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THE EFFECT OF SNOWMOBILE TRAILS ON COYOTE MOVEMENTS
WITHIN LYNX HOME RANGES

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B.S., Wildlife Biology
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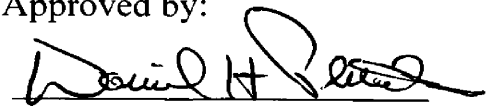
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For the degree of

Master of Science, Wildlife Biology

The University of Montana

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Approved by:



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The effect of snowmobile trails on coyote movements within lynx home ranges

Director: Daniel H. Pletscher 

Abstract:

Coyotes (*Canis latrans*) and Canada lynx (*Lynx canadensis*) are sympatric throughout much of the southern range of lynx. Researchers and managers have suggested that the presence of compacted snowmobile trails may allow coyotes to access lynx habitat in winter from which they would have otherwise been 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, throughout the year.

We investigated how coyotes interacted with compacted snowmobile trails by conducting carnivore track surveys and by snow tracking adult coyotes (4 males, 8 females) in areas with both documented lynx presence and moderate levels of recreational snowmobile use. Coyotes remained in lynx habitat having deep snow from January through March and traveled on compacted snowmobile trails more than random expectation. However, coyotes used compacted snowmobile trails for less than 8% of their travel, only traveled on them for a median distance of 124 m, and used compacted and uncompacted forest roads similarly. Coyotes did not travel closer to compacted snowmobile trails than random expectation (coyote mean distance = 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. Coyotes did, however, strongly select for shallower and more supportive snow surfaces when traveling off compacted snowmobile trails. Coyotes were primarily scavengers in winter (snowshoe hare kills comprised only 3% of coyote feed sites) and did not forage closer to compacted snowmobile trails than random expectation.

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INTRODUCTION

In its decision to list Canada lynx as a threatened species under the Endangered Species Act (Federal Register Vol. 65(58): 16051-16086), the U.S. Fish and Wildlife Service stated that “snowmobile trails and roads that are maintained for winter recreation and forest management create packed snow corridors that give other species access to lynx habitat...Coyotes use packed snow trails and now occupy the winter habitats of lynx and, therefore, are a concern as a potential lynx competitor in winter”. The decision acknowledged, however, that no evidence yet existed demonstrating that competition between coyotes and lynx had negatively affected contiguous U.S. lynx populations. The inter-agency Canada Lynx Conservation Assessment and Strategy, a document that directs lynx management on federal lands in the United States, stated that snow compaction caused by recreational activities in lynx habitat should be minimized and the effects of compacted snowmobile trails on lynx should be evaluated (Ruediger et al. 2000).

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 lynx and may cause the two species to use different winter habitats. Researchers have 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 (Buskirk et al. 2000). Increased availability of compacted snowmobile trails might allow coyotes to hunt hares successfully in high elevation, deep snow environments and persist there year round, thus significantly decreasing the number of hares available to lynx.

Although activities such as skiing, snowshoeing, and snowmobiling all result in compacted snow trails, only snowmobiling creates trails of sufficient density and extent to potentially affect entire predator communities. Recent technological advances allow newer snowmobiles to travel through deeper snow and into rougher areas than older machines. Snowmobile sales have increased over the last 15 years (International Snowmobile Manufacturers Association 2004) and riders now routinely travel into remote areas in search of challenging terrain.

The coyote can be a formidable competitor with lynx. Parker (1986), Murray et al. (1995), and O'Donoghue et al. (1998a) demonstrated that coyotes could successfully hunt snowshoe hares, the lynx's primary winter prey, in deep snow environments. The coyote's range has expanded dramatically in recent decades (Fuller and Kittredge 1996) and coyotes have killed both bobcat (*Felis rufus*; Anderson 1986, Jackson 1986, Toweill 1986) and, rarely, lynx (O'Donoghue et al. 1995).

If compacted snowmobile trails facilitate coyotes' presence in lynx habitat during the winter, then it is important to know whether the 2 species use food resources in a similar way. 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 on our study area prey almost exclusively on hares in winter (J. Squires unpublished data) and significant additional depletion of hares by coyotes during winter has the potential to negatively affect lynx distribution and abundance.

Interspecific competition is difficult to demonstrate in natural communities. This is especially true when one of the constituent species (the coyote in this case) is known to have plastic habitat use patterns and catholic feeding habits. We were unable to establish a large, representative control area within which snowmobile use could have been administratively manipulated. Therefore, we studied coyotes near Seeley Lake, MT from 2002 to 2004 to document the degree of lynx and coyote sympatry during winter in a deep snow environment, characterize coyote travel behavior relative to compacted snowmobile trails and changing snow conditions, and describe coyote winter food habits.

STUDY AREA

The study area was located in the Clearwater River drainage, near the town of Seeley Lake, Montana. This area is about 1800 km² and included state, federal, and private lands that supported intensive commercial forestry. An extensive road network associated with timber harvest and a high snow pack 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 range from 1,200 - 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 (U. S. Forest Service 1997). Low-elevation forests were open or park-like, but dense stands occurred where fire had been absent. Low-elevation sites are usually less than 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 are often greater than 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 multi-storied and multi-aged, often with a dense shrub understory.

The study area supported ungulates including white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*) and elk (*Cervus elaphus*). Common carnivores included black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), mountain lion (*Felis concolor*), bobcat, and American marten (*Martes americana*). This area supports an established lynx population (B. Giddings, Montana Dept. 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.

