kJ/g DMI and 15.4 kJ/g FMI (relatively high, due to the low water content of seeds); nectarivore, 16.0 kJ/g DMI and 3.76 kJ/g FMI; and frugivore, 6.6 kJ/g DMI and 1.50 kJ/g FMI. These factors were used to calculate all feeding rates reported in this review, even though more detailed conversion factors and feeding rate estimates are reported in a few of the research articles on individual species. The differences resulting from this simplification will have only a small influence on the regression of log-transformed data.

The calculated feeding rates for 79 species of mammals, 95 species of birds, and 55 species of reptiles for which FMRs have been measured are shown in Table 1. Also shown are details regarding

Table 1. Summary of feeding rates calculated from measured field metabolic rates in free-living mammals, birds, and reptiles (sorted by body mass). Values are daily intake rates for dry matter (DMI) and fresh matter (FMI), both in grams of food per day.

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
MAMMALS							
Pipistrellus pipistrellus	Pipistrelle	7.30	1.57	4.75	Ch	ND	I
Plecotus auritus	Brown long-eared bat	8.50	1.48	4.47	Ch	ND	I
Myotis lucifugus	Little brown bat	9.00	1.60	4.85	Ch	ND	I
Gerbillus henleyi	Northern pygmy gerbil	9.25	1.57	1.72	Ro	D	G
Tarsipes rostratus	Honey possum	9.90	2.15	9.15	Tr	ND	N
Anoura caudifer	Flower-visiting bat	11.5	3.24	13.8	Ch	ND	N
Macrotus californicus	Big-eared bat	13.0	1.15	3.48	Ch	D	I
Peromyscus crinitus	Cactus mouse	13.4	2.81	8.77	Ro	D	O
Mus domesticus	Wild house mouse	15.1	3.37	10.5	Ro	D	O
Cleithrionomys rutilus	Bank vole	16.0	5.76	17.5	Ro	ND	H
Sminthopsis crassicaudata	Narrow-footed marsupial mouse	16.6	3.67	11.1	Da	ND	I
Perognathus formosus	Long-tailed pocket mouse	17.9	2.67	2.93	Ro	D	G
Peromyscus maniculatus	Deer mouse	17.9	3.81	11.9	Ro	D	O
Peromyscus leucopus	White-footed deer mouse	19.2	2.96	9.24	Ro	ND	O
Microtus arvalis	Meadow mouse	20.0	6.43	20.1	Ro	ND	O
Eremitalpa namibensis	Namib Desert golden mole	20.7	0.67	2.02	In	D	I
Eptesicus fuscus	Big brown bat	20.8	2.33	7.07	Ch	ND	I
Gerbillus allenbyi	Allenby's gerbil	22.8	2.11	2.31	Ro	D	G
Cleithrionomys glareolus	Bank vole	23.4	8.80	26.7	Ro	ND	H
Microtus agrestis	Field vole	26.8	7.78	23.6	Ro	ND	H
Gerbillus pyramidum	Greater Egyptian gerbil	31.8	2.67	2.94	Ro	D	G
Pseudomys albocinereus	Australian native mouse	32.6	4.44	13.9	Ro	ND	O
Antechinus stuartii	Brown antechinus	33.0	4.62	14.0	Da	ND	I
Phascogale calura	Wambenger	33.5	3.68	12.3	Da	ND	C
Dipodomys merriami	Merriam's kangaroo rat	34.3	2.82	3.09	Ro	D	G
Microtus pennsylvanicus	Meadow vole	36.9	11.5	34.9	Ro	ND	H

Table 1. *(Continued)*

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
Acomys cahirinus	Common spiny mouse	38.3	3.70	11.6	Ro	D	O
Sekeetamys calurus	Bushy-tailed jird	41.2	3.14	9.82	Ro	D	O
Microgale dobsoni	Shrew-tenrec	42.6	4.12	12.5	In	ND	I
Microgale talazaci	Shrew-tenrec	42.8	3.56	10.8	In	ND	I
Acomys russatus	Golden spiny mouse	45.0	3.41	10.7	Ro	D	O
Lemmus trimucronatus	Brown lemming	55.2	20.1	60.9	Ro	ND	H
Dipodomys microps	Chisel-toothed kangaroo rat	57.1	6.04	18.9	Ro	D	O
Praomys natalensis	Multi-mammate mouse	57.3	6.19	19.3	Ro	ND	O
Antechinus swainsonii	Broad-footed marsupial mouse	62.6	8.02	24.3	Da	ND	I
Meriones crassus	Jird	69.2	3.85	4.22	Ro	D	G
Phyllostomus hastatus	Spear-nosed bat	80.8	7.80	23.7	Ch	ND	I
Arvicola terrestris	Water vole	85.8	11.9	36.0	Ro	ND	H
Ammospermophilus leucurus	Antelope ground squirrel	87.0	6.29	19.6	Ro	D	O
Tamias striatus	Eastern chipmunk	96.3	10.2	31.9	Ro	ND	O
Thomomys bottae	Botta's pocket gopher	104	13.0	39.5	Ro	ND	H
Petaurus breviceps	Sugar glider	124	12.3	38.5	Pt	ND	O
Gymnobelideus leadbeateri	Leadbeater's possum	125	16.1	50.3	Pt	ND	O
Psammomys obesus	Fat sand rat	170	16.5	50.1	Ro	D	H
Spermophilus saturatus	Golden-mantled ground squirrel	214	22.6	68.5	Ro	ND	H
Isoodon auratus	Golden bandicoot	333	20.4	63.6	Pe	ND	O
Spermophilus parryi	Arctic ground squirrel	630	58.4	182	Ro	ND	O
Bassariscus astutus	Ring-tailed cat	752	28.1	93.7	Ca	D	C
Potorous tridactylus	Long-nosed potoroo	825	51.7	157	Ma	ND	H
Vulpes cana	Blanford's fox	972	38.2	127	Ca	D	C
Petauroides volans	Greater glider	995	52.0	158	Pt	ND	H
Pseudocheirus peregrinus	Ring-tail possum	1000	61.5	186	Pt	ND	H
Bettongia penicillata	Short-nosed rat kangaroo	1100	59.3	180	Ma	ND	H
Isoodon obesulus	Short-nosed brown bandicoot	1230	46.0	144	Pe	ND	O
Vulpes macrotis	Kit fox	1480	70.2	234	Ca	D	C
Lepus californicus	Black-tailed jackrabbit	1800	130	394	La	D	H
Setonix brachyurus	Quokka	1900	47.7	144	Ma	ND	H
Vulpes velox	Swift fox	2100	106	353	Ca	ND	C
Aepyrpimnus rufescens	Rufous rat kangaroo	2860	124	376	Ma	ND	H
Tachyglosssus aculeatus	Echidna	2860	46.8	142	Ta	ND	I
Marmota flaviventris	Yellow-bellied marmot	3190	243	736	Ro	ND	H
Bradypus variegatus	Three-toed sloth	4150	54.5	165	Xe	ND	H
Macropus eugenii	Tammar wallaby	4380	100	303	Ma	ND	H
Thylogale billiardieri	Red-bellied wallaby	5980	142	429	Ma	ND	H
Alouatta palliata	Mantled howler monkey	7330	258	782	Pr	ND	H
Phascolarctos cinereus	Koala	7520	171	518	Ph	ND	H
Proteles cristatus	Aardwolf	8540	98.9	300	Ca	D	I
Petrogale xanthopus	Rock wallaby	8900	192	582	Ma	ND	H
Lyacon pictus	African wild dog	25170	911	3036	Ca	D	C
Arctocephalus gazella	Antarctic fur seal	34600	1230	4501	Pi	M	C
Canis lupus	Timber wolf	37300	1054	3512	Ca	ND	C
Arctocephalus galapagoensis	Galapagos fur seal	37400	256	935	Pi	M	C
Odocoileus hemionus	Mule deer	39100	1565	4737	Ar	ND	H

