Ecological Monographs, 57(2), 1987, pp. 111–128
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FIELD METABOLIC RATE AND FOOD REQUIREMENT SCALING IN MAMMALS AND BIRDS[1]

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Abstract. Field metabolic rates (FMRs or $\dot{H}_F$), all measured using doubly labeled water, of 23 species of eutherian mammals, 13 species of marsupial mammals, and 25 species of birds were summarized and analyzed allometrically ($\log_{10}$–$\log_{10}$ regressions). FMR is strongly correlated with body mass in each of these groups. FMR scales differently than does basal or standard metabolic rate in eutherians (FMR slope = 0.81) and marsupials (FMR slope = 0.58), but not in birds (FMR slope = 0.64 overall, but 0.75 in passerines and 0.75 in all other birds). Medium-sized (240–550 g) eutherians, marsupials, and birds have similar FMRs, and these are ≈17 times as high as FMRs of like-sized ectothermic vertebrates such as iguanid lizards. For endothermic vertebrates, the energy cost of surviving in nature is enormous compared with that for ectotherms. Within the eutherians, marsupials, or birds, FMR scales differently for the following subgroups: rodents, passerine birds, herbivorous eutherians, herbivorous marsupials, desert eutherians, desert birds, and seabirds. Equations are given for use in predicting daily and annual FMR and food requirement of a species of terrestrial vertebrate, given its body mass.

Key words: allometry; daily energy expenditure; desert; doubly labeled water; ecological energetics; endothermy cost; energy budget; feeding rate; herbivory; passerine bird; rodent; seabird.

INTRODUCTION

The transient assemblage of chemicals that makes up an animal requires energy for construction, maintenance, and operation. Knowledge of the energy budget of an animal can provide much insight into its physiology, ecology, and evolution (Bennett and Ruben 1979, Bartholomew 1982, Schmidt-Nielsen 1983), especially if one knows the energetics of the animal while behaving normally in its natural habitat. Most of our knowledge of animal energetics comes from studies on captive wild animals and domestic animals (Brody 1945, Paynter 1974, Kleiber 1975, Hudson and White 1985). It is difficult to apply metabolic rate data from captive or domestic animals to free-living animals, which are responding to variations in food supply, food quality, predation, reproductive status, weather, and other circumstances that captive animals may not experience. Field metabolic rate (FMR or $\dot{H}_F$) is the total energy cost a wild animal pays during the course of a day. FMR includes the costs of basal metabolism (BMR), thermoregulation, locomotion, feeding, predator avoidance, alertness, posture, digestion and food detoxification, reproduction and growth, and other expenses that ultimately appear as heat, as well as any savings resulting from hypothermia.

Energy metabolism in the field can be measured routinely by means of doubly labeled water. This method involves measuring the washout rates of isotopes of hydrogen and oxygen injected in the form of water into animals in the field. The hydrogen isotope measures primarily water loss, while the oxygen isotope, which is in equilibrium with oxygen in water and in CO_2, measures primarily the sum of water and CO_2 loss. The difference between isotope washout rates represents CO_2 loss alone, and is a measure of metabolic rate (Lifson and McClintock 1966, Nagy 1975, 1980). A substantial number of wild eutherian mammals, marsupial mammals, and birds have now been studied with doubly labeled water, and it seems timely to do preliminary calculations and comparisons of the allometric relationships between FMR and body mass for these vertebrate classes. The data sets presently available need more representation for several animal groups (e.g., large terrestrial birds, very small eutherian mammals such as shrews, large ruminants, desert marsupials), and I hope this report will stimulate research on some of these species. Although these shortcomings preclude satisfactory application of some of the physiological purposes of allometric analysis, such as understanding the mechanistic basis of the slopes and intercepts (Heusner 1982), the data can be used to evaluate ecologically relevant questions about scaling of field metabolism.

This analysis is aimed at four goals. The first is to determine whether FMR scales as does basal metabolism in endothermic vertebrates. This is important because some models of ecological energetics have incorporated allometric equations for basal metabolism. Second, how do the FMRs of endotherms compare with those of ectothermic vertebrates in nature? Third,

[1] Manuscript received 28 April 1986; revised and accepted 2 September 1986.

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does FMR allometry reflect taxonomic, dietary, or habitat subgroups, as does BMR allometry? The fourth purpose is to present empirical models for FMR and food requirement that may be used by ecologists, physiologists, conservationists, ecosystem modelers, and wildlife managers for predicting food and energy demands of wild terrestrial vertebrates from knowledge of their body masses, diets, and habitats.

Methods

In this paper, the term "field metabolic rate" (FMR) is used to describe estimates of energy metabolism based only on doubly labeled water (DLW) measurements of CO_2 production in free-living animals. This was done to distinguish DLW measurements from other published estimates of field metabolism, such as "average daily metabolic rate" (ADMR), which are long-term continuous measurements of oxygen consumption in captive animals (Morrison and Grodzinski 1975), "daily energy budget" (DEB), which are based on measurements of existence metabolism (EM, the rate of metabolizable energy intake in caged animals maintaining constant body mass outdoors) plus estimates of the additional metabolic costs of free living, reproduction, etc. (Kendeigh et al. 1977), and "daily energy expenditure" (DEE), which involves field measurements of time–activity budgets and laboratory measurements of the energetic costs of various activities (King 1974, Walsberg 1980, 1983). Recent studies indicate that some DEB and DEE estimates of energy metabolism may differ from DLW measurements by up to ±50% in birds (Weathers et al. 1984, Williams and Nagy 1984*a*) and mammals (Nagy and Milton 1979, Nagy and Montgomery 1980).

The accuracy of DLW measurements of energy metabolism has been examined in captive animals by comparing simultaneous DLW measurements and CO_2 production measurement (gas chromatograph or infrared analyzer) or metabolizable energy intake measurements. In earlier studies on six species of mammals and one bird species, the agreement between methods was within 4% on average (summarized by Nagy 1980). More recent studies indicate similar agreement in humans (Schoeller and Van Santen 1982) and birds (Hails 1979, Weathers et al. 1984, Williams and Nagy 1984*b*, Goldstein and Nagy 1985, Williams 1985). When differences are smaller than 5%, it is difficult to determine whether the errors are in the DLW method or in the other methods used for independent measurement of energy metabolism, or both. Considering the additional sources of error that may occur in field situations but not in most laboratory studies (Nagy 1980), most DLW measurements of FMR in mammals and birds are probably accurate to ±8% or better. In this analysis, I used DLW results only.

FMR data for 23 species of eutherian mammals, 13 species of marsupial mammals, and 25 species of birds were available for this analysis (Table 1). These measurements were made in a variety of habitats and mi croclimates, at different seasons, and in animals havin different diets, behavior patterns, and ages. Becaus the difficulties of recapturing birds (which seem to lea how to avoid being captured more quickly than oth vertebrates) during nonbreeding seasons, when they a not compelled to return repeatedly to their nests, mo of the FMR measurements available are for breedin birds (see Season column in Table 1). I excluded on the FMR data for animals that were probably not e dothermic during DLW measurements, such as ove wintering desert rodents (Mullen 1971*a*, *b*, Mullen an Chew 1973) and nestling altricial birds (Fiala a Congdon 1983, Gettinger et al. 1985, Williams a Nagy 1985). Cohorts within species, such as mal females, and juveniles, may occupy different ecologic niches, and individual animals may have different m abolic rates at various times of the year. Where statistically significant differences in FMR were fou between groups within species, I used group me rather than a mean for the entire species. Thus, th data and the regressions derived from them reflect much as possible, the natural variation in the daily c of living in the field. This approach should make results more ecologically meaningful. (Recalculating regressions in Fig. 1 using species means alone reve no significant differences from cohort regressions.)

Allometric analyses were done by regressing lo transformations of mean FMR values (the depend variable) upon $\log_{10}$ transformations of the correspon ing mean body mass values (the independent variabl using the least-squares method (Dixon and Ma 1969). Results of the regression analyses are repor as follows: the equation for the regression line has form

$$\log y = \log a + b \log x,$$

where $\log y$ is $\log_{10}$FMR (measured in kilojoule day), $\log a$ is the intercept of the line and a i untransformed value of FMR (in kilojoules per d for a 1-g animal, b is the slope of the line, and $\log x$ $\log_{10}$body mass (measured in grams). The followi statistics are given in Table 2 for each regression eq tion: standard error of intercept ($SE_{\log a}$), confidence terval of intercept (95% $CI_{\log a}$), standard error of slo (SE_b), confidence interval of slope (95% CI_b), number data points (N), coefficient of determination (r^2), pro ability value (P) for significance of regression (from statistic), mean value of $\log_{10}x$ ($\overline{\log x}$), mean value $\log_{10}y$ ($\overline{\log y}$), and the equation for calculating the 95 confidence interval (95% $CI_{P\log y}$) of a predicted log value ($P \log y$) at any given $\log x$ value (Dunn a Clark 1974).

