

The Effect of Snowmobile Trails on Coyote Movements Within Lynx Home Ranges

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ABSTRACT Coyotes (*Canis latrans*) and Canada lynx (*Lynx canadensis*) are sympatric throughout much of the lynx's southern range. Researchers and managers have suggested that the presence of compacted snowmobile trails may allow coyotes to access lynx habitat from which they were previously excluded by deep, unconsolidated snow. This could then allow coyotes to more effectively compete with lynx for snowshoe hares (*Lepus americanus*), the lynx's primary prey. We investigated how coyotes interacted with compacted snowmobile trails by conducting carnivore track surveys and by snow tracking adult coyotes (4 M, 8 F) in areas of western Montana, USA, with both documented lynx presence and recreational snowmobile use. Coyotes remained in lynx habitat having deep snow throughout the winter months. They used compacted snowmobile trails for 7.69% of their travel distance and traveled on them for a median distance of 124 m. Coyotes used compacted forest roads (5.66% of total travel) and uncompacted forest roads (4.62% of total travel) similarly. Coyotes did not travel closer to compacted snowmobile trails than random expectation (coyote $\bar{x}$ distance from compacted trails = 368 m, random expectation = 339 m) and the distance they traveled from these trails did not vary with daily, monthly, or yearly changes in snow supportiveness or depth. However, they strongly selected for naturally shallower and more supportive snow surfaces when traveling off compacted snowmobile trails. Coyotes were primarily scavengers in winter (snowshoe hare kills composed 3% of coyote feed sites) and did not forage closer to compacted snowmobile trails than random expectation. The overall influence of snowmobile trails on coyote movements and foraging success during winter appeared to be minimal on our study area. The results of this study will allow land managers to better assess the effects of snow-compacting activities on coyotes and lynx. (JOURNAL OF WILDLIFE MANAGEMENT 71(5):1409–1418; 2007)

DOI: 10.2193/2005-682

KEY WORDS *Canis latrans*, competition, coyote, lynx, *Lynx canadensis*, recreation, snow compaction, snowmobile, snowshoe hare.

Coyotes have a high foot-load (ratio of body mass to foot area; Murray and Boutin 1991) compared to lynx. This high foot-load makes travel through deep snow more energetically costly to coyotes than to lynx (Crete and Lariviere 2003) and could cause the 2 species to use different winter habitats. Buskirk et al. (2000) suggested that spatial separation between lynx and coyotes due to deep snow might break down if human-caused snow compaction allowed coyotes to access lynx habitat. Parker (1986), Murray et al. (1995), and O'Donoghue et al. (1998a) demonstrated that coyotes may, at times, prey heavily on hares in winter. Increased availability of compacted snowmobile trails might allow coyotes to more successfully hunt hares in high-elevation, deep-snow environments, and persist there year-round, thus significantly decreasing the number of hares available to lynx (Ruediger et al. 2000). Although activities such as skiing, snowshoeing, and snowmobiling all result in compacted snow trails, only snowmobiling is likely to create trail systems of sufficient density and extent to potentially affect predator communities in western Montana, USA.

Interspecific competition may be either interference (the killing or physical displacement of a subordinate competitor) or exploitative (competition for food resources; Case and Gilpin 1974). Coyotes kill bobcats (*Felis rufus*; Anderson 1986, Jackson 1986, Toweill 1986) and, rarely, lynx

(O'Donoghue et al. 1995). However, O'Donoghue et al. (1998a) found no evidence that habitat selection by coyotes and lynx was affected by interference competition. Similarly, none of >75 radiocollared lynx marked during a 6-year lynx research project on our study area were killed by coyotes (J. Squires, United States Forest Service, unpublished data).

The degree to which coyotes and lynx compete for snowshoe hares in the western United States is unknown. A high dietary overlap between coyotes and lynx in winter, when alternative lynx prey species are less available and the hare population is at its annual low, could adversely affect lynx. Snowshoe hare densities in the southern boreal forests are low relative to densities observed in the northern portion of their range (Hodges 2000, Griffin 2004). Lynx in western Montana prey almost exclusively on hares in winter (Squires and Ruggiero 2007) and significant depletion of hares by coyotes during winter could negatively affect lynx.

Interspecific competition is difficult to demonstrate in natural communities (Schoener 1983), especially when one of the constituent species (the coyote in this case) is known to have plastic habitat-use patterns and catholic feeding habits (Beckoff 2001). We could not establish a large, representative control area within which we could experimentally manipulate snowmobile use and predator communities. Therefore, we studied coyotes near Seeley Lake, Montana, from 2002 to 2004 to 1) assess the degree of coyote and lynx sympatry during winter, 2) characterize coyotes' association with compacted snowmobile trails, and

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3) describe coyotes' winter food habits. Clearer understandings of these 3 aspects of coyote winter ecology may allow managers to better assess the potential implications of snow-compacting activities within lynx habitat.

STUDY AREA

The study area was located in the Clearwater River drainage, near the town of Seeley Lake, Montana. This area was about 1,800 km² and included state, federal, and private lands that supported intensive commercial forestry. An extensive road network associated with timber harvest and a high snowpack attracted private and commercial snowmobile operators during winter. The Bob Marshall and Mission Mountain Wilderness areas flank the east and west sides of the study area, respectively.

Elevations on the study area ranged from 1,200 m to 2,100 m. The warm and dry forests at lower elevations were dominated by Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*) on south to west aspects, usually as mixed forests, although Douglas-fir may form pure stands. Low-elevation forests were open or park-like, but dense stands occurred where fire had been absent. Low-elevation sites were usually <35% slope.

Mid-elevations supported primarily cool-moist to dry conifer forests. Dominant tree species included seral Douglas-fir, western larch, and lodgepole pine in mixed to single-species stands. Slopes at mid-elevations were often >35%.