METHODS

Capture

We trapped coyotes within known lynx home ranges during the snow free months. Lynx home ranges were defined as part of an ongoing study that has collared over 75 lynx on the study area since 1998. We attempted to distribute our capture effort so that monitored animals were distributed across the study area. Coyotes were captured using padded #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 radio collars (ATS Inc., Isanti, MN) without inducing anesthesia and released them at the capture location.

Track Survey Routes

We established three carnivore track/snow survey routes (combined length of 111 km) within the study area. Routes were located on established snowmobile trails and surveyed 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 penetrability (indexed by measuring the distance a 100 g brass weight 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 hand held GPS unit. Each time a coyote track was encountered we measured the snow depth and penetrability 10 m from, and perpendicular to, the edge of the survey route. Tracks >100 m from the last recorded track of the same species were treated as independent observations. The mean elevation of the survey routes ($n = 111$ survey stations, mean = 1587 m, SD = 177 m) was similar to the mean elevation at which radio collared lynx were relocated during winter on the same study area (J. Squires unpublished data).

Snow depth data have been recorded bi-monthly for 30 years at 2 permanent snow survey stations (USDA Natural Resources Conservation Service) located within our study area. These data allowed us to compare snow depths present during the three winters of our study to the 30-year average snow depth.

Backtracking

We backtracked radio-collared 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 “non-use” track (not used but available to the coyote that day), and all compacted snow within 1 km of either track (Figure 1). The coyote backtrack and non-use track data were then analyzed in a pair-wise fashion. We then assessed coyote selection for a series of ephemeral habitat variables including snow conditions, prey tracks, and the distance coyotes traveled from compacted snowmobile trails.

We located radio-collared coyotes in sequential order using radio telemetry. This prevented the introduction of road and track sightability biases while attempting to achieve a balanced 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 the track was located. We then radioed the field station with the track’s location where technicians used a computer program to generate a “non-use” track starting point that was randomly located between 2 – 3 km from the coyote track. Locating the non-use track starting point 2 – 3 km from the coyote track starting point assured that it was located in an area that a coyote could have used, but did not that day. The computer program then generated a list of bearings and

distances based on one of a series of previously digitized coyote backtracks. When followed, these directions enabled technicians to walk a randomly located non-use track similar to an actual coyote track and, therefore, to control for internal correlations due to track shape.

Technicians began digitizing both use and non-use tracks at the same time and followed them for 3 km using data logging, differentially-correctable Trimble GeoExplorer 3 GPS units (Trimble Navigation Ltd., Sunnyvale, CA) which logged points at 2 second intervals. Each track was comprised of a series of contiguous track segments (Figure 1). Technicians created a distinct track segment whenever they entered a different forest stand type, encountered a road or trail, or after traveling 200 m, whichever came first. 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) was recorded for each segment. All feeding site locations were recorded and the prey/carcass species was determined. Both technicians then digitized all compacted snowmobile trails within 1 km of any portion of his or her respective track (Figure 1).

Occasionally, marked coyotes were backtracked while traveling with other coyotes. These groups' tracks frequently split from and re-joined 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 (ESRI, Inc., Redlands, CA) to reduce the effect of fine-scale GPS scatter while maintaining biologically significant track tortuosity (DeCesare et al. in press). 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 three years of the study) to send to the Wyoming Game and Fish Lab Laramie, WY, for dietary analysis. We assumed that each unique food item found in an individual scat represented a minimum of one distinct feed site of that type of food item. Scats were washed and food items identified by family using internal hair characteristics and bone fragments (Moore et al. 1997).

Statistical Analyses

To increase the statistical power and the sensitivity of our tests, the track pair was considered the sampling unit for all analyses of backtracking data unless noted in the text. 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 (mean backtracks per animal = 10.1, range = 6 – 16, SE = 0.7, Otis and White 1999). Prior to data analysis, we employed a series of statistical tests to assess the within and among animal independence of

individual track-pair observations. A runs test applied for each animal did not indicate significant within-animal sample serial correlation (Zar 1999). We then conducted a one-way 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 tests employing both the track pair and animal as the sampling unit are presented.

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

We used the Nearest Features v.3.7 extension (Jenness Enterprises, Flagstaff, AZ) of ArcView 3.2 (ESRI, Inc., Redlands, CA) to compute the centroid point of each segment within a track. The distance of each segment centroid from the nearest compacted snowmobile trail was computed. These segment centroid adjacency distances were then averaged to derive the measure of each track's adjacency to compacted snow trails (Figure 1). The snow depth and snow penetrability measurements for each track segment were also averaged to produce a mean value for these variables for each track.

We used multiresponse 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 to test differences between sample medians and independent samples t tests to test for differences in the mean values of un-paired sample distributions. A χ^2 goodness of fit test was used to compare the frequency snowshoe hare remains occurred in coyote scats and feed sites documented on coyote backtracks. We used one-way ANOVAs to evaluate differences among groups of sample means (Zar 1999).

RESULTS

Capture

Twenty-five adult coyotes (10 Males, 15 Females) were captured and radio-collared between Sept. 2001 and Oct. 2003. Seven marked coyotes died and 3 dispersed off the study area before they could be adequately sampled. Three additional animals primarily used areas with administrative access restrictions and were not sampled. The 12 remaining animals (4 males, 8 females) were sampled and included in the analysis.

