

The relationship between foot size of wild canids and regional snow conditions: evidence for selection against a high footload?

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Abstract

Mammals occupying northern areas may experience reduced fitness through the deleterious effects of snow on locomotion, energy expenditure, and food acquisition. Accordingly, in areas of deep and soft snow, selection may favour mammals possessing disproportionately large feet and lower footload (body mass/foot surface area). We collected carcasses of coyote *Canis latrans* ($n=472$), red fox *Vulpes vulpes* ($n=199$), arctic fox *Alopex lagopus* ($n=52$), grey fox *Urocyon cinereoargenteus* ($n=17$), and wolf *Canis lupus* ($n=14$) and compared body mass, total foot area, difference in surface area between front and hind feet, and footload, among species and populations. All measured morphological attributes differed significantly among canid species; grey fox had the smallest feet, whereas arctic fox had both the lightest mass and lowest footload of all canids. For all species, adult males tended to be heavier and have larger feet than did adult females, and for most species adults were heavier and larger than were juveniles. Foot area in red foxes increased significantly with latitude, with populations found north of 48 °N (i.e. approximate latitude where snow may become limiting) averaging 12% larger feet than those found farther south. For coyotes, body mass increased with latitude, with populations found north of 48 °N averaging 26% heavier mass than those occurring farther south. Coyote foot area also increased with latitude, with populations found north of 48 °N averaging 25% larger feet than those found farther south. When indices of snow severity (mean annual snowfall, mean number of days with snowcover) were considered, foot area for red foxes was correlated with annual snowfall as well as latitude, whereas coyote morphology failed to correlate with any snow-related variables. These results suggest that snow may have contributed to selection for foot size in some wild canids (i.e. arctic fox, red fox), but such selective forces were probably relatively weak and inconsistent across species.

Key words: Canidae, foot size, snow, morphology

INTRODUCTION

Morphological variation among species or populations is often used as an indicator of adaptation to particular ecological conditions (e.g. Fuentes & Jaksic, 1979; Gitelman, 1985; Nagorsen, 1985). Accordingly, this variation in morphology is perceived as being a result of higher fitness among animals possessing attributes that are better suited to a particular environment. The speed and magnitude of morphological change in a species or population may be related to genetic diversity, rate of mutation, and intensity of selective forces acting for or against morphological change (Reznick *et al.*, 1997).

When selective pressures are long-term and intensive, and fitness is influenced by morphology, both the rate and magnitude of morphological change in a given population should be higher relative to others facing shorter term or weaker pressures. However, because morphological change is typically a slow process requiring multiple generations being subject to selection, few empirical studies have drawn clear causal relationships between morphology and the environment (Boyce, 1978).

Northern environments may impose upon resident animals strong selective pressures, with snow conditions being an important constraint on mammalian locomotion, energy expenditure, food acquisition, foraging behaviour, and activity (e.g. Fuller, 1991; Huggard, 1993; Murray *et al.*, 1995). When the effects of snow are

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intensive or sustained, they may favour changes in foot size or morphology that minimize deleterious outcomes to survival or reproduction (Telfer & Kelsall, 1984; Murray & Boutin, 1991). However, the effects of limb characteristics on locomotor performance, and the implications of such performance on fitness of terrestrial mammals, generally remain poorly understood (Harris & Steudel, 1997).

Not all northern mammals possess long limbs or large feet, suggesting that other ecological or behavioural factors may mitigate selection for morphological change. For instance, northern populations of coyotes *Canis latrans* are morphologically ill-equipped for travel in snow relative to similar-sized lynx *Lynx canadensis* or snowshoe hare *Lepus americanus*; the latter species being the primary prey of both predators in northern areas (Murray & Boutin, 1991). Northern coyotes apparently alleviate negative impacts of snow on movements by behavioural means such as extensive trail use, and travel and hunting in areas with hard snow (Murray & Boutin, 1991; Murray *et al.*, 1995); such behaviour may weaken selective forces favouring morphological change in this species.

Body mass, foot morphology (foot surface area and the difference in surface area between the front and hindfeet), and footload (body mass/foot surface area) of species and populations of wild canids were compared. We predicted that if snow acts as a selective force on canid morphology, feet should be disproportionately larger and/or footload should be lighter in species whose range is restricted to areas with substantial snow cover. Furthermore, feet should be larger and footload should be lighter in northern populations of wide-ranging species, and morphological attributes should be strongly correlated to indices of local snow severity. Thus, a significant correlation between foot size and/or footload and snow severity would support the contention that snow exerts a selective force on footload. This prediction contradicts conventional ecological theory: Allen's rule predicts that size of extremities (i.e. limbs or feet) will be smaller, and Bergman's rule predicts that body mass (and as a result, footload) should be heavier, in northern populations of a given species (Scholander, 1955; Mayr, 1956, 1966). Finally, we also predicted that morphological selection would be reduced in species having only recently expanded their range to include areas of substantial snowcover, as opposed to those having had longstanding exposure to snow-induced selective forces.