These analyses were done on the data sets for eutherian mammals, all marsupial mammals, and birds. The resulting slopes were tested for signific differences ($P < .05$) from the slopes for basal me bolic rate (b_{BMR}) for these groups using the equatio

TABLE 1. Summary of field metabolic rates (FMR), measured with doubly labeled water, in free-living mammals and birds.

Species	Mass (g)	FMR (kJ/d)	Cohort*	Habitat†	Season‡	Diet§	Figure number‖	Reference¶
		Eutherian mammals						
Mus musculus#	13.0	39.8	A	SS	Au, W	O	1	1
Macrotus californicus	12.6	22.2	A	D	Sp	I	2	2
	13.3	20.8	A	D	W	I	3	2
Clethrionomys rutilus#	13.6	59.0	A	T	W	H	4	3
	18.3	52.8	A	T	Sp	H	5	3
	15.9	60.2	A	T	Su	H	6	3
	16.1	58.5	A	T	Au	H	7	3
Peromyscus crinitus#	13.4	39.3	A	D	W	O	8	4
Perognathus formosus#	16.3	25.4	A	D	Su	G	9	5
	16.8	44.7	A	D	Au	G	10	5
	18.0	53.0	A	D	W	G	11	5
	20.4	57.5	A	D	Sp	G	12	5
Peromyscus leucopus#	19.4	36.6	A	DF	Au	O	13	6
Dipodomys merriami#	32.0	37.3	A	D	Su	G	14	7
	33.0	52.9	A	D	Au	G	15	7
	39.1	63.6	A	D	W	G	16	7
Pseudomys albocinereus#	32.6	62.2	A	SS	Au, W	O	17	1
Acomys cahirinus#	38.3	51.8	A	D	Sp	O	18	8
Acomys russatus#	45.0	47.6	A	D	Sp	O	19	8
Sekeetamys calurus#	41.2	44.0	A	D	Sp	O	20	8
Lemmus trimucronatus#	55.2	201	A	T	B	H	21	9
Dipodomys microps#	54.7	34.5	A	D	Au	O	22	7
	60.3	102	A	D	W	O	23	7
	58.4	137	A	D	Sp	O	24	7
	55.0	64.5	A	D	Su	O	25	7
Ammospermophilus leucurus#	90.0	114	A	D	Sp	O	26	10
	79.9	79.3	A	D	Su	O	27	10
	82.1	79.6	A	D	F	O	28	10
	96.1	79.0	A	D	W	O	29	10
Arvicola terrestris#	81.9	149	A	TM	Sp	H	30	11
	89.7	88.7	M	TM	Su	H	31	11
Tamias striatus#	96.3	143	A	DF	Au	O	32	6
Thomomys bottae#	99.4	127	A	CS	Su	H	33	12
	108	128	A	CS	W	H	34	12
	104	136	A	CS	Sp	H	35	12
Lepus californicus	1800	1416	A	D	Sp	H	36	13
	1800	1175	A	D	W	H	37	13
Alouatta palliata	3200	1110	J	TF	D	H	38	14
	6250	2304	F	TF	D	H	39	14
	8415	2861	M	TF	D	H	40	14
Arctocephalus gazella	37 000	29 108	F	M	B	C	41	15
Callorhinus ursinus	51 100	43 200	F	M	B	C	42	15
	51 100	28 992	F	M	B	C	43	15
Odocoileus hemionus	39 975	23 375	F	TM	Sp	H	44	16
	67 100	40 000	M	TM	Sp	H	45	16
Zalophus californicus	84 000	38 445	F	M	B	C	46	15
		Marsupial mammals						
*Sminthopsis crassicaudata***	6.1	29.1	J	TM	Sp	I	1	17
*Antechinus stuartii***	16.6	68.8	A	TM	Sp	I	2	17
	18.4	48.7	F	EF	W	I	3	18
	20.4	71.6	F	EF	W	I	4	18
	29.3	75.0	M	EF	W	I	5	18
*Antechinus swainsonii***	26.3	66.2	JF	EF	Sp	I	6	19
	32.1	92.1	JM	EF	Sp	I	7	19
	47.4	126	F	EF	Sp	I	8	19
	54.2	221	F	EF	B	I	9	19
	52.5	124	F	EF	B	I	10	19
	72.7	177	M	EF	B	I	11	19
Petaurus breviceps	112	153	F	EF	W	O	12	20
	135	192	M	EF	W	O	13	20

TABLE 1. Continued.

Species	Mass (g)	FMR (kJ/d)	Cohort*	Habitat†	Season‡	Diet§	Figure number‖	Reference¶
Gymnobelideus leadbeateri	117	219	F	EF	Sp	O	14	21
	133	232	M	EF	Sp	O	15	21
Pseudocheirus peregrinus	278	249	J	EF	Sp	H	16	22
	717	556	A	EF	Sp	H	17	22
Petauroides volans	934	690	F	EF	W	H	18	23
	1042	570	M	EF	W	H	19	23
Setonix brachyurus	1507	486	J	SS	Su	H	20	24
	2472	662	A	SS	Su	H	21	24
Isoodon obesulus	1232	690	A	EF	Au	O	22	25
Macropus eugenii	4555	1229	A	SS	Su	H	23	24
Thylogale billardieri	5445	1489	A	EF	Sp	H	24	26
Phascolarctos cinereus	7800	2050	F	EF	W	H	25	27
	10 800	2030	M	EF	W	H	26	27
Macropus giganteus	27 000	5611	F	EF	Sp	H	27	26
	61 900	11 734	M	EF	Sp	H	28	26
		Birds						
Calypte anna	4.5	26.7	A	CS	Su	N	1	28
Zosterops lateralis††	9.1	35.3	A	EF	Au	F	2	29
	9.7	39.2	A	EF	Sp	F	3	29
	9.6	50.7	A	EF	Sp	F	4	29
Hirundo tahitica††	14.1	76.6	A	TF	B	I	5	30
Riparia riparia††	14.3	81.7	A	TM	B	I	6	31
Passerculus sandwichensis††	19.1	80.3	M	SM	B	O	7	32
	17.0	67.7	F	SM	B	O	8	33
Delichon urbica††	20.1	77.1	A	TM	Su	I	9	34
	20.3	71.2	M	TM	B	I	10	34
	20.3	79.0	F	TM	B	I	11	34
	18.9	74.2	F	TM	B	I	12	34
	18.9	79.8	M	TM	B	I	13	34
	18.2	94.4	A	TM	B	I	14	34
	17.8	77.5	M	TM	B	I	15	35
	17.8	84.1	F	TM	B	I	16	35
	19.3	79.6	M	TM	B	I	17	31
	18.7	80.7	F	TM	B	I	18	31
Hirundo rustica††	20.4	104	F	TM	B	I	19	31
Phainopepla nitens††	22.7	79.1	A	D	Sp	O	20	36
Merops viridis	33.8	74.4	A	TF	B	I	21	30
Mimus polyglottos††	47.6	121	M	DF	B	O	22	37
Progne subis††	47.7	183	F	DF	B	I	23	38
	50.3	143	M	DF	B	I	24	38
Oceanites oceanus	42.3	81	A	M	B	C	25	39
	42.2	157	A	M	B	C	26	39
Sturnus vulgaris††	85.0	231	F	DF	B	O	27	40
	78.7	246	F	DF	B	O	28	40
	74.1	327	F	DF	B	O	29	40
	76.9	272	M	DF	B	O	30	40
Callipepla gambelii	145	90.8	A	D	Su	O	31	41
Sterna fuscata	188	141	A	M	B	C	32	42
	184	340	A	M	B	C	33	42
Ammoperdix heyi	156	122	J, A	D	Su	O	34	43
	206	150	A	D	Sp	O	35	43
	209	172	A	D	Au	O	36	43
Anous stolidus	195	352	A	M	B	C	37	44
Rissa tridactyla	386	913	A	M	B	C	38	45
Alectoris chukar	333	220	J, A	D	Su	O	39	43
	432	259	A	D	Sp	O	40	43
	419	302	A	D	Au	O	41	43
Puffinus pacificus	384	614	A	M	B	C	42	46
Diomedea immutabilis	3069	1447	A	M	B	C	43	47
	3064	2157	A	M	B	C	44	47

TABLE 1. Continued.