Table 1. *(Continued)*

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
Antidorcas marsupialis	Springbok	43300	2096	6342	Ar	D	H
Macropus giganteus	Eastern grey kangaroo	44500	754	2282	Ma	ND	H
Callorhinus ursinus	Northern fur seal	51100	1930	7065	Pi	M	C
Zalophus californianus	California sea lion	78000	2064	7554	Pi	M	C
Neophoca cinerea	Australian sea lion	83500	2112	7730	Pi	M	C
Phoca vitulina	Common seal	99000	2807	10274	Pi	M	C
BIRDS							
Archilochus alexandri	Black-chinned hummingbird	3.7	1.82	7.74	Ap	TeF	N
Calypte anna	Anna's hummingbird	4.5	1.99	8.46	Ap	CS	N
Thalurania colombica	Crowned woodnymph	4.9	2.37	10.1	Ap	TF	N
Auriparus flaviceps	Verdin	6.6	1.67	5.05	Pa	D	I
Chalybura urochrysia	Bronze-tailed plumeleteer	7.2	3.62	15.4	Ap	TF	N
Malurus cyaneus	Superb blue wren	8.3	1.90	5.76	Pa	TeF	I
Lampornis clemenciae	Blue-throated hummingbird	8.8	5.11	21.7	Ap	TeF	N
Zosterops lateralis	Grey-breasted silvereye	9.5	6.32	27.8	Pa	EF	F
Parus ater	Coal tit	9.5	2.63	7.98	Pa	CF	I
Nectarinia violacea	Orange-breasted sunbird	9.5	4.14	17.6	Pa	FY	N
Acanthorhynchus tenuirostris	Eastern spinebill	9.7	3.31	14.1	Pa	TeF	N
Troglodytes aedon	House wren	10.6	3.38	10.2	Pa	TeF	I
Parus cristatus	Crested tit	11.1	2.26	6.84	Pa	CF	I
Parus montanus	Willow tit	11.4	2.45	7.42	Pa	CF	I
Parus caeruleus	Blue tit	11.5	3.56	10.8	Pa	CF	I
Eremiornis carteri	Spinifexbird	12.0	2.86	8.67	Pa	D	I
Parus cinctus	Siberian tit	12.8	2.86	8.65	Pa	CF	I
Ficedula hypoleuca	Pied flycatcher	13.5	3.66	11.1	Pa	OW	I
Riparia riparia	Sand martin	14.3	4.54	13.8	Pa	TM	I
Muscicapa striata	Pacific swallow	14.4	2.89	8.75	Pa	TeF	I
Hirundo tahitica	Spotted flycatcher	14.4	3.61	10.9	Pa	TF	I
Phylidonyris pyrrhoptera	Crescent honeyeater	14.6	4.74	20.2	Pa	TeF	N
Ficedula albicollis	Collared flycatcher	15.9	4.37	13.2	Pa	TeF	I
Phylidonyris novaehollandiae	New Holland honeyeater	17.3	4.85	20.6	Pa	TeF	N
Parus major	Great tit	18.0	6.96	21.7	Pa	TeF	O
Erithacus rubecula	Robin	18.7	3.96	12.0	Pa	TeF	I
Passerculus sandwichensis	Savannah sparrow	18.7	5.74	17.9	Pa	SM	O
Delichon urbica	House martin	19.0	4.43	13.4	Pa	TM	I
Junco phaeonotus	Yellow-eyed junco	19.5	5.27	16.5	Pa	TM	O
Junco hyemalis	Dark-eyed junco	19.6	5.47	17.1	Pa	TM	O
Tachycineata bicolor	Tree swallow	20.2	11.6	35.2	Pa	TM	I
Hirundo rustica	Barn swallow	20.4	5.32	16.1	Pa	TM	I
Prunella modularis	Dunnocky	21.2	4.78	14.5	Pa	TeF	I
Phainopepla nitens	Phainopepla	22.7	5.65	17.7	Pa	D	O
Cormobates leucophaeus	White-throated treecreeper	23.7	4.52	13.7	Pa	TeF	I
Oenanthe oenanthe	Northern wheatear	24.3	5.08	15.4	Pa	TM	I
Pyrrhula pyrrhula	Bullfinch	25.1	5.21	5.71	Pa	TeF	G
Philetairus socius	Sociable weaver	25.5	3.48	10.9	Pa	D	O
Sialia mexicana	Western bluebird	27.4	5.28	16.0	Pa	TeF	I
Melopsittacus undulatus	Budgerigar	27.9	4.22	13.2	Ps	D	O

