BASAL METABOLIC RATE OF CANIDAE FROM HOT DESERTS TO COLD ARCTIC CLIMATES

Vincent Careau, Julie Morand-Ferron, and Don Thomas*

Département des Sciences Biologiques, Université du Québec à Montréal, P.O. Box 8888, Stn Centre-Ville, Montréal, Quebec H3C 3P8, Canada (VC)
Department of Biology, McGill University, Montréal, Quebec H3A 1B1, Canada (JM-F)
Département de Biologie, Université de Sherbrooke, Sherbrooke, Quebec J1K 2R1, Canada (DT)

Canids form the most widely distributed family within the order Carnivora, with members present in a multitude of different environments from cold arctic to hot, dry deserts. We reviewed the literature and compared 24 data sets available on the basal metabolic rate (BMR) of 12 canid species, accounting for body mass and climate, to examine inter- and intraspecific variations in mass-adjusted BMR between 2 extreme climates (arctic and hot desert). Using both conventional and phylogenetically independent analysis of covariance, we found that canids from the arctic climate zone had significantly higher mass-adjusted BMR than species from hot deserts. Canids not associated with either arctic or desert climates had an intermediate and more variable mass-adjusted BMR. The climate effect also was significant at the intraspecific level in species for which we had data in 2 different climates. Arctic and desert climates represent contrasting combinations of ambient temperatures and water accessibility that require opposite physiological adaptations in terms of metabolism. The fact that BMR varies within species when individuals are subjected to different climate regimes further suggests that climate is an important determinant of BMR.

Key words: basal metabolic rate, canids, carnivores, climate, phylogenetically independent contrasts

Cold arctic and hot desert climates each offer great physiological challenges to mammals living there. Limiting factors in these environments are usually physical rather than biotic (Bartholomew 1964). In arctic climates, ambient temperatures are generally below freezing for more than 8 months and can be as much as 90°C colder than an animal's core body temperature during winter (Scholander et al. 1950a). In deserts, the ambient temperatures can reach more than 50°C and be accompanied by intense solar radiation, desiccating winds, and an absence of drinkable water (Bartholomew 1964). Extreme climatic situations such as these have forced animals to adapt their physiology to manage energy and water flow.

Basal metabolic rate (BMR, minimum metabolic rate of postabsorptive inactive endotherms while in their resting phase and within their thermoneutral zone) gains ecological significance when one considers that it is correlated with both field and maximum rates of metabolism (energy expenditure) in mammals (Rezende et al. 2004; Ricklefs et al. 1996). Although body mass (M_b) has long been recognized as the main factor affecting BMR (Kleiber 1932, 1961), there remains uncertainty concerning the precise allometric scaling exponent between BMR and M_b (White and Seymour 2005a, 2005b). Several studies have attempted to explain the residual variation in BMR (i.e., mass-adjusted BMR, after correlations with M_b have been controlled statistically) by looking at associations with various climatic factors such as water accessibility (Williams et al. 2004), temperature (Lovegrove 2003), and environmental productivity (White 2003). The combination of water accessibility and ambient temperature could affect BMR because high temperatures and low water accessibility may favor a low BMR to avoid overheating and enhance water conservation (Bartholomew 1964; Thomas et al. 2001). In contrast, low temperatures could favor high BMR through an enhanced thermoregulatory capacity (e.g., ability to withstand cold challenge—Lovegrove 2003).

Canids are the most widely distributed family in the order Carnivora, with members on every continent except Antarctica (Ginsberg and Macdonald 1990). As a family, they are present in a great variety of habitats ranging from deserts to ice fields, (Macdonald and Sillerio-Zubiri 2004). The arctic fox (*Alopex lagopus*) is highly adapted to cold arctic climates (Fuglei and Oritsland 1999), whereas many other foxlike canids are mainly restricted to hot and dry deserts (e.g., Blanford's fox [*Vulpes cana*], fennec fox [*V. zerda*], kit fox [*V. macrotis*], and Rüppell's fox [*V. ruppellii*]—Golightly and Ohmart 1983;

* Correspondent: donald.thomas@usherbrooke.ca

TABLE 1.—Basal metabolic rate (BMR in kJ/day) of 12 canid species related to body mass (g) and climate. Canids that were not associated with arctic or desert climates were classified in the intermediate category. When a study involved more than 1 individual (n), we used mass and BMR means.

