Estimating the costs of locomotion in snow for coyotes

M. Crête and S. Larivière

Abstract: Carnivores living in areas of deep snow face additional energy expenditures during winter owing to increased locomotory costs. Such costs may vary in function of snow depth and hardness (sinking depth of animal) and travel speed. We estimated energetic costs of locomotion through snow in wild coyotes (*Canis latrans*) using three coyote-sized domestic dogs (*Canis familiaris*) to develop regression models predicting heart rate (as surrogate for energy expenditure) in relation to sinking depth and travel speed. In the absence of snow, heart rates of dogs increased linearly with travel speed (R^2 = 0.24), whereas when snow was present, track sinking depth affected heart rate substantially more than did travel speed. To assess whether our results with domestic dogs could help explain the behaviour of wild coyotes, we snow-tracked coyotes in southeastern Quebec, Canada, during two winters. During a normal harsh winter, coyotes relied on artificially packed snow (snowmobile and animal trails) more than during a mild winter. Coyotes typically exerted a fine-scale selection for snow depth and hardness that effectively reduced their sinking depth by ~2 cm. We estimated that travelling over snow increased coyote heart rate by 4%–6% in comparison with locomotion on hard surfaces, whereas fine-scale selection saved a similar amount of extra energy. We hypothesize that the use of snow packed by anthropogenic activities, especially snowmobile trails, may not only facilitate coyote movements in deep snow environments but also allow occupation of marginal habitats such as forested areas of northeastern North America.

Résumé : Les carnivores qui vivent dans les régions où la neige est épaisse ont des dépenses énergétiques additionnelles durant l'hiver à cause des coûts accrus de la locomotion. Ces coûts peuvent varier en fonction de l'épaisseur et de la consistance de la neige (profondeur d'enfoncement de l'animal) ainsi que de la vitesse de déplacement. Nous avons estimé les coûts énergétiques de la locomotion dans la neige de coyotes (*Canis latrans*) sauvages en utilisant trois chiens domestiques (*Canis familiaris*) de la taille de coyotes pour mettre au point des modèles de prédiction du rythme cardiaque (comme indice de la dépense d'énergie) en fonction de la profondeur d'enfoncement et de la vitesse de déplacement. En l'absence de neige, le taux cardiaque des chiens augmente avec la vitesse de déplacement selon une fonction linéaire (R^2 = 0,24); dans la neige, cependant, la profondeur d'enfoncement des pistes affecte considérablement plus le rythme cardiaque que ne le fait la vitesse de déplacement. Pour vérifier si les résultats obtenus chez les chiens pouvaient servir à expliquer le comportement de coyotes sauvages, nous avons suivi durant deux hivers les pistes de coyotes dans le sud-est du Québec, Canada. Durant un hiver rigoureux ordinaire, les coyotes utilisent la neige tassée artificiellement (par les motoneiges ou par le passage des animaux) plus que durant un hiver doux. Les coyotes font normalement une sélection de la profondeur et de la consistance de la neige à une échelle fine, ce qui réduit leur profondeur d'enfoncement d'environ ~2 cm. Nous estimons que les déplacements sur la neige font augmenter le rythme cardiaque des coyotes de 4 % – 6 % par rapport aux déplacements sur des surfaces dures; la sélection fine conserve une quantité similaire d'énergie supplémentaire. Nous formulons l'hypothèse selon laquelle l'utilisation de la neige tassée par les activités humaines, en particulier les pistes de motoneige, non seulement facilite les déplacements des coyotes dans des environnements de neige épaisse, mais qu'elle leur permet d'occuper des habitats marginaux, tels que les régions forestières du nord-est de l'Amérique du Nord.

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Introduction

In temperate areas, terrestrial animals remaining active throughout winter face two major constraints: food limitation and increased costs of locomotion through snow (e.g., Parker et al. 1984; Dumont et al. 2000). The costs of locomotion through snow may incur significant selective pressure resulting in differential survival and (or) reproduction. It follows that morphological and (or) behavioural adaptations facilitating travel in snow have evolved among many

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terrestrial mammals (Telfer and Kelsall 1984; Murray and Boutin 1991; Murray and Larivière 2002).

