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Coyote Diet and Movements in Relation to Winter Recreation in Northwestern Wyoming: Implications for Lynx Conservation

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COYOTE DIET AND MOVEMENTS IN RELATION TO WINTER RECREATION IN NORTHWESTERN WYOMING: IMPLICATIONS FOR LYNX CONSERVATION

by

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ABSTRACT

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by

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Increased snowmobile use in mountainous terrain has been highlighted as a conservation concern for some Canada lynx (*Lynx canadensis*) populations. Snow compaction resulting from winter recreation may potentially facilitate access by coyotes (*Canis latrans*) to habitats used by lynx during winter. Increased interactions could result in either exploitation or interference competition between the two species. Two recent, yet geographically distinct, studies showed contrasting findings regarding coyote movements and their use of snow-compacted trails during the winter. These findings suggest coyote association with snow-compacted trails may be regionally specific and dependent upon ecosystem dynamics and snow characteristics. The objectives of this study were to document diet, space use, and movements of coyotes occupying deep snow regions and explore whether a potential existed for increased interactions between coyotes and lynx due to snowmobile activity. We documented seasonal variation in coyote diets using scat

collections to assess dietary overlap with lynx. Coyote resource use within and among habitats containing snowmobile activity was examined using coyote backtrack surveys during two consecutive field seasons in northwestern Wyoming.

Although scat analysis findings suggest dietary overlap was not significant between coyotes and lynx during the winter or overall (all seasons combined), we lacked adequate sample size of lynx scats to determine if dietary overlap occurred during the fall, when coyote use of snowshoe hare peaked (24.1 % of all fall occurrences). Coyote backtrack surveys revealed that coyotes not only persisted in habitats used by lynx throughout the winter, but that snow compaction resulting from winter recreation use appeared to influence coyote movements during the winter months. Microhabitat analysis revealed that snow conditions influenced coyote behaviors and habitat use.

This research provided insight into the impacts of winter recreation on coyote diet and habitat use during the winter months in northwestern Wyoming. In addition, these results have implications for local lynx populations in the southern periphery of their natural range. These results may assist land management agencies in planning and implementing management strategies to enhance lynx recovery, and may be used to guide decisions regarding areas designated for winter recreation and areas proposed for expansion of winter activities.

(170 pages)

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CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

The question of how human recreation impacts threatened or endangered species has long been of concern to biologists and researchers. How a species responds within complex ecosystems (where single alterations to the system may result in a chain reaction causing indirect impacts to be as influential as direct impacts) is also uncertain because of the web of interactions taking place. With outdoor recreation on the rise (Wyoming Department of State Parks and Cultural Services 2008), information is needed to assess how a species will respond to increased human interactions as well as changes to their surrounding ecosystem. Canada lynx (*Lynx canadensis*) are a threatened North American felid species (listed in March 2000) that may be directly influenced by seasonal outdoor recreation, but are thought to be more likely impacted by secondary influences produced as a result of outdoor winter recreation (U. S. Department of the Interior 2000). Interactions between lynx and other predators, especially during the winter months, have been suggested to negatively impact lynx populations in the southern periphery of their natural range (Bunnell et al. 2006).

Coyotes (*Canis latrans*) have been highlighted as a major concern to lynx because of their expansive distribution, high reproductive rate and ability to dominate modified environments (Buskirk et al. 2000, Heilman et al. 2002). Coyotes demonstrate notable versatility to human-altered environments as well as plasticity in their behavior, social ecology and diet (Gese and Bekoff 2004). They are highly adaptive, generalist predators that can compete for resources (food and habitat) both directly and indirectly with multiple predators of smaller or similar body size (Knowlton and Tzilkowski 1979,

Litvaitis and Harrison 1989, Cypher and Spencer 1998, Fedriani et al. 2000, Thompson and Gese 2007). In the case of lynx, it has been suggested that winter recreation (particularly snowmobile use) facilitates coyote activity within lynx habitat resulting in possible competition and potential impacts to lynx recovery in the western United States (Halfpenny et al. 1999, Buskirk et al. 2000, Ruediger et al. 2000, Bunnell et al. 2006). Declines of lynx populations have also been attributed to loss of prey base, competition with other predators, habitat loss and/or fragmentation, and direct human disturbance (Halfpenny et al. 1999, Meaney and Beauvais 2004, Hoving et al. 2005).