Species	n	Body mass (g)	Climate	BMR (kJ/day)	Source
Canis lupus	9	35,000	Intermediate	3,872.23	Okarma and Kojeta 1987
C. lupus pallipes	3	20,194	Hot desert	2,410.56	Afik and Pinshow 1993
C. lupus	4	18,950	Intermediate	3,041.40	Hayssen and Lacy 1985
C. lupus dingo	4	18,000	Intermediate	3,487.17	Shield 1972
C. latrans incolatus	3	10,300	Arctic	2,173.94	Shield 1972
C. latrans mearnsi	3	10,000	Hot desert	1,295.88	Golightly and Ohmart 1983
C. mesomelas	4	7,720	Intermediate	1,811.54	Downs et al. 1991
Vulpes lagopus	2	7,600	Arctic	2,058.76	Korhonen et al. 1983
Nyctereutes procyonoides	4	7,575	Intermediate	1,705.03	Korhonen et al. 1983
Cerdocyon thous	2	5,444	Intermediate	734.45	Henneman et al. 1983
Lycalopex culpaeus	11	5,259	Intermediate	930.11	Silva et al. 2004
A. lagopus	2	5,090	Arctic	1,033.24	Klir and Heath 1992
V. vulpes alascensis	1	4,725	Arctic	1,195.64	Irving et al. 1955
A. lagopus	3	4,700	Arctic	1,192.27	Scholander et al. 1950a
A. lagopus	9	4,650	Arctic	1,075.65	Fuglei and Oritsland 1999
V. vulpes	4	4,045	Intermediate	906.97	Klir and Heath 1992
A. lagopus	3	3,600	Arctic	662.16	Casey et al. 1979
V. vulpes	4	3,060	Intermediate	724.33	Williams et al. 2004
V. vulpes arabica	5	1,967	Hot desert	418.02	Williams et al. 2004
V. macrotis	12	1,819	Hot desert	485.78	Golightly and Ohmart 1983
V. rueppellii	6	1,546	Hot desert	385.01	Williams et al. 2002
V. cana	4	1,285	Hot desert	304.53	Williams et al. 2004
V. zerda	7	1,215	Hot desert	281.06	Maloiy et al. 1982
V. zerda	8	1,106	Hot desert	190.79	Noll-Banholzer 1979

Lindsay and Macdonald 1986; Noll-Banholzer 1979). Additionally, some more-broadly distributed canids are present in both arctic and desert regions. For example, the gray wolf (*Canis lupus*), formerly the world's most widely distributed terrestrial mammal, still inhabits deserts at the margin of its arctic circumpolar distribution (Afik and Pinshow 1993). The coyote (*C. latrans*) is present from the arctic coast of Alaska to the tropics, including deserts in Nevada and New Mexico (Burt and Grossenheider 1992). The red fox (*V. vulpes*) currently has the widest geographical range of any member of the order Carnivora and is present in a variety of habitats ranging from arctic tundra to dry deserts (Macdonald and Sillerio-Zubiri 2004).

Measures of BMR have been made for 12 canid species, representing 33% of the family (36 species, according to Macdonald and Sillero-Zubiri 2004), placing the canids among the most studied group of mammals in terms of BMR. For some species, measures of BMR are available for more than 1 climatic region. Therefore, canids offer an opportunity to explore the effect of climate on BMR at both inter- and intra-specific levels. The aim of this study is to test the hypothesis that BMR is related to climate among and within canid species. We predict that canids associated with hot desert climate will have a relatively lower mass-adjusted BMR than canids associated with arctic climate.

MATERIALS AND METHODS

Data collection.—All BMR data were obtained from the literature except for 1 datum on the gray wolf that Hayssen and Lacy (1985) obtained from a personal communication with B. K. McNab (Table 1). We used data when individuals were weighed as adults and when metabolic measures were taken in their thermoneutral zone while animals were inactive and post-absorptive. Data reported as watts or as oxygen consumption rate were converted to kJ/day assuming an energy equivalent of 20.08 J/ml O_2.