Upper-elevation forests consisted of subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and Engelmann spruce (*Picea engelmannii*), with lesser components of lodgepole pine, Douglas-fir, and western larch. Subalpine forests were multistoried and multiaged, often with a dense shrub understory.

The study area supported ungulates including white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*). Common carnivores included black bear (*Ursus americanus*), grizzly bear (*U. arctos*), mountain lion (*Felis concolor*), bobcat, wolf (*Canis lupus*), and American marten (*Martes americana*). This area supports an established lynx population (B. Giddings, Montana Department of Fish Wildlife and Parks, personal communication). Snowshoe hare, red squirrel (*Tamiasciurus hudsonicus*), blue grouse (*Dendragapus obscurus*), and ruffed grouse (*Bonasa umbellus*) were present during winter.

Snow depths on the study area averaged 69 cm during the winters 2002–2004 (see “Track Survey Routes” in Methods).

METHODS

Capture

We trapped coyotes within lynx home ranges during the snow-free months. We defined lynx home ranges as part of an ongoing study that has collared >75 lynx on the study area since 1998. We distributed our capture effort so that

monitored coyotes were spatially distributed across the study area. We captured coyotes using padded number 3 Victor Softcatch® foot-hold traps (Oneida Victor Inc., Ltd., Euclid, OH) modified with stronger coil springs and 2 additional chain swivels to increase capture efficiency and to reduce foot damage. We checked traps every 12–24 hours. We fitted coyotes with radiocollars (Advanced Telemetry Systems Inc., Isanti, MN) without anesthesia and released them at the capture location.

Track Survey Routes

We established 3 carnivore track and snow survey routes (combined length of 111 km) within the study area. We located routes on established snowmobile trails and surveyed them twice monthly from mid-December through late March. We established permanent snow survey stations, located 10 m from the edge of the route, at 1-km intervals where we measured snow depth and supportiveness (indexed by measuring the distance a 100-g brass wt dropped from 1 m penetrated the snow surface) during each survey. We also recorded all carnivore tracks encountered along the survey routes by species and location using a handheld Global Positioning System (GPS) unit. Each time we encountered a coyote track, we measured the snow depth and supportiveness 10 m from, and perpendicular to, the edge of the survey route. We treated tracks >100 m from the last recorded track of the same species as independent observations. The mean elevation of the survey routes ($n = 111$ survey stations, $\bar{x} = 1,587$ m, $SD = 177$ m) was similar to the mean elevation at which radiocollared lynx were relocated during winter on the same study area (J. Squires, unpublished data).

The United States Department of Agriculture Natural Resources Conservation Service had recorded snow-depth data bimonthly for 30 years at 2 permanent snow survey stations located within our study area. We compared snow depths present during the 3 winters of our study to the 30-year average snow depth.

Backtracking

We backtracked radiocollared adult coyotes within lynx home ranges to quantify how they interacted with compacted snowmobile trails (both forest roads compacted by snowmobiles and dispersed snowmobile trails) and to document coyote winter food habits. The goal of the backtracking component of our study was to create a series of daily digital maps of a coyote backtrack, a randomly located nonuse track (not used but available to the coyote that day), and all compacted snowmobile trails within 1 km of either track type (Fig. 1). We analyzed the coyote backtrack and nonuse track data in a pair-wise fashion. We then assessed coyote selection for a series of habitat variables including snow conditions, prey tracks, and the distance coyotes traveled from compacted snowmobile trails.

We located radiocollared coyotes in sequential order using radiotelemetry. This prevented the introduction of road and track sightability biases while maintaining a balanced