Track Survey Routes

We conducted 20 route surveys for a total of 2220 km of effort. Coyote tracks accounted for 65% (1483 of 2291 total tracks) of all carnivore tracks documented. Coyote tracks were encountered throughout the winter months at a mean elevation of 1591 m ($n=1483$, SE = 16.86) that did not differ significantly from the elevation of the routes as a whole (1587 m, $n = 111$, $t = -0.35$, $P = 0.73$; Table 1). Lynx tracks accounted for 32% of carnivore tracks encountered and were found at higher elevations (1626 m, $n = 760$, SE = 5.9) than generally available on the routes ($t = - 2.47$, $P = 0.01$). The

elevations at which the two species were detected on survey routes largely overlapped (Figure 2).

Snow was more supportive 10 m off compacted survey routes where coyote tracks were located (11.9 cm, $n = 1483$, $SE = 0.22$) than snow along coyote backtracks (mean = 15.9 cm; $n = 119$, $t = -5.46$, $P < 0.01$) and along the survey routes in general (mean = 17.8 cm; $n = 2200$; $t = -5.21$, $P < 0.01$). However, we found no significant difference ($t = 0.25$, $P = 0.81$) between the snow depths (10 m off the routes) when coyotes were present (mean = 69.3 cm, $n = 1483$, $SE = 0.81$) and on the survey routes in general (mean = 69.1 cm, $n = 2200$, $SE = 0.69$).

The mean elevation at which coyote tracks were detected varied significantly by winter month (ANOVA, $F = 72.25$, $df = 2$, 1480 , $P < 0.01$). Coyotes were detected at a mean elevation of 1592 m in January ($n = 561$, $SE = 7.69$), 1493 m in February ($n = 324$, $SE = 10.15$), and 1643 m in March ($n = 598$, $SE = 7.24$). Lynx were detected at similar elevations throughout the winter (ANOVA, $F = 1.06$, $df = 2$, 757 , $P = 0.348$).

Backtracking

We backtracked 12 adult coyotes (4 Males, 8 Females) a total of 322 km between January 2002 and March 2004. In addition, 358 km of paired non-use tracks were digitized during the same period. Our sampling intensity averaged 10.1 track pairs per animal (range = 6 - 16, $SE = 0.7$); backtracks averaged 2705 m in length ($n = 119$, $SE = 72.20$ m) and each track was comprised of an average of 26.2 individual segments (range = 5 - 55, $SE = 0.7$).

Adjacency to and use of compacted snowmobile trails.— 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 while <0.01% of non-use tracks intersected such surfaces. Backtracked coyotes used forest roads compacted by snowmobiles 5.66% of the time while the remaining 2.03% of coyotes' travel on compacted snowmobile trails was on dispersed snowmobile trails.

Coyotes used roads that were not compacted by snowmobiles for 4.62% of their travel (Table 2). Non-use 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 mean = 71.37 cm, coyote backtrack mean = 63.71; ANOVA, $F = 1.81$, $df = 1, 158$, $P = 0.18$) nor more supportive (uncompact road mean = 15.07 cm, coyote back track mean = 15.93; ANOVA, $F = 0.03$, $df = 1, 158$, $P = 0.86$) snow conditions than coyote backtracks in general. Coyotes' travel distance on forest roads with snow compacted by snowmobiles was similar to their travel distance on forest roads with unmodified snow (MRBP; $P = 0.17$).

However, 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 - 3623 m, SE = 44 m) from compacted snowmobile trails compared to 339 m ($n = 119$, range = 39 - 1979 m, SE = 30; Table 2) for non-use tracks.

While both 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., Figure 3), 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 mid-winter, coyote travel distance from compacted snow (relative to availability) did not differ by winter month (ANOVA, $F = 0.04$, $df = 2, 118$, $P = 0.96$, Figure 3).

Coyotes used compacted snowmobile trails on 35% (42 of 119) of the 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 uncompacted forest road surfaces. When a coyote backtrack encountered an uncompacted 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 track than uncompacted roads (Mann-Whitney U, $Z = -0.36$, $P = 0.72$) nor did they travel on them for greater distances (Mann-Whitney U, $Z = -1.31$, $P = 0.19$).

Snow conditions on coyote backtracks.—Although only 7.7% of coyote travel was on compacted snowmobile trails, coyotes did select strongly for naturally supportive snow. Coyotes used less penetrable snow surfaces (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 the track segments on which coyotes were traveling on compacted snowmobile trails (7.69% of total travel distance) were removed from the analysis, coyotes still selected for more supportive (coyote backtrack penetrability mean = 16.68 cm, $SE = 0.78$; non-use track penetrability mean = 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 mean = 64.89 cm, $SE = 2.76$; non-use

track mean = 71.69 cm, SE = 2.91; MRBP, $n = 119$ track pairs, $P < 0.01$) snow conditions. There was no correlation between a coyote track's distance from compacted snowmobile trails and the supportiveness of the snow surface the day the track was made ($n = 119$, supportiveness on coyote backtracks correlated with coyote adjacency to snowmobile trails, $r^2 = 0.02$; supportiveness on non-use tracks correlated with coyote adjacency to snowmobile trails, $r^2 < 0.01$, Figure 4).

Although the mean snow depth on survey routes varied significantly among years on the survey routes (ANOVA, $F = 3.65$, $df = 2, 18$; $P = 0.04$), the supportiveness of the snow surface did not (ANOVA, $F = 0.79$, $df = 2, 18$; $P = 0.69$, Figure 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 (Figure 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 (Figure 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 non-use 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 per km (SE = 3.03) while paired non-use tracks encountered hare tracks at a mean rate of 27.61 tracks per km (SE = 2.57). The difference between the coyote and non-use track hare encounter rates was not significant (MRBP, $n = 119$ pairs, $P = 0.08$) but coyotes tended to encounter hare tracks more frequently on coyote backtracks than non-use 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) of scavenge sites were of snowshoe hares. Eleven of 88 feed sites (13%) were kills, three (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 ($n = 88$, $SE = 52$ m) which was similar to the mean distance coyotes traveled from compacted snowmobile trails in general (368 m, $SE = 44$ m; $t = -0.96$, $df = 204$, $P = 0.92$) and random expectation (339 m, $SE = 30$ m; $t = 0.61$, $df = 204$, $P = 0.55$).