We assigned a climate category (arctic, intermediate, and hot desert) to each datum according to the location of the capture site and the general distribution range of each species reported in Macdonald and Sillerio-Zubiri (2004). For instance, coyotes captured and measured in Alaska by Shield (1972) and in Arizona by Golightly and Ohmart (1983) were associated with arctic and hot desert climates, respectively. Arctic and hot desert climates were easily associated with each datum we obtained because original authors were usually explicit when they measured animals associated with these environments. However, this was not always the case for studies conducted on canids living in other moderate environments that may not offer as great a challenge as desert or arctic climates. Therefore, our intermediate category includes a variety of habitats ranging from temperate broadleaf forests (i.e., gray wolf in Poland) to African savannas (i.e., *Canis mesomelas*), Atlantic forests of eastern Brazil (i.e., *Cerdocyon thous*), montane grasslands (i.e., *Lycalopex culpaeus* in Chile), and Arabian highlands (i.e., *V. vulpes*). Hence, along a cold-to-hot gradient combined with water scarcity, the intermediate category represents a broad range of climates located in between the extremes of arctic and hot desert climates, so one might expect a more variable mass-adjusted BMR.
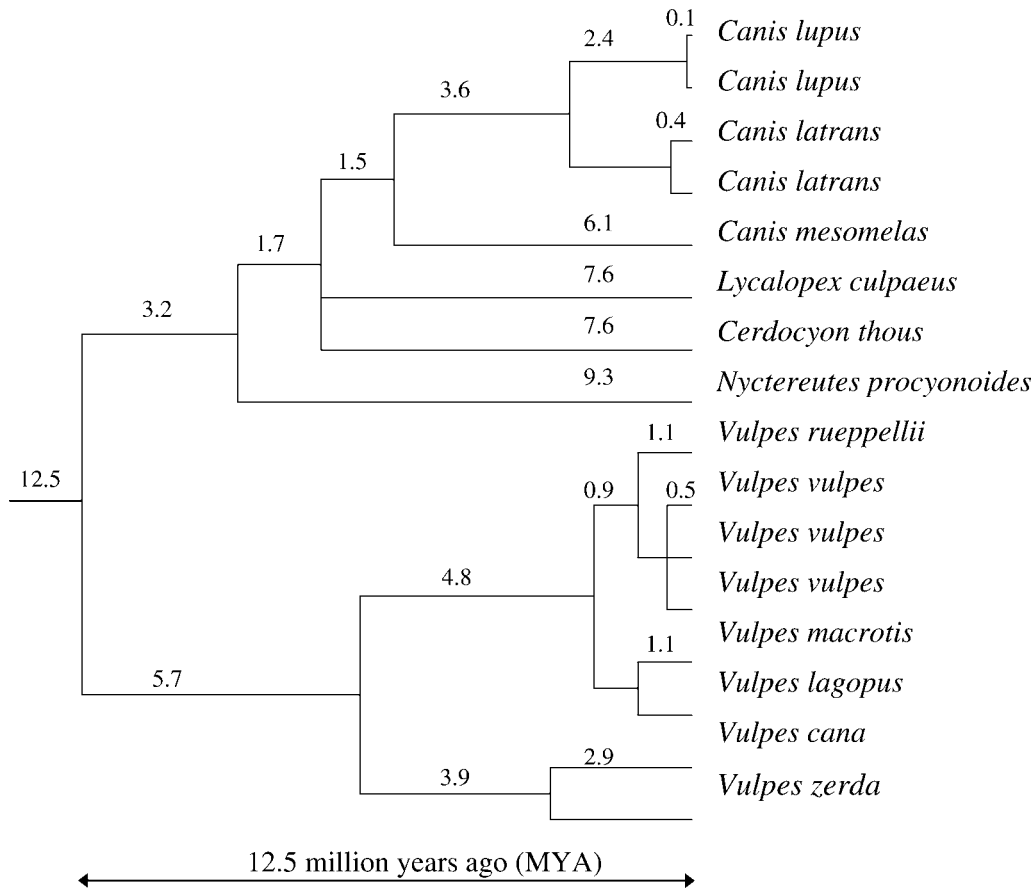
Fig. 1.—The canid phylogenetic supertree with branch lengths used to generate the phylogentically independent contrasts. The supertree is based on Bininda-Emonds et al. (1999) and includes subspecies of gray wolf, coyote, and red fox.

Canid phylogeny.—We used the phylogenetic supertree of Bininda-Emonds et al. (1999), to which we added subspecies of gray wolves, coyotes, and red foxes associated with different climates (Fig. 1). Because sufficient information on branch lengths was not available for subspecies of gray wolves, we used an arbitrary short branch length of 0.1 million years ago (mya—sensu Williams et al. 2004). According to Vilà et al. (1999), the 2 subspecies of coyotes (*mearnsi* and *incolatus*) diverged 0.42 mya (Williams et al. 2004). The red fox evolved in Eurasia during the Pleistocene (Frati et al. 1998); hence we assumed that subspecies for which we had data separated 0.5 mya. Independent contrasts are reasonably robust with respect to errors in branch lengths (Diaz-Uriarte and Garland 1998). Adequacy of our tree was indicated by nonsignificant relations ($P > 0.05$) between standardized contrasts and the square root of the sum of branch length for M_b and BMR after log-transformation of branch lengths (Garland et al. 1992). We obtained similar results using Pagel's (1992) arbitrary branch lengths, so we present results using log-transformed branch lengths only.

Statistical analysis.—Means (± 1 *SE*) are presented throughout the paper. BMR and M_b data were transformed using the $\log_{10}$ function to ensure a normal distribution of the residuals. To incorporate the complete variance in BMR, we kept and analyzed all data available because individuals from different studies had different M_b or different BMR despite a similar M_b. All observations on a single species in a single climate are weighted according to the number of individuals measured in the study. However, when different studies reported BMR of a species from different climatic zones, we treated these as subspecies from different geographic locations with possibly minimal gene flow.

Because of the hierarchical nature of phylogenetic descent, species and subspecies may not represent statistically independent points, degrees of freedom may be inflated, and significance level derived from conventional tests cannot be trusted (see Garland et al. 2005 for a recent review). Therefore, we used both conventional least square regression (CSLR) and phylogenetically independent (PI) statistical methods. For CLSR and PI analyses, respectively, we used JMP 5.0.1 statistical package (SAS Institute Inc., Cary, North Carolina) and the Phenotypic Diversity Analysis Program (PDAP— Garland and Ives 2000; Garland et al. 1999). We 1st described the allometric equation between BMR and M_b with a CLSR. We then used the PDTREE program to calculate the PI contrasts of BMR and M_b and plotted these forcing the regression through the origin. To examine the effect of climate after controlling for the effect of M_b, we performed a CLSR analysis of covariance (ANCOVA) with climate as a fixed factor and M_b as a covariate. Post hoc Tukey's honestly

significant difference tests were conducted to test for differences in mass-adjusted BMR between groups, using $P < 0.05$ as the criteria for rejection of the null hypothesis.

