

Basal Metabolic Rate in Carnivores Is Associated with Diet after Controlling for Phylogeny

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ABSTRACT

Studies of basal metabolic rate (BMR), the minimum metabolic rate of postabsorptive, inactive endotherms while in their rest phase and thermal neutral zone, have contributed significantly to our understanding of animal energetics. Besides body mass, the main determinant of BMR, researchers have invoked diet and phylogenetic history as important factors that influence BMR, although their relative importance has been controversial. For 58 species within the Carnivora, we tested the hypothesis that BMR is correlated with home range size, a proxy for level of activity, and diet, using conventional least squares regression (CLSR) and regression based on phylogenetic independent contrasts (PIC). Results showed that BMR of Carnivora was positively correlated with home range size after controlling for body mass, regardless of the statistical method employed. We also found that diet and mass-adjusted home range size were correlated. When we simultaneously tested the effect of diet and mass-adjusted home range on mass-adjusted BMR, home range size was insignificant because of its colinearity with diet. Then we eliminated home range size from our model, and diet proved to be significant with both CLSR and PIC. We concluded that species that eat meat have larger home ranges and higher BMR than species that eat vegetable matter. To advance our understanding of the potential mechanisms that might explain our results, we propose the “muscle performance hypothesis,” which suggests that selection for different muscle fiber types can account for the differences in BMR observed between meat eaters and vegetarian species within the Carnivora.

Introduction

Studies of basal metabolic rate (BMR), the minimum metabolic rate of postabsorptive, inactive endotherms while in their rest phase and thermal neutral zone, have contributed significantly to our understanding of animal energetics (Kleiber 1961; King 1974; McNab 1986; Ricklefs et al. 1996; Lovegrove 2000; Gillooly et al. 2001; Darveau et al. 2002; Rezende et al. 2004). BMR gains ecological significance when one considers that it is correlated with field metabolic rate (FMR) in mammals (Nagy 1987; Koteja 1991; Ricklefs et al. 1996; Nilsson 2002) and that it is related to reproductive output (McNab 1980).

In mammals BMR is a power function of body mass, its main determinant, where the exponent ranges between 0.67 and 0.75 (Kleiber 1961; Dodds et al. 2001; Symonds and Elgar 2002; White and Seymour 2003). Even among species of mammals of the same body mass, BMR varies sixfold (McNab 1988a; Blaxter 1989). Factors that have been invoked to explain residual variation in BMR include climate (Scholander et al. 1950; Lovegrove 2003), biogeography (Lovegrove 2000), habitat (McNab and Morrison 1963; MacMillen and Hinds 1983; Hinds and MacMillen 1985), parasite species richness (Morand and Harvey 2000), life history (Harvey et al. 1991), demography (McNab 1980; Kurta and Ferkin 1991), diet (McNab 1992a, 2003), and phylogenetic history (Hayssen and Lacy 1985; Elgar and Harvey 1987; Harvey et al. 1991). Among these factors, diet and phylogenetic history have received the most attention, although researchers disagree about their relative importance (Derrickson 1989; Harvey and Elgar 1989; McNab 1992a).

For 151 eutherian mammals, McNab (1986) found that species that consumed vertebrate prey had a high BMR; those that ate invertebrates, fruits, or leaves of woody plants had low BMR; and species that ate a mixed diet had an intermediate value. Believing McNab's methods flawed, Elgar and Harvey (1987) readdressed the hypothesis of association between diet and metabolic rate in mammals and, after ostensibly removing the effects of phylogeny, failed to find a relationship between BMR and diet. In another study, Harvey et al. (1991) did not find that diet influenced BMR in eutherian mammals after performing analyses based on phylogenetic independent contrasts (PIC; Felsenstein 1985). McNab (1992a) pointed out errors in Elgar and Harvey's (1987) data set such as incorrect values of body mass and BMR and at least 28 incorrect assignments of food habits. He reanalyzed mammalian BMR using ANCOVA and concluded that ecological factors such as food habits and

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activity levels were more important than phylogeny in explaining variation in BMR.

Although most studies relating BMR to diet included species within the entire class Mammalia, restricting data to species within a single order or family of mammals could be more instructive when utilizing the comparative method (Leroi et al. 1994). In support of this view, Hayssen and Lacy (1985) found different slopes for orders of mammals when they regressed BMR against body mass. If different factors affect BMR, we might expect different slopes for the relationship between BMR and body mass among orders (McNab 1992a). To avoid some of these problems, we restricted our study to species of Carnivora, a taxon composed of 270 species with a variety of dietary habits ranging from vegetarian to species that consume only meat.

Even when studies have been restricted to a single family, researchers have found contrasting results depending on the method of analysis. Using conventional ANCOVA, McNab (1992a) concluded that body mass and food habits were the only significant factors explaining variance in BMR in the family Phyllostomidae (Chiroptera). However, Cruz-Neto et al. (2001) failed to find an association between BMR and diet in bats when they employed PIC. McNab (2003) disagreed with these findings and claimed that “the concept that quantitative physiological characters can be transmitted via phylogeny without regard to the habits of animals and the characteristics of their environments cannot be defended” (p. 357).

McNab (1989, 1992a) found that the primary determinant of mass-adjusted BMR in Carnivora was diet, with climate and activity as secondary factors. Species within this order that preyed almost entirely on vertebrates had high BMR (McNab 2000), whereas species that ate invertebrates, fruits, and/or leaves exhibited low metabolic rates (McNab 1995). Although McNab (1992a) used taxonomic affiliation in his analyses, he did not remove effects of phylogenetic history (Garland et al. 1993).

To explain the association between metabolic rate and food habits, McNab (1986, 1989) argued that properties of food influence rates of energy acquisition by mammals and, therefore, energy expenditure. Factors that restricted energy availability were seasonal variation in food supply (fruits), low energy density of food (some invertebrates), or foraging methods (ant and termite eaters). However, one might think that some correlate of food habits, such as the level of activity required to procure prey, could potentially also be responsible for variation in BMR among mammals. Carnivorous mammals tend to have larger home ranges than herbivorous species (Harvey and Pagel 1991), and foraging over a larger area could result in higher field metabolic rate. Given that mammals with high FMR also tend to have high BMR (Ricklefs et al. 1996), covariation between BMR and diet could be a product of an association between BMR and activity level. Nevertheless, Garland et al. (1993) failed to find a relationship between home

range size and diet using data from three orders of mammals (Carnivora, Artiodactyla, and Perissodactyla) after they controlled for mass and phylogeny.

Here, we compile data for BMR, diet, and home range size, a proxy for level of activity, for 58 species of Carnivora. Our assignment of diet as a continuous variable—percentage of meat in the diet—rather than to discrete categories minimizes ambiguity over placement of species in diet categories (e.g., Cruz-Neto et al. 2001). We tested the hypothesis that BMR is associated with home range size and diet among members of the Carnivora. BMR and home range size were significantly correlated after adjusting for body mass using both conventional statistics and regressions based on PIC. We also found evidence that diet was correlated with home range size after controlling for mass and phylogeny. In a multiple regression model, results showed that home range size was not a significant variable when mass, diet, and phylogeny were included. We then eliminated home range size from our model, and we found a positive association between BMR and the proportion of meat in the diet, using both conventional statistics and statistics based on PIC. From these results, we concluded that species that eat meat forage over larger home ranges and have higher BMR than vegetarian species. Our findings are the first to bridge the gap between colleagues whose approaches to addressing correlations between BMR and diet have differed.