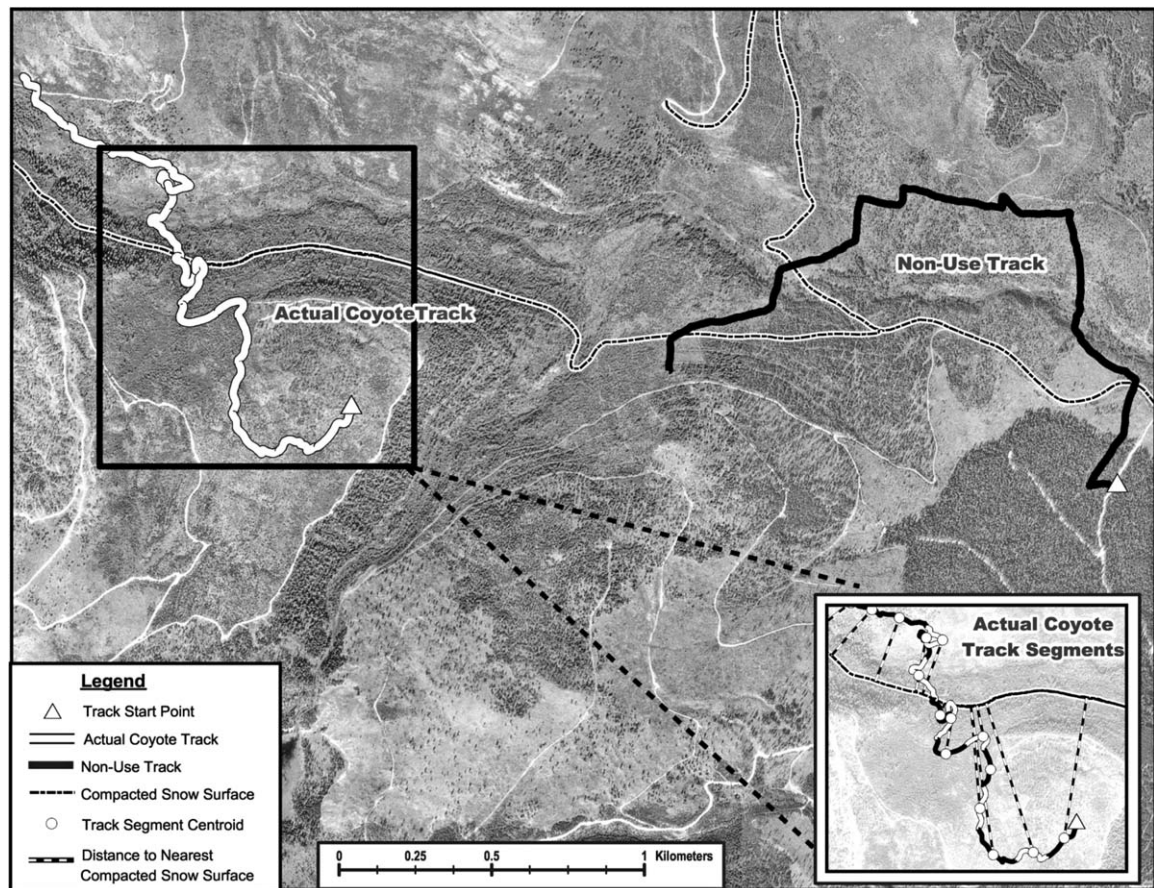


Figure 1. An example of daily coyote backtracking data overlaid on an aerial photo (summer) using data collected on 10 February 2004 near Seeley Lake, Montana, USA. Inset shows the track's segments, centroid point locations, and the individual measures of the segments' distance to compacted snow that were used to compute the mean distance that track was from compacted snowmobile trails.

sampling intensity across animals. We triangulated the coyote's location from a snowmobile and then walked to it from preexisting snowmobile trails to avoid compacting additional snow on the study area. When we were approximately 80 m from the coyote (determined by the signal's attenuation and change in direction relative to our movements), we circled the coyote until we located the track. We then radioed the field station with the track's location, and technicians used a computer program to generate a nonuse track starting point that was randomly located between 2 km and 3 km from the coyote track. Locating the nonuse track starting point 2–3 km from the coyote track starting point ensured that it was located in an area that a coyote could have used but did not use that day. The computer program then generated a list of bearings and distances based on previously digitized coyote backtracks. When followed, these directions enabled technicians to walk a randomly located and oriented nonuse track that was similar to an actual coyote track in shape.

Technicians began digitizing both use and nonuse tracks at the same time and followed them for 3 km using data-logging, differentially correctable Trimble GeoExplorer 3 GPS units, which collected track data as a series of distinct, consecutive segments (Fig. 1). Technicians created a track segment whenever they entered a different forest stand type,

encountered a road or trail, or after traveling 200 m, whichever came first. We recorded snow depth, snow supportiveness (indexed by measuring the distance a 100-g brass weight dropped from 1 m penetrated the snow surface), the number and species of prey track crossings, and whether the coyote was traveling on a road or trail (and, if so, what type) for each segment. We recorded all feeding-site locations and determined the prey or carcass species. Both technicians then digitized all compacted snowmobile trails within 1 km of any portion of their respective tracks (Fig. 1).

Occasionally, we backtracked marked coyotes while traveling with other coyotes. These groups' tracks frequently split from and rejoined each other as the animals traveled. When it was not possible to determine which track was made by the marked animal (for example, by assessing track size or stride length) technicians alternated between taking the right and left set of tracks each time the group split.

Variations in canopy cover and topography affect GPS fix rates and location quality (Moen et al. 1996, D'Eon et al. 2002, Di Orio et al. 2003, Frair et al. 2004). We used a Bezier smoothing algorithm in the ET GeoWizards® extension for ArcGIS® Desktop 8.3 to reduce the effect of fine-scale GPS scatter while maintaining biologically significant track tortuosity (DeCesare et al. 2005).

Smoothed track length corresponded closely to technicians' paced distances recorded while in the field.

Scat Analysis

We randomly selected 30 of 85 scats collected along coyote backtracks (10 from each of the 3 yr of the study) to send to the Wyoming Game and Fish Lab, Laramie, USA, for dietary analysis. We assumed that each unique food item found in an individual scat represented ≥1 distinct feed site of that type of food item. We washed scats and identified food items by family using internal hair characteristics and bone fragments (Moore et al. 1974).

Statistical Analyses

To increase the statistical power and the sensitivity of our tests, we considered the track pair the sampling unit for all analyses of backtracking data unless otherwise noted. We recognize that pseudoreplication is a concern when treating repeated observations of a single animal as replicates (Hurlbert 1984). With this in mind, we sampled animals sequentially to maintain temporal independence between observations of the same animal, and we attempted to sample evenly across animals ($\bar{x}$ backtracks/animal = 10.1, range = 6–16, SE = 0.7; Otis and White 1999). Prior to data analysis, we statistically assessed the within- and among-animal independence of individual track-pair observations. Runs tests applied for each animal did not indicate significant within-animal sample serial correlation (Zar 1999). We then conducted a 1-way analysis of variance (ANOVA), factoring on animal, for each of the variables considered in our analysis of backtracking data. Only one variable (snow supportiveness) varied significantly by animal (ANOVA, $F = 2.03$; $df = 11, 118$; $P = 0.03$). Therefore, when analyzing this variable, we present tests employing both the track pair and animal as the sampling unit.

We divided the number of prey and carnivore track crossings encountered on each track segment by the length of that segment. We then computed the mean of these individual track-segment encounter rates for each track. To test whether coyotes were closer to compacted snow during any particular year or month of the winter (relative to the amt of compacted snow available), we computed the differences between the distance the coyote and nonuse tracks were from compacted snow for each track pair and analyzed them by month and year.

We used the Nearest Features v.3.7 extension of ArcView 3.2 to compute the centroid point of each segment within a track. We then computed the distance each segment centroid was from the nearest compacted snowmobile trail. We averaged these segment centroid adjacency distances to derive a measure of each track's adjacency to compacted snow trails (Fig. 1). We also averaged the snow-depth and snow-supportiveness measurements for each track segment to produce a mean value for these variables for each track.