Energetic costs of locomotion through snow undoubtedly change according to snow characteristics (snow depth, hardness, etc.), and these vary not only among areas but also temporally. Mammals may respond adaptively to the costs of travel through soft snow by adapting their gait or by selecting areas where snow is hard and compact (Telfer and Kelsall 1984; Murray and Boutin 1991). Such behavioural plasticity might account for the limited evidence for morphological change among some canid populations residing in northern areas; effective behavioural responses to snow could minimize selective pressure on morphological traits (Murray and Larivière 2002).

Coyotes (*Canis latrans*) evolved in the open landscape of central and southwest North America (Young and Jackson 1951) where snow cover is minimal, and thus, selective forces favouring reduced track sinking depth should not be operational (Murray and Boutin 1991; Murray and Larivière 2002). However, the geographic distribution of coyotes expanded considerably both northward and eastward during the last 50–100 years, and the species has colonized southeastern Canada in the last few decades (Moore and Parker 1992). In southeastern Quebec, snow cover typically exceeds 1 m in midwinter and persists from early December to late April (Dumont et al. 2000). Coyote populations in southeastern Quebec have remained at low densities since colonization, but rural populations have reached a higher density than populations inhabiting large forest tracts (Todd 1985; Richer et al. 2002).

We hypothesized that snow increases the locomotory costs among free-ranging canids living in areas where winter snowfall is substantive. We tested the following two predictions: (1) canid heart rate (a surrogate for energy expenditure) should increase exponentially with sinking track depth in snow, as is observed among ungulates and (2) free-ranging coyotes should exhibit behavioural adaptations such as selection of hard and shallow snow conditions in order to reduce energy expenditure for travel, and such selection should be correlated with winter severity.

Study area

The study area covered approximately 1200 km^2 of rolling hills on the south shore of the St. Lawrence River in southeastern Quebec. Annual precipitation averages 1105 mm in the centre of the study area, with 33% falling as snow during early December to late April (Environment Canada 1993). As a result of the decline of agriculture in the region, the rural landscape (473 km^2) was a mosaic of cultivated fields interspersed with old fields and regenerating forest, woodlots, and open water. Contiguous forest blocks of various ages covered the rest (721 km^2) of the study area (Tremblay et al. 1998; Richer et al. 2002). Dominant tree species include sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) on hill tops and south-facing slopes and balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*) elsewhere. Large mammals common to the area include moose (*Alces alces*) (~0.18/km^2), white-tailed deer (*Odocoileus virginianus*) (~1.1/km^2), and black bear (*Ursus americanus*) (~0.4/km^2) (Richer et al. 2002). Other carnivores present include red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), American marten (*Martes americana*), and Canada lynx (*Lynx canadensis*).

Methods

Evaluating costs of locomotion in dogs

All experimental procedures were approved by the Université Laval Council for Animal Care (protocol 96-258) and followed standard guidelines for animal welfare (Canadian Council on Animal Care 1984). We used three coyote-sized domestic dogs (*Canis familiaris* of mixed breed, 15.7 ± 0.9 kg (mean ± SE)) equipped with heart-rate transmitters (HR-300; Telonics, Inc., Mesa, Ariz.) to model costs of energy expenditure that coyotes may experience in snow. Heart rate has been shown to be closely associated with oxygen consumption, and thus energy expenditure, in several species of ungulates (Holter et al. 1976; Robbins et al. 1979; Mautz and Fair 1980; Kautz et al. 1981) and carnivores (Fisher et al. 1987; Griffin and Gilbert 1993). Although our sample size was small, it is comparable with that used by other researchers in similar energetic trials and other physiological studies (e.g., Griffin and Gilbert 1993).