METHODS

Morphological attributes relevant to snow were examined in 5 species of North American canids: (1) arctic fox *Alopex lagopus*, which has a circumpolar distribution (Garrott & Eberhardt, 1987); (2) grey fox *Urocyon cinereoargenteus*, which ranges across the southern United States and into south-eastern Canada (Fritzell, 1987); (3) red fox *Vulpes vulpes*, found throughout

Canada and the United States (Voigt, 1987); (4) coyote cited previously, which occurs throughout the contiguous United States and south-eastern Canada and into Alaska and Yukon (Voigt & Berg, 1987); (5) wolf *Canis lupus*, which currently ranges throughout most of Canada and Alaska (Carbyn, 1987). Before European settlement, red foxes were apparently common north of 40°–45°N but southward range expansion occurred in the last 350 years (Churcher, 1959). In contrast, the northern distribution of coyotes was restricted to the central prairies (49°–50°N) and expanded to the east and north in the last 200 years (Moore & Parker, 1992).

Carcasses from each species were collected (1992–97) from trappers and animal damage control personnel across Canada and the United States. Most animals were obtained during standard trapping seasons (November–April) using traditional capture methods; a smaller number of canids were shot opportunistically. Age (adult or juvenile, based on tooth wear and body size), weight and gender were recorded for each carcass. Unskinned paws were removed from carcasses and traced 3–5 times on a sheet of paper to obtain a measure of foot area (Telfer & Kelsall, 1979). All 4 paws were traced from most carcasses, but for some samples a single front and hind limb were traced. The tracing procedure was such that the pencil was pressed against the periphery of the digital bones as it circled the paw, thereby compressing fur and toes. We felt that this technique was less biased and provided a minimum measure that was more reflective of true foot size than was a measure that enabled toes to be splayed. Foot surface area was calculated using a digital planimeter (Murray & Boutin, 1991).

Foot measurements were standardized by having both authors trace paws from a sample of coyotes ($n = 28$) and arctic foxes ($n = 52$). The same magnitude of difference (12%) characterized the untransformed mean size obtained by each author for both species, suggesting that the correction factor between observers was consistent across a range of canid foot sizes. Thus, all foot-size measurements obtained by 1 of the 2 observers were scaled according to the correction factor.

Most (54%) carcasses were skinned before weighing; mass loss due to skinning was corrected for. For arctic foxes ($n = 52$) and red foxes ($n = 52$), the mass of skinned carcasses was found to be 21% and 18% less than unskinned carcasses (adjusted for age and sex) taken from the same area, respectively. Thus, for all species of foxes an average 20% reduction in body mass was assumed to be the result of skinning. Similar comparisons were not possible for the remaining species, but elsewhere the loss of mass in skinned coyote carcasses was reported to average 10% (Sabeau, 1993). Thus, for wolves and coyotes, a correction factor of 10% was applied. This disparity in the correction factor applied to the smaller foxes vs the larger coyotes and wolves makes intuitive sense; the surface area:volume ratio, and therefore, the relative mass of hide and fur, should be proportionally heavier in the smaller foxes. However, the choice of correction factor (ranging from 10% to

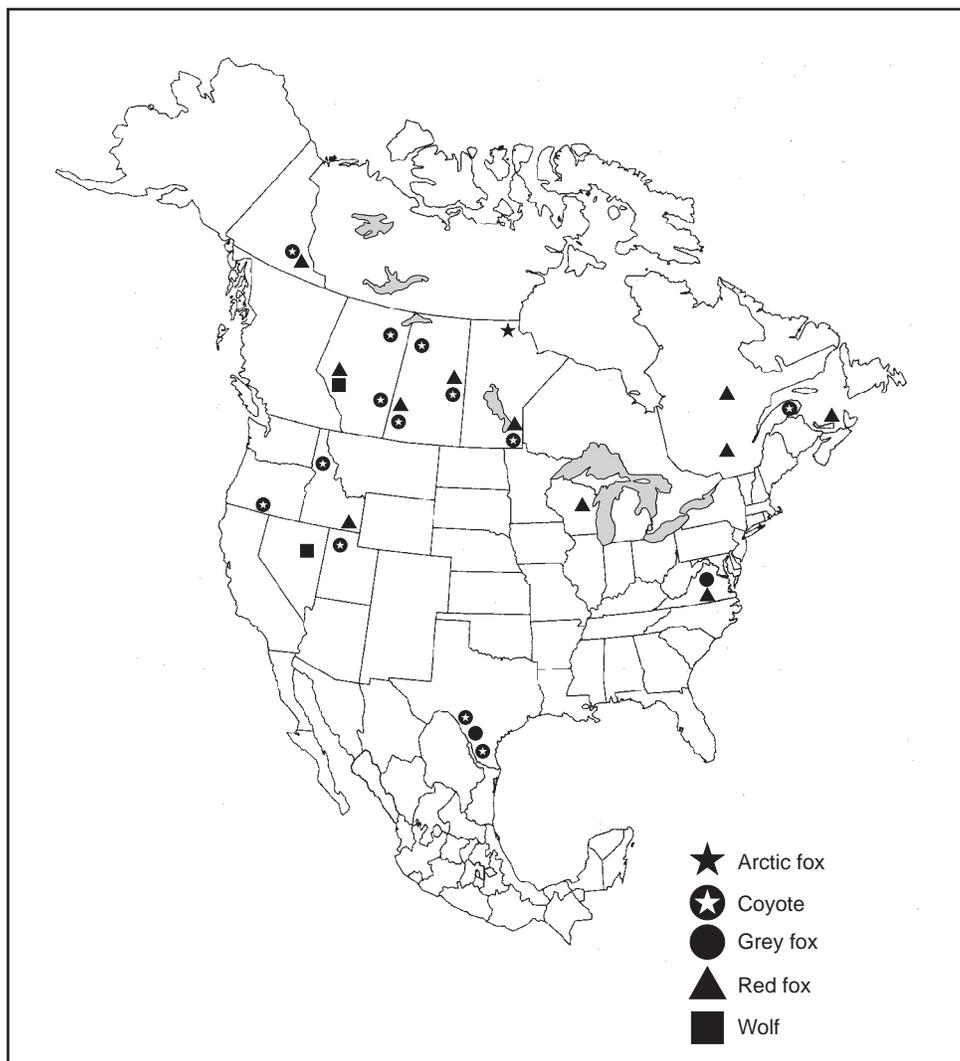


Fig. 1. Distribution of canid populations sampled for carcasses to measure morphological attributes potentially related to snow.