We used multi-response randomized block permutation procedures (MRBP) to test for differences in variable means between the aggregated pairs of coyote and random tracks (Mielke and Berry 2001). We used Mann–Whitney U tests

Table 1. The mean elevation of carnivore tracks documented along 2,200 km of survey route, the probabilities that the species' mean track elevations do not differ from the mean survey route elevation of 1,587 m, and track encounter rates in western Montana, USA, 2002–2004.

Species	<i>n</i> (tracks)	$\bar{x}$ track elevation (m)	<i>P</i> ^a	Track encounter rates ^b		
				Jan	Feb	Mar
Coyote	1,483	1,591	0.73	0.84	0.77	0.94
Lynx	760	1,626	0.01	0.53	0.50	0.38
Mountain lion	20	1,533	0.18			
Bobcat	13	1,610	0.35			
Marten	10	1,410	0.13			
Wolf	5	1,387	0.15			

^a Independent samples t -test.
^b Tracks/km. We did not compute encounter rates for species with sparse records.

to test differences between sample medians and independent samples t -tests to test for differences in the mean values of unpaired sample distributions. We used a chi-square goodness-of-fit test to assess the similarity of sample frequencies. We used 1-way ANOVAs to evaluate differences among groups of sample means (Zar 1999).

RESULTS

Capture

We captured and radiocollared 25 adult coyotes (10 M, 15 F) between September 2001 and October 2003. Seven marked coyotes died and 3 dispersed off the study area before we could adequately sample them. Three additional animals primarily used areas with administrative access restrictions and we did not sample them. We sampled the 12 remaining animals (4 M, 8 F) and included them in the analysis.

Track Survey Routes

We conducted 20 route surveys for a total of 2,220 km of effort. Coyote tracks accounted for 65% (1,483 of 2,291 total tracks) of all carnivore tracks documented. We encountered coyote tracks throughout the winter months at a mean elevation of 1,591 m ($n = 1,483$, SE = 16.86) that did not differ significantly from the elevation of the routes as a whole (1,587 m; $n = 111$, $t = -0.35$, $P = 0.73$; Table 1). Lynx tracks accounted for 32% of carnivore tracks encountered, and we found them at higher elevations (1,626 m; $n = 760$, SE = 5.9) than generally available on the routes ($t = -2.47$, $P = 0.01$). The elevations at which we detected the 2 species on survey routes largely overlapped (Fig. 2).

Snow was more supportive 10 m off compacted survey routes where coyote tracks were located (11.9 cm; $n = 1,483$, SE = 0.22) than snow along the survey routes in general ($\bar{x} = 17.8$ cm; $n = 2,200$, $t = -5.21$, $P < 0.01$). However, we found no significant difference ($t = 0.25$, $P = 0.81$) between the snow depths (10 m off the routes) where we detected coyote tracks ($\bar{x} = 69.3$ cm; $n = 1,483$, SE = 0.81) and on the survey routes in general ($\bar{x} = 69.1$ cm; $n = 2,200$, SE = 0.69).

The mean elevation at which we detected coyote tracks

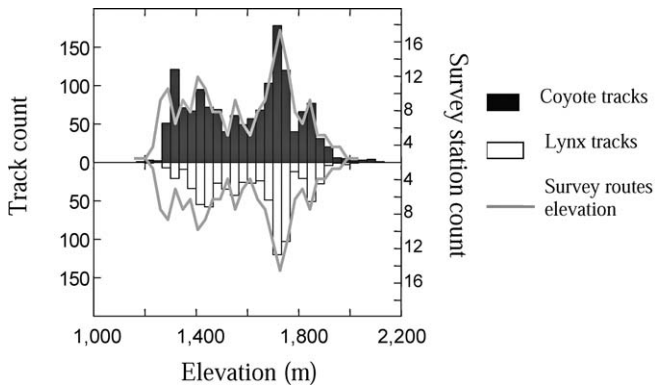


Figure 2. The elevations at which we located coyote and lynx tracks along track survey routes located near Seeley Lake, Montana, USA, 2002–2004. The gray line represents the distribution of the elevations of 111 snow survey stations evenly distributed along the survey routes.

along survey routes varied significantly by winter month (ANOVA, $F = 72.25$, $df = 2$, $1,480$, $P < 0.01$). We detected coyotes at a mean elevation of 1,592 m in January ($n = 561$, $SE = 7.69$), 1,493 m in February ($n = 324$, $SE = 10.15$), and 1,643 m in March ($n = 598$, $SE = 7.24$). We detected lynx at similar elevations throughout the winter ($\bar{x} = 1,626$ m; ANOVA, $F = 1.06$, $df = 2$, 757 , $P = 0.348$).

Backtracking

We backtracked 12 adult coyotes (4 M, 8 F) a total of 322 km between January 2002 and March 2004. In addition, we digitized 358 km of paired nonuse tracks during the same period. Our sampling intensity averaged 10.1 track pairs per animal (range = 6–16, $SE = 0.7$); backtracks averaged 2,705 m in length ($n = 119$, $SE = 72.20$) and each track comprised an average of 26.2 individual track segments (range = 5–55, $SE = 0.7$).

Adjacency to and use of compacted snowmobile trails.—Backtracked coyotes used snow compacted by snowmobiles more than random expectation (MRBP, $P < 0.01$; Table 2). Backtracked coyotes were on compacted snowmobile trails for 7.69% of their total travel distance whereas <0.01% of nonuse tracks intersected such surfaces. Backtracked coyotes used forest roads compacted by snowmobiles 5.66% of the time, whereas the remaining 2.03% of coyotes' travel on compacted snowmobile trails was on dispersed snowmobile trails.