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, $n = 11$, $SE = 241$) 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 ($n = 3$, $SE = 315$ m) from compacted snowmobile trails, which was also farther from compacted snowmobile trails 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, $F = 0.2$, $df = 1, 117$, $P = 0.90$).

A minimum of 49 independent food items were found in 30 analyzed scats (Table 4). Cervid remains made up 61% of all food items detected and twelve percent 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

Winter coyote distribution

Coyotes were consistently present in deep snow areas used by lynx on our study area. We detected coyote tracks on survey routes throughout the winter and at similar elevations as lynx tracks and lynx tracks were commonly encountered on coyote backtracks. Although we detected coyote tracks along survey routes at significantly lower elevations during the month of February, this apparent elevational shift in coyote track detections did not correspond with monthly changes in either snow depth or supportiveness along the same routes. Snow depths increased most during February and the observed elevational shift in coyote track detections may have been a result of reduced detection rates at higher elevations due to frequent snowfalls. The location of coyote backtracks was not influenced by the frequency of snowfall events and the elevation of these digitized backtracks did not vary by winter month.

Coyote association with compacted snowmobile trails

Coyotes used compacted snowmobile trails more than random expectation on our study area although this use represented a relatively small proportion of their overall travel distance. Coyotes traveled on compacted forest roads 5.7% of the time and used dispersed snowmobile trails for 2.0 % of their travel. Coyotes used these compacted snowmobile trails infrequently and traveled on them for relatively short (median = 124 m) distances.

However, backtracked coyotes also used forest roads with unmodified snow for 4.6% of their travel. There was no significant difference between coyotes' travel distance on compacted and uncompacted forest road surfaces. Coyotes did not use roads compacted by snowmobiles more often per track than uncompacted roads nor did they travel on them for greater distances. Compacted snowmobile trails and uncompacted forest roads were similarly available to coyotes and it is possible that coyotes' use of forest roads was, in part, a function of the roads' structure (a cleared travel corridor) and location rather than the snow conditions on them. Dispersed snowmobile trails were often located along man made corridors such as summer foot trails, fire lines, and power lines. We observed that coyotes often used these man made corridors when snow machine trails were absent but unfortunately we did not quantify use of these structures.

Coyotes did not travel closer to compacted snow than random expectation and the distance they traveled from snowmobile trails did not vary with daily, monthly, or yearly changes in snow supportiveness or depth. Coyote tracks on the survey routes were not more likely to be present in areas where snow was generally less supportive and we observed no elevational shift in the habitat use of backtracked coyotes as the winter progressed. Similarly, the distance coyotes traveled from compacted snow (relative to its availability) did not vary by winter month or as snow depths varied over the three years of the study.

Behavioral adaptations may allow coyotes to travel and forage in deep snow environments despite their relatively high foot-load. Both Murray and Boutin (1991) and Crete and Lariviere (2003) found that coyotes used areas with more supportive and shallower snow than was generally available. Similarly, Todd et al. (1981) and Murray et

al. (1994) found that coyotes selected for more supportive and shallower snow than lynx using the same areas. We also found that coyotes on our study area selected for shallower and more supportive snow conditions than were generally available. Although our measurements of snow supportiveness only provided an index of actual coyote track sinking depths, it is clear that shallower and more supportive snow offers significant energetic advantages to traveling coyotes (Crete and Lariviere 2003). On our study area, coyotes largely found these snow conditions where they occurred naturally in forested stands.

Coyote winter food habits

Coyotes did not appear to use compacted snowmobile trails to locate or acquire food on our study area. Neither scavenging sites nor kill sites were significantly closer to compacted snowmobile trails than coyote backtracks in general or random expectation. Snowshoe hare kill sites ($n = 3$) were located an average of 773 m from compacted snowmobile trails.

Although snowshoe hares kills did not comprise a large proportion (3% of documented feed sites) of coyotes' winter diets, we could not assess the degree to which this level of hare predation during winter impacted lynx on our study area. Exploitation competition between coyotes and lynx may actually be highest 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 on their study area. 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. Two of the 3 hare kills we documented on coyote backtracks occurred in late March, near the end of the winter season.

Eighty eight percent of the feed sites found along coyote backtracks were scavenge sites and most of those (74%) were of ungulate carrion. Coyotes in northern snowshoe hare habitat exhibit a clear functional response to changes in hare densities (Todd and Keith 1983, Staples 1995, O'Donoghue et al. 1998b). Scavenged ungulate carrion often becomes coyotes' primary winter food source when hare densities drop to densities similar to those in western Montana (Ozoga and Harger 1966, Nellis and Keith 1976, Todd et al. 1981, Staples 1995, Hodges 2000, Griffin 2004). In southwestern Yukon, Murray et al. (1995) observed coyotes killing one hare per 9.4 km of travel distance when hares were at their cyclic high while we found that coyotes traveled 107.3 km between hare kills on our study area. This is similar to the distance coyotes traveled between snowshoe hare kills in northern Minnesota (127.3 km/hare kill, 509 km surveyed, Berg and Chesness 2001).

