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The influence of snow on lynx and coyote movements: does morphology affect behavior?

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Summary. We studied sympatric lynx *(Lynx canadensis)* and coyotes *(Canis latrans)* to assess how morphological disadvantages to locomotion over snow affected movement patterns. Both species are of similar size and mass, but the feet of lynx are much larger, and coyotes were found to have 4.1–8.8 times the foot-load (ratio of body mass to foot area) of lynx. This resulted in greater mean sinking depths of coyote limbs, although the magnitude of the difference was less than that in foot-load. Coyotes exhibited stronger use of behavioral patterns that reduced negative effects of snow on movements. Coyotes were most abundant at low elevations where snow was shallow, whereas lynx were mostly at higher elevations. Coyotes also used areas at both elevations where snow was shallower than average, while lynx used areas where snow was deeper. Further, both species used travel routes where snow was shallower than it was near the track. Coyotes traveled on harder snow and used trails more frequently, thereby tending to reduce sinking depths to those similar to lynx. The behavioral repertoire of coyotes reduced the morphological advantage of large feet possessed by lynx; however, overall sinking depths were still greater in coyotes. Snowshoe hares *(Lepus americanus)* were the main prey of both species, and their foot-load was less than that of either predator. Hare kills by coyotes occurred after fewer bounds than did those by lynx, and the large difference between foot-loads of both species of predators may have forced coyotes to ambush rather than chase hares, as did lynx.

Key words: Lynx – Coyote – Snow – Morphology – Behavior

Snow may hinder the movements of animals, and its effect on locomotion depends on snow depth and hardness, as well as animal height, weight, and foot morphology (Formozov 1946). Mammals may also alter behavior to offset the disadvantages of moving through snow. Telfer and Kelsall (1984) described behavioral adaptations to snow shown by different species of ungulates, but no study has yet collected empirical data on the use of behaviors to reduce the negative effects of snow on movements.

We examined traits (either morphological or behavioral), which appeared to alleviate adverse effects of snow on animal locomotion. Chest height and foot-load (ratio of body mass to foot surface area), have been considered relevant to locomotion in snow (Telfer and Kelsall 1979), whereas behavioral advantages to snow may consist of techniques of locomotion that facilitate movement, use of favorable snow conditions, and specific foraging tactics that reduce deleterious effects of snow on food acquisition (Telfer and Kelsall 1984).

Lynx *(Lynx canadensis)* and coyotes *(Canis latrans)* are mid-sized carnivores that range where snowcover occurs (Quinn and Parker 1987, Voigt and Berg 1987). Lynx morphology is well suited for travel in snow because of a low foot-load (Parker et al. 1983) and relatively long limbs, whereas coyotes appear disadvantaged in snow because of their high foot-load (Todd and Keith 1976). This study examines differences in morphological advantages to snow between the species, and then measures the actual physical disadvantages, as determined by sinking depth. One possible scenario is that morphology translates into direct disadvantages, leading to one of the following outcomes; 1) Coyotes compensate through behavior that enables them to employ similar snow to that used by lynx. 2) Coyotes compensate by using snow of different depth and hardness than that used by lynx. 3) Coyotes do not compensate, but this does not lead to differential use of snow conditions. Alternatively, morphological differences between coyotes and lynx may not disadvantage the former, and use of snow by coyotes is unaffected by footload.

Study area

Lynx and coyotes were studied on 175 km^2 within a valley in southwestern Yukon (61° N, 138° W), and we

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worked from the base of the valley (830 m) to an elevation of 1169 m. Snowfall increased with elevation, and total snow accumulation during the year of study averaged 65 cm, which was typical for that site (Krebs et al. 1986). Based on locations of radiocollared animals and associated tracks, we estimated that at least 16 lynx and 12 coyotes resided in the area during winter 1988–89. Snowshoe hares *(Lepus americanus)* were an important prey for both species; mean hare density on the site was 3.4 ± 0.7 (SD) hares per hectare (C.J. Krebs, unpubl.).

Method

Morphology

Skinned lynx and coyote carcasses were obtained from trappers during winter 1988–89; all lynx had been trapped, whereas all coyotes were shot. We recorded weight, sex, and age class (subadult or adult, according to skull size and tooth wear) of each lynx. Coyote age was not estimated.