Recent findings by Bunnell et al. (2006) support the hypothesis that snow compaction and the presence of hard-packed trails have the potential to break down seasonal spatial segregation between lynx and coyotes (Buskirk et al. 2000, Ruediger et al. 2000). In Utah, Bunnell et al. (2006) found that "coyotes required the presence of packed trails to exploit areas of deep snow" in the Intermountain West, suggesting important findings for lynx conservation and supporting steps taken by land management agencies to limit potential impacts of coyotes on lynx populations (U.S. Forest Service and U.S. Fish and Wildlife Service 2000, U.S. Forest Service and U.S. Bureau of Land Management 2004). In contrast, research conducted in northwestern Montana concluded it was "unlikely that snowmobile recreation increased competition between coyotes and lynx" in their study site (Kolbe et al. 2007). While these two studies were similar in regards to the questions being addressed, several differences existed between them including study design and data collection methods, as well as differences in species composition within the study sites, distribution of snowmobile trails, levels of snowmobile activity, and spatial variability of snow column characteristics representative

of their geographical locations. Based on comparisons of snow depth and snow water equivalent measurements documented on local SNOTEL sites (North Fork Jacko, Burgess Junction, Island Park, Hayden Fork, and Bug Lake) the Montana study area had dense, wet snow resulting in a firm, compacted snow column. Conversely, the Intermountain west study was conducted in locals characterized by high elevation and cold, dry snow resulting in a powdery snow column for much of the winter (Natural Resources Conservation Service 2010).

The question concerning potential influences of increased snowmobile activity and its ability to create snow-compacted corridors, thereby facilitating use and travel by coyotes within habitats used by lynx in winter (Bider 1962, Ozoga and Harger 1966, Murray and Boutin 1991, Koehler and Aubrey 1994, Murray et al. 1995, Lewis and Wenger 1998, Buskirk et al. 2000) remains controversial (Bunnell et al. 2006, Kolbe et al. 2007). Additionally, it has not been addressed whether impacts would differ between geographical regions with varied snow columns, levels of outdoor winter recreation, and predator dynamics. Consequently, large portions of federal land have been mandated to disallow an increase in groomer-compacted trails established for winter recreation use (U.S. Forest Service and U.S. Fish and Wildlife Service 2000, U.S. Forest Service and U.S. Bureau of Land Management 2004) until more concrete information is available to make informed management decisions and minimize impacts across a broader geographical range.

The lynx population in Wyoming is the southernmost naturally occurring population in the contiguous United States, and was listed as a Distinct Population Segment (DPS) to be reviewed for lynx critical habitat designation (U.S. Department of

the Interior 2003). Regulatory measures within critical habitats designations and neighboring areas are continuously being reviewed for implementation in an effort to preserve and restore core areas showing evidence of lynx persistence. This research will help provide insight into what impacts winter recreation has on coyote habitat use and diet during the winter months, and what implications that may have for local lynx populations within Wyoming's DPS. Results will help agencies effectively plan and implement management strategies to enhance lynx recovery, and guide decisions regarding winter recreation use in areas currently open for winter sports as well as areas that are proposed for expansion of winter recreation.

This study was designed to mimic data collection protocols from research previously conducted by Kolbe et al. (2007) allowing for comparison of coyote behavior in relation to winter recreation from a separate geographical region with different snow characteristics. In Chapter 2 we examined the diet of coyotes, as well as lynx diets during the winter months, to determine if dietary overlap was occurring between coyotes and lynx. In Chapter 3 we examined coyote movements in relation to snow compaction and how winter recreation influenced coyote access to different habitats used by lynx during winter. In Chapter 4 we investigated microhabitat use and sequential track data to explain what drives coyote movements and the relationship between habitat patches and coyote use of snow-compacted trails. Chapter 5 discusses management implications derived from results of the study.