We further tested the effect of climate on BMR with a PI ANCOVA using PDANOVA and PDSIMUL modules in PDAP (Garland et al. 1993). We used Monte Carlo computer simulations ($n = 1,000$) made along our phylogeny to generate a null distribution of F values that incorporate phylogenetic effects, and took the 95th percentile as the critical value. M_b and BMR were simulated as correlated traits with a coefficient of 0.926 determined from the regression of PI contrasts of these variables. A Brownian evolutionary speciation model was used. The starting values for M_b and BMR were $\log_{10}M_b = 3.586$ (i.e., 3,850 g) and $\log_{10}BMR = 2.904$ (i.e., 800.8 kJ/day). This M_b is the approximate size of *Leptocyon vafer*, considered to be the common ancestor of all living canids, estimated from skull length and m1 values of 89 and 11.8 mm, respectively (X. Wang, pers. comm.), and using the equations described in Van Valkenburgh (1990). The BMR value was estimated using the CLSR regression, assuming that the BMR of ancestral canids was not significantly different from that of the extant species. Values that exceeded the algorithm boundaries were excluded ("throw out" limits in PDSIMUL). The lower M_b limit was $\log_{10}M_b = 2.903$ (i.e., 800 g) and the upper limit $\log_{10}M_b = 4.792$ (i.e., 62 kg). These limits are the lower and upper end of the range size of the smallest (fennec fox) and largest (gray wolf) living canids (Macdonald and Sillerio-Zubiri 2004). BMR upper and lower limits were 3.699 (i.e., 5,000.3 kJ/day) and 2.176 (i.e., 149.9 kJ/day), respectively.

To examine whether the climate effect is present at the intraspecific level, we performed a 1-tailed paired *t*-test on the 3 species (gray wolf, coyote, and red fox) for which we obtained physiological data in more than 1 climate. We compared the weighted mass-adjusted BMR between either arctic or intermediate or both to the paired hot desert data.

RESULTS

Using CLSR, M_b explained 92.7% of the variation in BMR ($F = 281.4$, *d.f.* = 1, 22, sum of weights = 16, $P < 0.001$; Fig. 2A). The slope of the relationship (0.84 ± 0.05; lower bound of 95% confidence interval [CI] = 0.74) did not differ significantly from 0.75, but was significantly higher than 0.67. Using PI contrasts, M_b explained 82.9% of the variation in BMR ($F = 83.3$, *d.f.* = 1, 14, $P < 0.001$; Fig. 2B). Although the slope of the relationship between BMR and mass (0.95 ± 0.10) tended to be higher, the lower bound of the 95% CI (0.73) included both the slope of the CLSR analysis and 0.75 and thus did not differ significantly from either.

The CLSR ANCOVA model including climate as a fixed effect and M_b as a covariate explained 95.2% of the variance in BMR. Climate effect yielded an F value of 5.0 and was significant ($P < 0.05$). The 95th percentile of the PI ANCOVA was 3.5; hence climate effect is significant at $P < 0.05$ even when considering phylogeny. High mass-adjusted BMR is associated with arctic climate, whereas low mass-adjusted BMR is asso-
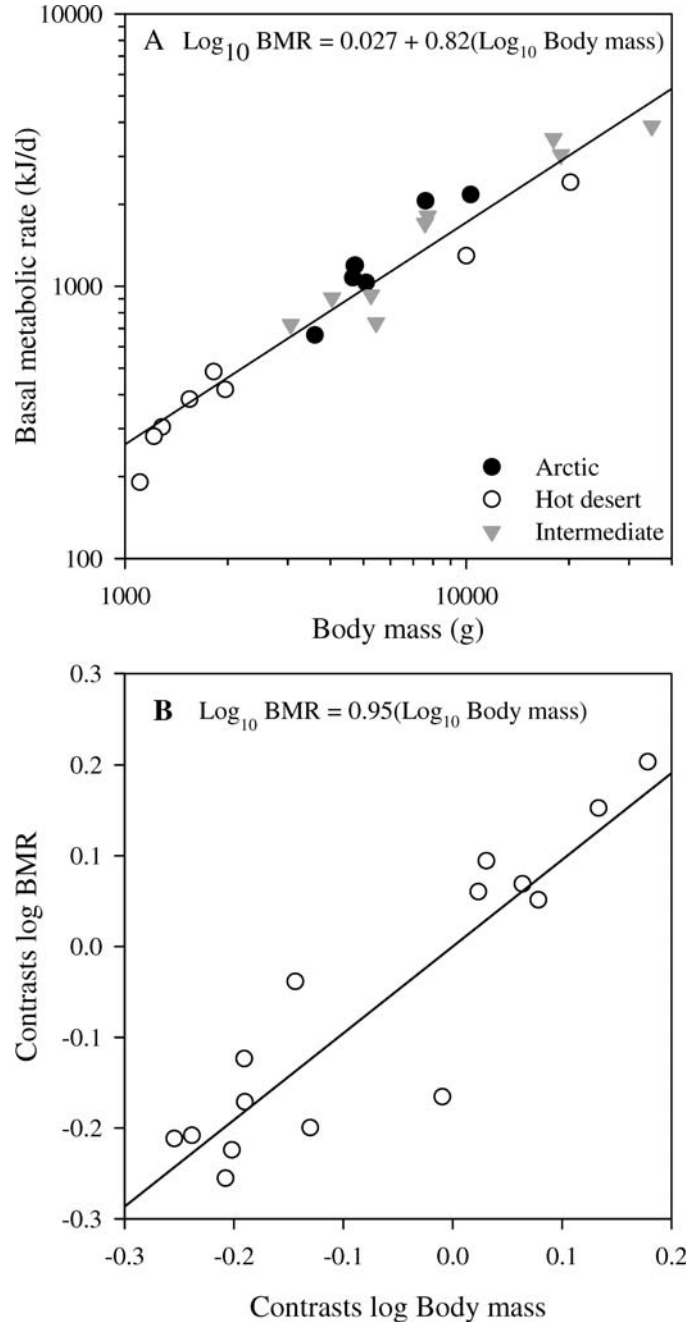