Chest height was measured from the distal tip of toes to midline of the brisket (Kelsall 1969). Foot-load ratio was calculated by dividing carcass weight by the total area of the 4 unskinned paws. Paw area was obtained by placing the sole of a fore and hindlimb on paper, tracing the contour, and measuring with a digital planimeter. All toes were compressed against each other, and the claws of lynx were retracted before tracing. Parker et al. (1983) found that skinned lynx carcasses weighed 10% less than fresh carcasses; we assumed the same reduction for coyotes.

We obtained hares by snaring during December 1989. Hares were skinned, weighed, sex was determined, and foot-load of each carcass was measured, as described above. Skinning reduced the weight of carcasses by 10%.

General snow conditions

Mean snow depth and snow hardness (measured by the sinking depth of a penetrometer, see below) representative of the entire area were obtained at 16 sites near a 30-km snowmobile trail along the valley floor. We divided the sites by elevation into 9 low (837–887 m) and 7 high (935–1035 m). Each site was visited 8 times during the winter, and 4 measures were taken within a 1 m range, and averaged.

Track counts

To index relative abundance of lynx and coyotes at different elevations, we recorded the location of all lynx and coyote crossings of a network of snowmobile trails, between November 1988 and April 1989. Tracks were grouped into those occurring at high (>900 m) and low (<900 m) elevations. Tracks were usually counted up to 8 days after a snowfall, and an average of 30 km of trails were checked each day.

Predator response to snow conditions

Between November 1988 and March 1989 we followed fresh predator tracks in snow (208 km for lynx and 188 km for coyote). Tracking was undertaken daily after snowfall, and continued until fresh tracks could no longer be distinguished from older trails (usually 7–10 days). Distances were estimated by converting number of paces to kilometers (Parker 1981).

To measure predator response to snow conditions, we made the following measurements as the beginning, end, and at every 500 paces (approximately 600 m) of a tracking session. At each site we measured 1) snow depth between predator steps (on-track) and 1 m perpendicular to the track (off-track), and 2) sinking depth of a single predator step (from top of snow to top of imprint). In addition, we obtained an index of snow hardness by measuring the sinking depth of a penetrometer (lead filled soft-drink can, 150 g) that was dropped from a height of 50 cm above the snow surface. When dropped from a height of 50 cm, penetrometer sinking depth was intermediate to the step sinking depth of lynx and coyote. The penetrometer was dropped between steps of the animal being tracked (on-track) and 1 m off-track. If the animal being tracked was following the track of another animal (trail), on-track penetrometer sinking depth was obtained on the trail itself. Percent distance that a tracked animal spent on trails was estimated in each block (500 paces).

Predator chases of prey

All chases of prey were recorded as encountered during a tracking session. We noted the prey species chased, number of bounds by the predator, chase outcome (successful or unsuccessful), and snow depth and penetrometer sinking depth on- and off-track. We also recorded sites where predators appeared to have scavenged food. We noted when chases or scavenging occurred on trails.

Track identification

Coyote and red fox *(Vulpes vulpes)* tracks appeared similar in southwestern Yukon. We identified coyote tracks by a combination of track size, known home ranges of radio-collared animals, locations of visual sightings, and knowledge of spatial exclusion of foxes from coyote areas (Voigt and Earle 1983; Harrison et al. 1989).

Statistical analyses

We used ANOVA, Stepwise Linear Regression, G-test (with Williams' correction), and Student t-test (Sokal and Rohlf 1981) to analyse data, and P-values less than 0.05 were considered significant. To maximize independence between observations, a tracking session was considered the experimental unit. However, when we compared snow conditions on-track to those off-track, we did not pool data from an entire session. This may have violated the assumption of independence, but all pairs of observations were 500 paces apart, which reduced the likelihood of interdependence between observations. Data obtained on percent of movement distances spent on trails were normalized with an arcsin of the square-root transformation (Krebs 1989). We divided the study period into 18- to 22-day intervals.