Species	Mass (g)	FMR (kJ/d)	Cohort*	Habitat†	Season‡	Diet§	Figure number‖	Reference¶
Spheniscus demersus	3170	1945	A	M	B	C	45	48
Macronectes giganteus	3583	4149	F	M	B	C	46	49
	4505	4737	M	M	B	C	47	49
Pygoscelis adeliae	3868	4002	A	M	B	C	48	50
Diomedea exulans	7360	2632	F	M	B	C	49	51
	9440	3973	M	M	B	C	50	51

* Cohort: A = adult, F = female, M = male, J = juvenile.
† Habitat: SS = semiarid scrub, D = desert, T = taiga or tundra, DF = deciduous forest, TM = temperate meadow, CS = chaparral scrub, TF = tropical forest, M = marine, EF = eucalypt forest, SM = salt marsh.
‡ Season: Sp = spring, Su = summer, Au = autumn, W = winter, B = breeding, D = dry.
§ Diet: O = omnivore, H = herbivore, I = insectivore, G = granivore, N = nectarivore, F = frugivore, C = carnivore (primarily fish-eaters).
‖ Figure number corresponds to those in Fig. 1.
¶ References: 1. K. Nagy and K. Morris, *personal observation*, 2. Bell et al. 1986, 3. Holleman et al. 1982, 4. Mullen 1971*a*, 5. Mullen and Chew 1973, 6. Randolph 1980, 7. Mullen 1971*b*, 8. Degen et al. 1986, 9. Peterson et al. 1976, 10. Karasov 1981, 1983, 11. Grenot et al. 1984, 12. Gettinger 1984, 13. Shoemaker et al. 1976, 14. Nagy and Milton 1979, 15. Costa et al. 1985, 16. K. Nagy and N. Jacobsen, *personal observation*, 17. K. Nagy, A. K. Lee, R. Martin, and M. Fleming, *personal observation*, 18. Nagy et al. 1978, 19. A. K. Lee and K. Nagy, *personal observation*, 20. Nagy and Suckling 1985, 21. Smith et al. 1982, 22. K. Nagy, R. Martin, and A. K. Lee, *personal observation*, 23. W. Foley and K. Nagy, *personal observation*, 24. K. Nagy, A. Bradley, and K. Morris, *personal observation*, 25. K. Nagy, B. Clay, and S. D. Bradshaw, *personal observation*, 26. K. Nagy and G. Sanson, *personal observation*, 27. Nagy and Martin 1985, 28. D. Powers and K. Nagy, *personal observation*, 29. I. Rooke, S. D. Bradshaw, and K. Nagy, *personal observation*, 30. Bryant et al. 1984, 31. Westerterp and Bryant 1984, 32. Williams and Nagy 1984*a*, 33. Williams and Nagy 1985, 34. Bryant and Westerterp 1980, 35. Hails and Bryant 1979, 36. Weathers and Nagy 1980, 37. Utter 1971, 38. Utter and LeFebvre 1973, 39. Obst et al. 1987, 40. Ricklefs and Williams 1984, 41. Goldstein and Nagy 1985, 42. Flint and Nagy 1984, 43. Kam et al. 1987, 44. Ellis 1984, 45. Gabrielsen et al. 1987, 46. Ellis et al. 1983, 47. H. Ellis, K. Nagy, T. Pettit, and G. C. Whittow, *personal observation*, 48. Nagy et al. 1984, 49. B. Obst and K. Nagy, *personal observation*, 50. K. Nagy and B. Obst, *personal observation*, 51. Adams et al. 1987.
\# Rodent.
** Dasyurid marsupial.
†† Passerine bird.

$(b - b_{BMR})/SE_b$, where t is the Student's t statistic (Afifi and Azen 1979). Analysis of covariance (ANCOVA, Dixon and Massey 1969) was then used to test for differences among the three regressions. First, the slopes were examined, and if the slopes did not differ significantly between regressions, the common slope was calculated, and the adjusted regressions were then tested for differences between intercepts. Subsequently, subgroups within the data sets for eutherians, marsupials, and birds were also compared using ANCOVA. Regression statistics shown are those derived from least-squares analyses, unless ANCOVA indicated that slopes did not differ. In those cases, the statistics shown are those derived via ANCOVA on the basis of the common slope.

Feeding rates required to provide metabolizable energy to animals as fast as they were oxidizing it (as measured by DLW) were calculated from information about diet energy content and assimilability. Details are given in the section on food requirements below.

RESULTS AND DISCUSSION

Eutherians, marsupials, and birds

Like BMR, FMR is strongly correlated with body mass in eutherian mammals (Fig. 1A). The regression equation for eutherians is:

$$\log y = 0.525 + 0.813 \log x, \qquad (1)$$

with $r^2 = 0.967$. However, the slope of the FMR regression, 0.813, is significantly higher ($P < .025$) than Kleiber's (1975) BMR slope of 0.75 and much higher ($P \ll .005$) than the BMR slope of 0.696 recently reported by Hayssen and Lacy (1985). Thus, FMR in the eutherians studied to date is not a constant multiple of BMR. Most of the large eutherians are marine mammals, which are known to have relatively high BMRs (Robbins 1983), and this may contribute to the steep slope. However, the data for deer (points 44 and 45 in Fig. 1A) fall in the middle of the marine mammals. It would be useful to know if deer are representative of large ruminants in general. Also, no FMR measurements have yet been made on shrews or other very active, very small eutherians.

Marsupial mammals also have FMRs that correlate strongly with body mass (Fig. 1B). The regression equation for marsupials is:

$$\log y = 1.072 + 0.576 \log x, \qquad (2)$$

with $r^2 = 0.970$. For marsupials, the FMR slope is significantly lower ($P < .001$) than the BMR slopes of 0.737 reported by Dawson and Hulbert (1970) and 0.747 reported by Hayssen and Lacy (1985). The ratio of FMR to BMR decreases with increasing body mass

TABLE 2. Regression statistics for allometry of field metabolic rates (kJ/d) and feeding (dry matter ingestion) rates (g/d) of terrestrial vertebrates.

Group	Units of y	log a ($SE_{\log a}$)	95% CI of log a	b (SE_b)	95% CI of b	N	r^2	P
			Eutherian mammals					
All eutherians	kJ/d	0.525 (0.057)	0.410 0.640	0.813 (0.023)	0.767 0.859	46	0.967	<.001
	g/d	−0.629 (0.065)	−0.760 −0.497	0.822 (0.026)	0.769 0.874	46	0.958	<.001
Rodents	kJ/d	1.022 (0.141)	0.734 1.310	0.507 (0.087)	0.330 0.684	33	0.524	<.001
	g/d	−0.207 (0.194)	−0.602 0.189	0.564 (0.119)	0.322 0.807	33	0.421	<.001
Other than rodents	kJ/d	0.239 (0.153)	−0.097 0.575	0.885 (0.039)	0.800 0.971	13	0.979	<.001
Herbivores	kJ/d	0.774 (0.109)	0.541 1.007	0.727 (0.039)	0.644 0.809	17	0.959	<.001
	g/d	−0.239 (0.109)	−0.472 −0.006	0.727 (0.039)	0.645 0.809	17	0.960	<.001
Other than herbivores	kJ/d	0.412 (0.058)	0.292 0.532	0.862 (0.026)	0.809 0.915	29	0.977	<.001
Desert eutherians	kJ/d	0.507 (0.053)	0.382 0.633	0.786 (0.023)	0.731 0.841	23	0.963	<.001
	g/d	−0.825 (0.101)	−1.035 −0.615	0.874 (0.056)	0.757 0.992	23	0.920	<.001
Other than desert species	kJ/d	0.663 (0.072)	0.493 0.833	0.786 (0.023)	0.731 0.841	23	0.963	<.001
			Maruspial mammals					
All marsupials	kJ/d	1.072 (0.054)	0.962 1.183	0.576 (0.020)	0.535 0.617	28	0.970	<.001
	g/d	−0.308 (0.046)	−0.403 −0.212	0.673 (0.017)	0.638 0.708	28	0.984	<.001
Herbivores	kJ/d	0.804 (0.123)	0.507 1.101	0.644 (0.034)	0.562 0.725	12	0.936	<.001
	g/d	−0.321 (0.181)	−0.724 0.081	0.676 (0.050)	0.564 0.788	12	0.948	<.001
Other than herbivores	kJ/d	0.978 (0.063)	0.825 1.131	0.644 (0.034)	0.562 0.725	16	0.936	<.001
			Birds					
All birds	kJ/d	1.037 (0.064)	0.908 1.166	0.640 (0.030)	0.580 0.699	50	0.907	<.001
	g/d	−0.188 (0.060)	0.310 −0.067	0.651 (0.028)	0.595 0.707	50	0.919	<.001
Passerines	kJ/d	0.949 (0.059)	0.809 1.088	0.749 (0.037)	0.663 0.835	26	0.899	<.001
	g/d	−0.400 (0.075)	−0.554 −0.247	0.850 (0.053)	0.741 0.960	26	0.915	<.001
Other than passerines	kJ/d	0.681 (0.102)	0.442 0.920	0.749 (0.037)	0.663 0.835	24	0.899	<.001
	g/d	−0.521 (0.132)	−0.794 −0.248	0.751 (0.048)	0.652 0.850	24	0.919	<.001
Desert birds	kJ/d	0.703 (0.067)	0.568 0.838	0.660 (0.021)	0.617 0.703	8	0.953	<.001
	g/d	0.045 (0.238)	−0.536 0.627	0.445 (0.103)	0.192 0.698	8	0.755	<.01
Other than desert species	kJ/d	1.052 (0.046)	0.960 1.145	0.660 (0.021)	0.617 0.703	42	0.953	<.001
Seabirds	kJ/d	0.904 (0.187)	0.501 1.307	0.704 (0.061)	0.572 0.836	15	0.911	<.001
	g/d	−0.306 (0.187)	−0.709 0.098	0.704 (0.061)	0.572 0.836	15	0.911	<.001

TABLE 2. Continued.