MANAGEMENT IMPLICATIONS

The influence of snowmobile trails on coyote movements and foraging success during winter appeared to be minimal on our study area. Although coyotes used compacted snowmobile trails more often than expected, the vast majority of coyote travel was on unmodified snow. Coyotes also used uncompacted forest roads more than expected and traveled on them similarly to compacted snowmobile trails. Coyotes did not generally travel closer to compacted snowmobile trails than expected and snowmobile trails were not used by coyotes to locate or acquire food during winter. The

distance coyotes traveled from compacted snowmobile trails did not vary with changes in snow depth or supportiveness and when coyotes did encounter compacted snowmobile trails they did not travel on them often or for great distances. However, coyotes strongly selected for shallower and more supportive snow conditions than were generally available as they traveled through lynx habitat.

The importance of compacted snow corridors to coyote persistence may differ in areas where naturally occurring snowpacks do not allow coyotes to freely travel and effectively forage. Further study of these relationships in areas having different snow conditions, lynx and hare densities, carrion availability, and recreational snowmobile use patterns are necessary to assess how consistent the coyote behaviors that we documented on our study area are throughout the southern range of lynx.

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Table 1. The mean elevation of carnivore tracks documented along 2200 km of survey route, the probabilities that the species' mean track elevations do not differ from the mean survey route elevation of 1587 m, and track encounter rates in western Montana, 2002-2004.

Species	<i>n</i> (tracks)	Mean track elevation (m)	<i>P</i> ^a	Track encounter rates ^b		
				Jan.	Feb.	Mar.
Coyote	1483	1591	0.73	0.84	0.77	0.94
Lynx	760	1626	0.01	0.53	0.50	0.38
Mtn. lion	20	1533	0.18	-	-	-
Bobcat	13	1610	0.35	-	-	-
Marten	10	1410	0.13	-	-	-
Wolf	5	1387	0.15	-	-	-

^a Independent samples T-test

^b Tracks per km. Encounter rates were not computed for species with sparse records.

Table 2. Summary of data collected along both coyote (322 km) and non-use (358 km) snow tracks between December 2001 and March 2004.

Variable	Coyote tracks	Non-use tracks	<i>P</i> value ^a
	mean (SE)	mean (SE)	
Distance to snowmobile trails (m)	368 (44)	339 (30)	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 uncompacted roads	4.62%	<0.01%	<0.01
Snow depth (cm)	63.71 (2.73)	71.54 (2.92)	<0.01
Snow penetrability (cm)	15.93 (1.46)	18.83 (1.72)	<0.01
Lynx tracks encountered (tracks/km)	0.48 (0.15)	0.38 (0.11)	0.83
Snowshoe hare tracks encountered (tracks/km)	33.08 (3.03)	27.61 (2.57)	0.08

^a MRBP test.

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

	Snowshoe hare	Cervid	Grouse spp.	Red squirrel	Microtine spp.	Other	Total
Kills	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

Table 4. A comparison of independent food items present in 30 analyzed winter coyote scats and feeding sites located along 322 km of coyote back track, western Montana, 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 (<i>spp.</i>)	2%	5%

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

Figure 1. Daily coyote backtracking data overlaid on an (summer) aerial photo using data collected on 10 February 2004 near Seeley Lake, Montana. 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 adjacency distance for that track.