In November 1996, dogs were equipped with heart rate implants weighing 60 g that were placed ventrally via a <5 cm incision in a subcutaneous pocket near the lower abdomen; anesthesia was achieved with ketamine hydrochloride and diazepam and maintained with isofluorine. We ensured that the transmitter was offset laterally from the point of entry so as to minimize direct pressure on the incision wound. Two additional incisions were made near the thoracic cavity to allow suture of the electrode wires (20 cm) to muscle tissue. Dogs were allowed to recover from surgery during 4 weeks while housed individually at the Jardin Zoologique de Québec; animals were provided with food and water ad libitum throughout the recovery period. In early January 1997, animals were relocated to the study area where they were housed outdoors in individual cages. Each dog was fed approximately 500 mL of pelleted dog food per day and ad libitum water.

Costs of locomotion were measured during a sequence of trials conducted during late January – February 1997; we spent about 2 weeks training dogs to walk on command without pulling on a leash so that measurements of energy expenditure would not be biased by our restraint procedures. Each trial lasted while the animal travelled approximately 300 m. During each trial, we counted the number of heart beats using a tape recorder connected to a telemetry receiver (TR2; Telonics, Inc.) and calculated the average heart rate by dividing total number of beats by the duration of the trial. Whenever necessary, the speed of the tape recorder was slowed to facilitate data extraction. To minimize the potential bias incurred from having dog heart rates acclimate during a trial to specific trial conditions, we usually walked the animals for several minutes on similar substrate and at a similar pace prior to the onset of the trial.

We first estimated the basal heart rate of the dogs by monitoring on several occasions their sleeping heart rates between the hours of 0000 and 0300. Ambient temperature

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was determined prior to each trial. Second, in our locomotion trials, we attempted to differentiate between the effect of travel speed versus snow conditions on heart rate by first conducting a series of tests on a hard surface lacking snow (i.e., a plowed road) at varying speeds. We counted all heart pulses for two-thirds of the trials (62/94) and estimated mean heart rate for each remaining trial by sampling three 30-s bouts (if pulse rates were fast and thus difficult to count). Third, we conducted trials in a variety of snow conditions by walking dogs at varying speeds and estimating mean heart rate by either counting all pulses or systematically subsampling three 30-s bouts during a trial. All pulse rates are reported on a per minute basis.

Snow-tracking of free-ranging coyotes

We snow-tracked coyotes in southeastern Quebec during December 1995 – March 1996 and January–March 1998. During early morning, we monitored the study area either in a truck or on snowmobiles in search of fresh (<12 h old) coyote tracks. Once detected, we back-tracked coyote tracks on snowshoes while measuring tracked distances using a hip-chain. Every 50 m, we measured mean coyote track sinking depth, snow depth and snow hardness on the trail, and snow depth and hardness 1 m off the trail (see Murray and Boutin 1991). Snow hardness was measured using a penetrometer designed to mimic the pressure exerted by a coyote foot in snow. The penetrometer consisted of a copper pipe partially filled with lead (length 60.3 cm, diameter 5.2 cm, mass 2811 g); preliminary trials revealed that across a range of snow conditions, dropping the penetrometer from 10 cm above the snow surface yielded sinking depths comparable with that of coyote tracks. Because travel on modified snow such as preformed trails could constitute an important behaviour allowing for minimization of energy expenditures by coyotes, we also estimated the length (metres) of coyote travel on modified snow and classified such movements into one of three categories: anthropogenic (snowmobile trails, other), animal (snowshoe hare (*Lepus americanus*), coyote, other species), and frozen waterways. Because use of modified snow surface was expressed in terms of proportion of the total distance tracked, we obtained the proportion of distance travelled in fresh snow by difference.

During winters 1995–1996 and 1997–1998, we monitored snow depth and hardness using a permanent snow station located in the Pohénégamook white-tailed deer wintering area (Dumont et al. 2000). In 1996–1997, we further compared snow depth and hardness between forest and rural landscapes using 12 snow stations located in forest stands. Every 2 weeks, we measured snow depth and hardness in each forest stand at five points spaced at 3-m intervals along a straight line.