$\overline{\log x}$	$\overline{\log y}$	95% CI of predicted log y^*		
		c	d	e
2.196	2.311	0.371	1.022	0.015
2.196	1.176	0.425	1.022	0.015
1.598	1.831	0.316	1.030	0.313
1.598	0.695	0.434	1.030	0.313
3.715	3.528	0.386	1.077	0.049
2.566	2.639	0.406	1.059	0.041
2.566	1.626	0.405	1.059	0.041
1.980	2.119	0.321	1.035	0.027
1.701	1.844	1.995	0.031	0.0005
1.700	0.662	0.311	1.044	0.142
2.692	2.778	1.995	0.031	0.0005
2.494	2.509	0.231	1.036	0.031
2.494	1.370	0.199	1.036	0.031
3.534	3.079	2.060	0.012	0.0011
3.534	2.066	0.256	1.083	0.192
1.714	2.081	2.060	0.011	0.0011
1.983	2.305	0.368	1.020	0.026
1.983	1.102	0.347	1.020	0.026
1.378	1.981	2.014	0.026	0.0014
1.378	0.772	0.158	1.038	0.480
2.638	2.657	2.014	0.026	0.0014
2.638	1.460	0.401	1.042	0.061
2.266	2.199	2.014	0.019	0.0005
2.266	1.053	0.275	1.125	0.848
1.929	2.326	2.014	0.018	0.0005
2.958	2.985	0.399	1.067	0.109
2.958	1.775	0.399	1.067	0.109

in marsupials, whereas in the eutherians studied thus far, FMR/BMR increases with increasing body mass. The FMR of a large (62 kg) male grey kangaroo is much lower than the FMR of a large (67 kg) male mule deer (compare point 45 in Fig. 1A with point 28 in Fig. 1B).

For birds, FMR is highly correlated with body mass as well (Fig. 1C). The regression equation for birds is:

$$\log y = 1.037 + 0.640 \log x, \qquad (3)$$

with $r^2 = 0.907$. In birds the FMR slope does not differ ($P > .20$) from the BMR slope of 0.668 for all birds (Lasiewski and Dawson 1967).

Judging by the differences in slopes, FMR scales differently than does BMR in mammals, but not in birds. What about the elevations of the relationships: do marsupials have lower FMRs than eutherians, and birds have higher FMRs than eutherians, as occurs with BMR? Plotting the three regression lines together (Fig. 1D) reveals that the lines cross each other, and do not sort into the hierarchy clearly evident with BMR. ANCOVA applied to all three groups indicates that the slopes are not identical ($F_{2,118} = 25.1$, $P \ll .001$). Pairwise ANCOVA comparisons show that the slopes for eutherians and marsupials differ ($F_{1,70} = 46.4$, $P \ll .001$), the slopes for eutherians and birds differ ($F_{1,92} = 21.6$, $P \ll .001$), but the slopes for marsupials and birds do not differ significantly ($F_{1,74} = 2.69$, $P > .10$). However, the intercepts for marsupials and birds, recalculated using the common slope of 0.611, are significantly different ($F_{1,75} = 7.42$, $P < .01$), with birds having a higher intercept than marsupials.

Zerbe et al. (1982) provide a statistical method for determining the range of x values over which two regressions with unequal slopes are too close to each other to differ significantly. This method indicates that the regressions for eutherians and marsupials do not differ between body masses of 71 and 548 g, and eutherians do not differ from birds between body masses of 241 g and 9.44 kg. This suggests that the FMRs of eutherians, marsupials, and birds are similar for medium-sized (241–548 g) animals. It is not possible, on the basis of FMR measurements presently available, to determine whether a 250-g endotherm is a eutherian, a marsupial, or a bird from knowledge of its FMR alone. Thus the FMRs of medium-sized eutherians do not fall into the pattern of marsupial < eutherian < bird that is predicted on the basis of BMR regressions. Small eutherians have lower FMRs than small marsupials and birds, but large eutherians have comparatively high FMRs.

Endotherms and ectotherms

The energy cost of living in nature for endotherms is enormous compared to that of ectotherms such as reptiles. The regression line for FMR in iguanid lizards, $\log y = -0.650 + 0.799 \log x$, $r^2 = 0.981$ (Nagy 1982) has a much lower elevation than those of mammals and birds (Fig. 1D). A 250-g mammal or bird typically

TABLE 2. Continued.

Group	Units of y	Log a ($SE_{Log\ a}$)	95% CI of Log a	b (SE_b)	95% CI of b	N	r^2	P
Other than seabirds	kJ/d	1.325 (0.081)	1.161 1.489	0.440 (0.049)	0.340 0.540	35	0.709	<.001
			Iguanid lizards					
All iguanids	kJ/d	−0.650 (0.029)	−0.711 −0.589	0.799 (0.023)	0.751 0.847	25	0.981	<.001
Herbivores	g/d	−1.713 (0.123)	−2.104 −1.321	0.841 (0.059)	0.652 1.029	5	0.985	<.001
Insectivores	g/d	−1.890 (0.037)	−1.967 −1.812	0.773 (0.038)	0.693 0.853	20	0.958	<.001

* Equation for calculating the 95% CI of a predicted log y value at any log x value is of the form:

$$95\%\ CI_{\log y} = \log y \pm c[d + e(\log x - \overline{\log x})^2]^{0.5}.$$

spends ≈320 kJ of energy daily for oxidative metabolism. This is 17 times as much as the 19 kJ required by a 250-g iguanid lizard during a spring or summer day. This difference results partly from a three- to sixfold greater capacity of endotherm tissues to process energy at the cellular level, as reflected in greater mitochondrial densities, relative membrane surface areas, enzyme activities, sodium transport, and thyroid activities (Bennett 1972, Else and Hulbert 1981, Hulbert and Else 1981). However, most of the difference is due to metabolic responses to daily thermal regimes. As ambient temperature drops at night, a lizard's body temperature and energy metabolism both decline, but an endotherm facing the same environment maintains a high body temperature at the expense of increasing metabolic heat production. For example, at an ambient temperature of 10°C, a typical 250-g endotherm has a resting metabolic rate that is ≈200 times that of a 250-g lizard (calculated using the allometric regression of Hinds and MacMillen [1984] for mammals, and Bennett and Dawson's [1976] regression for lizards at 20°, assuming a Q_{10} of 3 between 10° and 20°).

Rodents, dasyurids, passerines

The allometry of BMR within some taxonomic orders of mammals differs from the BMR regressions for the Class Mammalia or the BMR regressions for the Infraclasses Eutheria and Metatheria (marsupials) (Hayssen and Lacy 1985). Similarly, the higher BMR of birds in the Order Passeriformes as compared with other birds (Lasiewski and Dawson 1967) is well known. Are these differences also apparent in FMR allometry?

The data set for eutherians (Table 1) contains an adequate number of FMR measurements on animals in the Order Rodentia to yield a statistically significant allometric regression, and hence permit ANCOVA comparisons of rodents with all other eutherians. The allometric slope for rodents is significantly lower ($F_{1,42} = 15.3$, $P < .001$) than that for other eutherians (Fig. 2A). The ANCOVA-generated regression line for rodents is:

$$\log y = 1.022 + 0.507 \log x, \quad (4)$$

with $r^2 = 0.524$. The regression line for other eutherians is:

$$\log y = 0.239 + 0.885 \log x, \quad (5)$$

with $r^2 = 0.979$. The FMR slope for rodents (0.507) does not differ significantly ($.10 > P > .05$) from the slope for BMR in rodents (0.669, Hayssen and Lacy 1985), but the confidence intervals for the FMR slope are relatively large (Table 2). Sixteen species of rodents have been studied (Table 1), but all are relatively small (<100 g); studies on larger rodents would be valuable.

Eutherians in the Order Edentata are known to have lower BMRs than other eutherians (Hayssen and Lacy 1985). FMRs of two edentates are also much lower than FMRs of other eutherians. Three-toed sloths (*Bradypus variegatus*, Nagy and Montgomery 1980) have a mass-corrected FMR of 0.70 $kJ \cdot g^{-0.813} \cdot d^{-1}$, which is only 21% of the rate of 3.35 $kJ \cdot g^{-0.813} \cdot d^{-1}$ for a typical eutherian (Eq. 1). Silky anteaters (*Cyclopes didactylus*, K. A. Nagy and G. G. Montgomery, *personal observation*) metabolize 1.27 $kJ \cdot g^{-0.813} \cdot d^{-1}$, only 38% of the expected FMR.