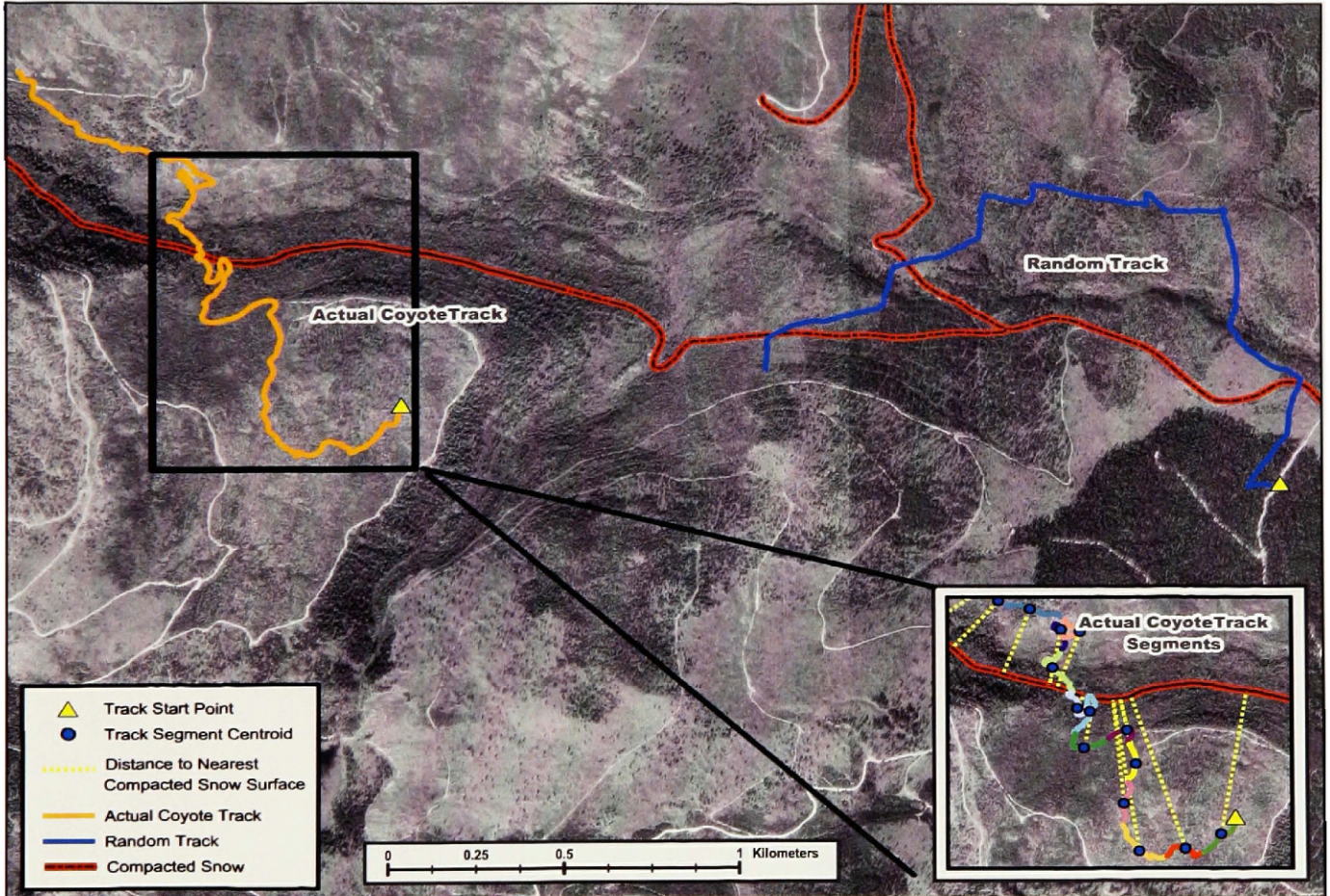


Figure 2. The elevations at which coyote and lynx tracks were recorded along track survey routes between December 2001 and March 2004. The gray line