Table 1. *(Continued)*

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
Mirafra erythrochlamys	Dune lark	28.5	4.59	14.4	Pa	D	O
Merops viridas	Blue-throated bee-eater	34.3	4.74	14.4	Co	TF	I
Oceanites oceanus	Wilson's storm-petrel	42.3	7.35	26.9	Pr	M	C
Oceanodroma leucorhoa	Leach's storm-petrel	45.9	7.28	26.6	Pr	M	C
Mimus polyglottos	Mockingbird	47.6	8.64	27.0	Pa	DF	O
Progne subis	Purple martin	49.0	9.06	27.4	Pa	DF	I
Actitis hypoleucos	Common sandpiper	51.6	9.01	33.0	Ch	M	C
Calidris alba	Sanderling	52.0	8.70	31.8	Ch	M	C
Neophema petrophila	Rock parrot	62.8	7.57	23.7	Ps	D	O
Cinclus cinclus	Dipper	63.7	10.9	33.0	Pa	TM	I
Charadrius hiaticula	Ringed plover	74.8	18.6	68.2	Ch	M	C
Ceryle rudis	Pied kingfisher	76.0	13.6	45.6	Co	TF	C
Sturnus vulgaris	Starling	78.7	19.2	60.0	Pa	DF	O
Aethia pusilla	Least auklet	80.3	21.6	79.0	Ch	M	C
Melanerpes formicivorous	Acorn woodpecker	82.0	13.9	43.5	Pi	OW	O
Geophaps plumifera	Spinifex pigeon	87.0	4.50	4.94	Cl	D	G
Turdus merula	Blackbird	96.0	9.94	30.1	Pa	TeF	I
Sterna paradisaea	Arctic tern	101	20.7	75.6	Ch	M	C
Arenaria interpres	Ruddy turnstone	108	21.7	79.5	Ch	M	C
Pelecanoides georgicus	South Georgia diving petrel	109	28.6	105	Pr	M	C
Sterna hirundo	Common tern	127	21.2	77.4	Ch	M	C
Pelecanoides urinatrix	Common diving petrel	137	34.4	126	Pr	M	C
Callipepla gambelii	Gambel's quail	145	6.49	20.3	Ga	D	O
Barnardius zonarius	Port Lincoln parrot	145	13.5	42.2	Ps	D	O
Pachyptila desolata	Antarctic prion	149	24.1	88.3	Pr	M	C
Alle alle	Dovkie	164	43.0	157	Ch	M	C
Ptychoramphus aleuticus	Cassin's auklet	174	25.5	93.2	Ch	M	C
Sterna fuscata	Sooty tern	187	14.9	54.4	Ch	M	C
Ammoperdix heyi	Sand partridge	190	10.6	33.0	Ga	D	O
Anous stolidus	Brown noddy	195	21.7	79.5	Ch	M	C
Falco tinnunculus	Eurasian kestrel	211	22.1	73.9	Fa	TM	C
Cacatua roseicapilla	Galah	307	24.9	77.9	Ps	D	O
Phaethon lepturus	White-tailed tropicbird	370	48.0	175	Pe	M	C
Cepphus grylle	Black guillemot	380	53.1	194	Ch	M	C
Puffinus pacificus	Wedge-tailed shearwater	384	37.9	139	Pr	M	C
Rissa tridactyla	Black-legged kittiwake	386	49.1	179	Ch	M	C
Alectoris chukar	Chukar	395	18.6	58.0	Ga	D	O
Uria lomvia	Thick-billed murre	834	91.4	334	Ch	M	C
Uria aalga	Guillemot	940	115	422	Ch	M	C
Eudyptula minor	Little penguin	1050	64.8	237	Sp	M	C
Sula sula	Red-footed booby	1070	75.3	275	Pe	M	C
Centrocercus urophasianus	Sage grouse	2500	91.1	100	Ga	D	G
Morus capensis	Cape gannet	2580	209	763	Pe	M	C
Diomedea immutabilis	Laysan albatross	3070	82.1	300	Pr	M	C
Spheniscus demersus	Jackass penguin	3170	120	440	Sp	M	C
Sula bassanus	Northern gannet	3210	301	1099	Pe	M	C
Diomedea chrysostoma	Grey-headed albatross	3710	148	540	Pr	M	C