Results

Morphology

Foot-loading differed significantly among lynx ($n = 58$), coyotes ($n = 10$), and snowshoe hares ($n = 21$) (one-way ANOVA; $F = 354.6$; $df = 2{,}86$; $P < 0.001$). Mean foot-load of coyotes was 3.4 to 8.8 times greater than that of lynx, and 5.8 to 8.1 times greater than that of snowshoe hares (Table 1). Subadult lynx had a lower foot-load than did adults (two-way ANOVA; $F = 58.88$; $df = 1{,}54$; $P < 0.001$), whereas similar foot-loads characterized males versus females among both lynx ($F = 3.13$; $df = 1{,}54$; $P = 0.082$) and coyotes ($t = 2.10$; $df = 8$; $P = 0.069$). Mean chest height did not differ between these 2 predator species

Table 1. Mean mass, total foot area, foot-load, and shoulder height of skinned lynx, coyote, and snowshoe hare carcasses. Sample sizes in parentheses. M = male, F = female

Species	Mass (kg) Mean ± SD		Foot Area (cm^2) Mean ± SD		Foot-Load (g/cm^2) Mean ± SD		Chest Height (cm) Mean ± SD	
Lynx								
Adult								
M (30)	8.99	1.19	286.4	28.4	31.6	5.2	46.7	10.4
F (15)	7.08	1.36	275.6	27.7	25.9	5.5	42.2	6.3
Subadult								
M (7)	4.03	0.50	262.9	35.1	15.6	4.0	38.6	4.9
F (6)	4.32	0.50	265.0	23.8	16.5	2.9	35.5	5.5
Coyote								
M (5)	10.32	1.16	77.0	10.7	136.8	30.9	43.1	2.8
F (5)	8.00	0.58	75.8	5.2	106.0	11.1	42.3	4.0
Snowshoe hare								
M (12)	1.60	0.13	92.2	10.5	16.8	1.4	–	
F (9)	1.65	0.15	87.9	6.8	18.4	1.4	–	

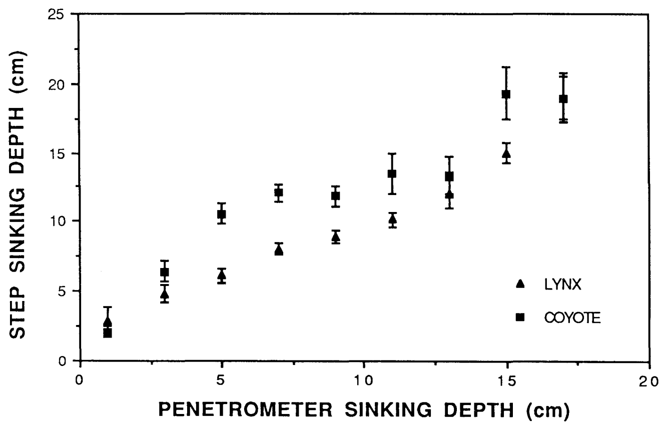

Fig. 1. Mean (± SE) step sinking depths of lynx and coyotes as a function of penetrometer sinking depth. Consecutive penetrometer sinking depths have been pooled in increments of 2

(two-way ANOVA; F = 0.000; df = 1,64; $P = 0.995$), nor were differences detected between chest height of males and females (F = 0.90; df = 1,64; $P = 0.346$), though adult lynx had higher chests than subadults (t = 3.03; df = 56; $P = 0.004$). Mean foot-load of female hares was higher than that of males (t = 2.54; df = 19; $P = 0.020$).

Physical disadvantages

Morphological differences between lynx and coyotes caused coyotes to sink deeper than lynx at specific levels of snow hardness (two-way ANOVA; F = 28.39; df = 1,196; $P < 0.001$; Fig. 1). However, this difference was never more than 4 cm (75% of mean lynx step sinking depth), which was less than the magnitude of the difference in foot-load between the two species. Both predators sank deeper as snow hardness decreased (F = 26.48; df = 6,196; $P < 0.001$), but the rate of change in sinking depth was different for lynx than for coyotes (species × penetrometer sinking depth; F = 3.24; df = 6,196; $P = 0.005$). Rarely did sinking depths of either species exceed 20 cm, and this depth was much less than chest height of either predator.