Material and Methods

Data Collection and Treatment of Variables

For BMR, we selected 58 measurements made on postabsorptive animals from eight families of Carnivora at rest and within their thermoneutral zone (Table 1). When several measurements existed for a species, values of BMR and body mass were averaged if the authors had not reported sample size; if sample sizes were reported, we weight-averaged the values based on sample size.

For 54 species, we expressed diet as a percentage of meat (vertebrates), invertebrates, and vegetable matter eaten (Table 2). In tabulating diets, mostly quantified from contents of fecal samples, we favored data based on biomass rather than frequency of occurrence. Percentage of meat in the diet was not normally distributed (Kolmogorov-Smirnov test, $KS = 0.24$; $P < 0.01$). Therefore, for this variable we used the logit transformation ($\log [Y/1 - Y]$; Zar 1996), which normalized the data ($KS = 0.11$; $P > 0.11$).

We obtained values of home range size for 41 species of Carnivora (Table 3). Group-living species were excluded because group size might affect estimates of home range size. Only estimates of female home range size were included because, in most species of Carnivora, male home range size is

related not only to resource availability but also to mating behavior (Sandell 1989).

Some of our analyses are complicated by the fact that variables are interrelated. To make the variables independent, we used in our analyses residuals obtained from regressions. The effect of mass on BMR was eliminated using residuals from the regression between those two variables (mass-adjusted BMR). We used the same procedure with home range size and body mass (mass-adjusted HR). To make home range size independent of mass and diet simultaneously, we used residuals of the multiple regression equation, $\text{home range size} = a + b_1 \times \text{mass} + b_2 \times \text{diet}$. We refer to the latter variable as “res HR.”

Construction of Phylogeny

We constructed a phylogenetic tree of species for which we had physiological data based on both the fossil record and molecular data (Fig. 1). Branches are given in million years from divergence (see Appendix).

Phylogenetic Signal

We tested for phylogenetic signal in body mass, BMR, percentage of meat in the diet, and home range size using the test of serial independence (Abouheif 1999) and the test for phylogenetic signal in the Phenotypic Diversity Analysis Program (PDAP; Garland et al. 1999; Garland and Ives 2000). We used two different tests for signal because they have different underlying assumptions.

Conventional Least Squares Regressions versus Regressions Using Phylogenetic Independent Contrasts: A Note of Caution

We have used both conventional least squares regression (CLSR) and regression based on PIC, a procedure that some of our colleagues may question. Some might argue that PIC, the most common model currently in use, is the preferred or even obligatory method because using contrast data adjusts for relatedness among species, “correcting” for phylogenetic history (Harvey et al. 1995; Garland et al. 1999; Bennett and Owens 2002; Rezende et al. 2004). Incorporation of phylogenies into comparative physiology has provided an important tool for guiding the selection of species in comparative studies and for thinking about the adaptive significance of traits (Bennett 1997; Ackerly and Donoghue 1998; Feder et al. 2000)—the significance of both contemporary trait values and of their evolutionary history. We embrace inclusion of phylogenies into comparative analyses when tests for phylogenetic signal indicate that these methods are warranted. But insistence on PIC as the only method to use in comparative analyses could lead to errors

of interpretation; we encourage caution in interpreting results obtained using PIC. New models currently being developed, based on the assumption that species mean values reflect adaptation to current environment, emphasize the importance of evaluating the proper evolutionary model and in some cases obviate the necessity of incorporating phylogenetic relationships of species (Kelly and Price 2004). In addition, the development of phylogenetic models that incorporate stabilizing and directional selection may soon supersede models of PIC based on Brownian motion (Butler et al. 2004).

The primacy ascribed to PIC is based on the idea that this method solves a problem inherent in CLSR, namely, that sister species are not independent (Felsenstein 1985). In our use of CLSR, we do not assume a “star phylogeny,” or any phylogeny, as some would argue (Garland et al. 1992, 1999). Rather we assume that traits are held by natural selection near their optimum for a given environment and that trait A in species X is not similar to the same trait in species Y merely because they have a common ancestor. At present there exists no mechanism for testing the degree to which natural selection has operated in the past to bring about speciation or to test whether stabilizing selection is currently creating stasis in a trait. Similarities among closely related species can result from similarities in selection pressures and need not imply phylogenetic constraint (Williams 1992; Ridley 1996). We are circumspect in using only PIC in this study because we violate many, if not all, of the assumptions of the PIC method. For example, PIC assumes that a correct topology is known (Felsenstein 1985, 1988), a condition unfilled in this study and probably all others (Lake and Moore 1998). Even phylogenetic trees based on molecular data typically are constructed from one or two genes, often from mitochondria. These “gene trees” are assumed to represent the “species tree,” but this may be untrue (Coyne and Orr 2004). The evolutionary model implicit in PIC is that of stochastic evolution or Brownian motion (Diaz-Uriarte and Garland 1996). If the evolution of physiological traits in carnivores deviates significantly from a stochastic model, then PIC may provide inappropriate parameter estimates of allometric relationships across species (Price 1997; Kelly and Price 2004). Evidence suggests that natural selection and/or sexual selection, and not genetic drift, are the dominant forces promoting speciation (West-Eberhard 1983; Coyne and Orr 2004), invalidating the Brownian motion model.

PIC can provide values that are nonindependent when clades have different rates of evolution or when change in a trait varies with time, that is, position within the tree (Price 1997). When alternate phylogenies are incorporated into comparative analyses, results and conclusions can be markedly different (Price 1997; McKechnie and Lovegrove 2002), although comparisons between simulated phylogenies indicate that results of PIC analyses may be relatively insensitive to the topology (Garland and Adolph 1994). Ricklefs and Starck (1996) reported that contrasts from short branch lengths contribute to a larger pro-

