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Winter space use of coyotes in high-elevation environments: behavioral adaptations to deep-snow landscapes

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Abstract In the last century, coyotes (*Canis latrans*) have expanded their range geographically, but have also expanded their use of habitats within currently occupied regions. Because coyotes are not morphologically adapted for travel in deep snow, we studied coyote space use patterns in a deep-snow landscape to examine behavioral adaptations enabling them to use high elevations during winter. We examined the influence of snow depth, snow penetrability, canopy cover, and habitat type, as well as the rates of prey and predator track encounters, on coyote travel distance in high-elevation terrain in northwestern Wyoming, USA. We backtracked 13 radio-collared coyotes for 265.41 km during the winters of 2006–2007 and 2007–2008, and compared habitat use and movement patterns of the actual coyotes with 259.11 km of random travel paths. Coyotes used specific habitats differently than were available on the landscape. Open woodlands were used for the majority of coyote travel distance, followed by mixed conifer, and closed-stand spruce–fir. Prey track encounters peaked in closed-stand, mature Douglas fir, followed by 50- to 150-year-old lodgepole pine stands, and 0- to 40-year-old regeneration lodgepole pine stands. Snowmobile trails had the most variation between use and availability on the landscape (12.0 % use vs. 0.6 % available). Coyotes increased use of habitats with dense canopy cover as snow penetration increased and rates of rodent and

red squirrel track encounters increased. Additionally, coyotes spent more time in habitats containing more tracks of ungulates. Conversely, use of habitats with less canopy cover decreased as snow depth increased, and coyotes traveled more directly in habitats with less canopy cover and lower snow penetration, suggesting coyotes used these habitats to travel. Coyotes persisted throughout the winter and effectively used resources despite deep snow conditions in a high-elevation environment.

Keywords *Canis latrans* · Coyote · Habitat · Snow compaction · Snow penetrability · Space use

Introduction

Carnivore persistence in deep snow habitats is reliant on their ability to maximize energetic trade-offs (Pouille et al. 1995; Crete and Larivière 2003; Zub et al. 2009). Resource selection is dependent on balancing energy expenditures associated with locomotion versus energy intake from prey while minimizing predation risk. Deep snow and cold temperatures, both characteristic of harsh winter climates, can exacerbate locomotion costs for cursorial predators (Shield 1972; Crete and Larivière 2003) causing a high energetic budget and the need for acquiring substantial food resources. Because of these energetic demands, behavioral and/or morphological adaptations are necessary for a species to effectively travel, hunt, and exploit resources within such deep snow habitats, as demonstrated in Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*; Murray and Boutin 1991; Lesage et al. 2001; Murray and Larivière 2002).

Coyote (*Canis latrans*) encroachment into deep-snow landscapes is a concern because of their association with

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snowmobile compacted trails, and subsequent possible competition with lynx (Murray and Boutin 1991; Koehler and Aubry 1994; Murray et al. 1995; Lewis and Wenger 1998; Bunnell et al. 2006). Although one study found snow compaction did not result in competition between coyotes and lynx (Kolbe et al. 2007), other studies suggest that geographically distinct regions differing in snow profile, predator communities, and expanse of snow compaction resulting from snowmobile use could result in different findings (Bunnell et al. 2006). Canids may demonstrate a higher level of energetic tolerance in response to deep snow (Crete and Lariviere 2003). Behavioral traits facilitating coyote use of deep-snow habitats include their ability to actively select travel paths with shallower, more supportive snow (Murray and Boutin 1991; Kolbe et al. 2007); flexibility in prey selection and feeding habits (Patterson et al. 1998; Bartel and Knowlton 2004); and hunting in groups to acquire larger prey (Gese and Grothe 1995). Studies have observed behaviors of coyotes dwelling in deep-snow habitats (Murray and Boutin 1991; Litvaitis 1992; Crete and Lariviere 2003; Thibault and Ouellet 2005). However, few have examined how coyotes use the landscape from a spatial perspective, and how extrinsic factors such as snow depth, snow supportiveness, prey availability, canopy cover, and habitat type influences space use. Although a recent study investigated the influence of groomed trails on coyote movements (Kolbe et al. 2007), no studies to date have specifically analyzed the influence of groomed trails on habitat use within specific cover types.

Our objective was to document space use by coyotes in high-elevation terrain characterized by long winters and deep snow to determine what variables influenced coyote use of deep-snow environments, and to understand what enables year-round persistence under presumably unfavorable conditions. Accordingly, we examined variables encountered within specific habitats and compared coyote use of those habitats to availability across the landscape. Specifically, we were interested in understanding how snow characteristics (snow depth and supportiveness), canopy cover, habitat type, prey track encounter rates, and predator track encounter rates influenced coyote travel distance in different habitats. We hypothesize that (1) coyotes will select for groomed trails to travel to and from sites that are rich in prey; however, (2) the benefits of increased prey encounters within habitats with high snow penetration could outweigh the costs of travelling on unsupported snow. Here, we will address these competing hypotheses by establishing first whether coyotes preferentially use groomed trails to travel by comparing availability versus use of groomed trails, and by quantifying which habitats are preferentially selected based on characteristics such as snow characteristics (snow depth and

supportiveness), canopy cover, habitat type, prey track encounter rates, and predator track encounter rates. We predict that (1) coyotes will increase their use of snowmobile trails as snow depth increases and snow penetration increases (i.e., snow compaction decreases), (2) coyotes will increase use of habitats with high canopy cover as this canopy cover suspends the snow in the canopy and reduces snow cover under the canopy, (3) coyotes will increase their use of habitats containing high prey abundance, (4) coyotes will decrease their use of habitats containing larger sympatric predators (i.e., wolves, *Canis lupus*), and (5) the pattern of movement (convoluted versus straight-line travel) of coyotes will be influenced by habitat type, canopy cover, snow depth and penetrability, and prey and predator encounter rates, with the hypothesis that coyotes will travel in a more convoluted path while foraging, versus moving in a straight path when traveling between resource patches.