Fig. 2.—A) Relationship between basal metabolic rate and body mass in canids. All data from Table 1 are shown, but the regression line is weighted to account for multiple observations from a single species from a same climate. B) Contrasts of log basal metabolic rate (BMR) in relation to contrasts of log body mass. Regression line was forced through the origin.

ciated with desert climate (post hoc test: $P < 0.05$; Fig. 3). Canids in the intermediate climate category had more variable mass-adjusted BMR that was not significantly different from arctic and desert canids (post hoc test: $P > 0.05$; Fig. 3). Subspecies of gray wolf, coyote, and red fox adapted to arctic and intermediate climates had a higher mass-adjusted BMR than their hot desert counterparts (1-tailed paired *t*-test: $t = 3.35$, *d.f.* = 2, $P = 0.04$; see specific symbols in Fig. 3).
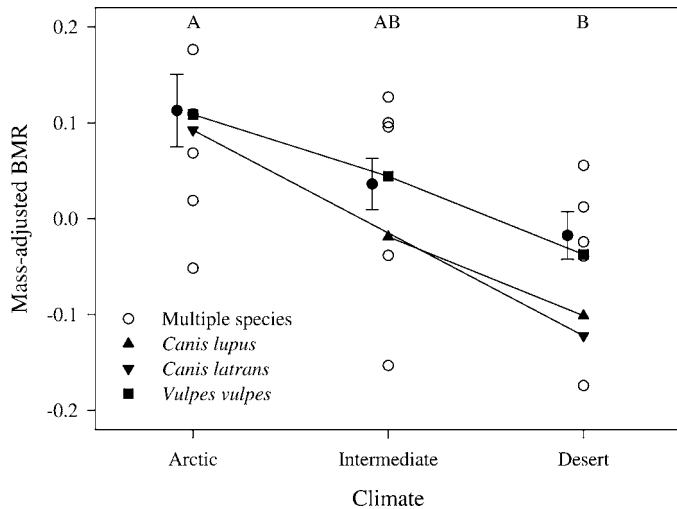
Fig. 3.—Mass-adjusted basal metabolic rate among canids associated with different climates. Intermediate category includes many environments ranging between arctic and hot desert climates that may not offer as great a temperature or water stress as arctic and desert climates. Means ($\pm SE$; indicated beside data for each climate category) are weighted to account for multiple observations on a single species and different letters indicate Tukey's post hoc honestly significant difference significant differences for a conventional least square ANCOVA. The climate effect remains significant when taking phylogeny into account (phylogenetically independent ANCOVA by computer simulations). Lines connect subspecies of *C. lupus*, *C. latrans*, and *V. vulpes* associated with different climate categories. For *C. lupus* and *V. vulpes*, the value for the intermediate climate category is the weighted mean for 3 and 2 studies, respectively.

DISCUSSION

Our study sheds little light on the exact allometric scaling exponent for BMR on mass. As White and Seymour (2005a) pointed out, small data sets with large size variation often result in high allometric exponents. The exponents for canids (0.84 and 0.95 for our CLSR and PI analyses, respectively) are intriguingly high and fall at the extreme upper bound of the frequency distribution for a sample size of 15 species (White and Seymour 2005a:figure 1C). However, these apparently high scaling exponents do not differ significantly from the value of 0.75 initially reported by Kleiber (1932) and subsequently supported by numerous analyses of the effects of body size on energy metabolism (e.g., see Hayssen and Lacy 1985; Peters 1983; White and Seymour 2005b).