Table 1. *(Continued)*

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
Pygoscelis antarctica	Chinstrap penguin	3790	346	1264	Sp	M	C
Macronectes giganteus	Giant petrel	3890	267	977	Pr	M	C
Pygoscelis adeliae	Adelie penguin	3990	234	856	Sp	M	C
Eudyptes chrysolophus	Macaroni penguin	4270	182	666	Sp	M	C
Pygoscelis papua	Gentoo penguin	6170	287	1050	Sp	M	C
Diomedea exulans	Wandering albatross	8420	207	756	Pr	M	C
Aptenodytes patagonicus	King penguin	12900	457	1673	Sp	M	C
Struthio camelus	Ostrich	88300	1286	4018	St	D	O
REPTILES							
Mesalina olivieri	Sand lizard	1.1	0.016	0.048	La	SA	I
Rhoptropus afer	Namib Desert gecko	2.6	0.013	0.038	Ge	D	I
Urosaurus nigricaudus	Black-tailed brush lizard	3.2	0.077	0.232	Ph	A	I
Uta stansburiana	Side-blotched lizard	3.2	0.037	0.112	Ph	D	I
Pedioplanis lineoocellata	Spotted sand lizard	3.3	0.030	0.091	La	D	I
Heliobolus lugubris	Bushveld lizard	3.8	0.044	0.135	La	D	I
Meroles anchietae	Namib Desert dune lizard	4.0	0.043	0.134	La	D	O
Cnemidophorus hyperythrus	Orangethroat whiptail	4.3	0.063	0.190	Te	A	I
Acanthodactylus pardalis	Sand lizard	4.5	0.013	0.039	La	SA	I
Sceloporus graciosus	Sagebrush lizard	5.0	0.045	0.137	Ph	SC	I
Sceloporus virgatus	Striped plateau lizard	6.3	0.059	0.178	Ph	A	I
Callisaurus draconoides	Zebra-tailed lizard	7.1	0.062	0.189	Ph	D	I
Podarcis lilfordi	Lacertid lizard	7.4	0.083	0.251	La	A	I
Sceloporus variabilis	Rosebelly lizard	7.7	0.106	0.322	Ph	TR	I
Chalcides sexlineatus	Gran Canarian skink	7.8	0.040	0.121	Sc	STR	I
Ptyodactylus hasselquistii	Negev Desert gecko	9.1	0.066	0.200	Ge	D	I
Varanus caudolineatus	Goanna/monitor lizard	10.4	0.193	0.644	Va	SA/SC	C
Gallotia atlantica	Agamid lizard	11.9	0.147	0.445	La	STR	H
Sceloporus occidentalis	Western fence lizard	12.1	0.099	0.300	Ph	SC	I
Cnemidophorus tigris	Western whiptail	16.5	0.225	0.682	Te	D	I
Pachydactylus bibroni	Bibron's gecko	16.6	0.122	0.370	Ge	A	I
Sceloporus jarrovi	Yarrow's spiny lizard	16.6	0.106	0.320	Ph	SC	I
Mabuya striata	Striped skink	19.5	0.161	0.488	Sc	D	I
Thamnophis sirtalis	Common garter snake	22.0	0.338	1.13	Co	SC	C
Phrynosoma platyrhinos	Desert horned lizard	22.6	0.152	0.460	Ph	D	I
Elgaria multicarinatus	Southern alligator lizard	25.3	0.113	0.342	An	SC	I
Lacerta viridis	Common lizard	25.5	0.324	0.981	La	TE	I
Gallotia galloti	Agamid lizard	25.6	0.459	1.39	La	STR	H
Microlophus albemariensis	Lava lizard	28.2	0.182	0.551	Tr	IT	I
Ctenophorus nuchalis	Central netted dragon	36.8	0.535	1.62	Ag	D	I
Gallotia stehlini	Giant agamid lizard	47.3	0.791	2.40	La	STR	H
Dipsosaurus dorsalis	Desert iguana	52.5	0.648	1.96	Ph	D	H
Agama impalearis	Bibron's agama	54.4	0.933	2.83	Ag	D	I
Angolosaurus skoogi	Skoog's lizard	57.4	0.297	0.900	Gr	D	H
Varanus acanthurus	Ridge-tailed monitor	60.0	0.242	0.809	Va	TE	C
Varanus scalaris	Goanna/monitor lizard	66.4	0.506	1.69	Va	EW	C
Vipera aspis	European viper	67.2	0.409	1.37	Vi	TE	C
Crotalus lepidus	Mottled rock rattlesnake	109	0.305	1.02	Vi	SC	C

Table 1. *(Continued)*

Genus, species	Common name	Mass, g	DMI, g/d	FMI, g/d	Taxon	Habitat	Diet
Masticophus flagellum	Coachwhip	124	0.760	2.54	Co	D	C
Crotalus cerastes	Sidewinder	129	0.324	1.08	Vi	D	C
Coluber constrictor	Racer	132	0.831	2.78	Co	W	C
Sauromalus obesus	Chuckwalla	167	1.57	4.74	Ig	D	H
Chlamydosaurus kingii	Frillneck lizard	635	2.91	8.82	Ag	W	I
Iguana iguana	Green iguana	860	6.01	18.2	Ig	SA	H
Tupinambis teguixin	Tegu	1170	13.9	46.4	Te	TR	C
Varanus rosenbergi	Goanna/monitor lizard	1180	6.49	21.7	Va	EW	C
Varanus mertensi	Merten's water monitor	1210	8.85	32.3	Va	M	C
Varanus gouldii	Sand monitor	1320	15.1	50.5	Va	TRW	C
Varanus panoptes	Goanna/monitor lizard	1350	11.7	39.0	Va	TRW/RI	C
Amblyrhynchus cristatus	Galapagos marine iguana	1610	9.12	27.6	Ig	M	H
Gopherus agassizzi	Desert tortoise	2120	4.29	13.0	Ts	D	H
Varanus bengalensis	Bengal monitor	2560	25.5	85.2	Va	TR	C
Varanus salvator	Goanna/monitor lizard	7530	58.8	197	Va	SA/TR	C
Varanus giganteus	Perentie	7700	52.4	175	Va	DTR	C
Varanus komodoensis	Komodo dragon	45200	158	527	Va	TR	C

TAXON: MARSUPIAL MAMMALS: 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 = Gerrhosauridae, Ig = Iguanidae, La = Lacertidae, Ph = Phrynosomatidae, Sc = Scincidae, Te = Teiidae, Tr = Tropiduridae, Va = Varanidae, Vi = Viperidae; TESTUDINES: Ts = Testudinidae; the clade Iguania includes families Ag, Ig, Ph, and Tr; clade Scleroglossa includes An, Co, Ge, Gr, La, Sc, Te, and Va.

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, IT = intertidal, ME = mediterranean

DIET: I = insectivore, G = granivore, N = nectarivore, O = omnivore, H = herbivore, C = carnivore, F = frugivore

taxonomic affiliation (order or family), habitat, and diet. These feeding rates are those needed to provide the metabolizable energy the animals burn in the field, so they represent "steady-state" conditions. Free-living animals that are growing or reproducing or storing fat for winter or migration will have feeding rates that are higher, perhaps even much higher, than estimated for the steady-state situation. Similarly, animals that are using body stores of energy during migration, rut, torpor, hibernation, etc. will have actual feeding rates that are lower than calculated, or even nonexistent. However, FMR data, and thus feeding rate estimates, from endothermic animals undergoing starvation were not included in this analysis, nor were data from reptiles during inactive seasons (e.g. winter) or from juvenile birds or mammals that were not self-supporting.