20%) for a given species did not affect our results qualitatively.

Analyses

The 4 measures used to compare canid adaptation to snow were: (1) body mass (kg); (2) total foot surface area (cm²); (3) difference in the size of the front and hind feet; (4) footload (body mass of unskinned carcass/total foot surface area). Changes in body mass that occur strictly as a result of selective forces imposed by snow seem unlikely, but mass should scale to body size and thus may serve as a reasonable index of both structural size and also potential snow-bearing pressure. Snow-induced selection for increased foot area and reduced footload has been hypothesized previously (Telfer & Kelsall, 1984; Murray & Boutin, 1991), with reduced footload simply providing a version of the former measure that has been scaled to body mass. However, the possibility that selection might favour individuals with disproportionately large forefeet only

(rather than large total foot surface area) was also considered, given the common practice by canids of placing hind feet in the track created by the front feet. Thus, we measured size differences between fore and hindfeet. Body mass and total foot-surface area were log-transformed before analysis, whereas values for foot-size differential and footload approached normality and therefore remained untransformed.

Canid morphology was compared using a factorial multiple analysis of variance. To test our prediction of differential morphological attributes among species, individual animals were used as the experimental unit, and species, sex, and age as independent variables. Next, geographical differences among populations were addressed by comparing morphological features measured from 11 populations of red fox and 13 populations of coyote. Site-specific averages were then calculated for each adult sex cohort, and a population average computed based on the assumption of parity of sexes. This approach was valid because our results did not differ qualitatively between sexes of the same species. The juvenile data was not analysed in the

Table 1. Morphological attributes (mean \pm SD) of five species of wild canids. Arctic fox and wolves were obtained from a single location, grey fox from two locations, and red fox and coyotes were collected from 11 and 13 locations, respectively. Foot area represents, total area encompassed by all four limbs, while foot area differential is the difference in size between the front minus the hind feet. Sample sizes are in parentheses

	Body mass (kg)	Foot area (cm ²)	Foot area differential (cm ²)	Footload (g/cm ²)
Arctic fox				
Adult male (23)	3.18 \pm 0.41	48.2 \pm 4.3	0.5 \pm 1.4	66.0 \pm 7.1
Adult female (19)	3.01 \pm 0.52	45.7 \pm 5.3	0.5 \pm 1.2	68.2 \pm 7.1
Juvenile (10)	2.55 \pm 0.39	46.9 \pm 4.6	0.5 \pm 1.0	55.0 \pm 10.6
Mean (52)	3.03 \pm 0.50	47.1 \pm 4.8	0.5 \pm 1.3	64.7 \pm 10.6
Grey fox				
Adult male (9)	3.40 \pm 0.77	38.3 \pm 3.6	0.5 \pm 0.9	88.6 \pm 17.5
Adult female (4)	3.85 \pm 0.15	40.6 \pm 5.3	-1.2 \pm 0.6	95.7 \pm 11.8
Juvenile (4)	2.76 \pm 0.61	33.8 \pm 3.8	0.1 \pm 1.0	83.4 \pm 24.8
Mean (17)	3.36 \pm 0.72	37.8 \pm 4.6	0.0 \pm 1.1	89.1 \pm 17.7
Red fox				
Adult male (91)	5.70 \pm 0.87	65.4 \pm 10.3	0.4 \pm 1.5	88.5 \pm 16.6
Adult female (41)	4.96 \pm 0.76	58.5 \pm 8.4	0.4 \pm 1.5	86.2 \pm 14.5
Juvenile (63)	4.03 \pm 0.70	55.7 \pm 7.3	0.2 \pm 1.5	72.7 \pm 11.3
Mean (196)	5.00 \pm 1.08	60.8 \pm 10.0	0.3 \pm 1.5	82.9 \pm 16.2
Coyote				
Adult male (192)	13.32 \pm 2.57	79.0 \pm 12.5	2.3 \pm 1.8	170.3 \pm 27.0
Adult female (117)	11.97 \pm 2.45	73.9 \pm 12.4	2.0 \pm 2.0	164.3 \pm 28.8
Juvenile (142)	9.59 \pm 2.11	72.0 \pm 9.9	1.8 \pm 1.6	133.8 \pm 26.7
Mean (451)	11.80 \pm 2.88	75.4 \pm 12.1	2.0 \pm 1.8	157.2 \pm 31.7
Wolf				
Adult male (4)	43.41 \pm 8.03	213.2 \pm 10.5	6.9 \pm 2.7	201.2 \pm 42.0
Adult female	37.09 \pm 4.66	191.4 \pm 15.8	6.2 \pm 3.5	195.5 \pm 34.7
Juvenile (5)	25.11 \pm 8.12	159.6 \pm 22.2	5.1 \pm 2.9	155.5 \pm 37.2
Mean (14)	34.62 \pm 10.13	186.3 \pm 27.6	6.0 \pm 2.9	183.7 \pm 41.1