Coyotes used roads that were not compacted by snowmo-

biles for 4.62% of their travel (Table 2). Nonuse tracks encountered uncompact roads at a frequency similar to compacted snowmobile trails ($n = 19$ uncompact road encounters, $n = 18$ compacted snowmobile trail encounters; $\chi^2 = 0.03$, $P = 0.86$). Uncompact roads traveled by coyotes had neither deeper (uncompact road $\bar{x} = 71.37$ cm, coyote backtrack $\bar{x} = 63.71$; ANOVA, $F = 1.81$, $df = 1$, 158 , $P = 0.18$) nor more supportive (uncompact road $\bar{x} = 15.07$ cm, coyote backtrack $\bar{x} = 15.93$; ANOVA, $F = 0.03$, $df = 1$, 158 , $P = 0.86$) snow than coyote backtracks in general. The overall distance coyotes traveled on forest roads with snow compacted by snowmobiles was similar to their travel distance on uncompact forest roads (MRBP, $P = 0.17$).

Coyotes did not generally travel closer to compacted snowmobile trails than random expectation (MRBP, $P = 0.56$). Coyote backtracks were located an average of 368 m ($n = 119$, range = 8–3,623 m, $SE = 44$) from compacted snowmobile trails compared to 339 m ($n = 119$, range = 39–1,979 m, $SE = 30$; Table 2) for nonuse tracks.

Mean snow depth (ANOVA, $F = 21.16$, $df = 2$, 18 , $P < 0.01$) and snow penetrability (ANOVA, $F = 7.04$, $df = 2$, 18 , $P < 0.01$) on the survey routes differed by month of the winter (Jan, Feb, and Mar; Fig. 3); however, the mean elevation of coyote backtracks did not vary by winter month (ANOVA, $F = 0.17$, $df = 2$, 118 , $P = 0.91$). Although we observed that the amount of compacted snowmobile trails on the study area was highest during midwinter, coyote travel distance from compacted snow (relative to availability) did not differ by winter month (ANOVA, $F = 0.04$, $df = 2$, 118 , $P = 0.96$; Fig. 3).

Coyotes used compacted snowmobile trails on 35% (42 of 119) of digitized backtracks. When a coyote traveled on a compacted snow surface, it did so an average of 1.76 times per backtrack ($n = 88$, $SE = 0.10$) and traveled on it for a median distance of 124 m. Thirty-four percent (40 of 119) of coyote backtracks intersected uncompact forest road surfaces. When a coyote backtrack encountered an uncompact road, the coyote used it an average of 1.80 times ($n = 72$, $SE = 0.11$) per backtrack and traveled on it a median distance of 102 m. Coyotes did not use compacted snowmobile trails more often per backtrack than uncompact roads (Mann–Whitney U , $Z = -0.36$, $P = 0.72$), nor did they travel on them for greater distances (Mann–Whitney U , $Z = -1.31$, $P = 0.19$).

Table 2. Data collected along both coyote (322 km) and nonuse (358 km) snow tracks, western Montana, USA, 2002–2004.

Variable	Coyote tracks $\bar{x}$	Nonuse tracks $\bar{x}$	P^a
Distance to snowmobile trails (m)	368	339	0.56
% of track distance on all snow surfaces compacted by snowmobiles	7.69%	<0.01%	<0.01
% of track distance on dispersed compacted snowmobile trails	2.03%	<0.01%	<0.01
% of track distance on forest roads compacted by snowmobiles	5.66%	<0.01%	<0.01
% of track distance on uncompact roads	4.62%	<0.01%	<0.01
Snow depth (cm)	63.71	71.54	<0.01
Snow penetrability (cm)	15.93	18.83	<0.01
Lynx tracks encountered (tracks/km)	0.48	0.38	0.83
Snowshoe hare tracks encountered (tracks/km)	33.08	27.61	0.08

^a Multi-response randomized block permutation procedures test.

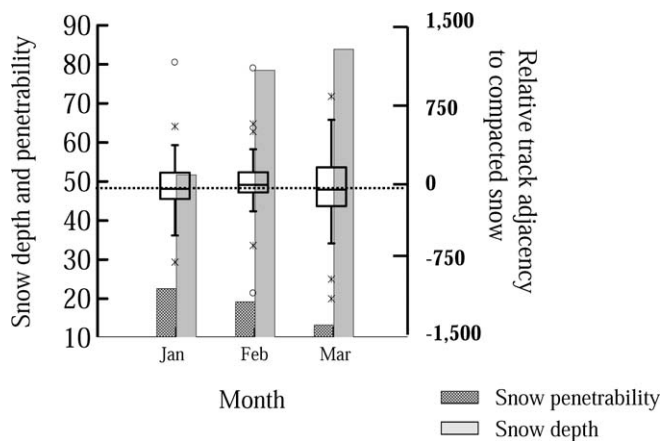


Figure 3. Snow depth, penetrability, and coyote association with compacted snowmobile trails by winter month, near Seeley Lake, Montana, USA, 2002–2004. Boxplots represent the distribution of the distances coyotes traveled from compacted snowmobile trails relative to their availability on the day we backtracked the coyotes. We computed relative adjacency distances by subtracting the nonuse track's average distance to compacted snowmobile trails from the actual coyote track's average distance from compacted snowmobile trails for each daily track pair. We pooled data from all 3 years of the study by winter month.

Snow conditions on coyote backtracks.—Coyotes consistently traveled in areas with more supportive snow conditions (MRBP, $n = 119$ track pairs, $P < 0.01$; MRBP, $n = 12$ animals, MRBP, $P < 0.01$) and shallower snow (MRBP, $n = 119$ track pairs, $P < 0.01$) than randomly available (Table 2). When we removed the track segments on which coyotes traveled on compacted snowmobile trails (7.69% of total travel distance) from the analysis, coyotes still selected for snow conditions that were more supportive (coyote backtrack penetrability $\bar{x} = 16.68$ cm, SE = 0.78; nonuse track penetrability $\bar{x} = 18.83$ cm, SE = 1.73; MRBP, $n = 119$ track pairs, $P < 0.01$; MRBP, $n = 12$ animals, MRBP, $P < 0.01$) and shallower (coyote backtrack

$\bar{x} = 64.89$ cm, SE = 2.76; nonuse track $\bar{x} = 71.69$ cm, SE = 2.91; MRBP, $n = 119$ track pairs, $P < 0.01$).