Regression analyses were done on the $\log_{10}$-transformed data for all mammals, all birds and all reptiles, as well as on every taxonomic, habitat and dietary category within those Classes, where sample sizes were adequate. Every regression for a category that was statistically significant, judging by a probability value < 0.05 according to an F-test for significance of the regression, is shown in Table 2 (mammals), Table 3 (birds), or Table 4 (reptiles). The regressions for desert marsupials (Equations 17 and 18) were calculated from new FMR data (Nagy and Bradshaw, 2000). Statistical tests to determine if allometric relationships in these tables differed from each other were beyond the scope of this review. Also not done were independent contrasts analyses (ICA), which adjust for phylogenetic relatedness (Garland *et al.*, 1993). However, the FMR data on which the feeding rates in this article were based were subjected to independent contrasts analysis, and the reader is referred to Nagy *et al.* (1999) for details. In general, ICA yielded statistically similar slopes (a) and intercepts (b) for conventional FMR regressions, and the same result would be expected for ICA of the feeding rate regressions reported here.

The probability values for the regressions for most groups in Tables 2–4 were quite low (<0.001), indicating that the relationships between $\log_{10}$ feeding rate and $\log_{10}$ body mass are robust for most groups. Some groups with smaller sample sizes (e.g. Pelecaniformes birds, with $n = 4$ and $P = 0.031$, Table 3) had much weaker relationships. The high coefficient of determination (r^2) values for many groups can be misleading. For example, the 0.947 value for the All mammal DMI that indicates that variation in $\log_{10}$ body mass explains 94.7% of the variation in $\log_{10}$ DMI. In fact, variation in the untransformed data is much higher than this implies. The column in Tables 2–4 labeled "Species deviation" is the average absolute percent difference between the actual feeding rate for a species and the feeding rate calculated for that species (using the regression line value at its body mass; Speakman, 2000). If the DMIs for all 79 species of mammals were predicted from body mass values using Equation 1 (the All mammal group, Table 2) and compared to the actual DMI values in Table 1, the average error (absolute error, ignoring sign) would be 41%.

Scaling of feeding rate

The allometric slope (*b* values) for feeding rate of the All mammal group (Table 2) is 0.74, substantially lower than the 1.0 value expected if there was a one-to-one relationship between food intake and body mass (i.e. a species ten times larger than another eats ten times as much food per day). To illustrate this, the scaling equation for DMI in All mammals, g DMI/d = 0.323(g body mass)$^{0.744}$, can be solved for two representative mammals, one weighing 100 g and another weighing ten times more, or 1000g. The results are: predicted DMIs = 9.94 g/d and 55.1 g/d, respectively. The larger representative mammal should consume only 5.5 times more dry food daily (55.1/9.94 = 5.5), not ten times. The allometric slopes for many other

Table 2. Equations for predicting food requirements of wild mammals. The equations are in the exponential form: y = a(grams body mass)^b, where y is either grams dry matter intake (DMI) per day, or grams fresh matter intake (FMI) per day. Species deviation is the average absolute difference between actual DMI or FMI (from Table 1) and those predicted for each species using the equations below. Group deviation is the difference between the predicted value for a 1.0 kg (or 50 g, in parentheses) mammal in that group versus the predicted value for a "typical" mammal (from the All mammals equations 1 and 2).

Group	y	a	b	n	r^2	P	Species deviation, % (absolute)	Predicted food intake (g/d) by a 1.0 kg (or 50 g) mammal	Group deviation, %	Equation number
All mammals	g DMI/d	0.323	0.744	79	0.947	<0.001	41	55 (5.9)	0 (0)	1
	g FMI/d	0.794	0.773	79	0.925	<0.001	51	166 (16)	0 (0)	2
Eutherians	g DMI/d	0.299	0.767	58	0.947	<0.001	43	60	+9	3
	g FMI/d	0.693	0.804	58	0.925	<0.001	56	179	+8	4
Marsupials	g DMI/d	0.483	0.666	20	0.983	<0.001	17	48	-13	5
	g FMI/d	1.667	0.649	20	0.982	<0.001	17	148	-11	6
Chiroptera (bats)	g DMI/d	0.365	0.671	7	0.730	0.014	23	(5.0)	(-15)	7
	g FMI/d	1.219	0.652	7	0.603	0.040	33	(16)	(-4)	8
Carnivora	g DMI/d	0.102	0.864	7	0.904	0.001	28	40	-28	9
	g FMI/d	0.348	0.859	7	0.889	0.001	30	131	-21	10
Rodentia	g DMI/d	0.332	0.774	30	0.785	<0.001	44	70	+26	11
	g FMI/d	0.588	0.864	30	0.643	<0.001	64	230	+39	12
Diprotodont marsupials (plant eaters, omnivores)	g DMI/d	0.546	0.654	14	0.978	<0.001	17	50	-9	13
	g FMI/d	2.128	0.633	14	0.976	<0.001	15	169	+2	14
Desert mammals	g DMI/d	0.192	0.806	25	0.950	<0.001	37	50	-9	15
	g FMI/d	0.327	0.878	25	0.923	<0.001	57	141	-15	16
Desert marsupials	g DMI/d	0.540	0.592	6	0.976	<0.001	9	32	-41	17
	g FMI/d	1.774	0.582	6	0.975	<0.001	9	99	-40	18
Terrestrial mesic mammals	g DMI/d	0.500	0.678	48	0.941	<0.001	37	54	-2	19
	g FMI/d	1.607	0.672	48	0.938	<0.001	38	167	+1	20
Desert rodents	g DMI/d	0.467	0.585	15	0.695	<0.001	27	(4.6)	(-22)	21
	g FMI/d	0.509	0.765	15	0.399	0.012	69	(10)	(-38)	22
Mesic rodents	g DMI/d	0.614	0.705	15	0.874	<0.001	35	80	+45	23
	g FMI/d	1.892	0.704	15	0.879	<0.001	34	245	+48	24
Carnivores	g DMI/d	0.153	0.834	13	0.954	<0.001	26	49	-12	25
	g FMI/d	0.469	0.848	13	0.956	<0.001	26	164	-1	26
Granivores	g DMI/d	0.659	0.413	6	0.861	0.008	8	(3.3)	(-44)	27
	g FMI/d	0.721	0.414	6	0.860	0.008	8	(3.6)	(-78)	28
Herbivores	g DMI/d	0.859	0.628	26	0.911	<0.001	40	66	+19	29
	g FMI/d	2.606	0.628	26	0.911	<0.001	40	200	+21	30
Insectivores	g DMI/d	0.373	0.622	14	0.891	<0.001	28	27	-50	31
	g FMI/d	1.130	0.622	14	0.890	<0.001	28	83	-50	32
Omnivores	g DMI/d	0.432	0.678	18	0.876	<0.001	26	47	-15	33
	g FMI/d	1.346	0.678	18	0.876	<0.001	26	146	-12	34