Within the marsupials, species in the Family Dasyuridae do not show a different allometric relationship than do other marsupials (Fig. 2B). ANCOVA indicates that no significant differences exist between slopes ($F_{1,24} = 2.34$, $P > .10$) or intercepts ($F_{1,25} = 2.98$, $P > .05$). Thus, the overall regression for marsupials (Eq. 2 above) best describes the FMR allometry of dasyurids. BMRs of dasyurids (MacMillen and Nelson 1969) also do not scale differently than BMRs of other marsupials (Dawson and Hulbert 1970). However, BMR in the dasyurids listed in Table 1 accounts for only 13–20% of FMR, with the remaining 80–87% allotted to activity, temperature regulation, and other energy costs

TABLE 2. Continued.

$\overline{\log x}$	$\overline{\log y}$	95% CI of predicted log y^*		
		c	d	e
1.565	2.014	0.297	1.029	0.113
1.075	0.209	0.161	1.040	0.088
1.896	−0.119	0.358	1.200	0.278
0.870	−1.217	0.151	1.050	0.279

of living in nature. Thus, it is surprising that the FMRs of dasyurids, which are active predators, do not have higher energy costs of living than other marsupials, which include omnivores and herbivores (Table 1).

Passerine birds, as a group, do have significantly higher FMRs than other birds (Fig. 2C). The slopes do not differ ($F_{1,46} = 0.296$, $P > .5$) but the intercepts do ($F_{1,47} = 17.3$, $P < .001$). The regression equation for passerine birds is:

$$\log y = 0.949 + 0.749 \log x, \quad (6)$$

with $r^2 = 0.899$. The regression equation for birds other than passerines is:

$$\log y = 0.681 + 0.749 \log x, \quad (7)$$

with $r^2 = 0.899$. The common slope for FMR of passerines and nonpasserines (0.749) does not differ significantly ($P > .20$) from the slopes for BMR of passerines (0.724) and nonpasserines (0.723, Lasiewski and Dawson 1967). This indicates that FMR may be a relatively constant multiple of BMR in birds, over a large range of body mass. The ratios of predicted FMR to predicted BMR for a 250-g bird are 2.49 for nonpasserines and 2.80 for passerines (BMR equations of Lasiewski and Dawson 1967), and passerine FMR is 2.50 times BMR measured during the active phase of the daily cycle, but 3.16 times BMR during the resting phase of the daily cycle (BMR equations of Aschoff and Pohl 1970). These ratios are close to the values of 2.6–2.8 times BMR estimated by Drent et al. (1978) as representative for breeding birds. (Most of the FMR measurements summarized in Table 1 were done on breeding birds.) Predicted FMR of a passerine bird is 85% higher than that of a nonpasserine bird. Caution should be exercised when interpreting Eq. 7, because most of the nonpasserines included in this regession (and all of the large nonpasserines) are seabirds. No terrestrial bird larger than 500 g has yet been studied. FMR measurements on eagles and vultures (for comparison with Giant Petrels and albatrosses) and on ostriches, emus and rheas would be especially interesting. Birds other than passerines are very diverse, and they probably should not be grouped together in an ecological context.

Diet

BMR may reflect the kinds of food resources used by different species of endotherms (McNab 1974, 1978*a*, 1980, Hayssen and Lacy 1985). Low BMRs may occur in small insectivorous, frugivorous, and granivorous mammals, and in some groups of herbivorous mammals as well (McNab 1986). Are dietary patterns reflected in FMRs of endotherms? The present FMR data sets are not complete enough to test for allometric differences for many diet types, but enough measurements are available to examine eutherian and marsupial herbivores, and to comment on eutherian granivores.

FMR scales differently in herbivorous eutherians than in nonherbivorous eutherians (Fig. 3A). The allometric slope for herbivores is significantly lower ($F_{1,42} = 9.39$, $P < .005$). The regression equation for herbivorous eutherians is:

$$\log y = 0.774 + 0.727 \log x, \quad (8)$$

with $r^2 = 0.959$. The equation for nonherbivorous eutherians is:

$$\log y = 0.412 + 0.862 \log x, \quad (9)$$

with $r^2 = 0.977$. Large herbivores tend to have somewhat lower FMRs than large nonherbivores, but small herbivores have somewhat higher FMRs than small, nonherbivorous eutherians.

In marsupials, FMR also scales differently in herbivores than in nonherbivores (Fig. 3C). The allometric slopes do not differ ($F_{1,24} = 1.11$, $P > .25$), but the intercepts do ($F_{1,25} = 5.69$, $P = .01$). The regression equation for herbivorous marsupials is:

$$\log y = 0.804 + 0.644 \log x, \quad (10)$$

with $r^2 = 0.936$. The equation for nonherbivorous marsupials is:

$$\log y = 0.978 + 0.644 \log x, \quad (11)$$

with $r^2 = 0.936$. Herbivorous eutherians generally have higher FMRs than herbivorous marsupials. The slopes of the two regressions do not differ ($F_{1,25} = 0.41$, $P > .50$), but the intercepts do ($F_{1,26} = 14.2$, $P < .001$).

Although seven data points for seed-eating eutherians are available, they span only a small range of body masses, and there is no significant allometric relationship among these points ($P > .25$). Field metabolic rates of granivorous eutherians fall among those of similar-sized eutherians having other diets (Fig. 3B), suggesting that no major difference exists in FMR.

Habitat

Climate and habitat type are known to affect the BMR of mammals and birds (Hulbert and Dawson 1974, McNab 1978*b*, 1979, Weathers 1979, 1980,

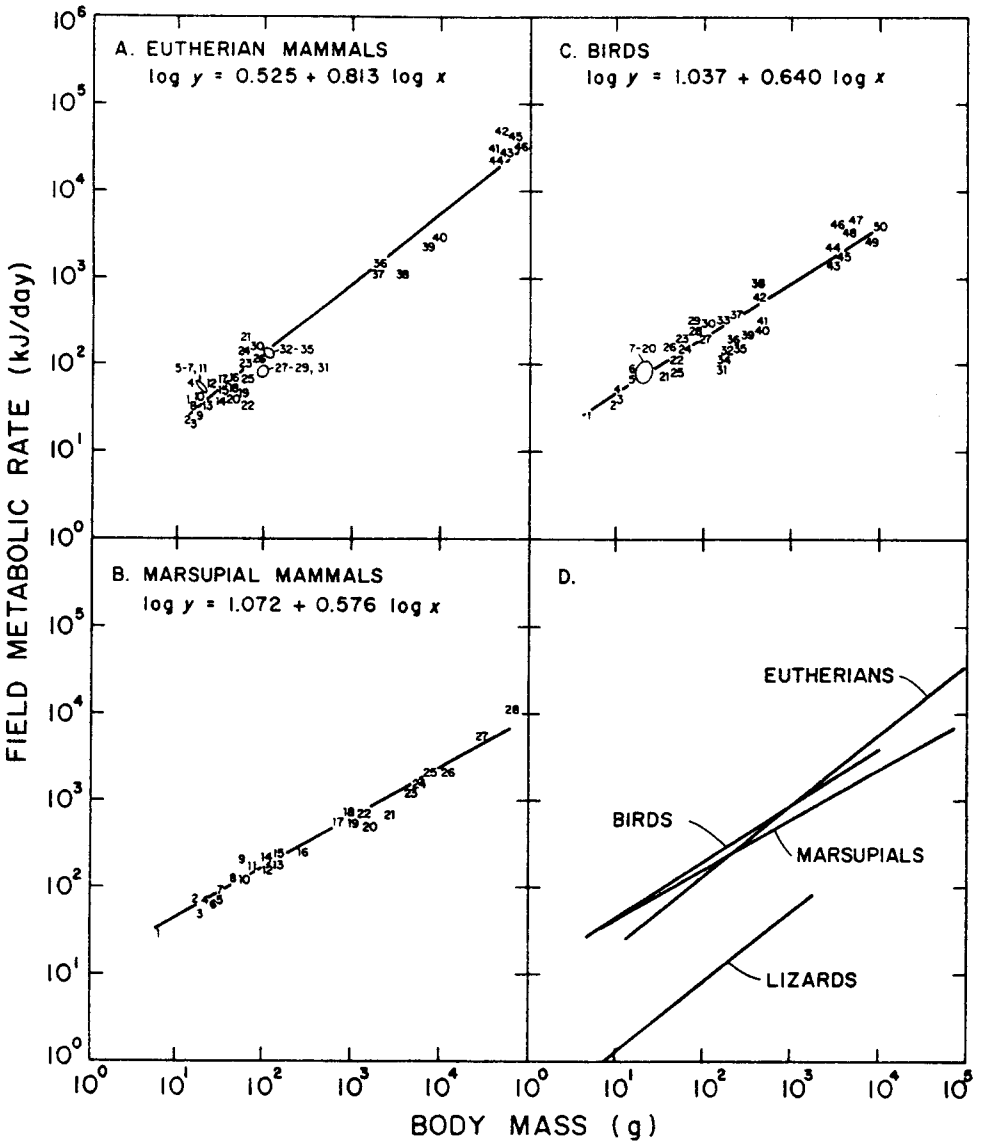

FIG. 1. Allometry of field metabolic rate among (A) eutherian mammals, (B) marsupial mammals, and (C) birds. Small numbers, which are offset in some cases to improve readability, correspond to the species numbers in Table 1. In (D), the regression lines for eutherians, marsupials, and birds are compared with each other and with that for iguanid lizards ($\log y = -0.650 + 0.799 \log x$, Nagy 1982).