We attempted to estimate energy conservation by coyotes, as determined by their observed behaviours while snow-tracking, by predicting heart rates under a range of snow conditions observed in the field; we used results from regression models derived from our assessment of costs of locomotion in dogs to help quantify the costs associated with travel in snow by coyotes. Although travel speed is seldom measured directly, movement rates as inferred from consecutive telemetry locations suggest that coyotes typically travel at speeds ranging from 1 to 5 km/h (Tremblay et al. 1998; Chamberlain et al. 2000; Kitchen et al. 2000; Grinder and Krausman 2001); we thus used this range when calculating our estimates.

Statistical analysis

In a preliminary analysis, we used linear regression with individual dog as a fixed factor (Proc GLM, SAS Institute Inc. 1999) to analyse the various relationships between dog heart rate and snow conditions, environmental conditions, and travel speed. Qualitative inspection of the plots generated by each of these regressions was used to determine the nature of relationships; we found that heart rate varied curvilinearly with sinking depth, and thus, we added a quadratic term to model heart rate when considering sinking depth in the snow. We computed general models by adjusting a random coefficient model using dogs as a random factor (Laird and Ware 1982; Rutter and Elashoff 1994; Proc Mixed, SAS Institute Inc. 1999). We log transformed heart rates to normalize residuals whenever necessary.

We determined if the relative utilization by coyotes of modified snow surfaces changed with respect to year (two), month (three), and landscape (two) using MANOVA (Proc GLM, SAS Institute Inc. 1999). This test was followed by an ANOVA on each snow category (six) to determine if utilization varied with respect to the main factors and their interactions; we conducted ANOVA on rank rather than raw data because we could not normalize residuals. We contrasted snow depth and snow hardness between the landscape during winter 1996–1997 using repeated-measures ANOVA, with habitat type (conifer, deciduous) and landscape as between-subject factors and sampling week (seven) as the within-subject factor (Proc Mixed, SAS Institute Inc. 1999). We evaluated the performance of the penetrometer by comparing its measurements with sinking depths of coyotes in the two landscapes, using linear regression with landscape as a dummy variable (Proc REG, SAS Institute Inc. 1999), and tested for differences between penetrometer readings on and off track and between sinking depths of coyotes by paired *t* tests.

Results

Modelling canid heart rate

The resting heart rate of the three domestic dogs was similar ($F_{[2,1]} = 0.66$, $P = 0.52$), with heart rates generally 72.4 ± 1.0 (mean ± SE) beats/min. Air temperature (range –25 to +3 °C) had a slight negative effect on recorded heart beats per minute (ln(heart rate) = 4.282 – 0.006(temperature); df = 34, $P < 0.0001$, $R^2 = 0.15$). The adjusted regression model thus estimated roughly a 0.6% increase in resting heart rate for each degree of drop in temperature.

When walking on a hard surface lacking snow, travel speed (range 1.5–11.3 km/h) had a substantive effect on dog heart rates (heart rate = 138.8 + 5.8(speed); df = 89, $P < 0.0001$, $R^2 = 0.24$), and such changes were consistent among animals (travel speed × dog interaction; $F_{[2,83]} = 0.24$, $P = 0.79$). On average, dog heart rate increased by 5.8 beats/min

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(~8% of resting heart rate) for every 1 km/h increase in travel speed.

In trials conducted in snow, dog sinking depth ranged between 1 and 35 cm, and animals travelled at speeds ranging from 1.6 to 9.4 km/h. When considering dog as a fixed factor, heart rate was more closely related to sinking depth (centimetres) (R^2 = 0.53) than travel speed (kilometres per hour) (R^2 = 0.12). Addition of a quadratic term to sinking depth and its interaction with dog improved the fit (R^2 = 0.59). The final model included sinking depth, its squared value, and travel speed (ln(heart rate) = 4.870 + 0.047(travel speed) – 0.003(sinking depth) + 0.007(sinking depth)^2; df = 284, P < 0.0001); considering dog as a random factor reduced R^2 to 0.55.