The distance coyotes traveled from compacted snowmobile trails was not affected by daily changes in snow supportiveness. There was no correlation between the snow penetrability on a coyote's backtrack and the distance it traveled from compacted snowmobile trails that day ($n = 119$, $r^2 = 0.02$; Fig. 4). Similarly, because we found that coyotes generally select for more supportive snow surfaces for travel, we also examined whether daily measures of snow supportiveness at a larger spatial scale were correlated with the distance coyotes traveled from compacted snowmobile trails. We found no relationship between the snow supportiveness on the nonuse tracks and the distance the paired coyote backtracks were from compacted snow ($n = 119$, $r^2 < 0.01$; Fig. 4).

Although the mean snow depth on survey routes varied significantly among years (ANOVA, $F = 3.65$, $df = 2, 18$, $P = 0.04$), the supportiveness of the snow surface did not (ANOVA, $F = 0.79$, $df = 2, 18$, $P = 0.69$; Fig. 5). Snow depths on the study area were 81% of the 30-year average in 2002, 93% of average in 2003, and 101% of average in 2004 (Fig. 5). Despite this year-to-year variation in snow depth, the distance coyotes traveled from compacted snowmobile trails relative to availability was not different among years of the study (Fig. 5).

Prey and carnivore tracks encountered along backtracks.—Coyotes encountered lynx tracks (0.48 tracks/km, SE = 0.15) at a rate similar to random expectation (0.38 tracks/km, SE = 0.11; MRBP, $P = 0.83$). Red squirrel tracks were encountered at nearly equal rates on both coyote (12.34 tracks/km, SE = 1.94) and nonuse tracks (11.71 tracks/km, SE = 1.56, MRBP, $P = 0.79$). However, coyotes encountered snowshoe hare tracks at a mean of 33.08 tracks/km (SE = 3.03), compared to 27.61 tracks/km (SE = 2.57) on nonuse tracks. Although the difference between the

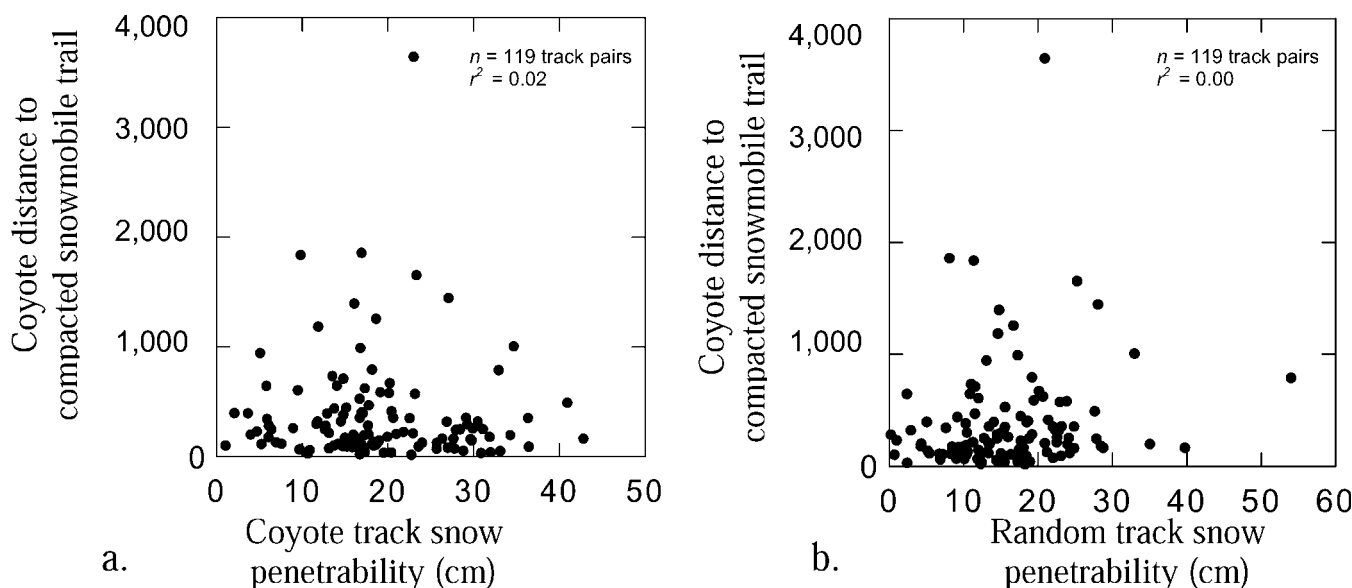


Figure 4. Regressions of the mean distance backtracked coyotes traveled from compacted snow and the snow supportiveness (penetrability) along (a) that backtrack and (b) the paired nonuse track, Seeley Lake, Montana, USA, 2002–2004.

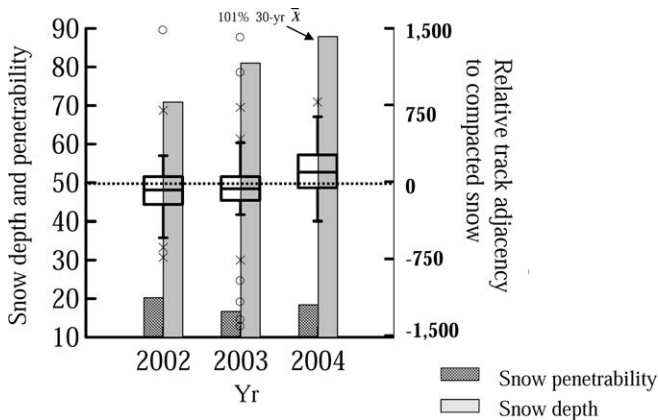


Figure 5. Snow depth, penetrability, and coyote association with compacted snowmobile trails by year, Seeley Lake, Montana, USA, 2002–2004. Boxplots represent the distribution of the distances coyotes traveled from compacted snowmobile trails relative to their availability on the day we backtracked the coyotes. We computed relative adjacency distances by subtracting the nonuse track's average distance to compacted snowmobile trails from the actual coyote track's average distance from compacted snowmobile trails for each daily track pair.

coyote and nonuse track hare encounter rates was not significant (MRBP, $n = 119$ pairs, $P = 0.08$), backtracked coyotes tended to encounter hare tracks more frequently than nonuse tracks.