Influence of snow on step sinking depth

We examined the influence of snow depth and snow hardness on sinking depths of lynx and coyotes. With lynx, snow hardness affected sinking depth (Stepwise Linear Regression: $R^2 = 0.44$; df = 1; $P < 0.001$), whereas snow depth had no effect on sinking depth ($R^2 = 0$; df = 1; $P > 0.015$). With coyotes, both snow depth ($R^2 = 0.03$; df = 2; $P < 0.001$) and snow hardness ($R^2 = 0.37$; df = 2; $P < 0.001$) influenced sinking depth. Thus, both attributes of snow may have affected sinking depth, and we examined their influence on lynx and coyote movements.

Use of elevation

Coyotes used low elevations more than did lynx (G = 44.67; df = 1; $P < 0.001$): 64% ($n = 104$) of coyote snowmobile trail crossings were located at low elevations compared to only 26% of crossings by lynx ($n = 250$). Snow tended to be shallower at low elevations (two-way ANOVA; F = 66.63; df = 1,112; $P < 0.001$; Fig. 2): mean depths for winter 1988–89 were 39.8 ± 13.8 cm ($n = 72$) at low elevations, versus 54.5 ± 16.2 cm ($n = 56$) at high ones.

Snow depth on predator tracks

Coyote tracks were generally on shallower snow than were those of lynx (three-way ANOVA; F = 15.71; df = 1,293; $P < 0.001$). In general, snow depth at the representative snow-measurement sites was intermediate to that of coyote and lynx tracks (Fig. 2). Snow depth on

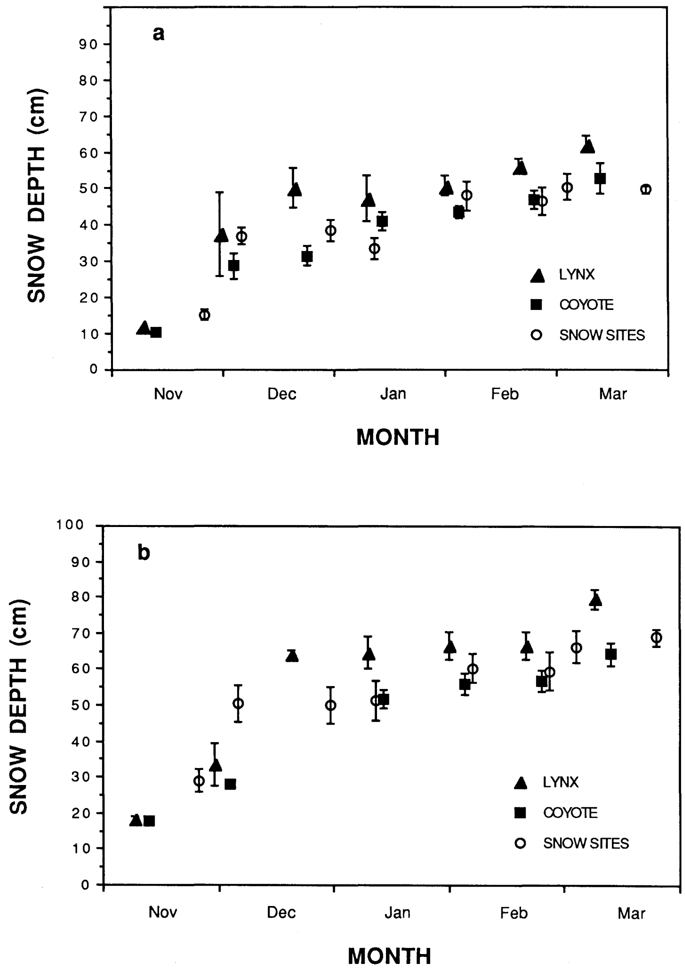

Fig. 2 a, b. Mean (±SE) snow depths on lynx and coyote tracks and at snow sites, at (**a**) low and (**b**) high elevations