Snow-tracking of free-ranging coyotes

During the first winter of snow-tracking coyotes (1995–1996), snow conditions were notably mild for our study area. In contrast, snow conditions were more severe during the second winter (1997–1998), with greater (~150%) snowfall and much later persistence of powdered snow than in winter 1995–1996 (Fig. 1). Thus, although we did not plan for such conditions, they provided a nice contrast to examine response to snow conditions by coyotes.

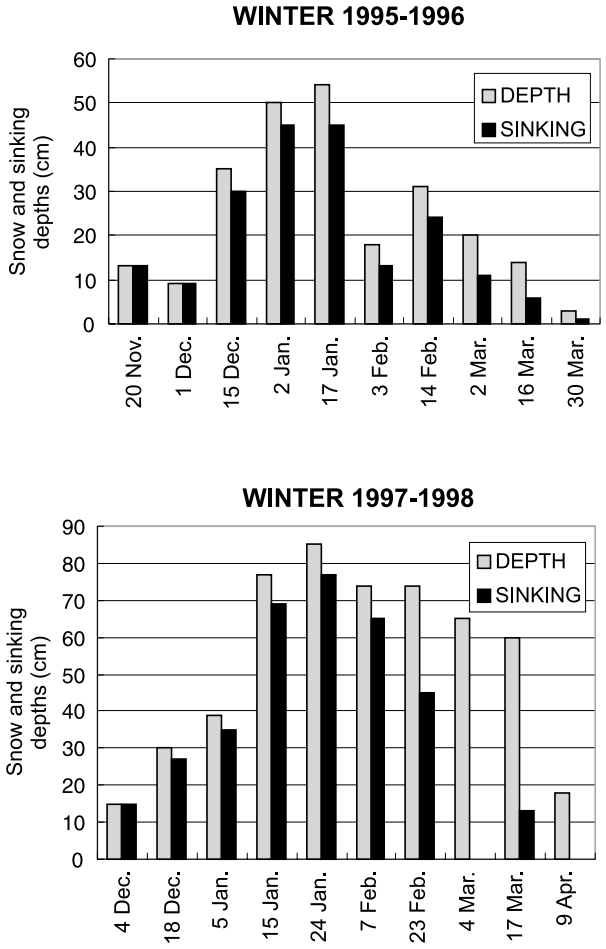
Our snow-tracking efforts revealed that coyotes responded to local snow conditions by travelling more on hardened snow during the harsh winter in both forested (48% vs. 28% for harsh and mild winter, respectively) and rural (63% vs. 17%) landscapes (Table 1). Overall snow conditions used by coyotes differed between the two winters (MANOVA, $F_{[6,62]}$ = 2.97, P = 0.01). Coyotes increased their use of snowmobile and animal trails in 1997–1998 compared with 1995–1996. Rural coyotes consistently travelled more in hare tracks than their forest counterparts, although infrequently (Table 1).

Our penetrometer closely mimicked sinking depth of coyotes in the rural landscape (y intercept = 0, slope = 1; $F_{[2,82]}$ = 0.64, P = 0.53, R^2 = 0.79). The fit was poorer in the forest landscape with the slope (0.69) deviating from 1 and the y intercept (4.0) from 0 ($F_{[2,82]}$ = 6.89, P < 0.01, R^2 = 0.46). The penetrometer tended to overestimate sinking depths <6 cm and underestimate those above. Within the range of sinking depths encountered in both landscapes, on-track measurements of the penetrometer did not differ from coyote sinking depths (P > 0.05 in both landscapes) (Table 2).

Coyotes selected shallower snow depth in both landscapes, depth being on average 3 cm shallower on track than 1 m off track (t = 2.41, P = 0.02). They also used harder snow as indicated by penetrometer sinking depths that were 2.3 cm deeper off track than on track (t = 6.31, P < 0.01) (Table 2).