Coyote winter food habits.—We documented 88 feed sites while backtracking coyotes; one feed site was found for every 3.7 km of coyote travel distance. Eighty-eight percent (77 of 88) of feed sites were scavenge sites; 74% of scavenge sites (57 of 77) were of ungulate carrion and 4% (3 of 77) were of snowshoe hares. Eleven of 88 feed sites (13%) were kills, 3 (3%) of which were of snowshoe hares (Table 3). Coyotes traveled an average of 107.3 km between snowshoe hare kills.

Feed sites were located an average of 375 m from compacted snowmobile trails (SE = 52, $n = 88$), which was similar to the mean distance coyotes traveled from compacted snowmobile trails in general (368 m, SE = 44; $t = -0.96$, df = 204, $P = 0.92$) and random expectation (339 m, SE = 30; $t = 0.61$, df = 204, $P = 0.55$). The mean distance between scavenge sites and snowmobile trails (327 m, SE = 47.82) was similar to random expectation (339 m; $t = 0.21$, df = 193, $P = 0.81$).

Kill sites were located farther (705 m, SE = 241; $n = 11$) from compacted snowmobile trails than random expectation (random expectation = 339 m; $t = 3.01$, df = 128, $P < 0.01$). Snowshoe hare kill sites were located a mean distance of 773 m (SE = 315, $n = 3$) from compacted snowmobile trails, which was also farther from compacted snowmobile trails

Table 4. A comparison of independent food items present in 30 analyzed winter coyote scats and feeding sites located along 322 km of coyote backtrack, western Montana, USA, 2002–2004.

Food item (by family)	% of total independent food items in scats ($n = 49$)	% of independent food items documented along backtracks ($n = 88$) ^a
Cervidae	61%	68%
Leporidae (snowshoe hares)	12%	7%
Bovidae	10%	0%
Sciuridae	8%	5%
Cricetidae	6%	2%
Bird (species)	2%	5%

^a Additional food items documented along backtracks but not detected in scats included coyotes, marten, skunks (*Mephitis mephitis*).

than random expectation (random expectation = 339 m; $t = 2.20$, df = 120, $P = 0.03$). Snow was not more supportive on those backtracks on which coyotes killed hares than on coyote backtracks in general (ANOVA, $F = 0.2$, df = 1, 117, $P = 0.90$).

We found ≥ 49 independent food items in 30 analyzed scats (Table 4). Cervid remains made up 61% of all food items detected, and 12% of food items were snowshoe hares. The percent of food items that were snowshoe hares was similar in both analyzed scats and on coyote backtracks ($\chi^2 = 1.07$, df = 1, $P = 0.35$).

DISCUSSION

We acknowledged a priori that assessing whether compacted snowmobile trails directly affect competitive interactions between lynx and coyotes would be difficult. Therefore, we evaluated 3 research hypotheses that we believed would be true if snowmobile trails facilitated competition between coyotes and lynx on our study area. These hypotheses include 1) coyotes would remain in lynx home ranges throughout the winter, 2) coyote predation on hares would be sufficient to affect lynx foraging success, and 3) coyote travel and foraging behavior would be spatially associated with compacted snowmobile trails.

Although coyotes on our study area remained in lynx habitat throughout the year, our results do not suggest that compacted snowmobile trails facilitated coyote movements or that snowshoe hares provided a large proportion of the coyote's winter diet.

Coyote and Lynx Winter Sympatry

Coyotes remained in lynx home ranges throughout the winter despite a deep snowpack. We detected coyote tracks on survey routes at similar elevations as lynx tracks (Fig. 2),

Table 3. Coyote feeding sites by type encountered along 322 km of coyote winter backtracks, western Montana, USA, 2002–2004.

Site type	Snowshoe hare	Cervid	Grouse species	Red squirrel	Microtine species	Other	Total
Kill sites	3	1 ^a	2	3	2	0	11
Scavenge sites	3	57	3	1	0	13 ^b	77

^a Mule deer.

^b Additional species scavenged included coyote, pine marten, skunk (*Mephitis mephitis*), and an unidentified bird.

and we commonly encountered lynx tracks on coyote backtracks (Table 2). In addition, we relocated radiocollared coyotes at similar elevations throughout winter despite significant variations in snow depth and penetrability. In Seeley Lake, coyotes would only have to travel 10–20 km to reach areas with little or no snow within a major big game wintering area. Despite the availability of snow-free winter habitat, they maintained their territories within the home ranges of resident lynx all year.

Coyote Winter Food Habits

Coyotes on our study area were primarily scavengers during winter and rarely preyed on hares. This observation is consistent with documented coyote winter food habits in other deep-snow areas with low hare densities and available ungulate carrion. Coyotes in northern latitudes exhibit a clear functional response to changes in hare densities (Todd and Keith 1983, Staples 1995, O'Donoghue et al. 1998b), and scavenged ungulate carrion often becomes a primary winter food when hare densities drop to levels similar to those in western Montana (Ozoga and Harger 1966, Nellis and Keith 1976, Todd et al. 1981, Staples 1995, Hodges 2000).