Materials and methods

Study area

We conducted this study on the east and west sides of Togwotee Pass in northwestern Wyoming, USA. The 512-km² study area was characterized by extensive recreational trails and roads (~2 km/km²) maintained year-round. The area was composed of the Bridger-Teton and Shoshone National Forests, and privately owned ranches. Elevations ranged from 1,800 to >3,600 m. The area was characterized by short, cool summers (mean temperature of 12 °C) and long winters (mean temperature of -8 °C). Precipitation occurred mostly as snow, and mean maximum snow depths ranged from 100 cm at lower elevations to >245 cm at intermediate elevations (2,000–2,400 m). Cumulative monthly snow depth for the winter (December–April) averaged 226.6, 149.4, and 228.9 cm in 2006, 2007, and 2008, respectively (Natural Resources Conservation Service 2008). Habitats varied between the east and west sides of the pass, with the east side classified as dry and the west side as wet (US Forest Service 1989). The plant communities on the east side consisted of more open dry meadows, sagebrush (*Artemisia* spp.), and stands of lodgepole pine (*Pinus contorta*), while the west side had more wet meadows and stands of Douglas fir (*Pseudotsuga menziesii*) and spruce (*Picea engelmannii*). On both sides of the pass, the plant communities included cottonwood (*Populus angustifolia*) riparian zones, interspersed with sagebrush uplands and willow (*Salix* spp.)—wetland communities at lower elevations. At intermediate elevations, aspen (*Populus tremuloides*), Douglas fir, and lodgepole pine were the dominant species. Whitebark pine

(*Pinus albicaulis*), spruce, and sub-alpine fir (*Abies lasiocarpa*) were the primary tree species at higher elevations.

The area around Togwotee Pass was a complex ecosystem with a diverse assemblage of predators. Although wolves (*C. lupus*) were extirpated from Wyoming by the 1930s, they have since re-established due to the 1995 re-introduction into Yellowstone National Park (US Fish and Wildlife Service 2006). Other carnivores included cougar (*Puma concolor*), wolverine (*Gulo gulo*), grizzly bear (*Ursus arctos*), black bear (*U. americanus*), bobcat (*L. rufus*), red fox (*Vulpes vulpes*), and pine marten (*Martes americana*). The main competitor and predator of coyotes was the wolf, while coyotes competed with bobcats, lynx, and red foxes for similar prey resources and habitat. Ungulate species found in the area included elk (*Cervus elaphus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*). Pronghorn antelope (*Antilocapra americana*) were in the area only during the summer. Other species included snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), Uinta ground squirrels (*Spermophilus armatus*), black-tailed jackrabbits (*L. californicus*), cottontail rabbits (*Sylvilagus* spp.), ruffed grouse (*Bonasa umbellus*), blue grouse (*Dendragapus obscurus*), deer mice (*Peromyscus maniculatus*), voles (*Microtus* spp.), gophers (*Thomomys* spp.), and various cricetid species. The main prey items in the diet of coyotes on the study area included mule deer (20.1 % occurrence), elk (12.5 %), montane vole (*Microtus montanus*, 12.0 %), and snowshoe hares (8.0 %) as found via scat analysis (Dowd and Gese 2012).

Snowmobiling was extensive during winter, allowing riders to access groomed trails and off-trail riding in and around the study area once snow conditions permitted (late October–May). Trail grooming operations typically began by mid-December with trails maintained through April 1 depending on snowfall. Wyoming's Continental Divide Snowmobile Trail was considered one of the top trail systems in the west (Wyoming Department of State Parks and Cultural Services 2008).

Habitat classifications

For our study area, habitat types were categorized according to vegetation age, stand structure, and species composition based on direct observation by field personnel during travel path sampling (see next section). Due to the scale of our study and the inadequacy of GIS layers currently available for the area, we used a vegetation classification system that combined dominant tree species and the stand's successional stage, representing a distinct 'cover type' (Despain 1990). Much of the variation in stand age was due to historic logging, fires, and other natural

disturbances (e.g., disease, avalanches, high winds). Cover types used a two-letter code paired with a number to classify a continuous patch (e.g., LP for lodgepole pine, 0 for a young stand = LP0). Lower numbers represented younger stands while higher numbers represented older stands; 0 = 0–40 years, 1 = 50–150 years, 2 = 150–300 years, and 3 = 300+ years old. A two-letter abbreviation lacking an attached number represented a climax stand (i.e., final successional stage). Specific cover types in our study area included aspen–conifer (AC), aspen (AS), Douglas-fir (DF0–DF3), lodgepole pine (LP0–LP3), mixed conifer (MC), open woodland (OW), spruce–fir (SF0–SF1), and whitebark pine (WB0–WB2). For the purpose of this study, we also classified groomed trail (GT) as a distinct habitat classification. Using this system, we documented a total of 20 distinct habitat types in our study area.

Coyote capture and backtracking

We captured coyotes in the summer and fall using padded-jaw leg-hold traps with attached tranquilizer tabs. We also captured coyotes during winter by placing road-killed deer and elk carcasses in large open meadows and using snowmobiles with nets, or net-gunning from a helicopter (Gese et al. 1987). Coyotes were radio-collared, ear-tagged, weighed, and released at the capture site; animals were handled without immobilizing drugs. Research protocols were approved by the Institutional Animal Care and Use Committees at Utah State University (#1294) and the USDA/National Wildlife Research Center (QA-1389).

We backtracked radio-collared coyotes during the winter months of 2006–2007 and 2007–2008 following methods of Kolbe et al. (2007) to document habitat use and spatial patterns on snow-compacted routes and non-compacted terrain (i.e., areas not used by snowmobiles). We used data collected during the backtracking to determine how extrinsic factors (prey and predator track encounter rates, snow depth, snow penetration, canopy cover, and habitat type) influenced the distance a coyote traveled within a given habitat. We randomly selected individual coyotes for backtracking using a computer generated randomization sequence (SAS Institute, Cary, NC, USA) to avoid bias and ensure all coyotes were sampled equally. The night before a backtracking session, we located coyotes by triangulation using ≥ 3 azimuths, and their position projected using LOCATE II, v.1.82 (Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). Once the travel path location was verified, a starting location for the actual travel path was used to generate a starting point for the random travel path. These random travel paths we generated allowed for direct comparison to the actual coyote travel paths and thus assess habitat selection. We created random travel paths using digital layers from

previously documented coyote travel paths in a random direction and projection (or “spin”), 2–3 km distance from the actual start point of the individual being backtracked that day. We used a projection distance to ensure sampling independence between the actual and random travel paths (Kolbe et al. 2007).