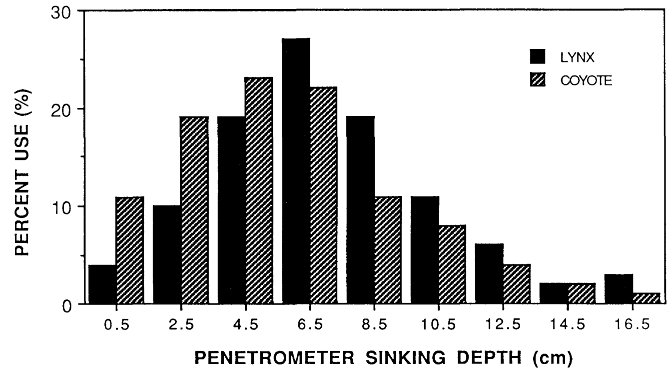

Fig. 3. Percent of surveyed lynx and coyote trail sites having different penetrometer sinking depths. Consecutive penetrometer sinking depths have been pooled in increments of 2

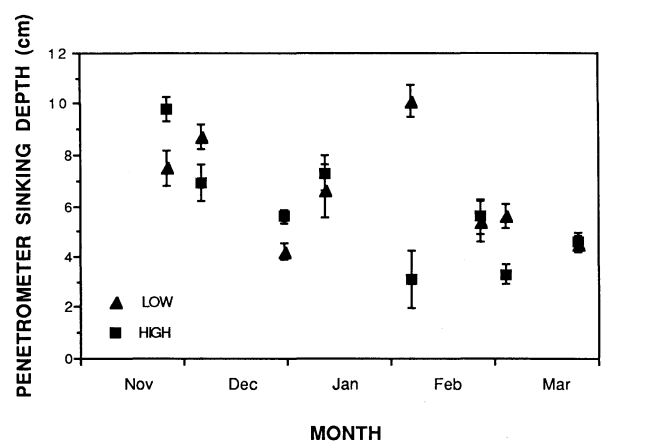

Fig. 4. Mean (±SE) penetrometer sinking depths on 8 days during winter 1988–89 at low and high elevations

tracks of both species was shallower at low elevations (F = 19.43; df = 1,293; $P < 0.001$), and snow on tracks became deeper as winter progressed (F = 37.11; df = 6,293; $P < 0.001$).

Travel routes

Both predators travelled where snow was shallower on-track than it was 1 m off-track. Mean snow depth on lynx tracks averaged 2.2 ± 8.7 cm less than it was off-track ($n = 460$; paired-t = 5.41; $P < 0.001$), whereas for coyotes, snow depth on-track was 3.1 ± 10.1 cm less than it was off-track ($n = 469$; paired-t = 6.73; $P < 0.001$). The shallow snow recorded on predator tracks was not entirely caused by the use of trails formerly compacted by other animals. When they were on untracked snow only, both lynx (paired-t = 3.55; df = 264; $P < 0.001$) and coyotes (paired-t = 4.74; df = 246; $P < 0.001$) employed snow that was shallower than it was 1 m off-track. In this case, mean difference between on-track and off-track snow depth was 1.9 ± 0.5 ($n = 265$) for lynx, and 2.5 ± 0.6 cm ($n = 247$) for coyotes.

Snow hardness on predator tracks

Snow used by coyotes was harder than that used by lynx (three-way ANOVA: F = 10.16; df = 1,293; $P = 0.002$; Fig. 3). Mean penetrometer sinking depth on lynx tracks was 8.5 ± 1.3 cm ($n = 136$), while penetrometer sinking depth on those of coyote was 6.7 ± 1.8 cm ($n = 185$), and these values were similar to those obtained throughout the winter at the snow sites (Fig. 4). Elevation did not affect snow hardness on predator tracks (F = 0.07; df = 1,293; $P = 0.798$), but snow hardened on tracks of both species as winter progressed (F = 8.07; df = 6,293; $P < 0.001$). Similarly, snow generally became harder in the study site as winter progressed (two-way ANOVA; F = 10.11; df = 7,112; $P < 0.001$). Snow hardness differed between elevations (F = 6.2; df = 1,112; $P = 0.014$), though neither level had consistently harder snow than the other (elevation x time; F = 10.11; df = 7,112; $P < 0.001$).