same manner because site-specific differences in juvenile morphology could be attributed to local trapping season timing and concomitant maturity of juveniles, as easily as to snow-induced selection. Site-specific attributes of adult red fox and coyote population morphology were then regressed against independent variables representing latitude, longitude, and latitude \times longitude interaction ((percentage across the range in degrees latitude + percentage across the range of degrees longitude)/2), using a stepwise procedure. This latter term does not represent a traditional statistical interaction term but rather a north-west gradient in the variables of interest (see Murray, 2000). Finally, independent variables representing site-specific indices of snow severity (mean number of days with snow-cover; mean total annual snowfall) were made available for inclusion in the regression models, and we evaluated their relationship to canid morphology relative to those representing geographic location. Snow values averaged over *c.* 50 years (1940–90) were obtained from Environment Canada and National Oceanic and Atmospheric Administration databases for the nearest weather station to each population site.

RESULTS

A total of 754 wild canids (arctic fox, $n = 52$; grey fox, $n = 17$; red fox, $n = 199$; coyote, $n = 472$; wolf, $n = 14$)

were collected from 12 states or provinces across North America (Fig. 1). All arctic foxes and wolves were collected from one area each (northern Manitoba and central Alberta, respectively), grey foxes were collected from southern Texas and Virginia, whereas red foxes and coyotes were collected from 11 and 13 separate areas, respectively (Fig. 1). For the red fox, latitudinal extremes in sampling locations ranged from Virginia (38°N) to southern Yukon (61°N), whereas for coyotes, latitude ranged from southern Texas (28°N) to southern Yukon (61°N).

Morphological differences among species

Pronounced differences were observed in the five morphological attributes of interest among canid species (Tables 1 & 2). Body mass was lightest in arctic and grey fox and heaviest in wolves, whereas foot surface area was least in grey fox and largest in wolves (Table 1). Males were heavier than females in all species. Footload was least in arctic fox, intermediate in grey and red fox, and heaviest in coyotes and wolves (Table 1).

Both body mass and foot area differed among sexes (Table 1), with mass being on average 11.9 \pm 7.2% (\pm SE) heavier, and foot size averaging 6.8 \pm 2.8% larger, for males of the five species. We also found that on average juveniles were 25.8 \pm 3.1% lighter in mass and had 10.4 \pm 3.4% lower foot surface area compared to adults

Table 2. Effects of species, sex, and age on morphological attributes of five species of wild canids. *F* and *P* values, results of MANOVA assessing differences in morphological attributes (see Table 1); foot area, total area encompassed by all four limbs; foot area differential, the difference in size between the front minus the hind feet

	Body mass (kg)		Foot area (cm ²)		Foot area differential (cm ²)		Footload (g/cm ²)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species	0.06	<0.001	259.49	<0.001	96.79	<0.001	909.48	<0.001
Sex	28.63	<0.001	27.57	<0.001	0.47	0.49	0.99	0.32
Age	203.55	<0.001	20.06	<0.001	2.05	0.15	110.93	<0.001
Species × sex	3.12	0.08	0.48	0.49	0.88	0.35	0.43	0.51
Species × age	0.06	0.80	1.58	0.21	0.01	0.94	16.30	<0.001
Sex × age	0.80	0.37	1.46	0.23	1.66	0.20	0.36	0.55
Species × sex × age	1.38	0.24	0.49	0.49	0.24	0.63	2.08	0.15