We began backtracking in the morning after night movements of coyotes had occurred and before the snow column deteriorated. Both actual and random paths were tracked simultaneously by teams of 2 field personnel, taking measurements and recording data for ≥ 3 km of tracking. During each actual or random travel path, we used a hand-held computer (Trimble GeoExplorer, Sunnyvale, California, USA) to collect data in a digital format using a datasheet generated with the computer software GPS Pathfinder Office (Trimble Navigation, Westminster, CO, USA). During each actual or random travel path, pathfinder software recorded locations every 5 s along the travel path. We marked point locations every time a habitat change was encountered, organizing the travel path into distinct but consecutive segments identified by habitat (Kolbe et al. 2007). We recorded canopy cover within each habitat using a densiometer to rank canopy closure into 4 categories: 0–10, 11–39, 40–69, and 70–100 % canopy cover. We recorded prey and predator track crossings as point locations by number and species every time a set of animal tracks crossed a travel path. We measured snow depth at every habitat change and every 200 m along the travel path using a probe (marked in cm) to measure from the snow surface to the ground. We recorded snow penetration whenever the habitat changed and every 200 m along the travel path by dropping a 100-g weight from 1 m above the snow surface and measuring penetration (Kolbe et al. 2007). Once the travel paths were completed, data recorded on the Trimble units were downloaded and imported into GPS Pathfinder Office, then differentially corrected. Travel paths were then smoothed to eliminate bounce or GPS scatter caused by canopy cover or varying topography which can influence location accuracy. We converted all travel paths to ArcGIS files for analysis.

Data and statistical analyses

We measured coyote habitat use at the landscape level by classifying the relative proportion of 20 habitats randomly encountered throughout the study area and comparing the habitats used by coyotes on actual travel paths (Thibault and Ouellet 2005). Randomly encountered habitats were documented along random travel paths in the same manner that habitats were encountered and recorded along simultaneously conducted actual travel paths of a coyote. Distances were referred to as the ‘control’ (random distance) and the ‘treatment’ (actual distance). Due to unequal

sample sizes resulting from differences in habitat encounters between actual and random travel paths, we used Levene’s test to assess the equality of variance in and between habitats. Unequal variances led to the use of a nonparametric Kruskal–Wallis test with Bonferroni corrections of *P* values in R v.2.10.1 (R Development Core Team 2010; package ‘Agricolae’, ‘Kruskal’ procedure) to compare differences across habitat types between the control and treatment groups, as well as differences within habitat types (actual distance traveled by coyotes within each habitat type to distance within control sites). All comparisons with a *P* value ≤ 0.10 were considered significant. All distance means and standard errors (SE) were presented for habitat types within control and treatment groups.

The covariates we hypothesized to be most important in determining how coyotes used the landscape included habitat characteristics (habitat ‘HAB’, canopy cover ‘CC’), snow characteristics (snow depth ‘SD’, snow penetration ‘SP’), predator track encounters (wolf ‘WF’), and prey track encounters (snowshoes hares ‘SSH’, red squirrels ‘RS’, grouse ‘GR’, rodents ‘ROD’, ungulates ‘UNG’). We separated red squirrels from rodents as the squirrels were principally arboreal prey, while most of the rodents were microtines. Ungulates were grouped to improve sample size (e.g., mule deer, elk, and moose). As an alternative to considering all of the prey species additively, we considered another covariate accounting for total prey abundance ‘TotPrey’, in an attempt to conserve degrees of freedom in the analysis conducted below. Because some of the covariates had the potential to be collinear (i.e., strongly correlated), we calculated variance inflation factor (i.e., package ‘car,’ procedure ‘vip’ in R v.2.10.1; R Development Core Team 2010) across covariates prior to model selection (Neter et al. 1996). A variance inflation factor of < 5 indicated a lack of collinearity, and vice versa. We conducted all the analyses below in R v.2.10.1 (R Development Core Team 2010).

Distance traveled within various habitats allowed us to examine movement patterns (convoluted use versus straight line use) and understand the behaviors associated with how coyotes used these habitats. To understand which of the above-mentioned factors could explain variability in the distance covered by coyotes within a given habitat, we compared actual distance traveled within a habitat segment to the shortest possible distance between the entrance and the exit points of that habitat. A distance ratio was then calculated by dividing the shortest possible distance by the actual distance traveled by a coyote, providing us with a proportion that ranged from 0 to 1, (i.e., ‘LRATIO’ = shortest distance/actual distance). This measure might seem counter intuitive since we would usually be interested in the distance covered by a coyote relative to the shortest possible distance; however, we needed this ratio to be constrained

between 0 and 1 in order to be able to conduct beta-regressions. This ratio is a reasonable proxy to the time spend in a given area, and thus can help us learn more about foraging behaviors across habitat types and snow characteristics, and as a function of both predator and prey encounter rates. To address this, we used a modification of the “empirical logistic transform” proposed by Collett (2002) for data that are not discrete. Such modification of the logistic regression is recommended in situations where the dependent variable (LRATIO) is continuous and restricted to the unit interval 0–1, such as proportions or rates. The dependent variable needs to be logit-transformed, such as $\log[\text{LRATIO}/(1 - \text{RATIO})]$, prior to conducting linear regression with an identity link (Warton and Hui 2011). We also included an individual random effect to account for both repeated measures across individuals, and spatial auto-correlation. Even though tracks were measured repeatedly in space within the same home range for a given individual, by accounting for an individual random effect that controls for repeated track measurements within an individual’s home range, we solve both the issue of individual and spatial autocorrelation at once. We used generalized linear mixed models (GLMMs) (Kuznetsova et al. 2013; package ‘lmerTest’, procedure ‘lmer’) to model the effects of various covariates on LRATIO, while accounting for both individual and spatial auto-correlation.

Due to the influence of canopy cover on snowpack accumulation in forests (Bernier and Swanson 1992; Murray and Buttle 2003; Talbot et al. 2006), we assessed coyote habitat use by comparing variables (snow characteristics, prey and predator encounters) documented along actual coyote travel paths using another habitat structure variable, canopy cover, within 4 levels: 0–10, 11–39, 40–69, and 70–100 % (percent’s reflect increased canopy closure). To determine differences in canopy cover use by coyotes, we analyzed the use of various CC measures, as a function of snow characteristics (i.e., snow depth ‘SD’, snow penetration ‘SP’), predator track encounters (i.e., wolf ‘WF’), and prey track encounters (i.e., snowshoes hares ‘SSH’, red squirrels ‘RS’, grouse ‘GR’, rodents ‘ROD’, ungulates ‘UNG’). As an alternative to considering all of the prey species additively, we again considered another covariate accounting for total prey encountered ‘TotPrey’. All explanatory covariates were treated as continuous, and the response variable, CC, was treated as an ordinal categorical variable (CC = 1 if canopy cover was between 0 and 10 %, CC = 2 if between 11 and 39 %, CC = 3 if between 40 and 69 %, and CC = 4 if >69 %). Here, we also used GLMMs (Kuznetsova et al. 2013; package ‘lmerTest’, procedure ‘lmer’) to model the effects of various covariates on a coyote’s choice of canopy cover levels (CC) while accounting for individual auto-correlation.