However, our study does shed light on the effect of climate on energy metabolism. Using both CLSR and PI analyses, we found that arctic canids have a significantly higher mass-adjusted BMR than desert canids. This is in accordance with several studies that have reported relatively high mass-adjusted BMR in Nearctic and Palearctic species (Lovegrove 2000) and low mass-adjusted BMR in desert species (Lovegrove 2000; MacMillen and Garland 1989; Shkolnik and Schmidt-Nielsen 1976; White 2003). Among many climatic variables, ambient temperature and precipitation have been identified as the most important climatic factors affecting mass-adjusted BMR of

small mammals (Lovegrove 2000). Therefore, we consider arctic and desert climates as contrasting combinations of these 2 abiotic factors that determine the optimum position along a slow–fast metabolic continuum. Arctic and desert climates may require opposing physiological adaptations that lead to inter- and intraspecific differences in BMR for canids.

In a cold arctic climate, the ambient temperature may regularly become much colder than the thermoneutral zone of an animal, so a high thermogenic capacity may be required to compensate for heat loss. The level of BMR, which is correlated with maximum metabolic rate, probably reflects the size of the metabolic machinery required for thermoregulation in cold arctic climates (Daan et al. 1990). Therefore, animals living at high latitudes may maintain larger organ masses and pay a maintenance cost, which we see as an elevated BMR (Speakman and Thomas 2003). However, in a hot and dry desert climate, the combination of water scarcity and extreme heat requires desert animals to limit water loss and energetic expenditure. When the ambient temperature approaches the core body temperature, thus reducing the thermal gradient, it becomes increasingly difficult to offload the metabolic heat produced by the BMR through convective heat transfer. As the thermal gradient decreases, homeotherms must increasingly rely on evaporation to offload metabolic heat production. However, evaporation is a costly strategy in a desert because it implies considerable water loss (Bartholomew 1964). Decreasing endogenous heat production can thus reduce dehydration risk because it reduces the quantity of heat that an animal is forced to evacuate by evaporation (Shkolnik and Schmidt-Nielsen 1976; Speakman and Thomas 2003).

One might argue that because the arctic fox has excellent insulation and an exceptionally broad thermoneutral zone, it never experiences any thermal constraints imposed by cold winter ambient temperatures (Prestrud 1991). Indeed, the thermoneutral zone for the arctic fox extends below -40°C (Casey et al. 1979; Scholander et al. 1950b; Underwood 1971). However, we found that other species (red fox and coyote) have a strong effect on the elevated BMR values for arctic canids in our analyses. Red foxes and coyotes have poorer insulation and their thermoneutral zone does not extend as low as that of the arctic fox (-13°C for red fox—Irving et al. 1955). These species may well face thermal constraints in winter and benefit from an elevated BMR, which probably reflects a large thermogenic capacity. It should be noted that for a given insulation value, increasing the BMR has the effect of broadening the thermoneutral zone and extending the lower limit to colder ambient temperatures (Schmidt-Nielsen 1997). For this reason, an increase in BMR in arctic species is likely to be adaptive.

Interspecific comparisons of mammalian BMR have reported a significant association with diet (or food habits) using conventional statistics (McNab 1986, 1989, 1992, 2003), but not with phylogenetically based methods (Cruz-Neto et al. 2001; Degen et al. 1998; Genoud 2002). However, a recent phylogenetic analysis suggests that BMR is correlated with diet among carnivores; species that eat meat have larger home ranges and higher mass-adjusted BMRs than species that eat vegetable matter (Muñoz-Garcia and Williams 2005). This

relation also was significant when restricted to 9 canid species, but did not take phylogeny into account. As seen in the data set of Muñoz-Garcia and Williams (2005), the 3 species with lower meat intake in their diet are not only closely related, but are also restricted to desert environments (*V. cana*, *V. zerda*, and *V. rueppellii*). Our results suggest that variation in mass-adjusted BMR may not be due to diet, but rather to climatic effects (which might be correlated with diet), meaning that simple "cause-and-effect" relationships must be taken with caution.

Although interspecific comparisons suggest that selection has acted on a suite of phenotypes (insulation, BMR, and core body temperature) to allow species to adapt to local or regional temperature regimes, the comparative method cannot un-ambiguously demonstrate "adaptation," meaning the tailoring of an ancestral condition to allow it to meet the needs of a new physical environment (Harvey and Pagel 1991). Our study cannot exclude the possibility that high BMR in arctic species and low BMR in desert species simply represent phenotypic plasticity whereby individuals adjust BMR in response to local environments. Further studies are needed to differentiate genetic and population-level adaptation from phenotypic plasti-city. However, it remains that climate plays a significant role in setting the level of basal metabolism.

ACKNOWLEDGMENTS

LITERATURE CITED

AFIK, D., AND B. PINSHOW. 1993. Temperature regulation and water economy in desert wolves. Journal of Arid Environments 24: 197–209.

BARTHOLOMEW, G. A. 1964. The roles of physiology and behaviour in maintenance of homeostasis in the desert environment. Symposia of the Society for Experimental Biology 18:7–29.

BININDA-EMONDS, O. R. P., J. L. GITTLEMAN, AND A. PURVIS. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74:143–175.