Dawson 1984). In particular, desert-dwelling endotherms often have lower BMRs than predicted from allometric equations, and seabirds tend to have high BMRs (Ellis 1984).

Eutherians living in desert habitats have FMRs that are 30% lower than nondesert eutherians (Fig. 4A). The slopes of the regressions do not differ significantly ($F_{1,42} = 0.24$, $P > .50$) but the intercepts, recalculated using the common slope, do differ ($F_{1,43} = 7.81$, $P < .01$). The regression equation for desert eutherians is:

$$\log y = 0.507 + 0.786 \log x, \qquad (12)$$

with $r^2 = 0.963$. The equation for nondesert eutherians is:

$$\log y = 0.663 + 0.786 \log x, \qquad (13)$$

with $r^2 = 0.963$.

Similarly, desert birds have FMRs that are less than half those in nondesert birds (Fig. 4B). The slopes of these regressions do not differ ($F_{1,46} = 3.46$, $.10 > P > .05$) (although the difference is close to statistical significance), but the intercepts are significantly different ($F_{1,47} = 46.8$, $P < .001$). The regression equation for desert birds is:

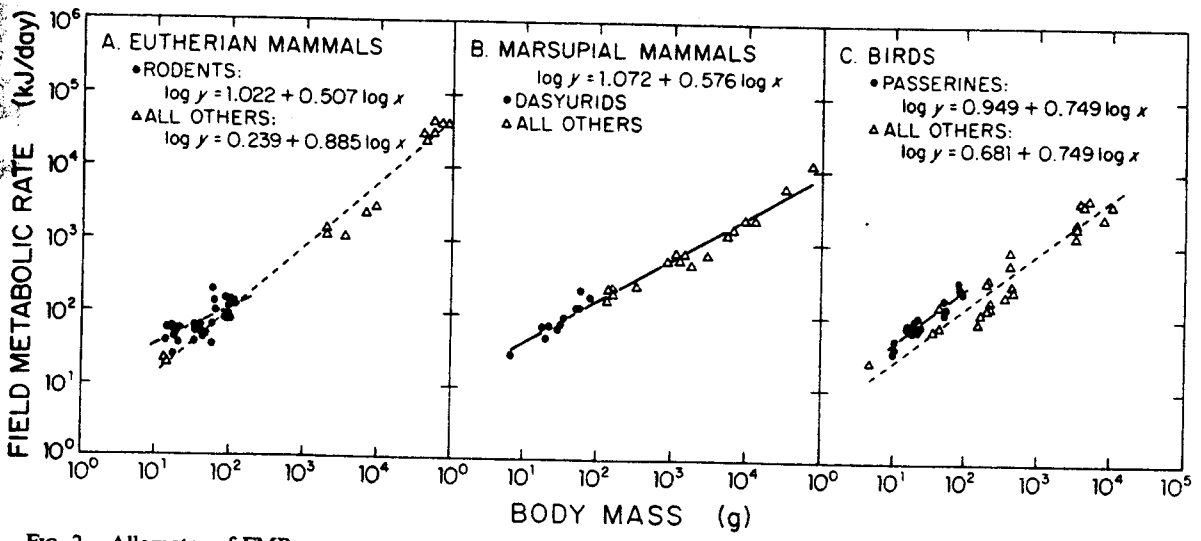

FIG. 2. Allometry of FMR among taxonomic subgroups: (A) rodents differ from other eutherians, (B) dasyurids do not differ significantly (ANCOVA) from other marsupials, but (C) passerine birds differ from other birds. The regression line for rodents (A) was extended beyond the data to improve clarity.

$$\log y = 0.703 + 0.660 \log x, \quad (14)$$

with $r^2 = 0.953$. The equation for nondesert birds is:

$$\log y = 1.052 + 0.660 \log x, \quad (15)$$

with $r^2 = 0.953$. The FMR regression for desert birds has a significantly lower slope ($F_{1,27} = 4.80$, $P = <.05$) than that for desert eutherians, but the two regression lines cross at a body mass of ≈35 g. McNab (1986) suggested that the low BMRs of small desert eutherians may be a consequence of diet rather than habitat. There are too few FMR measurements presently available to evaluate the relative importances of diet and habitat correlates of FMR scaling in eutherians or birds. Field studies of individual species, especially a species that has a seasonally changing diet, could test this hypothesis directly.

The allometry of FMR in seabirds differs from that of nonseabirds (Fig. 4C). Seabirds show a higher slope ($F_{1,46} = 12.6$, $P < .001$). The regression equation for seabirds is:

$$\log y = 0.904 + 0.704 \log x, \quad (16)$$

with $r^2 = 0.911$. The equation for nonseabirds is:

$$\log y = 1.325 + 0.440 \log x, \quad (17)$$

with $r^2 = 0.709$. The FMR slope for seabirds (0.704) does not differ significantly ($P > .40$) from the seabird BMR slope (0.721, Ellis 1984).

Season

Some species of endotherms have FMRs that differ greatly from season to season, but other species apparently have relatively constant FMRs through time (Table 1). For example, the pocket gopher *Thomomys bottae* had a maximum, mass-corrected FMR (during spring) that was only 8% higher than its minimum FMR, which occurred in winter (spring FMR = 12.9 $kJ \cdot g^{-0.507} \cdot d^{-1}$, winter FMR = 11.9 $kJ \cdot g^{-0.507} \cdot d^{-1}$, corrected for body mass differences on the basis of Eq. 4 for rodents). Similarly, the desert-dwelling partridges *Ammoperdix heyi* and *Alectoris chukar*, had maximum FMRs only 16 and 19% higher than minimum FMRs, respectively (mass corrections based on Eq. 14 for desert birds), while the desert jackrabbit *Lepus californicus* had a 20% higher FMR in spring compared to winter (mass-corrected using Eq. 12). On the other hand, maximum FMR (spring) was 283% higher than the minimum (summer) in the desert rodent *Dipodomys microps* and 105% higher in spring than in summer for the desert rodent *Perognathus formosus* (mass corrections based on Eq. 4). Seasonal variation in FMR has not been measured in enough species of endotherms at present to permit allometric analyses to be done by season. Seasonal changes in FMR have been measured in only one species of marsupial (*Antechinus swainsonii*), where lactating females had a mean FMR 75% greater than they did during the preceding mating period. Seasonal DLW measurements have been done on only two species of birds (*Ammoperdix heyi* and *Alectoris chukar*, Table 1). Birds present a problem in this regard, because many species are readily capturable only during the breeding season. As a result of this, the FMR data and allometric regressions reported herein for birds are biased strongly toward the breeding season (see Table 1).

Food requirements

The rate of food consumption an animal must achieve to provide the energy it uses in oxidative metabolism

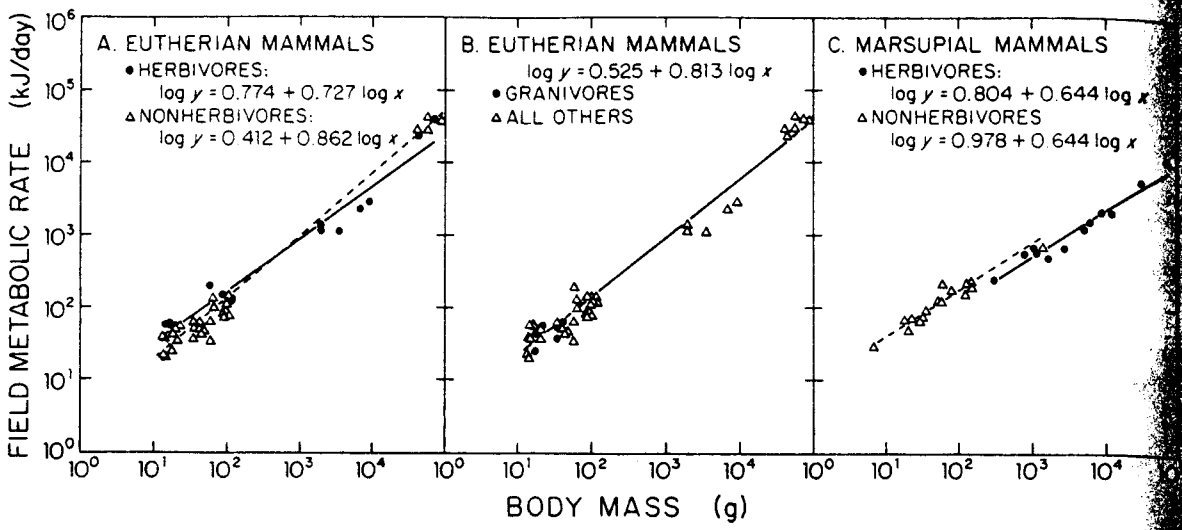

FIG. 3. Allometry of FMR among dietary subgroups: (A) herbivorous eutherians differ from nonherbivorous eutheria (B) seed-eating eutherians do not differ from other eutherians, and (C) herbivorous marsupials have lower FMRs th nonherbivorous marsupials.

can be calculated by dividing its FMR, in units of kilojoules per day, by the metabolizable (useable) energy in its food, in units of kilojoules per gram of food. Thus, the FMR data in Table 1 can be used to generate regressions for steady-state feeding rates that free-living mammals and birds must achieve over any considerable period of time.