Model selection

For both sets of analyses described above, we defined a global model testing for additive and interactive effects of all of the covariates of interest, but only when they made biological sense. For analysis where ‘LRATIO’ was the response variable, we specifically considered interactions between habitat and snow characteristics (i.e., canopy cover ‘CC’, snow depth ‘SD’, snow penetration ‘SP’) and predator or prey track encounters (e.g., wolf ‘WF’, snowshoes hares ‘SSH’, red squirrels ‘RS’, grouse ‘GR’, rodents ‘ROD’, ungulates ‘UNG’). For analyses where ‘CC’ was the response variable, we considered interactions between snow characteristics and predator or prey track encounters. Since the presence of predators and availability of prey could strongly depend on snow conditions, interactions between these sets of variables could help explain coyote habitat use.

We used a unique approach to model selection based on parameter significance (confidence intervals and *P* values) alone. Since we are interested in objectively testing hypotheses about which factors are important in explaining coyote habitat use, we simply fit a full model accounting for all biological variables of interest, as well as biologically relevant interaction terms, and base our inference solely on parameter estimates, associated confidence intervals and *P* values from the full model (Bolker 2008). For each estimated parameter (β_i) that appeared in the model, we assessed the precision of each β_i based on the extent to which 95 % confidence intervals for each β_i overlapped zero (Graybill and Iyer 1994), and associated *P* values, to discuss the significance of each covariate effect on the response variable (either LRATIO, or CC).

Results

A total of 15 (4 F, 11 M) coyotes were captured and radio-collared from August 2006 through February 2008. One individual was shot shortly after being radio-collared and 1 young coyote dispersed from the study area, leaving 13 individuals (4 F, 9 M) for sampling. A total of 59 coyote travel paths were followed for a combined distance of 265.43 km, for 1,154 individual habitat segments. We also collected 259.11 km of random travel paths (1,426 individual habitat segments) for comparative analysis. Although 20 distinct cover types were documented throughout the study area, only 18 habitats were encountered by coyotes (DF and DF1 were not used by coyotes). Additionally, one habitat type was encountered by coyotes, but not encountered on our control (random) surveys (WB1).

Coyote habitat selection and use

We compiled a ranking system based on how habitats were used. Assumptions regarding what criteria make a habitat

desirable to a coyote were made to rank each habitat by the number of prey encounters, predator encounters, snow depth, snow penetration, and travel distance ratio (Table 1). Coyotes used open woodlands (OW) for the

Table 1 Habitat use by coyotes (*Canis latrans*) from actual backtrack data in the Togwotee Pass study area, northwestern Wyoming, winters 2006–2007 and 2007–2008

Habitat type	Habitat use (%)	Habitat availability (%)	Prey encounters (#/km)	Predator encounters (no./km)	Snow depth (shallowest to deepest)	Snow penetration (most supportive to least supportive)	Ratio (start at lowest ratio = most to least hunting)
OW (Open woodland)	(1) 25.6	(1) 38.2	(16) 10.6	(18) 1.3	(16) 97.6	(4) 16.9	(16) 0.61
MC (Mixed conifer)	(2) 21.3	(2) 20.8	(6) 34.5	(13) 0.3	(12) 90.6	(13) 21.2	(6) 0.43
GT (Groomed trail)	(3) 12.0	(13) 0.6	(8) 29.0	(1) 0.0	(1) 42.2	(1) 4.9	(18) 0.70
SF1 (Spruce–fir closed stand)	(4) 9.6	(4) 8.5	(5) 36.8	(1) 0.0	(10) 88.6	(17) 24.0	(2) 0.36
LP2 (Lodgepole Pine 150–300 years)	(5) 6.5	(6) 3.4	(13) 22.5	(14) 0.6	(7) 81.6	(6) 17.8	(8) 0.44
SF0 (Spruce–fir open canopy)	(6) 4.9	(3) 9.1	(11) 23.6	(15) 1.0	(14) 91.2	(11) 20.4	(8) 0.44
LP1 (Lodgepole pine 50–150 years)	(7) 4.6	(5) 5.8	(2) 46.8	(1) 0.0	(6) 81.0	(8) 19.9	(13) 0.52
LP3 (Lodgepole pine 300+ w/spruce)	(8) 4.0	(7) 2.6	(10) 24.6	(16) 1.0	(9) 82.4	(15) 22.7	(4) 0.41
SF (Spruce–fir climax w/WBP)	(9) 3.9	(8) 2.6	(14) 18.2	(1) 0.0	(5) 80.1	(16) 23.1	(3) 0.37
AC (Aspen/conifer)	(10) 3.7	(9) 1.9	(12) 22.7	(17) 1.0	(11) 89.0	(10) 20.1	(12) 0.50
LP0 (Lodgepole pine 0–40 years)	(11) 1.6	(10) 1.9	(3) 41.1	(1) 0.0	(17) 104.0	(7) 19.5	(15) 0.54
WB3 (Pole to mature)	(12) 0.7	(16) 0.4	(9) 26.1	(1) 0.0	(2) 49.0	(12) 21.1	(1) 0.29
WB2 (Mature, codominance)	(12) 0.7	(14) 0.6	(15) 15.9	(1) 0.0	(13) 91.2	(18) 24.7	(7) 0.43
AS (Aspen, all age)	(14) 0.5	(11) 1.5	(7) 29.5	(1) 0.0	(8) 81.7	(3) 16.6	(14) 0.53
WB1 (Whitebark pine, pole)	(15) 0.2	(18) 0.0	(17) 5.9	(1) 0.0	(18) 110.0	(14) 22.0	(10) 0.49
LP (Lodgepole Pine 300+ climax)	(16) 0.1	(15) 0.6	(4) 37.9	(1) 0.0	(15) 97.2	(5) 17.0	(17) 0.63
DF2 (Douglas fir, closed, mature)	(17) 0.1	(12) 0.9	(1) 108.1	(1) 0.0	(4) 75.5	(9) 20.0	(5) 0.42
WB (All whitebark, overmature)	(18) 0.0	(17) 0.2	(18) 0.0	(1) 0.0	(3) 59.0	(2) 8.0	(10) 0.49