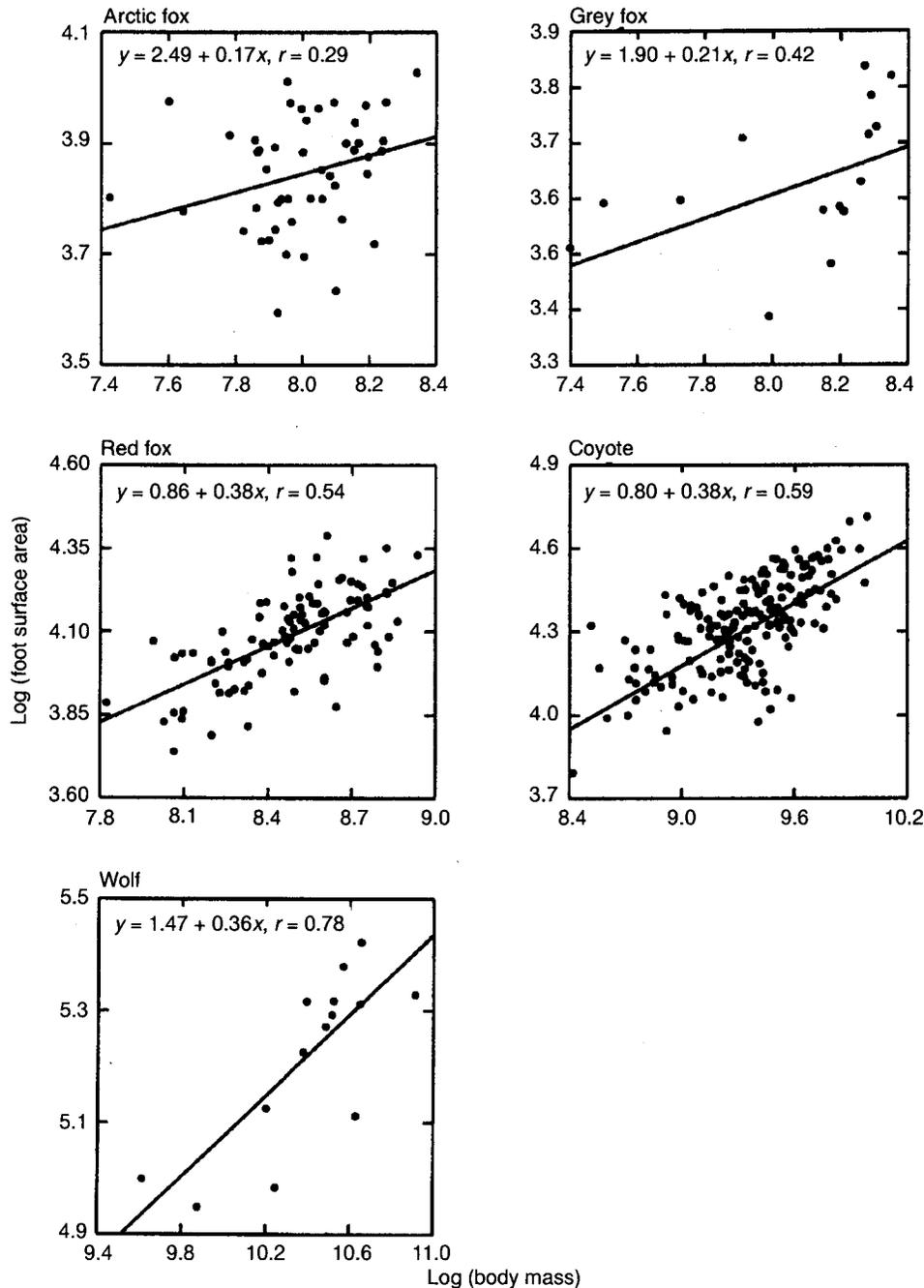


Fig. 2. Relationship between foot surface area (cm²) and body mass (g) for five species of wild canids.

Table 3. Effects of population, sex, and age on morphological attributes of red fox and coyotes from 11 and 13 populations, respectively. *F* and *P* values, results of MANOVA assessing differences in morphological attributes; foot area, total area encompassed by all four limbs; foot area differential, the difference in size between the front minus the hind feet

	Body mass (kg)		Foot area (cm ²)		Foot area differential (cm ²)		Footload (g/cm ²)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Red fox								
Population	19.428	<0.001	16.890	<0.001	5.630	<0.001	11.821	<0.001
Sex	29.015	<0.001	29.536	<0.001	0.011	0.92	0.312	0.58
Age	171.946	<0.001	15.460	<0.001	0.103	0.75	70.518	<0.001
Coyote								
Population	27.177	<0.001	48.486	<0.001	8.628	<0.001	12.134	<0.001
Sex	24.606	<0.001	24.600	<0.001	0.003	0.96	4.116	0.04
Age	312.417	<0.001	62.578	<0.001	2.262	0.13	153.709	<0.001

Table 4. Results of stepwise regression of latitude, longitude, and latitude × longitude interaction (an index of north–west gradient) on morphological attributes of red fox and coyotes

Dependent variable	Regression equation	<i>R</i> ²	<i>P</i>
Red fox			
Mass	–	–	All <i>P</i> > 0.09
Foot area	$y = 3.405 + 0.014 (\text{latitude})$	0.45	Latitude <i>P</i> = 0.03
Foot area differential	–	–	All <i>P</i> > 0.13
Footload	–	–	All <i>P</i> > 0.68
Coyote			
Mass	$y = 8.496 + 0.30 (\text{latitude}) - 0.008 (\text{latitude} \times \text{longitude})$	0.66	Latitude <i>P</i> < ; latitude × longitude <i>P</i> = 0.02
Foot area	$y = 4.385 + 0.011 (\text{latitude}) - 0.005 (\text{longitude})$	0.85	Latitude <i>P</i> < 0.001; longitude <i>P</i> = 0.001
Foot area differential	–	–	All <i>P</i> > 0.30
Footload	–	–	All <i>P</i> > 0.64

(Table 1). Remaining morphological attributes were similar among sex and age classes. Only one of 20 interaction terms was significant (Table 2), indicating that these results were generally consistent among canid species, sexes, and age classes. The only significant interaction terms were apparently attributable to the limited foot size differentiation between adult and juvenile grey foxes, compared to the remaining canid species (Table 1).

Foot surface area was correlated to body mass for four of five species (arctic fox: $t_{51} = 2.119$, $P = 0.039$; red fox: $t_{191} = 13.328$, $P < 0.001$; coyote: $t_{469} = 15.538$, $P < 0.001$; wolf: $t_{13} = 4.333$, $P < 0.001$), whereas for grey fox the correlation was only marginally significant ($t_{16} = 1.785$, $P = 0.094$). However, both correlation coefficients and regression slopes between body mass and foot surface area were lower for arctic fox compared to other species (Fig. 2), indicating that for arctic fox foot area may have been the least strongly related to body mass, and thus structural size. The slope of the body mass–foot area relationship was notably similar among red foxes and coyotes (Fig. 2).

Differences between size of front and hind feet were similar between male and female arctic foxes, but larger for female grey foxes, male coyotes, and male wolves. Overall, foot size differential was lower for juveniles than for adults (Table 1).