Metabolizable energy (ME) in a diet is the total (gross) energy in a unit of food consumed minus the energy lost as feces and urine resulting from that unit of food. Metabolizable energy efficiency (the ratio ME/total energy, or the fraction of gross energy that is metabolizable) is relatively constant among different species mammals and birds that are either carnivorous, in tivorous or granivorous (Hume 1982, Peters 19 Robbins 1983). In herbivorous mammals, metabo able energy efficiency for cell wall components creases with increasing body mass, because food ments for longer periods in larger herbivores (P 1978, van Hoven and Boomker 1985). However, herbivores generally select younger and more te vegetation that contains relatively low amounts o wall materials, so actual metabolizable energy effic cy tends to be independent of body mass (Parra 19

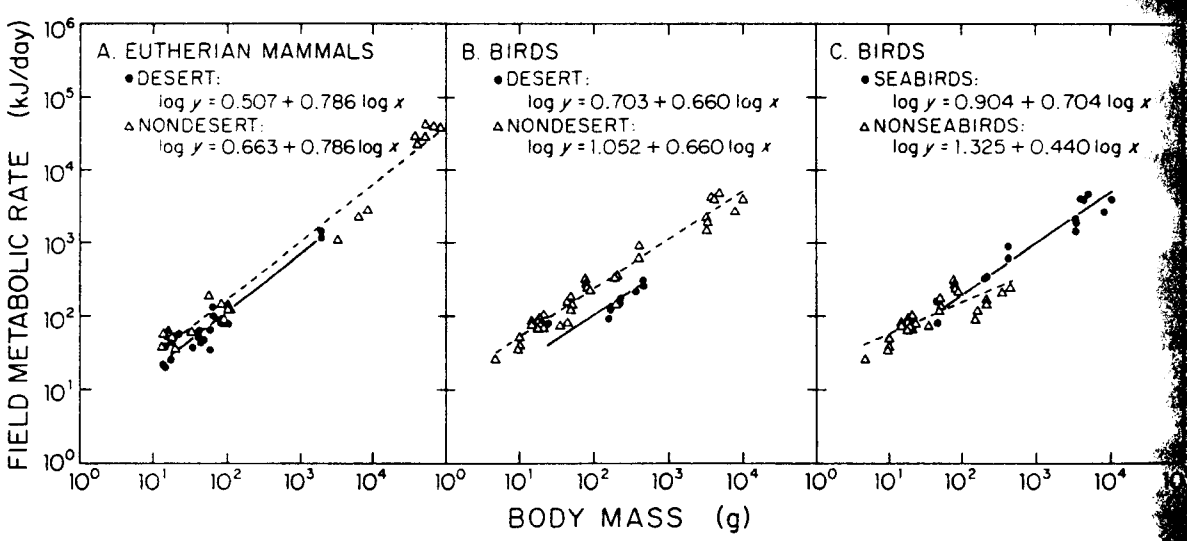

FIG. 4. Allometry of FMR among habitat subgroups: (A) desert eutherians have lower FMRs than nondesert eutheria (B) desert birds have lower FMRs than nondesert birds, and (C) seabirds differ from nonseabirds.

TABLE 3. Summary of allometric equations for field metabolic rates and feeding rates of free-living mammals, birds, and lizards. The equations have the form $y = ax^b$ where y is FMR (in kJ/d) or feeding (dry matter ingestion) rate (in g/d) and x is body mass (in g).

Group	Units of y	a	Units of x	b	95% CI of predicted y, as % of predicted y*	Equation
			Eutherian mammals			
All eutherians	kJ/d	3.35	g	0.813	−58 to +138%	18
	g/d	0.235	g	0.822	−63 to +169%	19
Rodents	kJ/d	10.5	g	0.507	−52 to +110%	20
	g/d	0.621	g	0.564	−64 to +176%	21
Herbivores	kJ/d	5.95	g	0.727	−62 to +161%	22
	g/d	0.577	g	0.727	−62 to +161%	23
Desert eutherians	kJ/d	3.21	g	0.786	−59 to +141%	24
	g/d	0.150	g	0.874	−52 to +108%	25
			Marsupial mammals			
All marsupials	kJ/d	11.8	g	0.576	−42 to +72%	26
	g/d	0.492	g	0.673	−37 to +59%	27
Herbivores	kJ/d	6.36	g	0.644	−40 to +67%	28
	g/d	0.321	g	0.676	−46 to +84%	29
			Birds			
All birds	kJ/d	10.9	g	0.640	−57 to +135%	30
	g/d	0.648	g	0.651	−55 to +124%	31
Passerines	kJ/d	8.88	g	0.749	−53 to +111%	32
	g/d	0.398	g	0.850	−31 to +45%	33
Desert birds	kJ/d	5.05	g	0.660	−47 to +91%	34
	g/d	1.11	g	0.445	−49 to +95%	35
Seabirds	kJ/d	8.01	g	0.704	−53 to +113%	36
	g/d	0.495	g	0.704	−61 to +159%	37
			Iguanid lizards†			
All iguanids	kJ/d	0.224	g	0.799	−32 to +46%	38
Herbivores	g/d	0.019	g	0.841	−59 to +146%	39
Insectivores	g/d	0.013	g	0.773	−30 to +43%	40

* Calculated at mean x for the regression (see text for details).
† Recalculated from Nagy (1982).

By combining average values for metabolizable energy efficiency for mammals and birds eating various diets (Hume 1982, Peters 1983, Robbins 1983) with typical gross energy contents of those diets (Golley 1961, Robbins 1983), I calculated the following mean metabolizable energy contents (in units of kilojoules of metabolizable energy per gram of dry matter): insects, 18.7 kJ/g for mammals and 18.0 kJ/g for birds; fish, 18.7 kJ/g for mammals and 16.2 kJ/g for birds (all carnivores listed in Table 1 eat primarily fish or marine invertebrates); vegetation, 10.3 kJ/g for mammals; seeds, 18.4 kJ/g for eutherians; and nectar, 20.6 kJ/g for hummingbirds. I estimated an intermediate value of 14 kJ/g for omnivorous mammals and omnivorous and frugivorous birds. Feeding rates were calculated using these values and FMR values for each cohort listed in Table 1, and allometric relationships for field food requirements of the various groups of mammals and birds were calculated via least-squares linear regression of the log-transformed data. In addition, allometric relationships for feeding rates of herbivorous and insectivorous iguanids were recalculated (as above, from data in Nagy 1982). Feeding rate regressions and associated statistics are shown in Tables 2 and 3.

Predicting FMR and food requirement

The allometric equations describing BMR in vertebrates have been very valuable to biologists. Those equations can be used to predict the BMR of animals from knowledge of body mass alone, or they can be used, for example, to evaluate the limits and constraints on body size or the interdependence of physiological and morphological properties of animals, and they establish the "standard," against which unusual species or groups of animals may be compared to reveal adaptations (Calder 1984, Schmidt-Nielsen 1984). The allometric relationships for FMR and feeding rate above can serve similar applications, in regard to the actual performance of wild animals living in their natural habitats. The exponential forms of these equations are the easiest to use on a day-to-day basis, so these forms are summarized in Table 3.