Ranking system based on assumption from the most desirable habitats (1 = most desirable, 18 = least desirable) reflecting observed encounters on actual travel paths shown in parentheses

majority of their travel distance, followed by mixed conifer (MC), and closed-stand spruce–fir (SF1). Prey encounters peaked in closed canopy, mature Douglas fir (DF2), followed by dense, young lodge pine (LP1), recently burned lodgepole pine (LP0), climax stand lodgepole pine (LP), and closed-stand spruce–fir (SF1). Wolf track crossings were most frequent in open woodland (OW), aspen conifer and 300+ year successional forest lodgepole pine (LP3). There were no wolf tracks crossed by coyotes in the majority of all habitat types (GT, SF1, LP1, SF, LP0, WB3, WB2, AS, WB1, LP or WB). The habitats with the shallowest snow were GT, mature whitebark pine co-dominated with spruce, fir, and lodgepole (WB3) and mature whitebark pine (WB). The most supportive snow was also on GT, followed by mature and AS. The greatest travel distance ratio was encountered in GT, meaning coyotes spent the least amount of time deviating from their projected entrance to exit points in this habitat. A high ratio demonstrated a straighter travel path, compared to a lower ratio which demonstrates convolutions in the travel path. Climax stands of lodgepole pine (LP) and open woodlands (OW) had the next highest distance ratios (Table 1).

When comparing habitats encountered on control paths to actual coyote backtracks, there were three habitat types that were not encountered in either dataset: WB1, DF, and DF1. For comparative purposes, these habitats were removed from the analysis. For the most part, coyote use of habitats ranked similarly to availability. The most readily available habitat across our study area based on our random travel paths was open woodland, followed by mixed conifer, young spruce–fir, and closed-stand spruce–fir (Table 1). Almost all the top ten ranking habitats used by coyotes were also in the top ten habitats available across the landscape (Table 1). However, according to our random path analysis, groomed trail was only available 0.6 % of the time, while it ranked third in coyote use, accounting for 12.0 % of their travel distance, meaning that, proportionally, they used groomed trails 18.5 times more than available. This was notably higher than any other habitat type encountered on the landscape. We further confirmed this result by conducting a Kruskal–Wallis test which indicated a significant difference in distance covered between the control (random distance) and the treatment (actual distance), across habitats ($X^2 = 154.39$, $df = 16$, $P < 0.001$) and between habitats (Table 2). Coyotes used only GT, LP2, and WB3 significantly more than expected, while they used only LP1 and SF0 less than expected (Table 2).

Effect of snow, prey, and predators on distance traveled

We did not experience any issues with collinearity when conducting regression analyses; all variance inflation

Table 2 Kruskal–Wallis test for differences in habitat use between the actual distance covered by the coyotes and the random distance, across 17 habitat types in the Togwotee Pass study area, northwestern Wyoming, winters 2006–2007 and 2007–2008; three habitats were excluded due to lack of encounter on either actual or random travel paths

Habitat	Random			Actual			P
	Mean	SE	n	Mean	SE	n	
AC	0.160	0.109	31	0.286	0.354	34	0.215
AS	0.127	0.084	30	0.181	0.139	38	0.023
DF2	0.171	0.072	13	0.121	0.025	2	0.248
GT	0.038	0.042	47	0.339	0.450	94	<0.001
LP	0.317	0.220	5	0.094	0.110	3	0.101
LP0	0.164	0.118	30	0.166	0.129	25	0.906
LP1	0.173	0.120	87	0.128	0.110	95	0.005
LP2	0.237	0.160	37	0.223	0.261	77	0.041
LP3	0.254	0.198	27	0.325	0.448	33	0.247
MC	0.250	0.231	216	0.254	0.266	222	0.246
OW	0.149	0.097	666	0.202	0.268	337	0.457
SF	0.416	0.397	16	0.338	0.563	31	0.181
SF0	0.239	0.170	99	0.196	0.197	67	0.020
SF1	0.230	0.206	96	0.256	0.247	100	0.881
WB	0.123	0.062	5	0.033	–	1	0.441
WB2	0.232	0.250	7	0.164	0.110	11	0.598
WB3	0.093	0.065	12	0.245	0.236	7	0.305

factors were <5 (Table 3; Neter et al. 1996). Results pertaining to the generalized linear mixed model testing for the effect of all covariates of interest on distance ratio ‘LRATIO’ while controlling for individual and spatial autocorrelation are presented (Table 4). The following covariates and interactions had a significant relationship with LRATIO: rodent track encounters ‘ROD’ and an interaction between snow depth and grouse track encounter ‘SD × GR’ both had a positive relationship with distance ratio (Table 4). However, CC, SP, an interaction between snow depth and rodent track encounters ‘SD × ROD’, as well as an interaction between canopy cover and rodent track encounter ‘CC × ROD’ all had a negative relationship with distance ratio (Table 4). These results indicated coyotes covered less distance (compared to the shortest possible distance and thus spent more time) in habitats with dense canopy cover (Table 4) and similarly when snow penetration increased, suggesting coyotes would tend to cover more distance (i.e., spend less time) in locales where snow penetration is low compared to the shortest possible distance (Table 4), and that coyotes covered less distance (i.e., spent more time) in ‘closed’ habitats (thick cover), and more distance (i.e., less time) in open habitats (Fig. 1). Coyotes tended to cover less distance (i.e., spend more time) in areas with more rodents than needed, especially as canopy cover and snow depth increased (Table 4).

Table 3 Variance inflation factors presented for all variables considered in *A* beta regressions testing for the effects of habitat, snow, and prey characteristics on LRatio (i.e., shortest possible distance by the actual distance traveled by a coyote), and *B* generalized linear mixed models testing for the effects of habitat, snow, and prey characteristics on CC (canopy cover categories)

Explanatory variables	VIF
A beta regressions	
Habitat type 'HAB'	2.07
Canopy cover 'CC'	1.15
Snow depth 'SD'	1.13
Snow penetration 'SP'	1.13
Snow shoe hare 'SSH'	1.31
Red squirrel 'RS'	1.48
Grouse 'GR'	1.03
Rodent 'ROD'	1.17
Wolf 'WF'	1.04
B generalized linear mixed models	
Habitat type 'HAB'	1.45
Snow depth 'SD'	1.13
Snow penetration 'SP'	1.04
Snow shoe hare 'SSH'	1.31
Red squirrel 'RS'	1.46
Grouse 'GR'	1.03
Rodent 'RD'	1.17
Wolf 'WF'	1.04