Columns: *n* is number of species, r^2 is the coefficient of determination, and *P* is the probability of a statistically significant regression (via *F*-test), with $P < 0.05$ indicating statistical significance.

mammalian, avian and reptilian groups are in or near the range of 0.6 to 0.9, but hummingbirds, desert lizards and lacertid lizards have slopes at or above 1.0 (Table 3 and 4), so a one-to-one relationship apparently does exist in these groups. Thus, with a few exceptions, we can say that among wild terrestrial vertebrates, larger species eat relatively less (kilogram for kilogram) than do their smaller relatives, while free-ranging in the field.

Table 3. Equations for predicting food requirements of wild birds. The equations are in the exponential form: $y = a(\text{grams body mass})^b$, where *y* is either grams dry matter intake (DMI) per day, or grams fresh matter intake (FMI) per day. Species deviation is the average absolute difference between actual DMI or FMI (Table 1) and those predicted for each species from the equations below. Group deviation is the difference between the predicted value for a 1.0 kg (or 50 g, in parentheses) bird in that group versus the predicted value for a "typical" bird (from the All birds equations 35 and 36).

Group	y	a	b	n	r^2	P	Species deviation, % (absolute)	Predicted food intake (g/d) by a 1.0 kg (or 50 g) bird	Group deviation, %	Equation number
All birds	g DMI/d	0.638	0.685	95	0.940	<0.001	30	72 (9.3)	0 (0)	35
	g FMI/d	2.065	0.689	95	0.893	<0.001	40	241 (31)	0 (0)	36
Passerines (perching birds)	g DMI/d	0.630	0.683	39	0.658	<0.001	23	(6.2)	(+34)	37
	g FMI/d	2.438	0.607	39	0.446	<0.001	32	(26)	(+14)	38
Charadriiformes (shore birds, gulls, auks)	g DMI/d	0.522	0.769	15	0.856	<0.001	21	106	+46	39
	g FMI/d	1.914	0.769	15	0.856	<0.001	21	388	+61	40
Procellariiformes (petrels, albatrosses)	g DMI/d	0.997	0.613	11	0.920	<0.001	32	69	-5	41
	g FMI/d	3.428	0.621	11	0.917	<0.001	33	250	+4	42
Sphenisciformes (penguins)	g DMI/d	0.277	0.796	7	0.809	0.006	22	68	-7	43
	g FMI/d	1.012	0.796	7	0.809	0.006	22	247	+3	44
Galliformes (quail, grouse)**	g DMI/d	0.088	0.891	4	0.992	0.004	8	41	-43	45
Pelecaniformes (tropic birds, gannets)	g DMI/d	0.279	0.845	4	0.938	0.031	15	96	+32	46
	g FMI/d	1.020	0.845	4	0.938	0.031	15	350	+45	47
Psittaciformes (parrots)	g DMI/d	0.361	0.735	4	0.999	<0.001	2	(6.4)	(+31)	48
	g FMI/d	0.948	0.735	4	0.999	<0.001	19	(17)	(-36)	49
Apodiformes (hummingbirds)	g DMI/d	0.344	1.216	5	0.978	0.001	5	*	*(+27)	50
	g FMI/d	1.466	1.216	5	0.978	0.001	5	*	*(+66)	51
Marine birds	g DMI/d	0.880	0.658	36	0.923	<0.001	28	83	+14	52
	g FMI/d	3.221	0.658	36	0.923	<0.001	28	303	+26	53
Temperate forest birds**	g DMI/d	1.020	0.511	16	0.693	<0.001	17	(7.5)	(-19)	54
Desert birds	g DMI/d	0.407	0.681	15	0.961	<0.001	25	45	-38	55
	g FMI/d	1.294	0.648	15	0.882	<0.001	38	114	-53	56
Temperate meadow birds	g DMI/d	1.048	0.567	9	0.754	0.002	19	(9.6)	(+4)	57
	g FMI/d	2.931	0.596	9	0.772	0.002	19	(30)	(-1)	58
Insectivorous birds	g DMI/d	0.540	0.705	26	0.754	<0.001	19	(8.5)	(-8)	59
	g FMI/d	1.633	0.705	26	0.754	<0.001	19	(26)	(-16)	60
Omnivorous birds	g DMI/d	0.670	0.627	18	0.911	<0.001	33	51	-30	61
	g FMI/d	2.094	0.627	18	0.911	<0.001	33	159	-34	62
Carnivorous birds	g DMI/d	0.849	0.663	38	0.925	<0.001	27	83	+14	63
	g FMI/d	3.048	0.665	38	0.924	<0.001	28	301	+25	64
Nectarivorous birds	g DMI/d	0.817	0.679	9	0.814	<0.001	14	*	*(+27)	65
	g FMI/d	3.475	0.679	9	0.814	<0.001	14	*	*(+66)	66

Columns: *n* is number of species, r^2 is the coefficient of determination, and P is the probability of a statistically significant regression (via *F*-test), with $P < 0.05$ indicating statistical significance.

*The Group deviations shown were calculated at a body mass of 5 g for these very small birds (3.7 to 8.8 g for hummingbirds, and 3.7 to 17.3 g for nectarivores).

