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

Author(s): Vincent Careau, Julie Morand-Ferron, and Don Thomas
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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 fossile 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;
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 Sillerio-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 O₂.

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.

### 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Body mass (g)</th>
<th>Climate</th>
<th>BMR (kJ/day)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Canis lupus</em></td>
<td>9</td>
<td>35,000</td>
<td>Intermediate</td>
<td>3,872.23</td>
<td>Okarma and Kojeta 1987</td>
</tr>
<tr>
<td><em>C. lupus pallipes</em></td>
<td>3</td>
<td>20,194</td>
<td>Hot desert</td>
<td>2,410.56</td>
<td>Afik and Pinshow 1993</td>
</tr>
<tr>
<td><em>C. lupus</em></td>
<td>4</td>
<td>18,950</td>
<td>Intermediate</td>
<td>3,041.40</td>
<td>Hayssten and Lacy 1985</td>
</tr>
<tr>
<td><em>C. lupus dingo</em></td>
<td>4</td>
<td>18,000</td>
<td>Intermediate</td>
<td>3,487.17</td>
<td>Shield 1972</td>
</tr>
<tr>
<td><em>C. latrans incolatus</em></td>
<td>3</td>
<td>10,300</td>
<td>Arctic</td>
<td>2,173.94</td>
<td>Shield 1972</td>
</tr>
<tr>
<td><em>C. latrans mearnsi</em></td>
<td>3</td>
<td>10,000</td>
<td>Hot desert</td>
<td>1,295.88</td>
<td>Golightly and Ohmart 1983</td>
</tr>
<tr>
<td><em>C. mesomelas</em></td>
<td>4</td>
<td>7,720</td>
<td>Intermediate</td>
<td>1,811.54</td>
<td>Downs et al. 1991</td>
</tr>
<tr>
<td><em>Vulpes lagopus</em></td>
<td>2</td>
<td>7,600</td>
<td>Arctic</td>
<td>2,058.76</td>
<td>Korhonen et al. 1983</td>
</tr>
<tr>
<td><em>Nyctereutes procyonoides</em></td>
<td>4</td>
<td>7,575</td>
<td>Intermediate</td>
<td>1,705.03</td>
<td>Korhonen et al. 1983</td>
</tr>
<tr>
<td><em>Cerdocyon thous</em></td>
<td>2</td>
<td>5,444</td>
<td>Intermediate</td>
<td>734.45</td>
<td>Henman et al. 1983</td>
</tr>
<tr>
<td><em>Lycalopex culpaeus</em></td>
<td>11</td>
<td>5,259</td>
<td>Intermediate</td>
<td>930.11</td>
<td>Silva et al. 2004</td>
</tr>
<tr>
<td><em>A. lagopus</em></td>
<td>2</td>
<td>5,090</td>
<td>Arctic</td>
<td>1,033.24</td>
<td>Klir and Heath 1992</td>
</tr>
<tr>
<td><em>V. vulpes alascensis</em></td>
<td>1</td>
<td>4,725</td>
<td>Arctic</td>
<td>1,195.64</td>
<td>Irving et al. 1955</td>
</tr>
<tr>
<td><em>A. lagopus</em></td>
<td>3</td>
<td>4,700</td>
<td>Arctic</td>
<td>1,192.27</td>
<td>Scholander et al. 1950a</td>
</tr>
<tr>
<td><em>A. lagopus</em></td>
<td>9</td>
<td>4,650</td>
<td>Arctic</td>
<td>1,075.65</td>
<td>Fuglei and Oritslan 1999</td>
</tr>
<tr>
<td><em>V. vulpes</em></td>
<td>4</td>
<td>4,045</td>
<td>Intermediate</td>
<td>906.97</td>
<td>Klir and Heath 1992</td>
</tr>
<tr>
<td><em>A. lagopus</em></td>
<td>3</td>
<td>3,600</td>
<td>Arctic</td>
<td>662.16</td>
<td>Casey et al. 1979</td>
</tr>
<tr>
<td><em>V. vulpes</em></td>
<td>4</td>
<td>3,060</td>
<td>Intermediate</td>
<td>724.33</td>
<td>Williams et al. 2004</td>
</tr>
<tr>
<td><em>V. vulpes arabica</em></td>
<td>5</td>
<td>1,967</td>
<td>Hot desert</td>
<td>418.02</td>
<td>Williams et al. 2004</td>
</tr>
<tr>
<td><em>V. macrotis</em></td>
<td>12</td>
<td>1,819</td>
<td>Hot desert</td>
<td>485.78</td>
<td>Golightly and Ohmart 1983</td>
</tr>
<tr>
<td><em>V. rueppellii</em></td>
<td>6</td>
<td>1,546</td>
<td>Hot desert</td>
<td>385.01</td>
<td>Williams et al. 2002</td>
</tr>
<tr>
<td><em>V. cana</em></td>
<td>4</td>
<td>1,285</td>
<td>Hot desert</td>
<td>304.53</td>
<td>Williams et al. 2004</td>
</tr>
<tr>
<td><em>V. zerda</em></td>
<td>7</td>
<td>1,215</td>
<td>Hot desert</td>
<td>281.06</td>
<td>Maloiy et al. 1982</td>
</tr>
<tr>
<td><em>V. zerda</em></td>
<td>8</td>
<td>1,106</td>
<td>Hot desert</td>
<td>190.79</td>
<td>Noll-Banholzer 1979</td>
</tr>
</tbody>
</table>
**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 Vila 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 MB 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 MB data were transformed using the log10 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 MB or different BMR despite a similar MB. 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 CSLR 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 first described the allometric equation between BMR and MB with a CSLR. We then used the PDTREE program to calculate the PI contrasts of BMR and MB and plotted these forcing the regression through the origin. To examine the effect of climate after controlling for the effect of MB, we performed a CSLR analysis of covariance (ANCOVA) with climate as a fixed factor and MB 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 \( \log_{10} \text{BMR} = 2.904 \) (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 \( m_1 \) 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 \((F = 281.4, df = 1, 22, \text{sum of weights} = 16, P < 0.001; \text{Fig. 2A})\). The slope of the relationship \((0.84 \pm 0.05; \text{lower bound of 95\% confidence interval} [\text{CI}] = 0.74)\) 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 \((F = 83.3, df = 1, 14, P < 0.001; \text{Fig. 2B})\). Although the slope of the relationship between BMR and mass \((0.95 \pm 0.10)\) 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 associated 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: \( t = 3.35, df = 2, P = 0.04 \); see specific symbols in Fig. 3).

![Figure 2](figure2.png)

**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.
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 $-40^\circ$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 ($-13^\circ$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).
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 unambiguously 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 plasticity. However, it remains that climate plays a significant role in setting the level of basal metabolism.

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