Habitat use within 4 levels of canopy cover

The results pertaining to the generalized linear mixed model testing for the effect of all covariates of interest on canopy cover 'CC' while controlling for individual and spatial autocorrelation are presented (Table 5). The best performing model indicated SD had a significant but weak negative effect on canopy cover (Table 5), whereby the deeper the snow, the larger the preference for low canopy cover habitats (Fig. 2). Snow penetration had the opposite effect on habitat use (Table 5); and as snow penetration increased, the use of habitats where canopy cover was dense increased as well (Fig. 2). The presence of wolves, snowshoe hares, red squirrels, and ungulates all had a significant effect on canopy cover as well, whereby the higher the encounter rate of wolves and snowshoe hares, the larger the preference for dense canopy covers by coyotes (Table 5; Fig. 2). We also considered biologically meaningful interactions between covariates that revealed interesting results: coyotes did not select for high canopy cover when snow penetration was high, even in the presence of increased track encounters of both rodents and ungulates (Table 5). Similarly, they avoided high canopy cover when snow penetration and wolf track encounters increased (Table 5). Finally, they selected for increased

Table 4 Results pertaining to the best performing generalized linear mixed model testing for the effects of habitat (canopy cover 'CC'), snow characteristics (snow depth 'SD', snow penetration 'SP'), small prey track crossing rates (snowshoe hare 'SSH', red squirrel 'RS', grouse 'GR', rodent 'ROD'), ungulate track crossing rates ('UNG'), and predator track crossing rates (wolf 'WF') on the distance covered by coyotes 'LRATIO'

	β Estimate	SE	<i>t</i> value	<i>P</i> value
CC ^a	-0.3611	0.1733	-2.0840	0.0379
SD	0.0010	0.0019	0.5630	0.5737
SP ^a	-0.0210	0.0099	-2.1230	0.0344
SSH	0.0167	0.0106	1.5690	0.1175
RS	0.0076	0.0349	0.2190	0.8268
GR	-0.3202	0.2333	-1.3730	0.1707
ROD ^a	0.0797	0.0473	1.6850	0.0930
UNG	-0.0492	0.0326	-1.5120	0.1315
WF	-0.0543	0.1313	-0.4130	0.6797
CC × SSH	-0.0027	0.0055	-0.4910	0.6238
SD × SSH	0.0001	0.0002	0.3300	0.7418
SP × SSH	-0.0007	0.0006	-1.1600	0.2468
CC × RS	0.0016	0.0079	0.1970	0.8437
SD × RS	0.0000	0.0004	-0.0370	0.9707
SP × RS	-0.0007	0.0009	-0.7370	0.4615
CC × GR	0.0378	0.1484	0.2550	0.7992
SD × GR ^a	0.0028	0.0016	1.8280	0.0684
SP × GR	0.0000	0.0043	0.0000	1.0000
CC × ROD ^a	-0.1129	0.0554	-2.0380	0.0423
SD × ROD ^a	-0.0017	0.0009	-1.9000	0.0582
SP × ROD	0.0093	0.0064	1.4520	0.1475
CC × UNG	-0.0039	0.0118	-0.3270	0.7436
SD × UNG	0.0003	0.0004	0.9420	0.3468
SP × UNG	0.0012	0.0013	0.9590	0.3383
CC × WF	0.0343	0.0572	0.5990	0.5493
SD × WF	0.0004	0.0014	0.2960	0.7677
SP × WF	0.0008	0.0019	0.4330	0.6650

^a Covariates that had a significant effect on LRATIO

canopy cover when snow depth and ungulate presence increased (Table 5); note that the relationship between canopy cover and snow depth mirrors that of canopy cover and snow penetration (Fig. 2).

Discussion

Coyote habitat use versus availability

Although habitat rankings were similar in regards to what was most and least used between random and actual habitat encounters, our distance comparisons showed proportional habitat use by coyotes did not reflect availability in the landscape; in many cases, coyotes used specific habitats

Fig. 1 Relationship between distance ratio (LRatio) and significant biological covariates of interest (Table 4): relationships between distance ratio and canopy cover ‘CC’ (top left panel), snow penetration ‘SP’ (top right panel), grouse ‘GR’ (bottom left panel), and rodent encounter rates ‘ROD’ (bottom right panel)

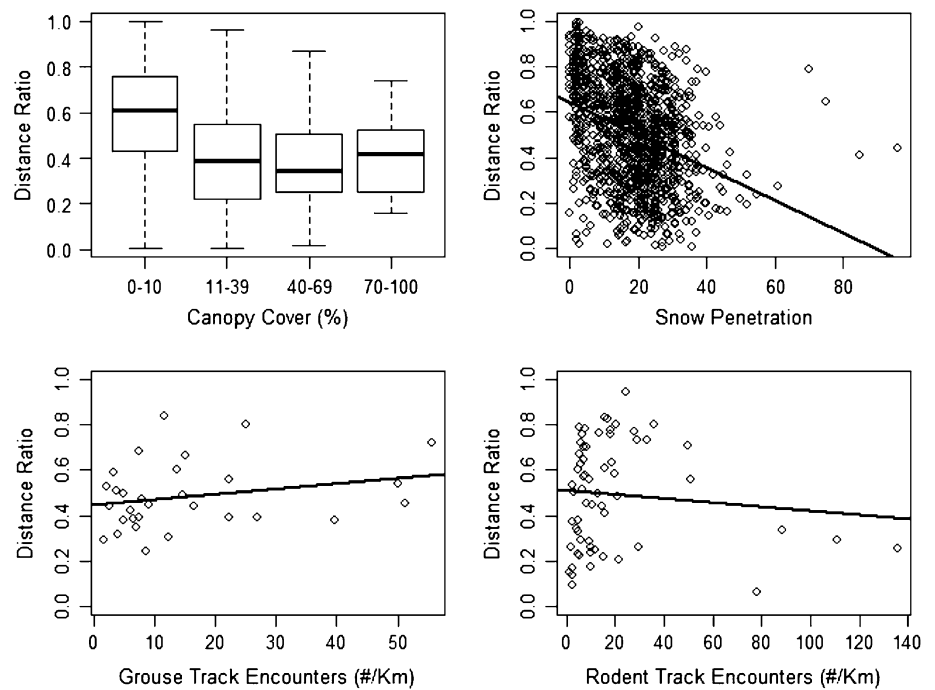


Table 5 Results pertaining to the best performing generalized linear mixed model testing for the effects of snow characteristics (snow depth ‘SD’, snow penetration ‘SP’), prey track crossing rates (red squirrel ‘RS’, grouse ‘GR’, rodent ‘ROD’, ungulates ‘UNG’), and predator track (wolf ‘WF’) crossing rates on canopy cover ‘CC’ selection by coyotes, while accounting for both individual and spatial auto-correlation