Table 1: Body mass and basal metabolic rate (BMR) of 58 species of Carnivora

Species	<i>n</i>	Body Mass (g)	BMR (kJ/d)	Source
Canidae:				
<i>Canis latrans</i>	4	10,300 ± 987	2,165.47 ± 356	Shield 1972
<i>Canis lupus</i>	...	18,950	3,028.97	McNab in Hayssen and Lacy 1985
<i>Cerdocyon thous</i>	2	5,444	731.67	Henneman et al. 1983
<i>Alopex lagopus</i>	7	4,100	929.3	Fugley and Øritsland 1999
<i>Vulpes zerda</i>	4	1,215	281.1	Maloiy et al. 1982
<i>Vulpes macrotis</i>	12	1,819	485.5	Golightly and Ohmart 1983
<i>Vulpes vulpes</i>	6	4,725	1,195.5	Irving et al. 1955; Williams et al. 2004
<i>Vulpes ruppellii</i>	6	15,45.7 ± 385	385.4 ± 73	Williams et al. 2002
<i>Vulpes cana</i>	4	1,285 ± 52	304.5 ± 32.3	Williams et al. 2004
Mustelidae:				
<i>Spilogale putorius</i>	...	624	140.77	Kilgore in McNab 1989
<i>Lutra lutra</i>	3	8,854.3 ± 1,777	2,997.3 ± 869	Iversen 1972
<i>Enhydra lutris</i>	10	29,625	9,570.1	Morrison et al. 1974
<i>Meles meles</i>	1	10,715.2	1,323	Iversen 1972
<i>Taxidea taxus</i>	6	9,000	1,301.2	Harlow 1981
<i>Gulo gulo</i>	3	13,133.4 ± 3,593	2,590.6 ± 445	Iversen 1972
<i>Eira barbara</i>	1	2,950	586.22	McNab 1995
<i>Martes americana</i>	5	1,038	329.34 ± 30	Worthen and Kilgore 1981
<i>Martes martes</i>	1	930.6	362.3	Iversen 1972
<i>Mustela vison</i>	8	834.9	283.6	Farrell and Wood 1968; Iversen 1972
<i>Mustela frenata</i> (females)	4	153 ± 3	84.35 ± 12	Brown and Lasiewski 1972
<i>Mustela erminea</i>	8	169.6	146.5	Iversen 1972; Casey and Casey 1979
<i>Mustela nivalis</i>	9	72.6	87.3	Iversen 1972; Casey and Casey 1979
Procyonidae:				
<i>Ailurus fulgens</i>	2	5,740	421.55 ± 23	McNab 1988b
<i>Nasua nasua</i>	2	3,850 ± 212	486.02 ± 38	Chevillard-Hugot et al. 1980
<i>Nasua narica</i>	4	3,630 ± 548	573.25 ± 77	Chevalier 1991
<i>Bassariscus astutus</i>	20	860.7	185.5	Chevalier 1991
<i>Bassariscus sumichrasti</i>	7	1,287.3 ± 133	305.24 ± 25	Chevalier 1991
<i>Potos flavus</i>	≥7	2,688	447.71	Müller and Kulzer 1977; Chevalier 1991; McNab 1995
<i>Procyon cancrivorus</i>	...	1,160	221.75	Scholander et al. 1950
<i>Procyon lotor</i>	≥8	4,847	742.23	Chevalier 1991; Mugaas et al. 1993; McNab 1995
Ursidae:				
<i>Ursus ursinus</i>	2	66,957 ± .3	4,049.56 ± 82	McNab 1992b
<i>Ursus arctos</i>	...	136,000	8,355.84	Watts 1989
<i>Ursus maritimus</i>	...	204,000	11,652.48	Watts 1989
<i>Ursus americanus</i>	...	143,000	5,559.84	Watts 1989
Herpestidae:				
<i>Herpestes sanguineus</i>	7	540	194.4	Kamau et al. 1979
<i>Herpestes auro punctatus</i>	8	611	193.56 ± 149	Ebisu and Whittow 1976
<i>Suricata suricatta</i>	5	850	148.92 ± 9	Müller and Lojewski 1986
Viverridae:				
<i>Arctitis binturong</i>	2	14,280 ± 3,514	541.5 ± 192	McNab 1995
<i>Fossa fossa</i>	1	2,260	435	McNab 1995
<i>Genetta tigrina</i>	2	1,698 ± 271	358.62 ± 16	Henneman and Konecny 1980
<i>Genetta felina</i>	2	1,203.2 ± 191	286.46 ± 25	S. Ostrowski, unpublished data
<i>Nandinia binotata</i>	1	4,270	414.02	McNab 1995
<i>Paradoxurus hermaphroditus</i>	2	3,160	365.55	McNab 1995

Table 1 (Continued)

Species	<i>n</i>	Body Mass (g)	BMR (kJ/d)	Source
<i>Arctogalidia trivirgata</i>	4	2,010 ± 260	265.32 ± 76	McNab 1995
Felidae:				
<i>Panthera tigris</i>	1	137,900	11,517.41	McNab 2000
<i>Panthera leo</i>	1	98,000	8,137.92	McNab 2000
<i>Panthera onca</i> (male)	2	69,000	6,160.32	McNab 2000
<i>Acinonyx jubatus</i>	2	37,900	4,311.5	McNab 2000
<i>Lynx rufus</i>	≥4	8,638.5	1,907.38	McNab 1989, 2000
<i>Herpailurus</i>				
<i>yagouaroundi</i>	2	8,350	833.66	McNab 2000
<i>Felis concolor</i>	4	37,175	4,246.87	McNab 2000
<i>Felis sylvestris lybica</i>	1	2,617.8	472.21	S. Ostrowski, unpublished data
<i>Felis margarita</i>	3	1,924.67 ± 143	431.43 ± 41	S. Ostrowski, unpublished data
<i>Leptailurus serval</i>	...	10,120	1,238.69	Downs et al. 1991
<i>Leopardus pardalis</i>	1	10,500	1,501.92	McNab 2000
<i>Leopardus wiedii</i>	2	3,550	482.23	McNab 2000
Hyaenidae:				
<i>Hyaena hyaena</i>	1	34,300	2,882.65	McNab 2000
<i>Proteles cristatus</i>	≥11	7,710	940	McNab 1984; Anderson et al. 1997

Note. Data presented as mean ± 1 SD.

portion of measurement variance than do contrasts from long branches and that these differences are magnified when contrasts are standardized. Moreover, if estimates of branch lengths are inaccurate in PIC, then the method can perform poorly (Björklund 1994; Diaz-Uriarte and Garland 1996; Gittleman et al. 1996; Price 1997; Abouheif 1999).

Taken together, these problems suggest that we should use both methods to achieve our goal of understanding the evolution of physiological traits such as BMR when tests for phylogenetic signal are significant. When tests for signal are insignificant, we see no reason to abandon the CLSR method. Where investigators have used both regressions based on PIC and CLSR, they have generally found similar correlations (Ricklefs and Starck 1996; Price 1997), and a comparison of results from the two methods may provide insights that otherwise would not have come to light (Price 1997). A reviewer of an earlier version of this article wrote, "Delete all of this section about controversies on the use of the comparative method; it is confusing for others that are starting to understand the statistics and evolutionary biology underlying PIC." Although we appreciate this commonly held perspective, we do not agree; we prefer, rather, to be honest about the problems in interpretation of our results. That we find identical trends with both methods strengthens our conclusion about the role of diet in influencing BMR in carnivores.

Conventional Least Squares Regression

We employed CLSR to determine interspecific allometric relationships of the form $\log Y = a + b \times \log X$. To detect dif-

ferences among groups, we first tested for homogeneity of slopes (following Zar 1996), and if slopes did not differ, we assumed a common slope and tested for differences in intercepts. We also utilized a multiple regression model to simultaneously investigate the relationship of BMR with mass, diet, and home range size. Statistical tests were performed using SPSS 11.5 with $\alpha = 0.05$.

Regression Based on Phylogenetic Independent Contrasts

We computed standardized independent contrasts with the PDTREE module in PDAP (Garland et al. 1999; Garland and Ives 2000). We checked for standardization of contrasts, and if necessary, log-transformed branch lengths (Garland et al. 1992).