BURT, W. H., AND R. P. GROSSENHEIDER. 1992. Les mammifères de l'Amérique du Nord. Les guides Peterson. Édition Broquet Inc., La Prairie, Quebec, Canada.

CASEY, T. M., P. C. WHITERS, AND K. K. CASEY. 1979. Metabolic and respiratory response of arctic mammals to ambient temperature during the summer. Comparative Biochemistry and Physiology 64:331–341.

CRUZ-NETO, A. P., T. GARLAND, AND A. S. ABE. 2001. Diet, phylogeny, and basal metabolic rate in phyllostomid bats. Zoology: Analysis of Complex Systems 104:49–58.

DAAN, S., D. MASMAN, AND A. GROENENWOLD. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. American Journal of Physiology 259:333–340.

DEGEN, A. A., M. KAM, I. S. KHOKHLOVA, B. R. KRASNOV, AND T. G. BARRACLOUGH. 1998. Average daily metabolic rate of rodents: habitat and dietary comparisons. Functional Ecology 12:63–73.

DIAZ-URIARTE, R., AND T. GARLAND. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Systematic Biology 47:654–672.

DOWNS, C. T., J. M. BOWLAND, A. E. BOWLAND, AND M. R. PERRIN. 1991. Thermal parameters of serval *Felis serval* (Felidae) and blackbacked jackal *Canis mesomelas* (Canidae). Journal of Thermal Biology 16:277–279.

FRATI, F., G. B. HARTL, S. LOVARI, M. DELIBES, AND G. MARKOV. 1998. Quaternary radiation and genetic structure of the red fox *Vulpes vulpes* in the Mediterranean Basin, as revealed by allozymes and mitochondrial DNA. Journal of Zoology 245:43–51.

FUGLEI, E., AND N. A. ORITSLAND. 1999. Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (*Alopex lagopus*) at Svalbard. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environ-mental Physiology 169:361–369.

GARLAND, T., A. F. BENNETT, AND E. L. REZENDE. 2005. Phylogenetic approaches in comparative physiology. Journal of Experimental Biology 208:3015–3035.

GARLAND, T., A. W. DICKERMAN, C. M. JANIS, AND J. A. JONES. 1993. Phylogenetic analysis of covariance by computer-simulation. Systematic Biology 42:265–292.

GARLAND, T., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

GARLAND, T., AND A. R. IVES. 2000. Using the past to predict the present: confidence intervals for regression equations in phyloge-netic comparative methods. American Naturalist 155:346–364.

GARLAND, T., P. E. MIDFORD, AND A. R. IVES. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. American Zoologist 39:374–388.

GENOUD, M. 2002. Comparative studies of basal rate of metabolism in primates. Evolutionary Anthropology 11:108–111.

GINSBERG, J. R., AND D. W. MACDONALD. 1990. Foxes, wolves, jackals and dogs: an action plan for the conservation of canids. World Conservation Union, Gland, Switzerland.

GOLIGHTLY, R. T., AND R. D. OHMART. 1983. Metabolism and body-temperature of two desert canids—coyotes and kit foxes. Journal of Mammalogy 64:624–635.

HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, United Kingdom.

HAYSSEN, V., AND R. C. LACY. 1985. Basal metabolic rates in mam-mals: taxonomic differences in the allometry of BMR and body mass. Comparative Biochemistry and Physiology 81:741–754.

HENNEMAN, W. W., S. D. THOMPSON, AND M. J. KONECNY. 1983. Metabolism of crab-eating foxes, *Cerdocyon thous*: ecological influences on the energetics of canids. Physiological Zoology 56: 319–324.

IRVING, L., H. KROG, AND M. MONSON. 1955. The metabolism of some Alaskan animals in winter and summer. Physiological Zoology 28: 173–185.

KLEIBER, M. 1932. Body size and metabolism. Hilgardia 6:315–353.

KLEIBER, M. 1961. The fire of life. John Wiley & Sons, Inc., New York.

KLIR, J. J., AND J. E. HEATH. 1992. Metabolic rate and evaporative water loss at different ambient temperatures in 2 species of fox: the

red fox (*Vulpes vulpes*) and the arctic fox (*Alopex lagopus*). Comparative Biochemistry and Physiology, A. Comparative Physiology 101:705–707.

KORHONEN, H., M. HARRI, AND J. ASIKAINEN. 1983. Thermoregulation of polecat and racoon-dog: a comparative study with stoat, mink and blue foxes. Comparative Biochemistry and Physiology 74:225–230.

LINDSAY, I. M., AND D. W. MACDONALD. 1986. Behavior and ecology of the Ruppell fox, *Vulpes ruppelli*, in Oman. Mammalia 50:461–474.

LOVEGROVE, B. G. 2000. The zoogeography of mammalian basal metabolic rate. American Naturalist 156:201–219.

LOVEGROVE, B. G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow–fast metabolic continuum. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology 173:87–112.

MACDONALD, D. W., AND C. SILLERIO-ZUBIRI. 2004. The biology and conservation of wild canids. Oxford University Press, Oxford, United Kingdom.