Regional differences in red fox and coyote morphology

The larger samples of red fox and coyotes were used to evaluate morphological attributes of each species relative to location of capture. For both red fox and coyotes, all measured morphological attributes differed among populations, and most differed among sex and age classes as well (Table 3). Assuming parity of sex ratio, an adult population average was calculated for each attribute and this value regressed against variables describing geographic gradients (latitude, longitude, and latitude × longitude interaction). Red fox foot area increased with latitude, but no other dependent variable was retained in the models (Table 4); on average, foxes captured north of 48°N (i.e. an arbitrarily chosen latitude that may represent the threshold where the effects of snow become significant) had 12% larger feet than those found to the south (Fig. 3). Alternately, body mass and foot area of coyotes scaled similarly with latitude (Table 4); coyotes found north of 48°N were 26% heavier and their feet were 25% larger compared to coyotes from farther south (Fig. 3). Weak correlations were also noted between coyote body mass and foot surface area versus a latitude × longitude interaction and latitude respectively (Table 4, Fig. 3).

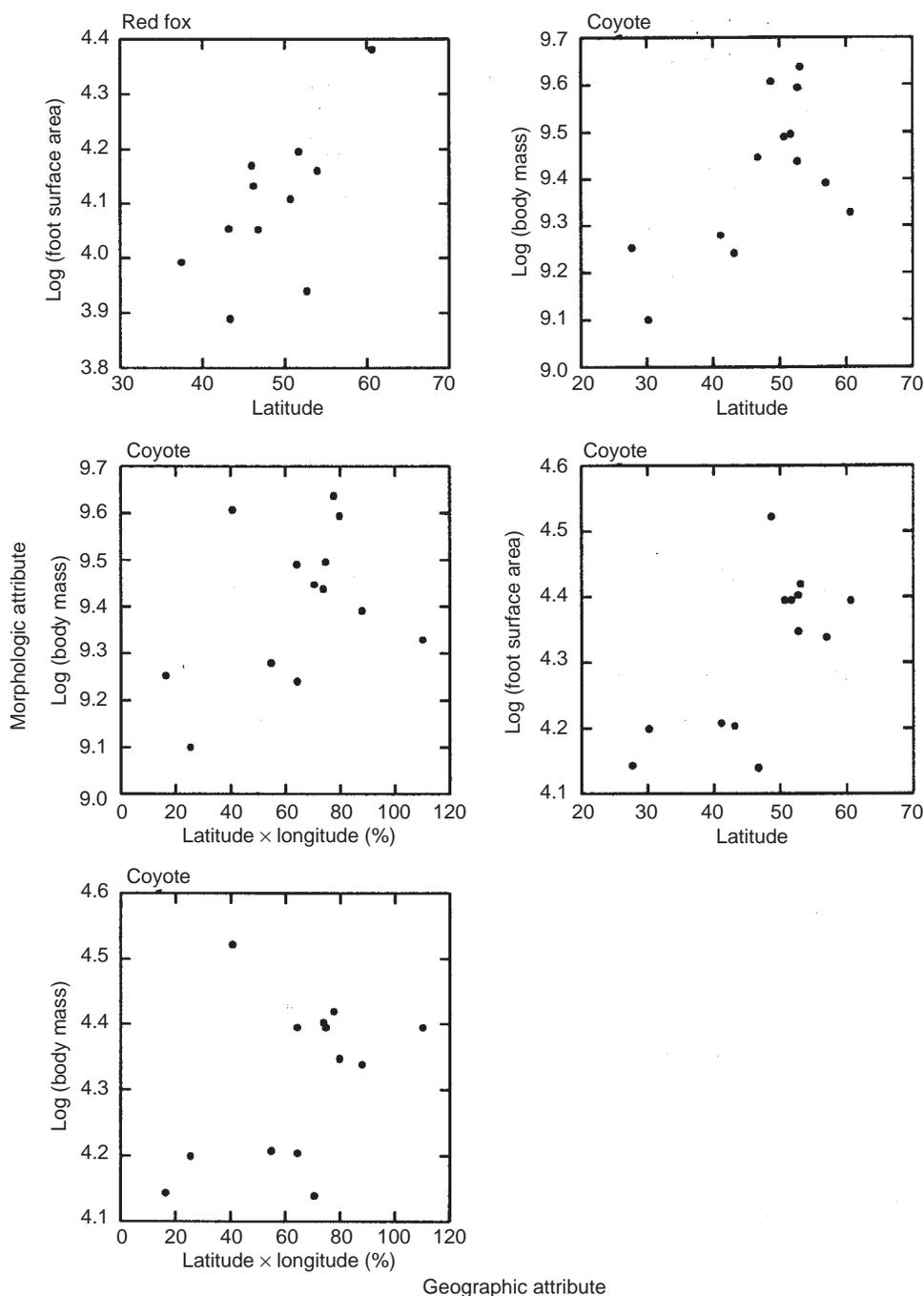


Fig. 3. Relationship between morphological characteristics of adult red fox and coyotes and geographic attributes found to be significant in stepwise regression models (see Table 4). Latitude \times longitude interaction is a measure of north–west gradient. Foot surface is in cm^2 and body mass is in grams.