represents the distribution of the elevations of 111 snow survey stations evenly distributed along the survey routes.

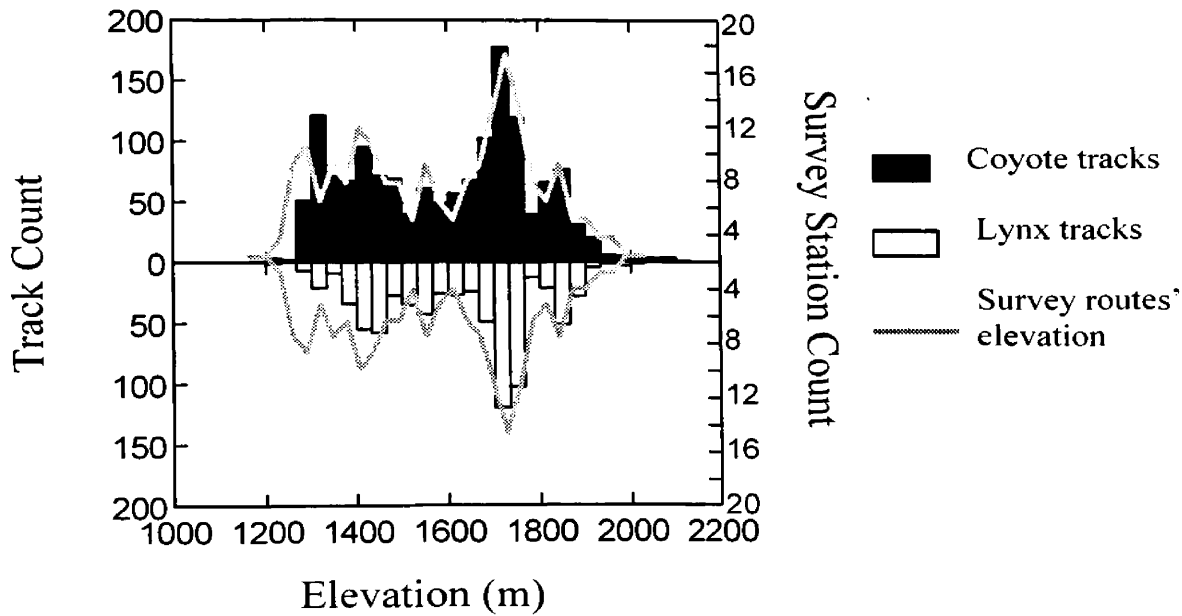
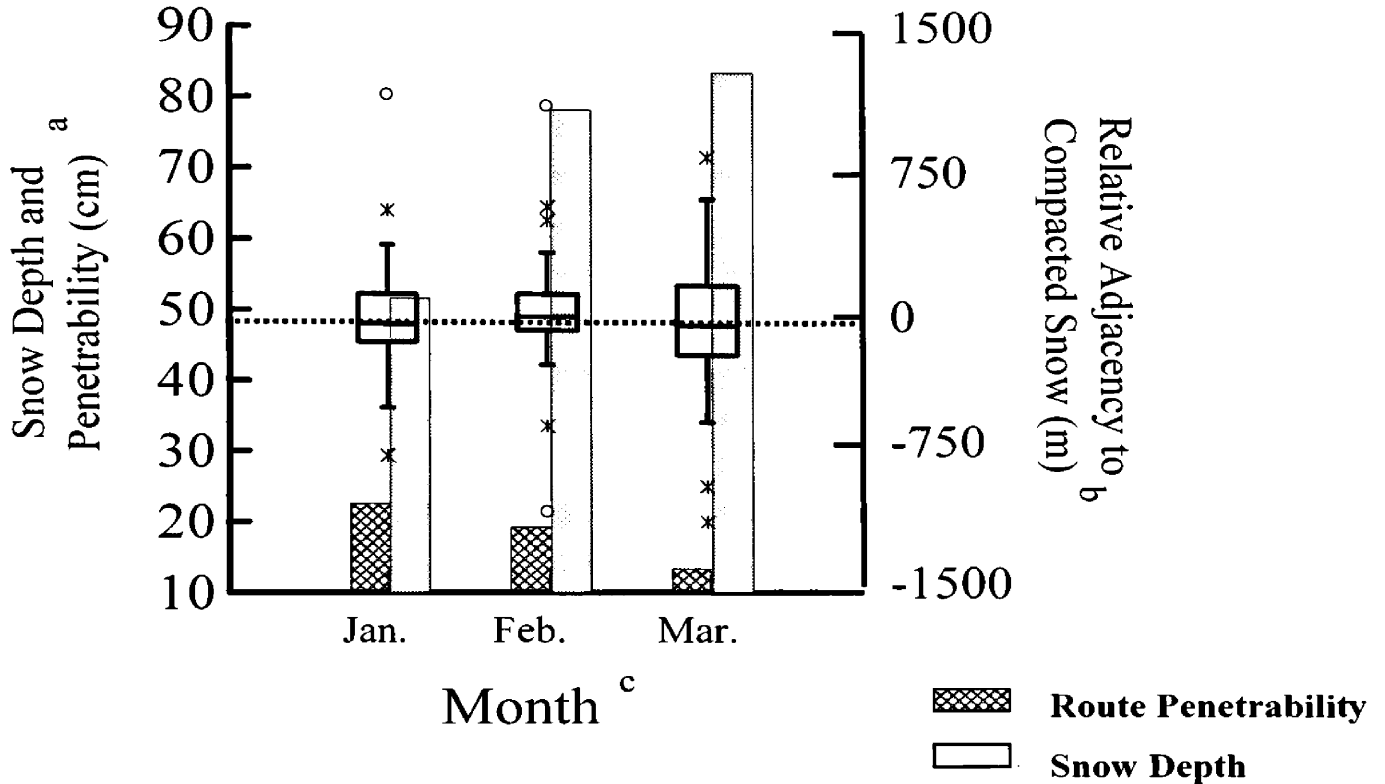