Based on the regression models developed with dogs, we evaluated how heart rate changed as a result of locomotion in snow. At 1 km/h, the heart rate of dogs was 136, 143, and 149 pulses/min for hard surface, on track in the snow, and off track in the snow, respectively. Thus, locomotion in snow increased heart rate by 5% (143 vs. 136 pulses/min) compared with locomotion on hard surfaces. Fine-scale selection of harder snow by coyotes likely yielded energy savings of similar magnitude (143 vs. 149 pulses/min). At higher travel speed (5 km/h), the heart rate of dogs was 165, 173, and 180 pulses/min for hard surface, on track in the snow, and off track in the snow, respectively. Thus, increasing travel speed from 1 to 5 km/h increased heart rate by 20% (e.g., 136 vs. 165 pulses/min for slow versus fast speed, respectively), regardless of snow conditions.

Fig. 1. Snow and sinking depth measured in the permanent Pohénégamook deer wintering area during the winters of 1995–1996 and 1997–1998. The compaction gauge used mimics coyote (*Canis latrans*) sinking depth.



Discussion

Snow exerts a strong effect on the locomotory abilities of terrestrial animals living at northern latitudes and higher altitudes. For carnivores, the ability to travel in snow is critical to enable the hunting and capture of prey. Using three domestic dogs as models, we estimated that coyotes likely experience a 4%–6% increase in energy expenditures when travelling in snow compared with travel on hard surfaces. Furthermore, sinking depth increased locomotory costs exponentially, as we predicted based on similar data for ungulates (Parker et al. 1984). When we compared our results from captive dogs with behavioural selection of snow attributes in free-ranging coyotes, we observed numerous behavioural adaptations to snow conditions. First, coyotes

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Table 1. Percentage (±SE) of distance travelled by coyotes (*Canis latrans*) on modified snow in forest and rural areas according to the types of perturbation that hardened the snow surface, southeastern Quebec, winters of 1995–1996 and 1997–1998.

	1995–1996 (mild winter)		1997–1998 (harsh winter)		ANOVA *P* values		
	Forest (n = 26)	Rural (n = 13)	Forest (n = 23)	Rural (n = 17)	Landscape	Year	Landscape × year
Human sources							
Snowmobile trails	7 (5)	0 (0)	15 (6)	10 (6)	0.13	0.03*	0.99
Other[a]	2 (2)	0 (0)	5 (2)	0 (0)	0.14	0.31	0.93
Animal sources							
Hare tracks	2 (1)	4 (1)	2 (1)	6 (3)	0.02*	0.32	0.33
Coyote tracks	13 (5)	8 (3)	22 (6)	38 (10)	0.99	0.01*	0.58
Other species	2 (1)	4 (1)	2 (1)	6 (3)	0.06	0.04*	<0.001*
Frozen water bodies	2 (1)	1 (1)	2 (1)	3 (2)	0.46	0.40	0.80
All modified snow	28	17	48	63			

Note: The probability that dependent variables varied according to years, landscapes, or their interaction is also presented. An asterisk indicates statistical significance.

[a]Paved or gravel roads, railroads, snowshoe tracks.

Table 2. Mean (±SE) sinking depth of forest and rural coyotes walking in the snow during the winters of 1995–1996 and 1997–1998 and snow depth and measurements of the penetrometer on track and 1 m off track.

	On-track measurements (cm)			Off-track measurements (cm)	
	Sinking depth of track	Penetrometer	Snow depth	Penetrometer	Snow depth
Forest (n = 51)	10.2 (0.6)	11.1 (0.6)	56.9 (2.8)	14.0 (0.7)	60.4 (2.8)
Rural (n = 35)	11.1 (0.9)	11.7 (1.0)	56.1 (3.7)	13.2 (1.0)	58.7 (3.6)

Note: n indicates the number of coyote tracks sampled.

routinely relied on snow hardened by other animal species and humans (also see Murray and Boutin 1991; O'Donoghue et al. 1998), and this selection was stronger during a harsh winter than during a mild winter. Moreover, coyotes also selected areas where snow cover was shallower and snow hardness greater. Selection of snow conditions that reduce sinking depth likely represents an adaptation by free-ranging coyotes living in deep-snow environments to reduce energy expenditure related to locomotion.