Travel routes

Snow was harder on tracks of both species than it was nearby. The mean penetrometer sinking depth on lynx

Table 2. Mean proportions of a tracking session in which single lynx and coyotes used trails. Number of tracking sessions are 102 for lynx and 144 for coyote

Trail type	Lynx Mean ± SD		Coyote Mean ± SD	
Snowshoe hare	31.3	23.7	34.3	27.6
Lynx	2.60	5.93	6.87	20.4
Coyote	0.41	2.21	2.42	6.85
Wolf	0.28	1.57	1.86	8.67
Wolverine	0.59	3.62	0.96	4.75
Moose	0.37	1.61	0.89	5.15
Human-snowshoe	0.31	1.59	0.73	5.10
Human-road	0.59	2.18	3.60	15.5
Total	36.5	25.1	51.6	30.2

Table 3. Snow depths, penetrometer sinking depths, and number of bounds taken by lynx and coyotes, according to success of hare chases

Characteristic	Lynx			Coyote		
	Mean ± SD		(*n*)	Mean ± SD		(*n*)
Snow depth (cm)						
successful	55.2	18.2	(33)	40.9	23.6	(24)
unsuccessful	63.1	20.8	(19)	44.0	29.4	(20)
Penetrometer sinking depth (cm)						
successful	7.1	3.0	(20)	5.1	3.1	(19)
unsuccessful	7.9	2.7	(30)	6.6	2.9	(11)
Bounds in the Chase (*n*)						
successful	2.21	1.89	(33)	0.48	1.05	(25)
unsuccessful	5.92	3.46	(20)	4.35	2.85	(20)

tracks was 1.0 ± 2.7 cm less than it was off-track ($n = 454$; paired-t = 8.04; $P < 0.001$), whereas for coyotes mean penetrometer sinking depth was 1.7 ± 3.3 cm less on-track than off-track ($n = 440$; paired-t = 10.88; $P < 0.001$). The use of hard-snow travel routes by predators was not entirely due to travel on trails hardened by other animals, as when they were on untracked snow only, hardness on both lynx (paired-t = 2.56; df = 244; $P < 0.001$) and coyote (paired-t = 4.74; df = 246; $P < 0.001$) tracks was lower than it was off-track. Mean difference between on-track and off-track penetrometer sinking depth in this case was 0.4 ± 0.2 cm ($n = 265$) for lynx, and 0.7 ± 0.2 cm ($n = 247$) for coyotes.

Trail use

We examined the difference in snow hardness when predators travelled on untracked snow versus trails. Though snow hardness was similar between untracked snow and trails (two-way ANOVA: F = 0.99; df = 1,156; $P = 0.321$); snow used by coyotes was generally harder than that used by lynx (F = 7.87; df = 1,156; $P = 0.006$). When on untracked snow, mean penetrometer sinking depth was 7.0 ± 3.3 cm ($n = 50$) on lynx tracks, and 5.8 ± 2.9 cm ($n = 58$) on those of coyotes. Mean penetrometer sinking depth was 4.9 ± 3.4 cm ($n = 29$) when lynx were on trails, and 4.9 ± 3.0 ($n = 23$) when coyotes used trails. The higher mean penetrometer sinking depth on untracked snow than on trails in both species, clearly demonstrates the advantage of using trails to reduce their sinking depth.

Use of animal trails by coyotes (52% of total distance tracked) exceeded that (37%) by lynx (t = 3.69; df = 196; $P < 0.001$). Both used hare trails similarly, but coyotes used other trails more frequently (Table 2).

Overall sinking depth

Coyotes used shallower and harder snow than did lynx, and travelled greater distances on trails, but on average still sank more deeply: 9.5 ± 4.4 cm ($n = 186$) versus 7.7 ± 3.2 cm ($n = 144$) (t = 2.52; df = 319; $P = 0.012$). This suggests that the strong behavioral patterns demonstrated by coyotes did not override the strong morphological and moderate behavioral traits expressed by lynx.