**The FMI regressions for Temperate forest birds and Galliformes were not significant ($P > 0.05$)

Table 4. Equations for predicting food requirements of wild reptiles. The equations are in the exponential form: $y = a(\text{grams body mass})^b$, where y is either grams dry matter intake (DMI) per day, or grams fresh matter intake (FMI) per day. Species deviation is the average absolute difference between actual DMI or FMI (Table 1) and those predicted for each species from the equations below. Group deviation is the difference between the predicted value for a 1.0 kg (or 10 g in parentheses) reptile in that group versus the predicted value for a "typical" reptile (from the All reptiles equations 67 and 68).

Group	y	a	b	n	r^2	P	Species deviation, % (absolute)	Predicted food intake (g/d) by a 1.0 kg (or 10 g) reptile	Group deviation, %	Equation number
All reptiles	g DMI/d	0.0111	0.920	55	0.952	<0.001	42	6.4 (0.09)	0 (0)	67
	g FMI/d	0.0333	0.932	55	0.953	<0.001	42	21 (0.29)	0 (0)	68
All lizards	g DMI/d	0.0109	0.944	48	0.966	<0.001	37	7.4	+16	69
	g FMI/d	0.0324	0.956	48	0.967	<0.001	38	24	+15	70
Iguanian lizards (agamas, iguanas, swifts)	g DMI/d	0.0141	0.884	17	0.956	<0.001	33	6.3	-1	71
	g FMI/d	0.0426	0.884	17	0.956	<0.001	33	19	-8	72
Scleroglossan lizards (skinks, snakes, goannas)	g DMI/d	0.0099	0.961	31	0.970	<0.001	39	7.6	+18	73
	g FMI/d	0.0296	0.976	31	0.970	<0.001	39	25	+20	74
Varanidae (goannas)	g DMI/d	0.0135	0.915	11	0.966	<0.001	32	7.5	+17	75
	g FMI/d	0.0452	0.915	11	0.966	<0.001	33	25	+21	76
Lacertidae (lacerta lizards)	g DMI/d	0.00778	1.166	10	0.890	<0.001	24	(0.11)	(+24)	77
	g FMI/d	0.0237	1.165	10	0.889	<0.001	24	(0.35)	(+22)	78
Iguanidae (iguanas, chuckwallas)	g DMI/d	0.0291	0.782	4	0.999	<0.001	2	6.5	+1	79
	g FMI/d	0.0881	0.782	4	0.999	<0.001	2	20	-6	80
Phrynosomatidae (horned lizards, bluebellies)	g DMI/d	0.0252	0.542	9	0.666	0.007	22	(0.09)	(-5)	81
	g FMI/d	0.0766	0.542	9	0.666	0.007	22	(0.27)	(-6)	82
Desert lizards	g DMI/d	0.00826	1.047	16	0.934	<0.001	30	(0.09)	(+2)	83
	g FMI/d	0.0252	1.045	16	0.933	<0.001	30	(0.28)	(-4)	84
Herbivorous reptiles	g DMI/d	0.0334	0.717	9	0.906	<0.001	35	4.7	-26	85
	g FMI/d	0.1012	0.717	9	0.906	<0.001	35	14	-31	86
Carnivorous reptiles	g DMI/d	0.00865	0.963	18	0.942	<0.001	44	6.7	+5	87
	g FMI/d	0.0289	0.964	18	0.942	<0.001	44	23	+8	88
Insectivorous lizards	g DMI/d	0.0109	0.914	27	0.853	<0.001	38	6.0	-6	89
	g FMI/d	0.0330	0.914	27	0.853	<0.001	38	18	-12	90

Columns: *n* is number of species, r^2 is the coefficient of determination, and *P* is the probability of a statistically significant regression (via *F*-test), with $P < 0.05$ indicating significance.

How do different groups compare?

One way to facilitate comparing the different categories of vertebrates is first to account for body size differences by calculating expected DMI and FMI values for a common body mass. The "Predicted food intake" columns in Tables 2–4 show these values for a body mass of one kilogram in most cases, or (in parentheses) for either 50 g (some mammals and bird groups) or 10 g (some reptile groups) for those groups where typical body masses are low and one kilogram is outside the range of masses in that group.

The common phrase "to eat like a bird" implies being very selective and eating only a small amount. In fact, Tables 2 and 3 reveal that a typical wild bird has a big appetite, consuming 31% more dry mass of food and 45% more fresh food each day than does a typical mammal (72 vs. 55 g DMI/d and 241 vs. 166 g FMI/d, respectively. The difference in food requirements between birds and reptiles is even more striking: a 1-kg reptile ingests only 9% of the food, fresh or dry matter, each day as does a 1-kg bird. Similarly, a 1-kg mammal requires over eight times as much food per day to fuel its cost of living as does a 1-kg reptile, which may be living in the same habitat and eating a similar diet. Thus, among the terrestrial vertebrates, birds eat the most.

In a similar way, we can compare the various groups of species within the Classes Mammalia, Aves and Reptilia. For example, in the "Group deviation" column of Table 2, the difference between the DMI rate predicted for a 1-kg eutherian mammal (60 g/d, from Eqn. 3) and the DMI rate for a 1-kg mammal from the All mammal group (55 g/d, Eqn. 1) is expressed as a percent of the All mammal prediction $\{100 \times [(\mathrm{DMI}_{\mathrm{euth}} - \mathrm{DMI}_{\mathrm{All\ mam}})/\mathrm{DMI}_{\mathrm{All\ mam}}] = +9\%\}$. This method is not as good as comparing the predicted eutherian value with the 1-kg value calculated from the combined data for all non-eutherian species, exclusive of the eutherian species, but such calculations for all the groups were beyond the scope of this review. Nevertheless, the "Group deviation" values can serve as relative indices. Among the mammal groups (Table 2), the "Group deviation" column suggests that eutherian mammals have somewhat higher feeding rates, and marsupials have somewhat lower feeding rates than all mammals combined, so that a 1-kg eutherian would have a daily feeding rate over 20% higher than a 1-kg marsupial. The seven species in the Order Carnivora have comparatively low field feeding rates. Desert mammals in general, and desert marsupials and desert rodents in particular apparently have relatively low food requirements for mammals. Similarly, insectivorous mammals and seed-eating (granivorous) mammals (many of whom are desert rodents) have relatively low daily food requirements. On the other hand, rodents in general, and especially mesic (moist habitat) rodents have relatively high feeding rates. Herbivorous mammals also have comparatively high food needs.