In regressions based on PIC, because of the presumed non-independence of values of species, *F* values obtained with ANOVA or ANCOVA cannot be compared for significance with those of usual tables. For this purpose we generated a null distribution of our *F* values using the PDSIMUL module of PDAP (Garland et al. 1993, 1999) and took the ninety-fifth percentile as the critical value. We performed computer simulations ($n = 1,000$) under five different models, gradual Brownian with and without limits, speciation Brownian with and without limits, and gradual Ornstein-Uhlenbeck (Garland et al. 1993).

To investigate relationships of independent contrasts of BMR with contrasts of mass, diet, and home range size, we used multiple regression analysis. For this analysis, we generated a tree containing the species for which we had data for mass, diet, and home range.

Table 2: Diet of 54 species of Carnivora expressed as percentage of meat, invertebrates, and vegetable matter

Species	Meat	Invertebrates	Vegetable Matter	Source
Canidae:				
<i>Canis latrans</i>	98.6	.9	.5	MacCracken and Hansen 1987; Huebschman et al. 1997
<i>Canis lupus</i>	100	0	0	Nowak 1999
<i>Cerdocyon thous</i>	68.9	22.9	7.9	Delgado 2002
<i>Alopex lagopus</i>	95	.4	4.6	Elmhagen et al. 2000, 2002
<i>Vulpes zerda</i>	33	33	33	Larivière 2002
<i>Vulpes macrotis</i>	98.5	1.5	0	Kilgore 1969
<i>Vulpes vulpes</i>	98.4	.1	1.5	Hockman and Chapman 1983; Jedrzejewski and Jedrzejewska 1992; Kauhala et al. 1998
<i>Vulpes ruellii</i>	78.5	7.4	13.2	Lindsay and MacDonald 1986
<i>Vulpes cana</i>	11.7	43.8	44.5	Geffen et al. 1992
Mustelidae:				
<i>Spilogale putorius</i>	50	50	0	Crabb 1941
<i>Lutra lutra</i>	97.5	2.5	0	Jedrzejewska et al. 2001; McDonald 2002
<i>Enhydra lutris</i>	11	89	0	Estes et al. 1978, 1986
<i>Meles meles</i>	13.5	62.2	24.3	Kauhala et al. 1998; Goszczynski et al. 2000; McDonald 2002; Virgós et al. 2004
<i>Taxidea taxus</i>	49	6.8	44.2	Sovada et al. 1999
<i>Gulo gulo</i>	100	0	0	Landa et al. 1999
<i>Eira barbara</i>	69.3	10	21	Bisbal 1986
<i>Martes americana</i>	99	.5	.5	Cumberland et al. 2001
<i>Martes martes</i>	77.3	11.3	11.4	Clevenger 1993; Helldin 1999; McDonald 2002
<i>Mustela vison</i>	58.5	41.5	0	Previtali et al. 1998; Jedrzejewska et al. 2001; McDonald 2002
<i>Mustela frenata</i>	100	0	0	Konecny 1989
<i>Mustela erminea</i>	91.5	.5	8	McDonald et al. 2000; Martinoli et al. 2001; McDonald 2002
<i>Mustela nivalis</i>	97.3	1.8	.9	Goszczynski 1999; McDonald et al. 2000; McDonald 2002
Procyonidae:				
<i>Ailurus fulgens</i>	0	0	100	Pradhan et al. 2001
<i>Nasua nasua</i>	2	58	41	Bisbal 1986
<i>Potos flavus</i>	0	21	78	Bisbal 1986
<i>Procyon cancrivorus</i>	13.5	20.5	65.5	Bisbal 1986; Dos Santos and Hartz 1999
<i>Procyon lotor</i>	0	73.5	26.5	Carrillo et al. 2001
Ursidae:				
<i>Ursus ursinus</i>	48	52	0	Laurie and Seidensticker 1977
<i>Ursus arctos</i>	20.6	1.5	78	Elgmork and Kaasa 1992; Frackowiak and Gula 1992; McLellan and Hovey 1995; Hilderbrand et al. 1999
<i>Ursus maritimus</i>	100	0	0	Derocher et al. 2002
<i>Ursus americanus</i>	11.2	27.4	61.5	Bull et al. 2001
Herpestidae:				
<i>Herpestes sanguineus</i>	36.5	63.4	.1	Ray and Sunquist 2001
<i>Herpestes auropunctatus</i>	50.7	25.5	22.4	Gorman 1975; Cavallini and Serafini 1995
<i>Suricata suricatta</i>	22.4	77.6	0	Doolan and MacDonald 1996
Viverridae:				
<i>Arctitis binturong</i>	20	0	80	Nowak 1999; MacDonald 2002
<i>Fossa fossa</i>	50	50	0	Nowak 1999; MacDonald 2002
<i>Genetta tigrina</i>	68.1	31.8	.1	Ray and Sunquist 2001
<i>Nandinia binotata</i>	15.1	24.4	43.6	Ray and Sunquist 2001

Table 2 (Continued)

Species	Meat	Invertebrates	Vegetable Matter	Source
<i>Paradoxurus hermaphroditus</i>	23.1	9.4	67.5	Joshi et al. 1995
<i>Arctogalidia trivirgata</i>	0	10	90	Nowak 1999; MacDonald 2002
Felidae:				
<i>Panthera tigris</i>	100	0	0	Kitchener 1991
<i>Panthera leo</i>	100	0	0	Kitchener 1991
<i>Panthera onca</i>	100	0	0	Kitchener 1991
<i>Acinonyx jubatus</i>	100	0	0	Kitchener 1991
<i>Lynx rufus</i>	99	1	0	Kitchener 1991
<i>Herpailurus yagouaroundi</i>	99.9	.1	0	Bisbal 1986; Kitchener 1991
<i>Felis concolor</i>	100	0	0	Kitchener 1991
<i>Felis sylvestris lybica</i>	97.1	1.9	1	Kitchener 1991
<i>Felis margarita</i>	98.2	1.8	0	Kitchener 1991
<i>Leptailurus serval</i>	98.9	1.1	0	Kitchener 1991; Bowland and Perrin 1993
<i>Leopardus pardalis</i>	98.2	1.7	.1	Bisbal 1986; Kitchener 1991; Villa Meza et al. 2002; Wang 2002
<i>Leopardus wiedii</i>	100	0	0	Kitchener 1991; Wang 2002
Hyaenidae:				
<i>Hyaena hyaena</i>	29.6	20	37.1	Leakey et al. 1999
<i>Proteles cristatus</i>	0	100	0	Nowak 1999

Nonparametric Tests

For three families—Canidae, Mustelidae, and Viverridae—that had considerable variation in food habits, we tested the idea that mass-adjusted BMR was related to percentage of meat in the diet. For Canids and Mustelids with $n = 9$ and 13, respectively, we used CLSR to search for a significant relationship between mass-adjusted BMR and diet. However, for Viverridae, $n = 6$, our data fell into two distinct groups, meat eaters and vegetarian. Hence we used Mann-Whitney U -test to test for differences between groups.

Results

Phylogenetic Signal

BMR, body mass, percentage of meat in the diet, and home range size exhibited significant phylogenetic signal as determined by the test of serial independence and the test for phylogenetic signal in PDAP (based on 1,000 randomizations, $P < 0.01$ in all cases).