Predator chases

All successful, and most unsuccessful, chases by lynx and coyotes were of snowshoe hare [lynx successful = 100% ($n = 32$), lynx unsuccessful = 92% ($n = 52$); coyote successful = 100% ($n = 25$), coyote unsuccessful = 83% ($n = 24$)]. Given the differences in foot-load of predators versus that of hare, we examined the characteristics of snow where hares were chased. Snow was both shallower (two-way ANOVA: F = 11.51; df = 1,87; $P = 0.001$), and harder (two-way ANOVA: F = 5.51; df = 1,75; $P = 0.022$) at the site of coyote chases than at those by lynx (Table 3). No differences were detected in snow depth (F = 0.023; df = 1,87; $P = 0.634$), and hardness (F = 2.91; df = 1,75; $P = 0.092$) at sites of successful versus unsuccessful chases. However, mean snow depths were less and hardness was greater at successful chases than at unsuccessful ones. This suggests that snow may, to a certain extent, influence the outcome of a chase between either predator and a hare. If this is the case, the actual length of a chase in the snow may also have affected hunting success. We found that the number of bounds in the chase was less at coyote chases (two-way ANOVA; F = 10.85; df = 1,127; $P = 0.001$) than at those by lynx, and at successful chases by both species (F = 57.03; df = 1,127; $P < 0.001$).

Forty-five percent ($n = 47$) of sites where coyotes scavenged food occurred while coyotes were on predator trails (10 on coyote trails and 8 on lynx trails). Conversely, only 25% ($n = 20$) of lynx scavenging bouts occurred while along trails, all having been made by lynx. The disproportionately high occurrence of scavenging by coyotes while travelling on predator trails versus their actual use of these, suggests that use of such routes was not strictly to decrease sinking depth, but also to obtain additional food.

Discussion

Advantages to snow

Coyotes are thought to have originated in areas where snowcover is negligible, and to have colonized the boreal forest only in the last century (Gier 1975; Nowak 1979). In contrast, lynx were present in pre-glacial times (Repenning 1967). Coyotes in the Yukon have a foot-load that is similar to that of coyotes from central Alberta (Telfer and Kelsall 1984), but one much greater than that of lynx.

As neither predator ever sank to its chest, our results suggest that decrease in foot-load is a major avenue of morphological advantage to snow. Yet despite a large difference in foot-load between lynx and coyotes, the magnitude of differences in sinking depth was less. The greater use of shallow and hard snow areas, as well as trails made by other animals, enabled coyotes to compensate for their apparent morphological disadvantage. On hard snow, the sinking depth of coyote feet was similar to that of lynx. However, the availability of such snow conditions was limited, and when coyotes were forced to use soft snow they sank deeper than lynx. Overall, snow was more disadvantageous to coyotes than to lynx, and this led to a greater overall sinking depth in the former species.

Keith et al. (1977) proposed that the much greater frequency of hare trails on snow near cyclic peaks, facilitates coyote movement. Our study was conducted near peak hare numbers in southwestern Yukon (C.J. Krebs, unpubl.), and we found that the use of hare trails was similar for coyotes and lynx. In contrast, distance travelled on other trails, was higher for coyotes. Though not necessarily a direct adaptation to snow, travelling on predator trails provided coyotes with a supplementary food source through scavenging. Scavenging is common among canids (Kleiman and Eisenberg 1973), and its practice by coyotes was probably not directly in response to the presence of snow. Nevertheless, this type of behavior has been considered as an advantage to snow (Telfer and Kelsall 1984). The amount of food obtained at sites where coyotes scavenged was relatively small (Murray 1991), making the use of predator trails probably not primarily to increase food intake.

Hunting tactics

Foot size of lynx and coyotes may have influenced the hunting tactics employed by each species. If foot-loads were the only consideration, the presence of snow should have benefited hare over both lynx, and coyotes. However, hare susceptibility to predation is more complex than simply the differential between foot-load of predator and prey. The behavioral patterns used by predators to reduce the adverse effects of snow on movements, may have facilitated capture of hares.

Although coyotes are among the fastest carnivores (Bakker 1983), their high foot-load would have slowed them down in snow. Because coyote chases of hare consisted of fewer bounds and were shorter (stride length of both species was similar) than those by lynx, it was perhaps necessary for coyotes to initiate chases at shorter distances. Felids are typically ambush or stalking predators (Kruuk 1986; Sunquist and Sunquist 1989), whereas canids typically run down their prey over long distances (Kleiman and Eisenberg 1973; Bakker 1983). It is therefore possible that snow influenced the hunting tactics used by each species.

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