	β Estimate	SE	<i>t</i> value	<i>P</i> value
SD ^a	-0.0020	0.0005	-3.7920	<0.001
SP ^a	0.0189	0.0020	9.6270	<0.001
SSH	0.0016	0.0016	0.9720	0.3315
RS	0.0040	0.0037	1.0930	0.2746
GR	0.0169	0.0272	0.6210	0.5348
ROD	-0.0008	0.0039	-0.2150	0.8297
UNG	-0.0004	0.0026	-0.1500	0.8807
WF ^a	0.0508	0.0281	1.8080	0.0709
SD × SSH ^a	0.0001	0.0000	-2.1040	0.0356
SP × SSH	0.0001	0.0001	1.2930	0.1963
SD × RS	0.0001	0.0000	1.3650	0.1726
SP × RS ^a	-0.0002	0.0001	-1.6620	0.0968
SD × GR	0.0000	0.0002	0.1940	0.8461
SP × GR	-0.0008	0.0009	-0.8520	0.3942
SD × ROD	-0.0001	0.0001	-0.9620	0.3363
SP × ROD	0.0001	0.0003	0.3190	0.7498
SD × UNG ^a	0.0002	0.0001	2.8570	0.0044
SP × UNG ^a	-0.0004	0.0001	-3.0150	0.0026
SD × WF ^a	-0.0005	0.0003	-1.7690	0.0771
SP × WF	-0.0006	0.0004	-1.4260	0.1542

^a Variables which have a significant effect on canopy cover selection by coyotes

more or less than were available. Differences in distance spent both between habitats and within habitats indicated that landscape use was not random, but rather an active selection process. Significantly more use of groomed trails, lodgepole pine, and mature whitebark pine co-dominated with spruce, fir, and lodgepole pine suggested that these habitats provided desirable habitat features and associated resources for coyotes.

Coyotes used groomed trails for a high proportion of their travel distance compared to availability (12.0 vs. 0.6 %) suggesting coyotes may be selecting groomed trails which could represent an important behavioral adaptation. Based on our rankings of desirable habitats which considered individual variables and basic assumptions from observed encounters (Table 1), we suspect the reason for the high use of groomed trails compared to availability could be due to a low predator encounter rate, low snow depth, and low snow penetration (of which GT received ‘1’ rankings for all the aforementioned variables). The combined influences of these variables suggested groomed trails presented a novel habitat in which coyotes would experience minimal threat from other predators and low resistance to winter travel.

Additionally, groomed trails received a relatively high ranking for prey encounters (rank = 6 out of 18, mean = 29.0 prey encounters/km). Although other habitats ranked higher, one should consider that, because of low snow depth and high level of supportiveness in this habitat, coyotes could cover more distance in a shorter time, expending less energy and encountering more prey due to

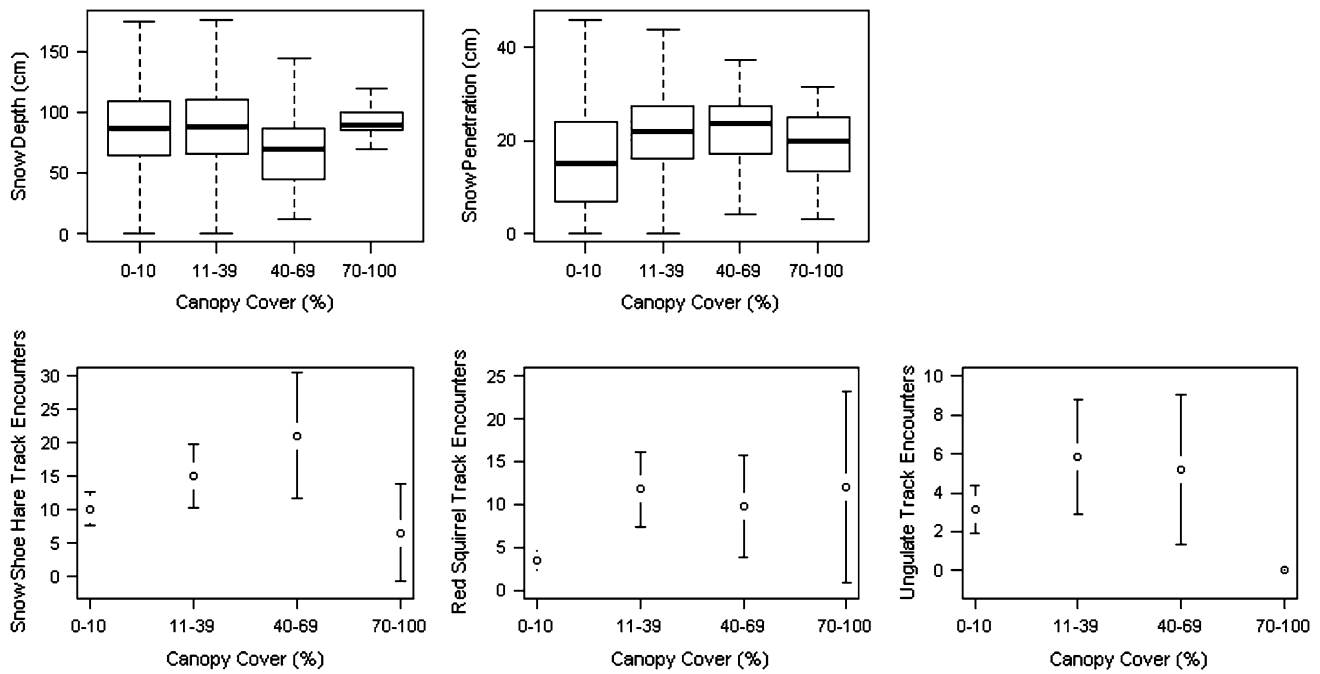


Fig. 2 Relationship between canopy cover and significant biological covariates of interest (Table 5): relationships between canopy cover and snow depth (*top left panel*), snow penetration (*top right panel*),

snowshoe hare track encounter rate (*bottom left panel*), red squirrel track encounter rate (*bottom center panel*), and ungulate track encounter rate (*bottom right panel*)

temporal constraints than compared to other habitats. It is also possible, based on the distance ratio (which showed coyotes were taking more direct travel routes when entering and exiting this habitat), that they may be using groomed trails to primarily travel, possibly to access other habitats with desirable prey or locate kills. Overall, groomed trails had the most desirable traits for any habitat encountered, suggesting that it could be the best habitat for minimizing energy expenditures and maximizing returns.