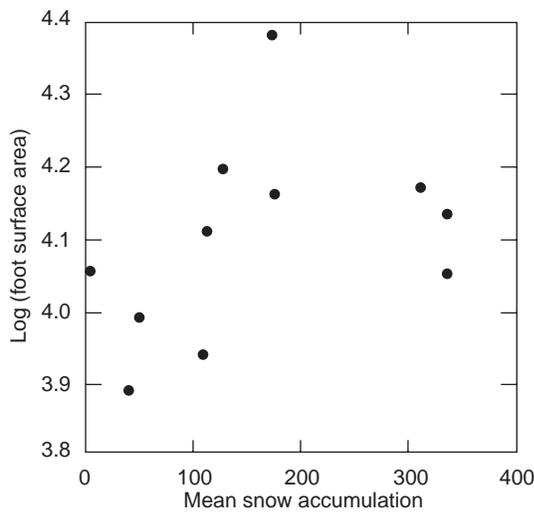
Relationship between snow and morphology

The gradients in red fox and coyote morphology were further examined by making available for inclusion in the above regression models, variables related to local snow severity. In order to detect potential snow-induced selection in morphology, independent variables related to snow severity were made available in the stepwise regression with geographic variables found to be significant in the previous analysis. For red foxes, mean

annual snowfall was among the two variables retained in the regression equation predicting red fox foot area (longitude was also retained), while latitude was now excluded (Table 5). On average, red fox populations experiencing >100 cm mean annual snowfall had 18% larger foot surface area than those faced with less annual snowfall (Fig. 4). Snow-related variables failed to be retained in the remaining regression equations, indicating that the effects of snow on red fox morphology probably were restricted to foot size.

Table 5. Results of stepwise regression of latitude, longitude, latitude \times longitude interaction (an index of north–west gradient), mean annual snowfall, and mean number of days with snow cover on morphological attributes of red fox and coyotes

Dependent variable	Regression equation	R^2	P
Ref fox			
Mass	–	–	All $P > 0.09$
Foot area	$y = 3.453 + 0.005 (\text{longitude}) + 0.001 (\text{snowfall})$	0.64	Longitude $P = 0.01$, snowfall $P = 0.01$
Foot area differential	–	–	All $P > 0.13$
Footload	–	–	All $P > 0.18$
Coyote			
Mass	$y = 8.496 + 0.30 (\text{latitude}) - 0.008 (\text{latitude} \times \text{longitude})$	0.66	Latitude $P < 0.01$; latitude \times longitude $P = 0.02$
Foot area	$y = 4.385 + 0.011 (\text{latitude}) - 0.005 (\text{longitude})$	0.85	Latitude $P < 0.001$; longitude $P = 0.001$
Foot area differential	–	–	All $P > 0.30$
Footload	–	–	All $P > 0.64$

**Fig. 4.** Relationship between foot surface area (cm^2) of 11 red fox populations (adults only) and mean annual snowfall. The relationship between mean annual snowfall and foot surface area was significant when degrees longitude was included in the regression model (see Table 5).

For coyotes, independent variables related to snow severity were not retained in any of the models (Table 5), indicating that no overriding influence of snow existed on coyote morphological attributes.

DISCUSSION

The hypothesis that in northern canid populations, selection favours morphological features mitigating the negative effects of snow on locomotion was tested. As predicted, arctic fox had feet that were larger relative to their body mass than those of other foxes. Also, foot surface area increased with latitude among red fox populations, but the correlation between annual snowfall and foot area also explained some variability. This was considered to serve as limited evidence for snow-induced selection in that species. For coyotes, both body mass and foot area increased similarly with lati-

tude, while no correlation with local snow severity was detected, implying a lack of snow-induced selection in that species. These results indicate that snow may elicit selection for morphological change among some wild canids, but that such selection seems to be relatively weak and inconsistent among species.

Snow, fitness, and mammalian morphology

Deep, soft snow is characteristic of winters across much of boreal North America, and such conditions undoubtedly affect mammalian locomotion, survival, and fitness. For instance, ungulates exhibit dramatic increases in energetic demands when forced to walk through deep and soft snow (Fancy & White, 1985, 1987; Dailey & Hobbs, 1989). Also, snow has been shown to influence a variety of canid behaviours, including feeding activity, prey choice, movement patterns, and habitat use (e.g. Halpin & Bissonette, 1988; Fuller, 1991; Murray & Boutin, 1991; Huggard 1993; Murray *et al.*, 1995). Therefore, snow probably acts as a selective force and may influence the morphology of northern mammals. Other studies (e.g. Gittleman, 1985; Iriarte *et al.*, 1990; Sikes & Kennedy, 1992; Dobson & Wiggington, 1996) have associated similar morphological variation among carnivore populations to selective forces imposed by local environmental conditions, thus, snow may be only one of a suite of environmentally mediated selective forces acting to shape carnivore morphology.