Effects of Body Mass on BMR

We found a positive association between log BMR and log body mass for Carnivora using both conventional least squares regression ($F = 592.8$, $P < 0.001$) and regression based on PIC ($F = 411.3$, $P < 0.001$; Table 4). Because the percentage of meat in the diet and log body mass were not correlated ($P > 0.37$,

CLSR; $P > 0.27$, PIC), we did not correct percentage of meat in the diet for body mass in analyses.

Log home range size was significantly correlated with log body mass using both CLSR (log home range [km^2] = $-2.36 + 0.846 \log \text{mass [g]}$; $n = 41$, $r^2 = 0.55$, $F = 47.78$, $P < 0.001$) and PIC (log home range [km^2] = $-2.617 + 0.825 \log \text{mass [g]}$; $n = 40$, $r^2 = 0.31$, $F = 17.67$, $P < 0.001$). Thus, larger species have larger home ranges, as one might expect.

BMR versus Body Mass among Families

We found significant differences in the slopes of equations relating BMR and body mass among families (ANCOVA, $F = 4.14$, $P = 0.007$; Table 4). The regression for Viverrids yielded an unusually low slope (0.25), for reasons that are not clear. When Viverrids were removed from the analyses, slopes were homogeneous ($F = 1.08$, $P = 0.37$) but intercepts were different ($F = 7.62$, $P < 0.001$).

Under all five models used in our simulations, 1,000 iterations each, PIC regressions of log BMR against log body mass showed homogeneity of slopes for families. Assuming a common slope, we then showed that intercepts did not differ significantly (Table 4). So our analysis using PIC suggested that the relationship between log BMR and log mass was the same for all families, whereas using CLSR viverrids had a significantly lower slope.

Table 3: Home range size of females of 41 species of carnivores

Species	Home Range (km ²)	Source
Canidae:		
<i>Canis latrans</i>	16.6	Kitchen et al. 1999
<i>Cerdocyon thous</i>	12.8	Macfadem Juarez and Marinho-Filho 2002
<i>Alopex lagopus</i>	15.1	Landa et al. 1998
<i>Vulpes macrotis</i>	11.0	List and MacDonald 2003
<i>Vulpes vulpes</i>	4.12	Trewhella et al. 1988
<i>Vulpes ruepellii</i>	13.1	Lenain et al. 2004
<i>Vulpes cana</i>	1.08	Geffen and MacDonald 1993
Mustelidae:		
<i>Spilogale putorius</i>	1.5	MacDonald 2002
<i>Lutra lutra</i>	19.2	Sandell 1989
<i>Meles meles</i>	12.4	Kowalczyk et al. 2003
<i>Taxidea taxus</i>	3.1	Minta 1993; Goodrich and Buskirk 1998
<i>Gulo gulo</i>	207.5	Sandell 1989; Landa et al. 1998
<i>Eira barbara</i>	16.03	Konecny 1989
<i>Martes americana</i>	15.15	Sandell 1989; Smith and Schaefer 2002
<i>Martes martes</i>	1.49	Zalewski et al. 1995
<i>Mustela vison</i>	2.9	Sandell 1989
<i>Mustela frenata</i>	.52	Gehring and Swihart 2004
<i>Mustela erminea</i>	.04	Sandell 1989; Robitaille and Raymond 1995
<i>Mustela nivalis</i>	.58	Jedrzejewski et al. 1995
Procyonidae:		
<i>Ailurus fulgens</i>	2.17	Johnson et al. 1988; Reid et al. 1991
<i>Bassariscus astutus</i>	1.85	Sandell 1989
<i>Potos flavus</i>	.2	Kays and Gittleman 2001
<i>Procyon lotor</i>	1.22	Kamler and Gipson 2003
Ursidae:		
<i>Ursus maritimus</i>	675	Nowak 1999
<i>Ursus arctos</i>	297.5	Sandell 1989; Dahle and Swenson 2003
<i>Ursus americanus</i>	20.58	Sandell 1989; Koehler and Pierce 2003
<i>Ursus ursinus</i>	10	Nowak 1999
Viverridae:		
<i>Genetta tigrina</i>	.06	Ikeda et al. 1982
<i>Nandinia binotata</i>	.45	Sandell 1989
<i>Paradoxurus hermaphroditus</i>	3.2	Rabinowitz 1991
Felidae:		
<i>Panthera tigris</i>	33.4	Sandell 1989; Kitchener 1991
<i>Panthera onca</i>	21	Kitchener 1991
<i>Acinonyx jubatus</i>	62.5	Kitchener 1991
<i>Lynx rufus</i>	21.7	Sandell 1989; Kitchener 1991
<i>Herpailurus yagouaroundi</i>	18.31	Konecny 1989; Nowak 1999
<i>Felis concolor</i>	175.8	Kitchener 1991; MacDonald 2002
<i>Leptailurus serval</i>	6.85	Kitchener 1991; Nowak 1999
<i>Leopardus pardalis</i>	8.24	Konecny 1989; Nowak 1999
<i>Leopardus wiedii</i>	10.95	Konecny 1989
Hyaenidae:		
<i>Hyaena hyaena</i>	44	Nowak 1999
<i>Proteles cristatus</i>	2.5	Nowak 1999