While snow depth was noticeably low in WB3 habitats and could provide the primary explanation for why coyotes used this habitat more than available (i.e., ease of travel), it should also be mentioned that diet analyses showed a high presence of whitebark pine seeds in the diet of coyotes during certain months (Dowd and Gese 2012). Because of stand structure and maturity of these trees (their ability to produce cones), combined with low snow depths (making access to seed caches more available), access to whitebark pine seeds would be advantageous for coyotes. Whitebark pine seeds are an important food source for several bird and mammal species including black bears, grizzly bears, and red squirrels (Mattson and Reinhart 1997). If coyotes use this resource with minimal energy expenditure and high energetic gain, the observed use versus availability analyses could reflect a preference for older whitebark pine habitats. In addition, lodgepole (especially trees similar in structure and age to LP2) were also found in or adjacent to WB3 habitats. While hunting and traveling in LP2 was

likely easier than in any of the other lodgepole habitats, and could explain coyote use of this habitat, proximity to whitebark pine could enhance coyote selection of LP2 by association when foraging on whitebark pine seeds.

Significantly less use of habitats LP1 and SF0 both suggest there are characteristics making these habitats less desirable for coyotes than other habitats. As suggested above, hunting and traveling maybe have been inhibited in LP1 due to stand structure, as it is categorized as a very dense, even-aged stand. As for SF0, it is possible that a high predator encounter rate (mean wolf encounters = 1.01/km) could account for the difference in use versus availability (Table 2). In North America, interference competition with wolves can be an important factor influencing the distribution and abundance of coyotes (Thurber et al. 1992; Peterson 1995; Berger and Gese 2007).

While open woodlands were ranked first in habitat use by coyotes, they still used open woodlands less than was available on the landscape (use = 25.6 %, $n = 337$; availability = 38.2 %). Several factors likely influenced this avoidance. High levels of snowmobile traffic and human presence (Dorrance et al. 1975; Richens and Lavigne 1978; Eckstein et al. 1979; Hamr 1988; Gander and Ingold 1997) occur in these open meadows, as this open landscape provides off-trail snowmobiling. Low prey track encounters (rank = 16 out of 18) was likely due to the deep snow (rank = 16 out of 18) limiting the availability

of small mammals (Wells and Bekoff 1982; Halpin and Bissonette 1988; Gese et al. 1996b) and hindering coyote movement in deep snow (Crete and Lariviere 2003). In addition, the high incidence of wolf tracks (rank = 18 out of 18, thus least desirable) in the open woodlands increased the likelihood of encountering wolves, and the coyotes thereby possibly avoided this habitat to reduce the risk of intraguild predation (Thurber et al. 1992; Berger and Gese 2007).

Coyote travel distance within habitats

As we hypothesized, distances traveled within habitats were related to snow supportiveness, suggesting the cost of locomotion influenced distance traveled within more energetically expensive habitats. Coyotes traveled further and straighter within habitats with more supportive snow, while coyote travel paths were more convoluted in habitats with less supportive snow. Canopy cover also had this effect on coyote travel distance, indicating coyotes traveled more distance (i.e., had a more convoluted travel path) in habitats with denser canopy cover. Essentially, this indicated that coyotes were using forested habitats (with less compacted snow) to hunt and non-forested habitats to travel. The effect of snow depth on distance traveled (coyotes traveled farther on more supportive snow when snow depths increased) supported this assumption, suggesting coyotes changed their behaviors to minimize energy expenditure in the presence of deeper snow.

Canopy cover and habitat use

The influence of canopy cover on habitat use was perhaps one of the most important variables for predicting prey use by coyotes. Canopy cover provides refuge for prey species and can increase survival (Litvaitis et al. 1985). While prey availability can be higher in forested habitats (Richer et al. 2002), coyotes are known to have the best hunting success in open habitats (Gese et al. 1996b). However, deep snow and compacted surfaces can limit prey availability and hinder hunting success in open habitats during the winter (Halpin and Bissonette 1988) forcing coyotes to adopt other strategies for acquiring prey (Gese et al. 1996a). In this regard, forested habitats could be advantageous to coyotes in our study area, as dense canopy cover yields lower snow accumulation on the forest ground, possibly making prey detection and acquisition more attainable in forested habitats during the winter than other habitats containing deep snow and compacted surfaces. Although it has been suggested that coyotes may be poorly adapted for hunting in forested habitats (Richer et al. 2002), if use of forested habitats is restricted to winter use and coyotes have access to open habitats during the spring, summer,

and fall months, use of forested habitats during the winter may be beneficial. Gese et al. (1996b) reported capture success rates of prey by coyotes to be higher in forested habitats, even though lower capture rates, lower detection rates, and fewer predation attempt rates were demonstrated by coyotes hunting in forested habitats. However, these data were obtained from an area where snow compaction and persistent human disturbance was not an issue during prey acquisition in open habitats (Gese et al. 1996b).

Coyotes in our study area demonstrated versatility to deep-snow conditions based on documented habitat use and behaviors associated with that use. During our study, coyotes appeared to be abundant and effectively used deep-snow habitats despite a light, non-supportive snow column. Coyotes have been shown to use compacted trails to negate the impacts of deep snow (Murray and Boutin 1991; Murray and Larivière 2002; Bunnell et al. 2006). In our study area, open woodland and groomed trails both had open canopies. Similar to our interpretation of hunting in dense canopies, we found coyotes used both open woodlands and groomed trails primarily for travel due their consistency in traveling straight-line projections. Similar to Thibault and Ouellet (2005), as snow supportiveness increased, coyote use of open canopy habitats increased, likely to minimize energy expenditure by traveling on more supportive surfaces. The deeper the snow, the more we observed coyotes using open habitats. This was likely due increased expenditures in dense habitats where snow was less compacted. As hypothesized, habitat use as a function of canopy cover resulted in preferential selection of open canopy covers for travel due to supportive snow characteristics, while dense canopy covers appeared to provide the most profitable strategy for winter foraging.

Our results have management implications for agencies charged with lynx recovery. Whether coyote use of these deep-snow habitats will impact other species in the ecosystem is unknown, but recovery of Canada lynx into these high-elevation areas could be jeopardized by increased competition with coyotes (Bunnell et al. 2006). Use of groomed trails within deep-snow environments may enable coyotes more access to a broader variety and expanse of habitat patches. When considering increased access to forested habitats, forests provide some of the best habitat for snowshoe hares (Litvaitis et al. 1985), and snowshoe hares are a major food item found in lynx and coyote diets throughout North America (Crete et al. 2001). Limiting the expanse of groomed trail systems may minimize coyote encroachment into these deep-snow environments.

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