Among birds, the Passerines (perching birds), the Apodidae (hummingbirds), the Pelecaniformes (gannets, tropicbirds), and especially the Charadriiformes (auks, gulls, shorebirds) have relatively high food requirements for birds (Table 3). Marine birds in general have somewhat elevated feeding rates, and temperate forest and desert birds apparently have reduced food needs. Regarding dietary categories, food requirements seem comparatively low for omnivores, but rather high among carnivores and especially nectarivores. For the reptiles during their activity seasons (Table 4), several groups of lizards have somewhat elevated food requirements (all lizards, Scleroglossans, varanids and Lacertids), and herbivorous reptiles have comparatively low feeding rates.

How to predict feeding rates

To obtain an estimate of the daily food intake of a species of mammal, bird or reptile in its natural habitat, first check Table 1 to see if that species has been studied. If so, the estimates in Table 1 (or better, in the original research article describing that study, if included) will be the most reliable. If the species of interest has not been studied with doubly labeled water, its food requirements can be estimated by inserting its average body mass (in grams) into one or more of the allometric equations in Tables 2–4. For example, assume we wish to predict the fresh food intake for a common raven (*Corvus corax*, 866 g body mass), an omnivorous bird living in the Mojave Desert in California. The equation for All birds (Eqn. 36) becomes g FMI/d $= 2.065 \times (866)^{0.689} = 2.065 \times 105.7 = 218$ g fresh matter intake per day. Equation 38 for Passerines, the taxon in which ravens belong, yields a prediction of 148 g FMI/d, Eqn. 56 for desert birds yields 104 g FMI/d, and the omnivorous bird equation (number 62) produces an estimate of 145 g FMI/d.

Which estimate is the most reliable? The Passerine estimate is probably least accurate because the raven's body mass of 866 g is far outside the range of masses of species used to derive Equation 38 (6.6 to 96 g; Table 1), so a substantial extrapolation is involved, along with its attendant uncertainty. The desert bird equation is also suspicious because, although the raven in this example lives in a desert, common ravens are a widespread and often migratory species, so they may not show the reduced energy and food requirement possessed by desert specialist species, which contributed much data to the derivation of the equations for desert birds. This leaves the estimates of 218 (all birds) and 145 (omnivores), the latter being 33% lower than the former. The average error in the ability of the All birds equation to predict the feeding rates of the species used to derive the equation is 40% ("Species deviation" column, Table 3), and this error should be a conservative estimate of the error in predicting values for new species. The average error of prediction for the omnivorous bird equation is 33%. Thus, either estimate (218 or 145 g FMI/d) is within the range of error of the prediction from the other equation. Another way to evaluate the reliability of a prediction made from these equations is to calculate the 95% confidence intervals for the prediction. These values will be much larger than the average errors indicated in Tables 2–4. If desired, the 95% confidence intervals may be calculated from equations given in Nagy *et al.* (1999) for FMR predictions, and then converted to DMI or FMI equivalents using the appropriate conversion factors given above.

The equations in Tables 2–4 yield estimated feeding rates that are needed for animals to obtain the metabolisable energy they used in their natural habitats, as determined with doubly labeled water. If the animal of interest to the reader is growing or reproducing or storing fat, its estimated feeding rate should be increased to include those avenues of metabolisable energy allocation. The literature on the species of interest or related species should be consulted to obtain rates of energy accumulation or allocation to production, which can then be added to estimated FMR. On the other hand, these equations will yield overestimates of food consumption for animals that are undergoing seasonal periods of weight loss due to relative or absolute starvation. Such periods include the nestling period for parent birds, the lactation period for nursing mammalian mothers, the migration period for many migratory terrestrial mammals, the cold seasons for temperate-zone reptiles, and the summer drought period for desert herbivores. Similarly, for wild animals held captive, such as in zoos, small outdoor enclosures or indoors in cages or pens, predicted feeding rates will probably be higher than actual food requirements. Probable reasons for this include: free-ranging animals must pay relatively higher costs of foraging for dispersed foods, avoiding or battling predators and parasites, dealing with more extreme climatic conditions, and interacting socially with conspecifics; and the foods given to captive animals are usually of higher quality (more metabolisable energy per gram of dry or fresh matter), so less biomass need be consumed, and this reduces food requirements a second way, which is a reduced metabolic cost of food processing due to its greater digestibility.

Conclusions

Birds are the most expensive group of vertebrates on Earth. Kilogram for kilogram, a typical bird eats about 31% more food each day than does a mammal, and endotherms (birds and mammals) consume eight to eleven *times* as much food daily as does a reptile. Within these groups, feeding rates increase with increasing size of animal, but in a less-than one-to-one manner, such that large animals use less food daily than that expected from their body mass (i.e. allometric slopes are usually less than 1.0). Feeding rates are strongly related to body mass within a variety of taxonomic, dietary and habitat groupings. The exponential (power) equations describing these relationships can be used to predict feeding rates in wild birds, reptiles, and mammals with an average error of about 40%, and an error as low as 5% in some groups. Such predictions should be adjusted up or down to account for higher expenses by breeding or growing animals or lower costs in captive animals.

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References

Garland TJ, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**, 265–292.

Lifson N, McClintock R (1966) Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* **12**, 46–74.

Nagy KA (1983) *The Doubly Labeled Water ($^3HH^{18}O$) Method: A Guide to its Use*. University of California Publication 12–1417, USA, Los Angeles, University of California.

Nagy KA, Peterson CC (1988) *Scaling of Water Flux Rate in Animals.* USA, Berkeley; University of California Press.

Nagy KA, Bradshaw SD (2000) Scaling of energy and water fluxes in free-living arid-zone Australian marsupials. *Journal of Mammalogy* **81**, 962–970.

Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition* **19**, 247–277.

Speakman JR (1997) *Doubly Labelled Water: Theory and Practice.* UK, London; Chapman and Hall.

Speakman JR (2000) The cost of living: Field metabolic rates of small mammals. *Advances in Ecological Research* **30**, 178–297.