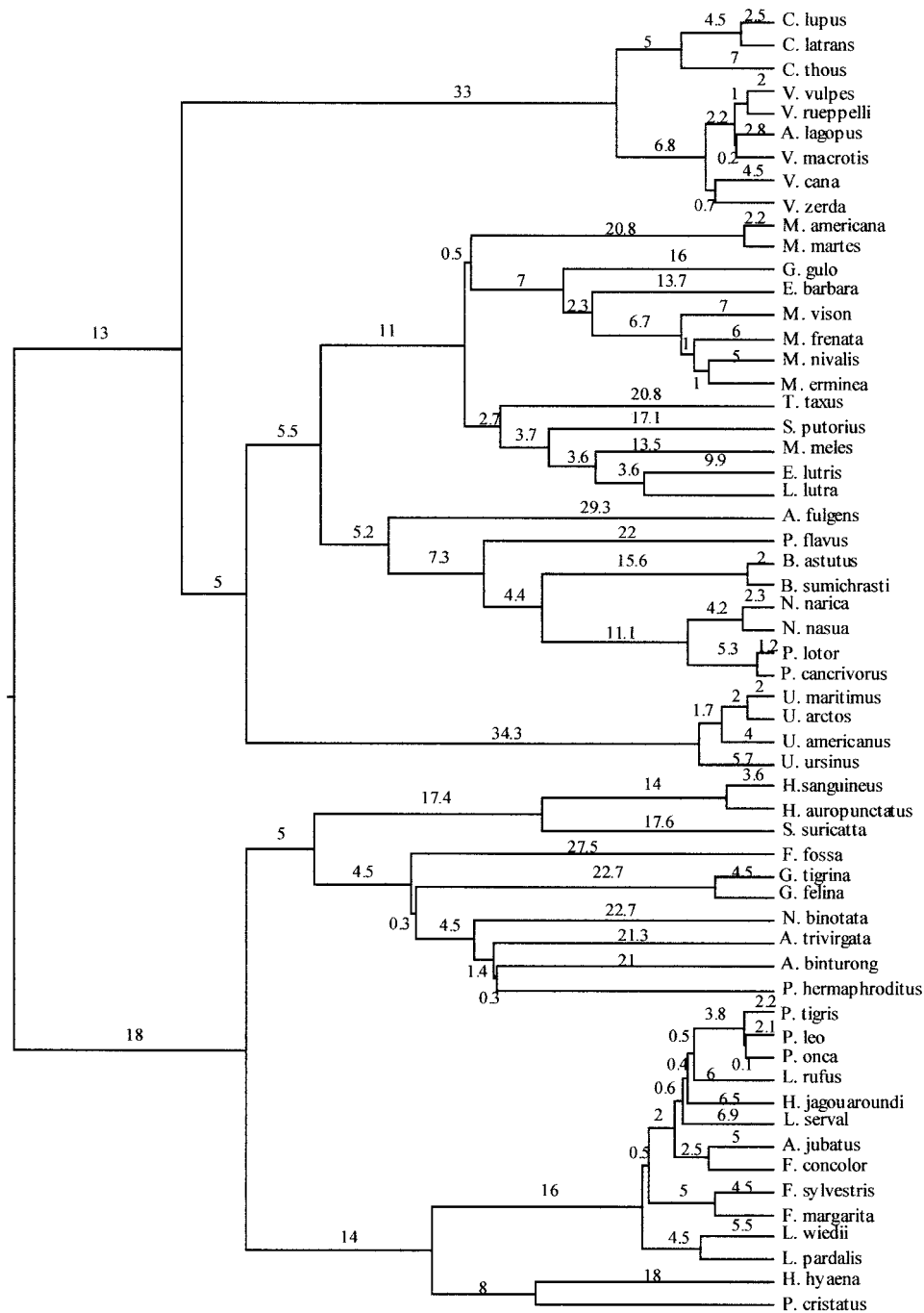


Figure 1. Phylogenetic hypothesis for carnivores. Basal node is set at 58 Ma.

BMR and Home Range

Mass-adjusted BMR was significantly correlated with mass-adjusted HR when we used CLSR (mass-adjusted BMR = $0.015 + 0.086$ mass-adjusted HR, $r^2 = 0.14$, $F = 6.1$, $P < 0.02$) and PIC regression (mass-adjusted BMR = $0.042 + 0.084$ mass-adjusted HR, $r^2 = 0.11$, $F = 4.95$, $P < 0.03$).

Diet and Home Range

With CLSR, we found a positive relationship between mass-adjusted HR size and percentage of meat in the diet (mass-adjusted HR = $-0.121 + 0.182$ [% meat]; $n = 40$, $r^2 = 0.31$, $F = 17.2$, $P = 0.001$; Fig. 2B). Using PIC, we also found a positive relationship between these two variables (mass-adjusted

Table 4: Allometric equations for log BMR (kJ/d) versus log body mass (g) generated by conventional least squares regressions (CLSR) and phylogenetic independent contrasts (PIC)

Taxon	<i>n</i>	Regressions from CLSR					Regressions from PIC				
		<i>b</i>	<i>a</i>	<i>r</i> ²	SE Slope	SE Intercept	<i>b</i>	<i>a</i>	<i>r</i> ²	SE Slope	SE Intercept
Carnivora	58	.70	.34	.92	.028	.104	.74	.12	.88	.037	.167
Canidae	9	.84 ^A	-.12 ^C	.96	.065	.233	.90	-.33	.95	.080	.294
Mustelidae	13	.73 ^A	.37 ^D	.93	.058	.189	.73	.35	.87	.086	.345
Felidae	12	.81 ^A	-.10 ^{CD}	.98	.041	.173	.81	-.08	.95	.057	.231
Viverridae	7	.25 ^B	1.72 ^E	.76	.078	.272	.30	1.52	.71	.087	.304
Procyonidae	8	.59 ^A	.60 ^C	.80	.121	.412	.83	-.28	.96	.072	.270

Note. The intercept is *a*, and *b* is the slope of the relationship $\log \text{BMR} = a + b(\log M)$. SE = standard error. All the regressions were significant ($P < 0.003$ in all cases). Values with different superscripts are significantly different ($P < 0.05$).

HR = $0.214 + 0.182$ [% meat]; $n = 40$, $r^2 = 0.31$, $F = 17.2$, $P < 0.001$; Fig. 2B). Thus, using both methods, we found that the higher the proportion of meat in the diet, the larger the home range size.

Multiple Regression of BMR, Diet, and Home Range Size

Because BMR may vary with diet as a result of covariation between diet and activity, we used a multiple regression model to assess effects of diet and home range size simultaneously on BMR. The overall multiple regression of mass-adjusted BMR against percentage of meat in the diet and res HR was significant using conventional statistics (mass-adjusted BMR = $-0.011 + 0.041$ [% meat] + 0.018 res HR; $n = 40$, $r^2 = 0.30$, $F = 8.02$, $P < 0.001$). However, the coefficient for res HR was not significantly different from 0 when diet was included in the model ($t = 0.46$, $P > 0.64$). In this model, then, home range was not a significant factor in explaining mass-adjusted BMR.

When we used independent contrasts of the same variables, the overall multiple regression was not significant (mass-adjusted BMR = $-0.011 + 0.031$ [% meat] - 0.030 res HR; $n = 38$, $r^2 = 0.13$, $F = 2.71$, $P > 0.08$). As when we used phenotypic values, coefficient for res HR was not significantly different from 0 ($t = -0.81$, $P > 0.43$), but the coefficient for diet was ($t = 2.18$, $P < 0.04$).

BMR and Diet

Because res HR was not a significant predictor variable in our multiple regression model when diet and mass were included, we dropped this variable and explored the effect of diet on BMR after controlling for body mass. Using CLSR, we found a positive relationship between mass-adjusted BMR and percentage of meat in the diet (mass-adjusted BMR = $-0.019 + 0.043$ [% meat]); $n = 54$, $r^2 = 0.22$, $F = 15.0$, $P < 0.001$; Fig. 2A). PIC regression analysis also showed a significant correlation between mass-adjusted BMR and percentage of meat in

the diet (mass-adjusted BMR = $0.039 + 0.041$ [% meat]; $n = 53$, $r^2 = 0.19$, $F = 12.4$, $P < 0.001$).

Differences in BMR and Diet within Families

For Canids and Mustelids, families for which we have sufficient data and that have high trophic diversity, we found that species with higher proportions of meat in the diet also exhibited higher mass-adjusted BMRs ($n = 9$, $r^2 = 0.58$, $F = 9.8$, $P < 0.02$ for Canids; $n = 12$, $r^2 = 0.48$, $F = 9.0$, $P < 0.02$ for Mustelids). Within the Viverrids, species with a diet >50% meat (*Genetta tigrina*, *Genetta felina*, and *Fossa fossa*) had a higher mass-adjusted BMR than the species that ate mainly vegetable matter (Mann-Whitney test, $U = 0$, $n = 6$, $P < 0.04$). These results indicate that the relationship between BMR and meat in the diet occurs not only within Carnivora in general but also within families.