In many applications, it is important to have some estimate of the variation around a FMR or feeding rate value predicted for a given body mass via these equations. Two measures of the variation around regression lines are available. One is the 95% confidence interval of the regression (dashed lines in Fig. 5), which is calculated from, and applies only to, the data set used in

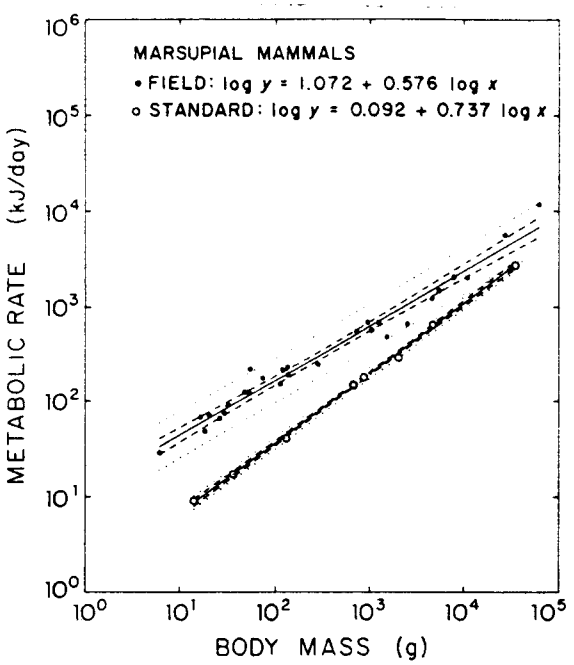

FIG. 5. Comparison of the scaling of FMR (●, ——) and standard metabolic rate (SMR, open circles, ——), along with the 95% confidence limits of the regressions (– – –) and the 95% confidence limits of the predictions (· · · · ·). The dotted lines apply to predictions of new y values at given x values.

the regression itself. In some earlier publications, this measure has erroneously been used to estimate confidence intervals of predicted values. The other is the 95% CI of the prediction (dotted lines in Fig. 5), which incorporates the additional uncertainty expected in new data points, and hence yields much wider confidence intervals (Fig. 5). The 95% CI of the prediction is the appropriate measure of variation to use when predicting new FMR or feeding rate values (Dunn and Clark 1974). The confidence intervals of the prediction expand toward the ends of the regression line (Fig. 5) because of increasing uncertainty with increasing distance from the mean log x value. For this and other reasons, it is risky to extrapolate these allometric equations beyond their empirical limits. In order to provide an idea of the confidence in predicted FMR or feeding rate values, I calculated the 95% CI for each equation at mean log x (where 95% CIs are smallest), took the antilog, and expressed the confidence limits as percents of predicted y (Table 3). The upper confidence limit is farther from predicted y than is the lower confidence limit after antilog transformation. For most equations, the lower confidence limit is 50–60% below predicted y, and the upper limit is between 100 and 170% greater than predicted y.

The FMR equations in Table 3 should yield predicted FMRs and 95% CIs that reflect the variability that actually occurs in the field. The data used to derive these regressions include variation due to differences in age, season, habitat, microclimate, behavior, etc. (Table 1). My intent was to generate the most general, widely applicable models of FMR possible with available measurements. The equations for birds are least successful in this regard, because most measurements for birds were made during the breeding season (when birds, especially seabirds, can be captured and recaptured reliably).

Predicted feeding rates are those required to achieve energetic steady-state, and do not include the additional food energy allocated to production (increase in biomass). The extra metabolic heat produced due to the added metabolic costs of growth and reproduction are already incorporated to some extent, because many of the FMR measurements in Table 1 were made on growing or reproducing animals. However, the chemical potential energy from the food that appears as new biomass is not accounted for in feeding rates estimated from FMR alone. Food consumption predicted from FMR, and calculated on a daily basis, should be close to actual feeding rates in adult mammals for most of the year, because nonbreeding adults usually do not grow much, and are maintaining energy budgets near steady-state conditions. For animals that become hyperphagic while undergoing prehibernation or premigratory fattening, feeding rates predicted from FMR will be underestimates during the fattening period, but they will be overestimates during the hibernation or migration periods, when feeding is reduced. Such predictions, if summed over the entire cycle of fattening and fasting, should be close to the actual, integrated feeding rate over the entire period, provided that the animal ends up with a body mass and chemical composition close to those it had at the beginning of the fattening period.

If annual food consumption by a population is predicted from the equations in Table 3, food ingestion will be underestimated by that amount of food appearing as new biomass (=production, the sum of reproduction and of growth of adults). This error should be <5% because endotherms in general channel only 0.5–3% of the energy they ingest into production on an annual basis (McNeill and Lawton 1970, Turner 1970, Humphreys 1979). However, on a daily basis, individual lactating female eutherians, or adult birds feeding large nestlings, may consume much more food energy than they themselves metabolize, so daily feeding rates predicted from FMR can be much too low in these situations.

To illustrate the predictive capabilities of these equations, assume we wish to estimate the daily and annual costs of living, as well as the food requirements, of spotted skunks (*Spilogale putorius*), for an individual animal and on a population basis. Assume males weigh 900 g and females average 500 g, and there are three pairs/ha of habitat. From Eq. 18, predicted FMR of a male is 845 kJ/d, and for the female, 524 kJ/d. Annual

FMR would be 308 MJ/yr (845 kJ/d·365 d/yr), for the male, and 191 MJ/yr for the female. Energy respired by the population would be 1497 $MJ \cdot ha^{-1} \cdot yr^{-1}$ [(3·308 MJ/yr) + (3·191 MJ/yr)]. From Eq. 19, predicted food (dry matter) requirements are 63 g/d for the male, and 39 g/d for the female. Annual food requirements for maintenance would be 23 kg/yr for the male, 14 kg/yr for the female, and 111 $kg \cdot ha^{-1} \cdot yr^{-1}$ for the population. These estimates of annual food consumption should be increased by 1–3% to account for the additional food chemicals appearing in biomass of weaned offspring and increased biomass of growing adults.

A more accurate prediction of food requirements can be made by incorporating measurements of diet and metabolizable energy efficiency specifically for *Spilogale putorius*. For example, if one knows that the diet is 90% animal matter and 10% vegetation, and that the dry matter in this diet contains 20.0 kJ/g, of which 16.0 kJ/g is metabolizable, then feeding rates can be calculated directly from predicted FMRs by dividing FMR by 16.0 kJ/g. Feeding rates estimated this way (dry matter) are 53 g/d for a male and 33 g/d for a female, ≈15% lower than the feeding rates predicted using Eq. 19 which assumes a more catholic diet.

Conclusions

1) Field metabolic rates are closely correlated with body mass (r^2 values for $\log_{10}$–$\log_{10}$ regressions are 0.91 to 0.97) in eutherian mammals, marsupial mammals, and birds.
2) FMR scales differently from BMR in eutherians and marsupials, but not in birds.
3) FMRs of medium-sized (240 to 550 g) eutherians, marsupials, and birds are similar, indicating that the energetic cost of living for a day in the field is about the same for medium-sized endotherms. This cost is ≈17 times greater than that paid by a similar-sized ectotherm (diurnal lizard).
4 FMR scales differently among rodents (compared with other eutherians), among passerine birds (compared with other birds), and among herbivorous eutherians and marsupials (compared with nonherbivorous eutherians and marsupials, respectively). Desert eutherians and birds have relatively low FMRs, and FMR scales differently in seabirds than in other birds.
5) Within different species, seasonal changes in FMR may be small (less than 10% in pocket gophers) or large (nearly four-fold in some kangaroo rats).
6) Equations are given for predicting FMRs and food requirements of free-living mammals, birds, and lizards.

Questions for future research

1) Do large terrestrial eutherians and birds have FMRs as high as large marine eutherians and birds?
2) Do desert marsupials have relatively low FMRs, as do desert eutherians and birds?
3) Do bats, which account for a large portion of the world's species of small eutherians, typically have FMRs as low as that of *Macrotus* (Table 1)?
4) What are the ecological bases of the observations (a) that medium-sized eutherians, marsupials, and birds all have similar FMRs but quite different BMRs, (b) that large herbivorous eutherians (deer) have much higher FMRs than do large herbivorous marsupials (kangaroos), and (c) that small eutherians have much lower FMRs than do small marsupials? Do these differences have physiological explanations as well?
5) How do habitat and diet effects on FMR interact with each other, and what are their physiological and behavioral bases?

Acknowledgments

This review and many of the studies cited herein were funded by the Ecological Research Division of the U.S. Department of Energy via Contract DE-AC03-76-SF00012 and by NSF grant DEB 79-03868. I am grateful to G. A. Bartholomew for the stimulus to undertake this task, to A. Bennett, T. Bucher, B. Henen, R. Peters, C. Peterson, and K. Schmidt-Nielsen for their patient assistance with statistics, to my collaborators A. J. Bradley, S. D. Bradshaw, B. Clay, A. A. Degen, H. I. Ellis, M. R. Fleming, W. J. Foley, N. K. Jacobsen, M. Kam, A. K. Lee, R. W. Martin, K. D. Morris, B. S. Obst, T. N. Pettit, D. R. Powers, I. Rooke, G. Sanson, and G. C. Whittow for permission to cite our as yet unpublished results, and to G. A. Bartholomew, A. F. Bennett, W. A. Calder III, A. A. Degen, H. B. Lillywhite, R. E. MacMillen, B. K. McNab, and W. A. Montevecchi for their comments on various versions of the manuscript.

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