Modelling costs of locomotion in snow for canids

Travel speed increased heart rate linearly in dogs. The regression model explained 24% of the variance in the data set, estimating an average increment of 6 pulses/min for each increment of 1 km/h in travelling speed. In mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and caribou (*Rangifer tarandus*), energy expenditure also exhibits a clear linear relationship with travelling speed (Parker et al. 1984; Fancy and White 1987). When considered in the context of the above studies, our results suggest that the linear relationship between energy expenditure and travel speed may be common among terrestrial mammals.

Our experiments with domestic dogs clearly showed an exponential relationship between heart rate and sinking depth, a phenomenon similar to that described for ungulates such as white-tailed deer, mule deer, elk, and caribou (Parker et al. 1984; Fancy and White 1987). This implies that common biomechanics may apply to both canids and cervids; in cervids, locomotory costs double when sinking depth represents between 50% and 60% of brisket height (Fancy and White 1987). We did not measure such a variable in dogs or coyotes, but heart rate would double at a sink depth of 33 cm when walking at 1 km/h according to our model. Given substantial differences in leg morphology, it would be interesting to determine if canids can better tolerate relative sinking depth in the snow than can cervids. Differences in energetic tolerance to deep snow may help understand the increased vulnerability of small ungulates such as white-tailed deer to coyote predation during winters of deep snow.

Travel speed, sinking depth, and range expansion in coyotes

Our modelling with dogs suggests that canids endure a high cost when accelerating their pace. Indeed, heart rate increased by 20% with changes in travel speed from 1 to 5 km/h, which corresponds to the same energy expenditure as sinking 19 cm in the snow when walking at 1 km/h. This may explain why all studies monitoring travel speed of coyotes resulted in estimates around 1 km/h or less (Andelt and Gipson 1979; Holzman et al. 1992; Tremblay et al. 1998; Chamberlain et al. 2000; Kitchen et al. 2000; Grinder and Krausman 2001). Other extremely mobile carnivores such as polar bears (*Ursus maritimus*) also move at speeds averaging 1 km/h (Amstrup et al. 2001). We propose that locomotion at slow speed in cursorial carnivores like coyotes has been selected for because predators must range over large areas to increase their chances of successful encounters with prey (predator pass-along hypothesis, Lima 2002), and fast travel would be too prohibitive to sustain.

Snow exacerbates locomotion cost, which is critical for the energy budget of cursorial predators. On average, heart rate increased by ~5% when domestic dogs walked over snow rather than on a hard surface, and in the wild, coyotes reduced energy expenditures by selecting hardened snow

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such as snowmobile or animal trails when travelling. The effects of sinking depth are compounded by travel speed, suggesting that chases at high speed through soft snow are extremely prohibitive for coyotes. This would explain why coyotes use ambush to capture hares over snow and make shorter pursuits than the large-footed Canada lynx (Murray and Boutin 1991; O'Donoghue et al. 1998).

Our models can allow a rough estimate of the fraction that locomotory costs represented in the field metabolic rate of coyotes in winter, assuming 10.9 km travelled per day (Andelt and Gibson 1979) at a speed of 1 km/h and a resting heart rate of 75 pulses/min. Locomotion would make up 27% and 29% of field metabolic rate when moving on a hard surface and in average snow conditions, respectively. In swift fox (*Vulpes velox*) and kit fox (*Vulpes macrotis*), locomotory costs averaged 21% of field metabolic rate when estimated with doubly labelled water (Covell et al. 1996; Girard 2001). Our models suggest that locomotion remains very costly in coyotes, as it is in foxes (Covell et al. 1996). The energetic savings of travelling on plowed roads, hare trails, and snowmobile trails probably enable coyotes to occupy marginal forest habitats (Tremblay et al. 1998; Crête et al. 2001; Richer et al. 2002) and may have facilitated their range expansion in northeastern North America.

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