Discussion

Within the Carnivora, we found that, after controlling for body mass and phylogeny, mass-adjusted BMR can be explained by home range size, our proxy for activity level. We also found evidence that diet is correlated with home range size, regardless of body mass and phylogenetic affiliation. Because diet and home range size covaried, we tested their simultaneous effect on BMR using multiple regression and found that home range size was not a significant predictor variable. From our results, we concluded that home range size is significantly correlated with diet, and diet significantly correlates with BMR in the Carnivora. Therefore, species that eat meat have large home ranges and high metabolic rates, vegetarian species have small home ranges and low BMRs, and species with mixed diet show intermediate values. This is the first time that a significant association between BMR and diet has been reported using PIC, a result that bridges the chasm, at least for carnivores,

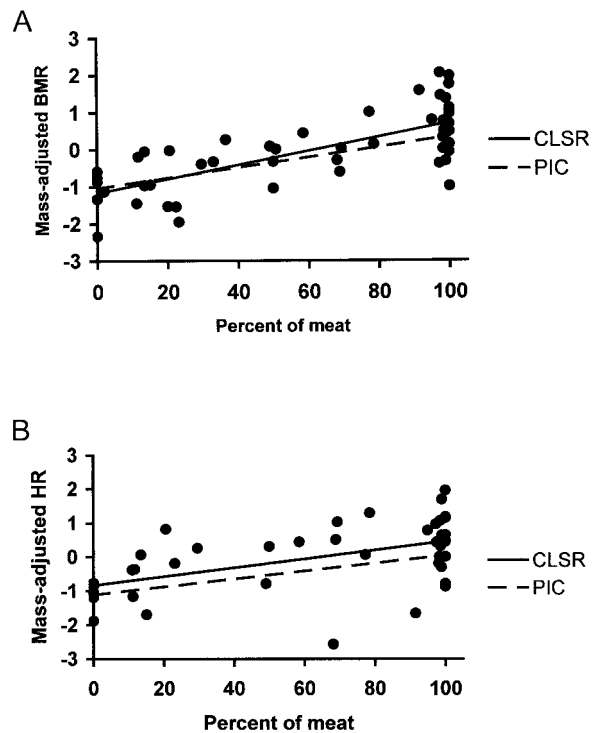


Figure 2. A, Relationship between mass-corrected BMR (kJ/d) and diet, expressed as percentage of meat, for 54 species of the order Carnivora, both using CLSR and PIC. B, Relationship between the residuals of home range size (km²) versus mass (g) and diet, expressed as percentage of meat, for 40 species of Carnivora, with either CLSR or PIC.

between McNab (1986, 2003) and others (Elgar and Harvey 1987; Cruz-Neto et al. 2001).

Activity Hypothesis

Carnivorous species tend to have larger home ranges than species that eat vegetable matter (Garland 1983; Harvey and Pagel 1991). According to Garland et al. (1993), “In simple (and adaptive) terms, this difference [in home range] has been explained by the higher trophic level occupied by carnivores, which means that their food is more widely dispersed and offers fewer joules per unit home range area than does the food of herbivores” (p. 268). Higher BMRs of carnivores, then, could be a consequence of the fact that they expend more energy to pursue, kill, and handle their prey. In this scenario, higher metabolic rates would be related to higher levels of activity as estimated by home range size. According to the activity hypothesis, correlation between BMR and diet would be a by-product of the relationship between activity and diet.

We found that diet was correlated with home range size, controlling for body mass, using both CLSR and PIC. Garland et al. (1993), using only PIC, analyzed data for three clades—Carnivora, Perissodactyla, and Artiodactyla—and failed to find

significant differences in the home range size between carnivorous and herbivorous species after controlling for mass and phylogeny. These authors noticed that food habits were confounded with phylogeny in their data, a situation that limited interpretation of results (Garland et al. 1993). In our study, the broad array of food habits in most clades reduced these problems.

Regression of BMR and home range size when adjusted for mass was significant using CLSR and PIC. These results can be explained by collinearity between diet and home range size: a diet composed of meat could be associated with a larger home range and a higher BMR. Since diet and home range size are not independent, they both affect BMR. However, home range size was not a significant predictor variable in our multiple regression model when we employed trait values or independent contrasts. Thus, home range size, our proxy for activity level, does not have an effect on BMR when we correct for mass, phylogenetic history, and diet.

Food Quality Hypothesis

The food quality hypothesis states that carnivorous species tend to have larger BMRs because the food items they consume are more digestible, are free from chemical deterrents, and are generally available throughout the year (McNab 1986, 1989). On the other hand, vegetarian species have lower metabolic rates because plant material is poorly digestible, is more likely to have chemical deterrents, and is less available during some seasons, and more nonnutritive substances are usually ingested with them. McNab (1986) said that it was “likely that the correlation of basal rate with food habits is causative in the sense that various properties of the foods may limit the rate in which energy is acquired by a mammal and therefore the rate at which the mammal can expend energy” (p. 7).

New Directions: “Muscle Performance” Hypothesis

We have confirmed an idea, originally espoused by McNab (1989), that species of carnivores that consume vertebrate prey tend to have higher BMR than species that include vegetable material in their diet, and we have eliminated the dissonance between previous tests of this hypothesis by using both CLSR and regressions based on PIC. Neither hypothesis that we have explored, the “activity hypothesis” or the “food quality hypothesis,” provides much insight into mechanisms responsible for elevation in metabolism of those species that eat entirely meat. Identification of a correlation among metabolism, diet, and home range size is necessary but not complete if one wants to understand how natural selection has brought about elevated oxygen consumption in meat eaters. So where do we go from here? We develop a new hypothesis, the “muscle performance hypothesis,” that states that BMR is elevated in vertebrate-eating carnivores because natural selection has designed their

muscle structure for endurance rather than power, and the resulting increase in mitochondria density in particular muscle fiber types requires elevated oxygen consumption.

Foraging for vertebrate prey typically requires movement over large distances; one can imagine that selection has maximized efficiency of muscle movement in these species. When species include vegetable material in their diet, home range size can be decreased; therefore, endurance requirements of their muscle tissue may be reduced, or power requirements of muscles may be increased as a result of species becoming more arboreal. We know that muscle tissue is the primary determinant of total oxygen consumption, accounting for 35% of BMR (Martin and Fuhrman 1955). Muscle tissue is a mixture of a variety of fiber types ranging from slow oxidative, characterized by high mitochondrial volume density and therefore relatively high O₂ consumption, to fast oxidative glycolytic, with an intermediate number of mitochondria, to fast glycolytic, which have fewer mitochondria, an extensive sarcoplasmic reticulum, and relatively low O₂ consumption (Hochachka 1994; Lieber 2002; Punkt 2002). In general, slow oxidative fibers are thought to have high endurance, high efficiency, and low power output; fast oxidative glycolytic fibers are intermediate; and fast glycolytic have high power output but low endurance and low efficiency (Lieber 2002). These differences are the result, at least in part, of different fibers containing unique isoforms of myosin, expressions of different genes. The “muscle performance” hypothesis predicts that vertebrate-eating carnivores have a higher proportion of slow oxidative fibers in their muscles, that mitochondria volume densities in muscle tissue will be relatively high, and that capillary abundance will be high. Concentrations of metabolic enzymes probably are different in muscle tissue of meat eaters compared with vegetarian species. The hypothesis predicts that concentrations of succinate dehydrogenase, an enzyme used in oxidative metabolism, will be relatively high, whereas concentrations of lactate dehydrogenase, an enzyme used in anaerobic metabolism, will be relatively low. Because slow oxidative fibers tend to use free fatty acids as a metabolic substrate (Hochachka 1994; Lieber 2002), the hypothesis also predicts that concentrations of free fatty acids are relatively high in muscle tissue of meat-eating carnivores and glycogen relatively low.