MACMILLEN, R. E., AND T. GARLAND. 1989. Adaptive physiology. Pp. 143–168 in Advances in the study of *Peromyscus* (Rodentia) (J. N. Lane and G. L. Kirkland, Jr., eds.). Texas Tech University Press, Lubbock.

MALOIY, G. M. O., J. M. Z. KAMAU, A. SHKOLNIK, M. MEIR, AND R. ARIELI. 1982. Thermoregulation and metabolism in a small desert carnivore—the fennec fox (*Fennecus zerda*) (Mammalia). Journal of Zoology (London) 198:279–291.

MCNAB, B. K. 1986. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56:1–19.

MCNAB, B. K. 1989. Basal rate of metabolism, body size, and food habits in the order Carnivora. Pp. 335–354 in Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Comstock, Ithaca, New York.

MCNAB, B. K. 1992. A statistical-analysis of mammalian rates of metabolism. Functional Ecology 6:672–679.

MCNAB, B. K. 2003. Standard energetics of phyllostomid bats: the inadequacies of phylogenetic-contrast analyses. Comparative Biochemistry and Physiology, A. Molecular and Integrative Physiology 135:357–368.

MUÑOZ-GARCIA, A., AND J. B. WILLIAMS. 2005. Basal metabolic rate in carnivores is associated with diet after controlling for phylogeny. Physiological and Biochemical Zoology 78:1039–1056.

NOLL-BANHOLZER, U. 1979. Body-temperature, oxygen-consumption, evaporative water-loss and heart-rate in the fennec. Comparative Biochemistry and Physiology, A. Comparative Physiology 62:585–592.

OKARMA, H., AND P. KOJETA. 1987. Basal metabolic rate in the gray wolf in Poland. Journal of Wildlife Management 51:800–801.

PAGEL, M. D. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology 156:431–442.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, United Kingdom.

PRESTRUD, P. 1991. Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter. Arctic 44:132–138.

REZENDE, E. L., F. BOZINOVIC, AND T. GARLAND. 2004. Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. Evolution 58:1361–1374.

RICKLEFS, R. E., M. KONARZEWSKI, AND S. DAAN. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. American Naturalist 147:1047–1071.

SCHMIDT-NIELSEN, K. 1997. Animal physiology. Cambridge University Press, Cambridge, United Kingdom.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, AND L. IRVING. 1950a. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biological Bulletin 99:259–271.

SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950b. Heat regulation in some arctic and tropical mammals and birds. Biological Bulletin 99:237–258.

SHIELD, J. 1972. Acclimation and energy metabolism of the dingo *Canis dingo* and the coyote, *Canis latrans*. Journal of Zoology (London) 168:483–501.

SHKOLNIK, A., AND K. SCHMIDT-NIELSEN. 1976. Temperature regulation in hedgehogs from temperate and desert environments. Physiological Zoology 49:56–64.

SILVA, S. I., F. A. JAKSIC, AND F. BOZINOVIC. 2004. Interplay between metabolic rate and diet quality in the South American fox, *Pseudalopex culpaeus*. Comparative Biochemistry and Physiology, A. Molecular and Integrative Physiology 137:33–38.

SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–490 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

THOMAS, D. W., J. BLONDEL, AND P. PERRET. 2001. Physiological ecology of Mediterranean blue tits (*Parus caeruleus*) 1. A test for inter-population differences in resting metabolic rate and thermal conductance as a response to hot climates. Zoology 104:33–40.

UNDERWOOD, L. S. 1971. The bioenergetics of the arctic fox (*Alopex lagopus* L.). Ph.D. dissertation, Pennsylvania State University, University Park.

VAN VALKENBURGH, B. 1990. Skeletal and dental predictors of body mass in carnivores. Pp. 181–205 in Body size in mammalian paleobiology: estimation and biological implications (J. Damuth and B. MacFadden, eds.). Cambridge University Press, Cambridge, United Kingdom.

VILÀ, C., et al. 1999. Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. Molecular Ecology 8:2089–2103.

WHITE, C. R. 2003. The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. Physiological and Biochemical Zoology 76:122–134.

WHITE, C. R., AND R. S. SEYMOUR. 2005a. Allometric scaling of mammalian metabolism. Journal of Experimental Biology 208:1611–1619.

WHITE, C. R., AND R. S. SEYMOUR. 2005b. Sample size and mass range effects on the allometric exponent of basal metabolic rate. Comparative Biochemistry and Physiology, A. Molecular and Integrative Physiology 142:74–78.

WILLIAMS, J. B., D. LENAIN, S. OSTROWSKI, B. I. TIELEMAN, AND P. J. SEDDON. 2002. Energy expenditure and water flux of Rüppell's foxes in Saudi Arabia. Physiological and Biochemical Zoology 75:479–488.

WILLIAMS, J. B., A. MUÑOZ-GARCIA, S. OSTROWSKI, AND B. I. TIELEMAN. 2004. A phylogenetic analysis of basal metabolism, total evaporative water loss, and life-history among foxes from desert and mesic regions. Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology 174:29–39.