Species living in snow often possess disproportionately long limbs or large feet relative to more southern species (e.g. Telfer & Kelsall, 1984; Murray & Boutin, 1991). For example, the large feet of lynx are well-suited for travel in snow and enable this species to hunt snowshoe hares more effectively during winter (Murray & Boutin, 1991). However, failure to detect differences in the morphology of mammals across a latitudinal gradient (e.g. Klein, Meldgaard & Fancy, 1987) could suggest that snow-induced selection is far from being ubiquitous among northern populations. In our study, arctic fox paws were *c.* 25% larger than those of the

more southerly grey fox, despite the 11% greater body mass among grey fox. When compared to red fox, foot size of arctic fox was only 22% less, compared to a body mass that was 40% less. These results imply that the lower footload of arctic fox is due to their having disproportionately large feet in comparison to the other two fox species. Arctic fox has allegedly been present in northern areas since at least the beginning of the Holocene (Kurtén & Anderson, 1980; Geiffen *et al.*, 1992), and are well-adapted morphologically to such areas through their shortened body extremities and counter-current body heat exchange (Prestud, 1991). This implies that adaptive morphological change in response to snow conditions could have occurred over an extended time period in this species. Yet, we are unable to dismiss the possibility that arctic fox foot size evolved primarily as a function of other selective forces, such as better traction on ice or improved insulation of digits (i.e. exaptation, *sensu* Gould & Vrba, 1982). Alternatively, the attributes of arctic fox feet may be caused by non-genetic effects if differential foot bone stress or foot growth rate is prevalent in northern environments (e.g. Patton & Brylski, 1988; Robinson & Wilson, 1995). However, if non-genetic factors were the cause of observed differences in foot size among canid species, it should be more likely that alterations in bone cross-sectional parameters and the degree of bone mineralization would be the most likely responses, rather than changes in foot size *per se* (e.g. Loitz & Zernicke, 1992; but see Kiiskinen, 1977). Nevertheless, the low footload of Arctic fox seems to contradict Allen's rule (Scholander, 1955), which predicts that extremities (including foot size) should become smaller among animals found in temperate areas.

The consistently lower footload of juvenile canids (for the four species exposed to snow) relative to adults may imply stronger selection for lighter footload in the former cohort. Yet, because other than our example for the grey fox, it remains unclear if morphological similarity between age classes also characterizes terrestrial mammal species not exposed to snow, we resist ascribing the observed age-specific differences specifically to selective forces imposed by snow. Doubtless, the potential effects of snow are mitigated in northern canids principally through selection for larger foot size, while body mass changes (and thus footload) fail to be similarly affected. Change in foot size may be the most direct response to snow-induced morphological selection, while body mass is probably subject to a number of competing selective forces, only one of which is snow. Clearly Bergman's rule (Mayr, 1956, 1966) would not favour mass reductions in northern populations. Finally, our failure to detect any significant relationships between local snow conditions and foot area differential implies that snow-induced selection acts similarly on front- and hindfeet.

Foot surface area of red fox populations was correlated to annual snowfall, but that of coyotes was not. This means that only some northern species or populations are subject to snow-induced selection, a result that

is consistent with one of our original predictions. The similar scaling of coyote body mass and foot area across latitude may signal that other factors influenced the morphology of this species across its range. Coyotes allegedly originated in the central prairies and immigrated to the far northern latitudes only in the last 50–100 years (Moore & Parker, 1992). Coyote populations colonizing northern areas surely were subject to ecological conditions (i.e. snow depth, snow hardness, and snow persistence) that differed from those present on their historical range, as on average the central prairies typically receive little or no snow overwinter, while snow accumulation in the northern range may exceed several metres. Thus, in theory, the potential existed to observe similar morphological change among coyotes and red fox.

The lack of morphological change in coyote footload may be related to several factors. For example, the use of areas of hard or shallow snow (Murray & Boutin, 1991) or dense vegetative cover (Murray *et al.*, 1995) by northern coyotes may render travel and hunting activities less energetically costly during winter, and thereby weaken selective forces for morphological change. It is also possible that the short historical duration of exposure to deep/soft snow by coyote populations, relative to those of red fox, may have precluded demonstrable change in foot morphology. If this is true, then snow exerts relatively weak selection on coyote morphology and it will be unlikely that such minor morphological changes can be detected over evolutionary time. Alternatively, it remains possible that non-genetic factors such as prey capture or general nutrition are linked to coyote morphology across the species' range (Thurber & Peterson, 1991; Peterson & Thurber, 1993; but see Larivière & Crête, 1993), and that such forces could mask the effects of snow-induced selection (e.g. see Klein *et al.*, 1987). Also, given the propensity for coyotes to disperse over long distances (Voigt & Berg, 1987), it remains possible that northern coyote populations are sufficiently panmictic with those from the south so as to obfuscate any detectable evidence of snow-induced selection. However, we should caution against the assumption that snow depth is necessarily the best index of snow severity, and that the absence of a correlation between snow depth and coyote foot morphology is unequivocal evidence for the absence of snow-induced selection in that species. Indeed, the major force selecting for foot morphology should be snow hardness (i.e. track sinking depth) rather than simply snow depth (see Telfer & Kelsall, 1984; Murray & Boutin, 1991), implying that future studies would be well served in using snow density or snow hardness measurements to complement similar analyses of snow-induced selection.

A fundamental problem with associating morphological change to environmentally induced selective forces is the general dearth of causal, rather than correlational, evidence (Boyce, 1978). Indeed, morphological differences among vertebrates are a function of numerous selective forces, many of which are either no longer important or difficult to associate with specific

morphological attributes. Accordingly, where possible, it will remain necessary to measure the effects of morphological variation on animal performance, and relate such effects to fitness (e.g. Arnold, 1983; Garland & Carter, 1994; Garland & Losos, 1994). Such integration is often difficult to undertake and thus has been rarely attempted for many taxonomic groups, including mammalian carnivores (Harris & Steudel, 1997). Accordingly, long-term studies on individual populations, combined with comparisons either among extant populations subject to different environmental conditions or else contrasts of various palaeontological specimens, are much needed to address questions related to selection and morphological change.

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