Figure 3. Snow depth, penetrability, and coyote association with compacted snowmobile trails by winter month, 2002 – 2004, Seeley Lake, MT.



- ^a Snow depth data were collected at two permanent USDA NRCS snow data collection stations on the study area. Snow penetrability is the mean of bi-weekly measurements taken at 111 permanent snow survey stations located within the study area.
- ^b Relative adjacency of coyotes to compacted snowmobile trails was computed by subtracting the random track's adjacency distance from the actual coyote track adjacency distance for each track pair.
- ^c Data from all three years of the study were pooled by winter month.

Figure 4. Regressions of the mean distance backtracked coyotes traveled from compacted snow and the snow supportiveness (penetrability) along that backtrack (a) and the paired non-use track (b), western Montana.

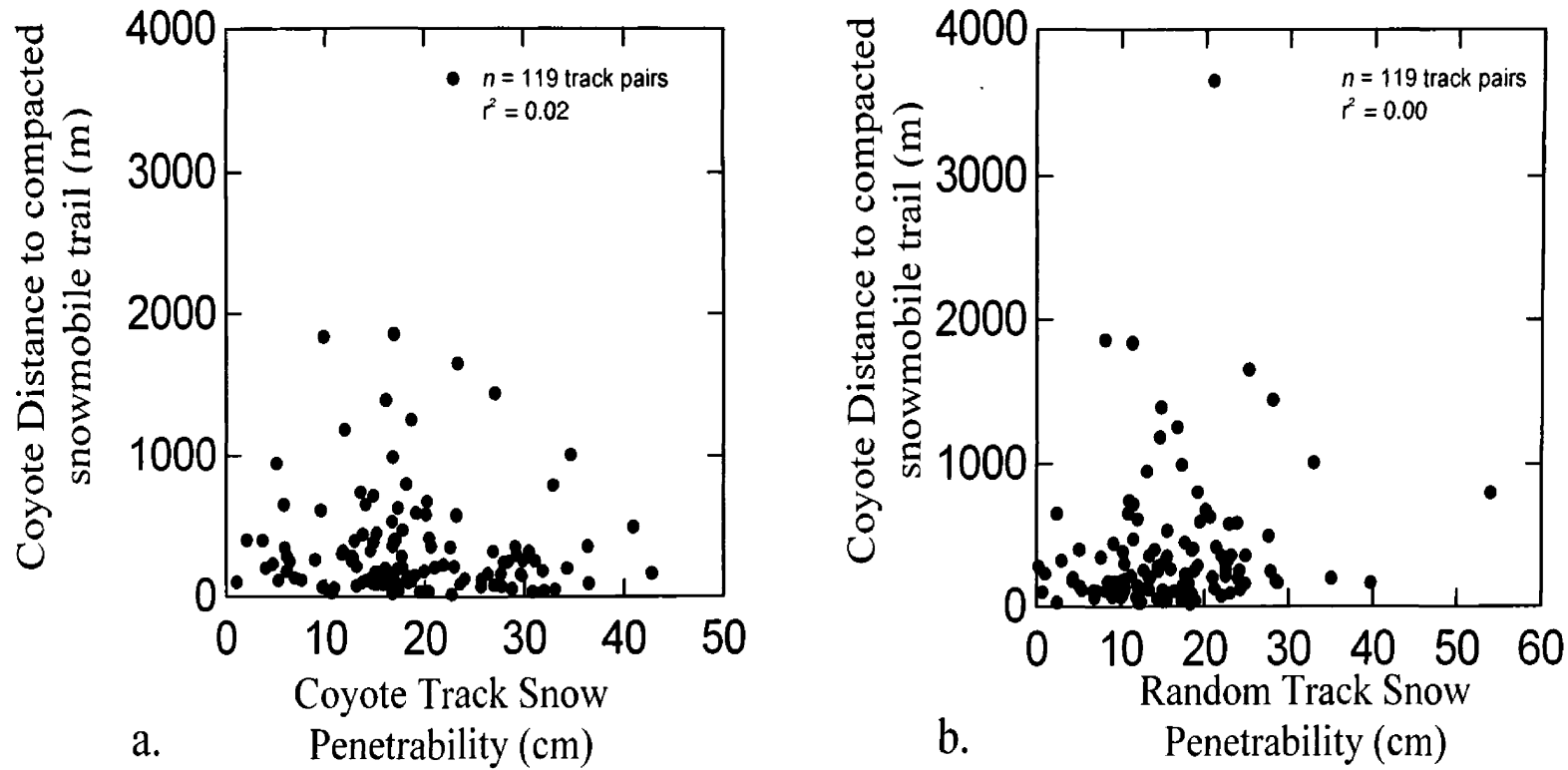
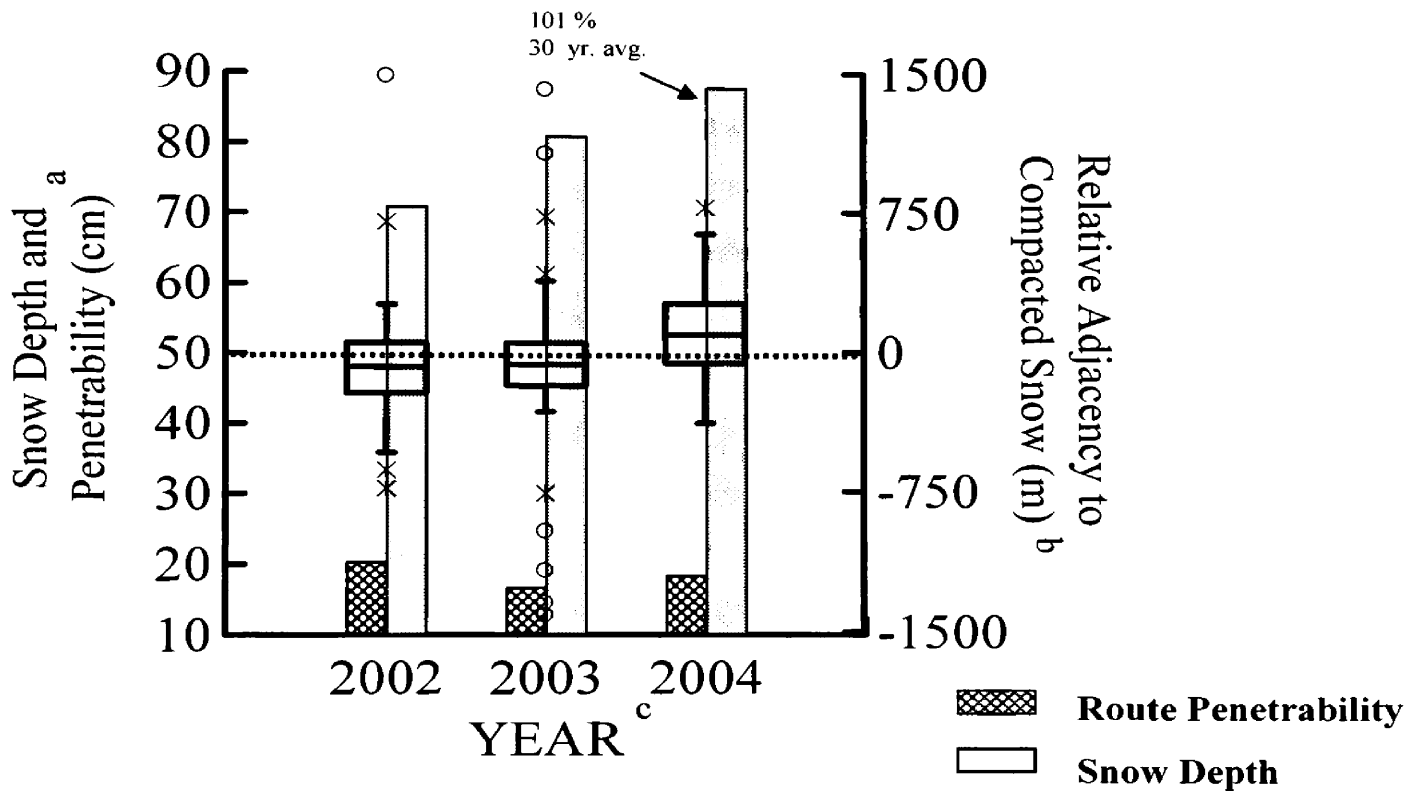


Figure 5. Snow depth, penetrability, and coyote association with compacted snowmobile trails by year, 2002 – 2004, Seeley Lake, MT.



- a Snow depth data were collected at two permanent USDA NRCS snow data collection stations on the study area. Snow penetrability is the mean of bi-weekly measurements taken at 111 permanent snow survey stations located within the study area.
- b Relative adjacency of coyotes to compacted snowmobile trails was computed by subtracting the random track's adjacency distance from the actual coyote track adjacency distance for each track pair.
- c Data from all three years of the study were pooled by winter month.