Recent evidence is consistent with our hypothesis. Wisløff et al. (2005) ran artificial selection experiments for low and high aerobic treadmill running capacity on white rats. After 11 generations, high- and low-capacity runners differed in running capacity by 347%. Rats with higher aerobic capacity expressed a higher quantity of proteins involved in mitochondrial function in skeletal muscle. Training experiments showed that differences between selection lines were partially genetic because rats with low aerobic capacity had a diminished adjustment to exercise training. Changes in gene expression may then affect metabolic performance in a relatively short time.

The “muscle performance” hypothesis provides a plausible,

testable, biochemical explanation for the relationship between BMR and diet. Furthermore, if it is supported, the hypothesis gives a possible scenario of how natural selection has modified the physiology of carnivores that have different ecologies.

Conclusions

BMR was significantly associated with mass and percentage of meat in the diet, and diet was correlated with mass-adjusted HR size in species of the Carnivora. Species that eat meat have larger home ranges and higher metabolic rates whereas those species that consume vegetable matter have smaller home ranges and lower BMRs. We propose that changes in the proportion of muscle fiber types can provide a mechanism to account for the differences in BMR observed between meat eaters and vegetarian species.

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Appendix

For the origin of Carnivora, we chose 58 Ma (Wayne et al. 1989). Early in its history, the order split into two major clades, Arctoidea and Feloidea. Arctoid evolutionary relationships are controversial. Some authors placed Mustelids and Procyonids as sister groups (Wozencraft 1989; Janis et al. 1998; Bininda-Emonds et al. 1999), whereas others claimed that Procyonids are more closely related to Ursids (Goldman et al. 1989; Hunt 1996). Position of *Ailurus fulgens* (red panda) is problematic because in some cases it is regarded as a sister group to the Mustelid-Procyonid clade, making Procyonidae paraphyletic (Hunt 1996; Bininda-Emonds et al. 1999), whereas other authors consider the red panda not a Procyonid but an Ursid (Wozencraft 1989). We have assumed that Procyonids include *A. fulgens* and are monophyletic, Procyonids and Mustelids are sister groups, and Ursids are a sister taxon to the Procyonid-Mustelid clade (Janis et al. 1998; Bininda-Emonds et al. 1999). Following Janis et al. (1998), we placed the origin of Mustelids at 34.5 Ma. Wayne et al. (1989) and Hunt (1996) traced the Ursids back to 40 Ma.

Feloidea appeared at 40 Ma (Wayne et al. 1989) and thereafter split into two clades consisting of two sister families each, Herpestids-Viverrids and Hyaenids-Felids. Herpestids-Viverrids diverged at 32.5 Ma (Bininda-Emonds et al. 1999) and Felids

and Hyaenids at 26 Ma (Garland et al. 1993). Described elsewhere (Williams et al. 2004), our Canid phylogeny assumed that Canids appeared at 12 Ma and then differentiated into two clades, one for *Canis* and South American dogs and another for foxes.

In general, we used Bryant et al. (1993) for the topology of the Mustelid clade. However, they suggested that the genus *Mustela* was an unresolved polytomy, but according to Kurose et al. (2000), *Mustela vison* was the first species to diverge, and *Mustela nivalis* and *Mustela erminea* are close relatives (Bininda-Emonds et al. 1999). There are no data available for *Mustela frenata*, so we assumed that this species branched after *M. vison*. Two main clades within the Mustelids split early in the history of the group: *Martes*, *Gulo*, *Eira*, and *Mustela* composed one of these clades and *Taxidea*, *Spilogale*, *Meles*, *Enhydra*, and *Lutra* the other. Bininda-Emonds et al. (1999) recognized the former but could not resolve relationships among species of the latter. These discrepancies have been resolved, incorporating the topology of Bryant et al. (1993) to this second clade.

Separation of *Martes*, the oldest of extant taxa, took place at around 23.5 Ma (Hunt 1996). We dated *Gulo* at 16 Ma as a minimum estimation since *Martes* can be found in North America as early as 15.8 Ma (Janis et al. 1998). We adopted Bininda-Emonds et al.'s (1999) divergence time for *Mustela* (11.4 Ma) because it fits well with the fossil record, at around 7 Ma (Martin 1989; Hunt 1996; Janis et al. 1998). There is no information available for *Eira*, so we placed this genus between *Gulo* and *Mustela* at 13.7 Ma, the mean branch length of the above taxa. A major point of disagreement is the position of skunk. Wayne et al. (1989) suggested 42 Ma for *Spilogale*, but this is likely an overestimation and has no support from the fossil record. We chose 17.1 Ma following Bininda-Emonds et al. (1999).

Our topology and branch lengths for Procyonids are mainly those reported in Bininda-Emonds et al. (1999). However, we included *A. fulgens* in the taxon, and we assigned 2 Ma for the divergence time between the two species of *Bassariscus* instead of 0.3 Ma.

The main source of our Ursid phylogeny was Goldman et al. (1989), although we modified some branch lengths. We assumed that *Ursus arctos* and *Ursus maritimus* are sister species that diverged at 2 Ma. *Ursus americanus* split at 4 Ma, and finally, *Ursus ursinus* diverged from the rest of the species of the family at 5.7 Ma (Bininda-Emonds et al. 1999).

Our topology of Felids follows Nowell and Jackson (1996). *Lynx* fossils were found up to 6 Ma (Martin 1989; Janis et al. 1998), whereas Nowell and Jackson (1996) dated the origin of the genus at 2 Ma. Because we adopted 6 Ma for the *Lynx*, we changed branch lengths for *Herpailurus jagouaroundi* and *Lepailurus serval*. For *L. serval* we used the divergence time given by Janczewski et al. (1995), and for *H. jagouaroundi* we assumed that the branch length was the mean between those for *L. serval* and *Lynx*. The polytomy of *Panthera* is controversial. Some

molecular data suggested that *Panthera leo* and *Panthera onca* are more closely related with each other than with *Panthera tigris* (Janczewski et al. 1995). This is the position we have adopted here, although we used branch lengths from Bininda-Emonds et al. (1999).

We based our topology of Herpestids and Viverrids on Bininda-Emonds et al. (1999). *Genetta felina* did not appear in their phylogeny, so we assumed that it diverged from *Genetta tigrina* at the time in which the genus appeared, 4.5 Ma. We followed Mills and Hofer's (1998) Hyaenid phylogeny with a divergence time of 18 Ma for the two species considered in this study.

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