Similarly, the hare kill rates that we observed suggest that snowshoe hares composed only a small proportion of coyotes' winter diet. Using techniques similar to ours, Murray et al. (1995) observed coyotes killing one hare per 9.4 km of travel distance when hares were at their cyclic high in southwestern Yukon, Canada. However, on our study area we found that coyotes traveled 107.3 km between snowshoe hare kills. This is similar to the distance coyotes traveled between hare kills in northern Minnesota, USA (127.3 km/hare kill, 509 km surveyed; Berg and Chesness 2001). Although we did not quantify coyotes' average daily travel distance as part of this study, Patterson et al. (1999) found that coyotes in Nova Scotia, Canada, traveled 14.3 km per day in winter. This distance is similar to that observed by Servin et al. (2003; 14.49 km, Durango, Mexico), but longer than travel distances noted by Andelt (1985; 7.8 km, TX, USA). If we conservatively assume that coyotes on our study area traveled 15 km per day, an individual coyote would kill, at most, one hare per week during the winter months. This predation rate would be insufficient to meet the estimated 0.7–0.9 hares per day required to meet coyotes' energetic needs when few other food resources are available (Keith et al. 1977, Litvaitis and Mautz 1980).

Although we were unable to quantify the summer diet of coyotes on our study area, predation of snowshoe hares may be more common during the snow-free months. O'Donoghue et al. (1998b) found that during the months of January, February, and March, hare predation by coyotes declined by as much as 90% from the high levels observed in late fall. Staples (1995) also found that the percent frequency of occurrence of hare remains in coyote scats was 2 times higher during the snow-free months than during winter. It is interesting to note that 2 of the 3 hare kills we documented on coyote backtracks occurred in late March, near the end of the winter season.

Coyote Association With Compacted Snowmobile Trails

Although compacted roads and trails were readily available on our study area, only a small proportion of coyotes' travel was on compacted snow surfaces and they only traveled on them for short distances. If compacted snow truly facilitated travel, we would also expect coyotes to repeatedly interact with compacted snow as they traversed the landscape. This was not the case on our study area. In general, coyotes did not repeatedly use a compacted trail during the same backtrack and did not travel closer to compacted snowmobile trails than randomly expected. In addition, the distances coyotes traveled from compacted trails did not vary with daily, monthly, or yearly changes in snow supportiveness or depth (Figs. 3–5). Coyotes did not exhibit elevational habitat shifts as winter progressed, despite significant changes in both snow depth and supportiveness. Therefore, although coyotes did use compacted snow more than random expectation, it is unlikely that snowmobile trails strongly affect either their movements in general or the potential for competitive interactions between coyotes and lynx.

Interestingly, we found no difference between coyotes' use of compacted and uncompacted forest roads, even though snow conditions on uncompacted roads were similar to those coyotes encountered when traveling off these man-made corridors. The similarity between the coyotes' selection for compacted and uncompacted forest roads suggests that coyotes may be selecting for the roads' structure (a cleared travel corridor) and location rather than the snow conditions on them. Our study area was heavily timbered and snowmobile users often followed foot trails, fire lines, and power lines. Like uncompacted roads, coyotes often traveled these corridors when the snow on them was not compacted, but unfortunately we did not quantify the use of these structures.

Large forest carnivores often use linear corridors, including roads, for travel and foraging (Thurber et al. 1992, James and Stuart-Smith 2000, Dickson et al. 2005). Coyotes have an affinity for corridors in general (Atwood et al. 2004), and forest roads specifically (Thurber et al. 1992, Staples 1995, Crete and Lariviere 2003, Arjo and Pletscher 2004), throughout the year. There is little evidence that coyotes avoid roads having a moderate level of human use (Staples 1995, Arjo and Pletscher 2004).

Behavioral adaptations may allow coyotes to travel and forage in deep-snow environments despite their relatively high foot-load. We observed coyote tracks on our survey routes more often in areas where snow was generally more supportive and backtracked coyotes demonstrated strong selection for shallower and more supportive snow conditions than randomly expected. Similarly, both Murray and Boutin (1991) and Crete and Lariviere (2003) found that coyotes used areas with more supportive and shallower snow than was otherwise available. Todd et al. (1981) and Murray et al. (1994) showed that coyotes selected for more supportive and shallower snow than lynx using the same areas. Shallower and more supportive snow offers significant energetic

benefits to traveling coyotes (Crete and Lariviere 2003), and coyotes largely found these advantageous snow conditions where they occurred naturally on our study area.

Finally, if coyotes depended on snowmobile trails to locate or acquire food, we would expect feeding sites to have been spatially associated with them. We did not find either coyote scavenging sites or kill sites closer to compacted snowmobile trails than backtracks in general or than random expectation. Specifically, the 3 snowshoe hare kills that we documented on coyote backtracks were located more than twice as far from compacted trails than randomly expected. Therefore, we found no evidence that snowmobile trails were associated with coyote foraging sites on our study area.

MANAGEMENT IMPLICATIONS

It is unlikely that limiting compacted snowmobile trails on our study area would significantly reduce exploitation competition between coyotes and lynx during winter.

ACKNOWLEDGMENTS

This study was a component of the Lolo Pass Redevelopment Project and was supported by the Federal Highways Administration; Idaho Department of Transportation; United States Forest Service (USFS) Clearwater National Forest; the United States Department of Agriculture Rocky Mountain Research Station; United States Department of Interior Bureau of Land Management; Montana Department of Fish, Wildlife and Parks; and the University of Montana. We thank S. Blum, C. Campbell, S. Connolly, J. Holiday, A. Kolbe, J. Martini, J. Miller, K. Morris, E. Patton, and R. Piehl for their assistance with field data collection. S. Blum, J. Jenness, and C. Copeland provided assistance with Geographic Information System analyses. T. Love, S. Tomson, and the staff of the USFS Seeley Lake Ranger District provided critical logistical support throughout the study. J. Copeland, N. DeCesare, D. Pearson, M. Schwartz, and T. Ulizio provided helpful comments on earlier drafts of this manuscript.

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Associate Editor: Morrison.