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CHAPTER 2

SEASONAL VARIATION OF COYOTE DIETS IN NORTHWESTERN WYOMING: IMPLICATIONS FOR DIETARY COMPETITION WITH LYNX

ABSTRACT

Exploitative competition through resource utilization may occur between coyotes (*Canis latrans*) and other carnivores in ecosystems where multiple predators co-exist. In the southern periphery of Canada lynx (*Lynx canadensis*) range, coyotes may reduce lynx numbers through exploitation competition of the lynx's main prey, snowshoe hares (*Lepus americanus*). There is concern that increased snowmobile activity may enable coyotes to increase their movements into deep snow areas during the winter months, thus avoiding the seasonal shifts previously dictated by snow depth and thereby potentially creating heightened resource competition with lynx. We studied the seasonal variation of coyote diets and the dietary overlap between coyotes and lynx in a 512-km^2 high elevation study area in northwestern Wyoming. Dietary shifts by coyotes were documented during the winter, spring, summer, and fall from August 2006 through June 2008. Although lynx are known to primarily prey on snowshoe hares, lynx scats were also collected to assess their diet for comparative purposes. In total, 470 coyote scats and 24 lynx scats were collected, dried, and analyzed. Mule deer (*Odocoileus hemionus*) was the predominant prey item for coyotes by percent occurrence (20.1%) for all 3 years combined, followed by elk (*Cervus elaphus*, 12.5%), montane vole (*Microtus montanus*, 12.0%), and snowshoe hare (8.0%). Snowshoe hares were the dominant prey item for

lynx, accounting for 85.2% of all prey occurrences. Coyote use of snowshoe hares peaked in the fall (24.1% of all fall occurrences). We found little dietary overlap between coyotes and lynx during the winter when lynx mainly fed on hares and coyotes fed mostly on ungulates. There was not sufficient data for lynx to assess dietary overlap during the non-winter seasons.

INTRODUCTION

Canada lynx (*Lynx canadensis*) were listed under the Endangered Species Act due to a lack of adequate management plans that incorporated monitoring and research to identify potential factors influencing their viability and protection of critical habitats (Ruediger et al. 2000). One of the key research needs for lynx management (Ruggiero et al. 2000, Murray et al. 2008) was the need to gain a better understanding of community interactions and how various predator species may compete with lynx for resources. Ruggiero et al. (2000) reported the number of generalist predators competing with lynx increased from the northern to southern part of their range. Understanding the factors giving generalist predators a competitive advantage over lynx may help determine what actions are needed in current management plans to enhance lynx recovery and population persistence.

Coyotes (*Canis latrans*), one of the most successful generalist predators in North America, have been recognized as a potential competitor with lynx (Buskirk et al. 2000, Ruediger et al. 2000, U.S. Forest Service and U.S. Bureau of Land Management 2004). Not only are coyotes highly adaptable, but they can thrive in human dominated landscapes (Toweill and Anthony 1988, Morey et al. 2007) and demonstrate behavioral

flexibility in their diet to changing environments (Patterson et al. 1998, Bartel and Knowlton 2004). One way to gain insight into what role coyotes play in an ecosystem is to document their food habits in a given environment (Bartel and Knowlton 2004). In addition, how other species may be impacted by coyote movements (Litvaitis and Shaw 1980) and habitat selection (Murray et al. 1994) are equally important when investigating competitive interactions. Because recent findings indicate humans may be facilitating coyote access to habitats used by lynx via increased winter recreation (Ruggiero et al. 2000, Bunnell et al. 2006), biologists have become increasingly concerned with interactions between coyotes and lynx.

Coyotes and lynx are sympatric in areas of Canada and the contiguous United States. In the southern periphery of lynx distribution, coyote populations have remained stable or increased while lynx numbers have declined (Buskirk et al. 2000). Sympatric predators, such as coyotes and lynx, have been able to coexist because morphological differences allowed them to occupy separate niches within an ecosystem and utilize different resources (Krebs 1978). A breakdown of niche separation between two species with similar requirements (typically caused by environmental alterations resulting in a lack of resource partitioning or limited resources) can result in an alteration of habitat selection and access to resources by the subordinate species (Witmer and deCalesta 1986, Ruggiero et al. 2000).

In the past, coyotes and lynx in many regions of North America have occupied different habitats during winter due to the inability of coyotes to travel and effectively hunt in deep snow (Litvaitis 1992, Crete and Lariviere 2003). The morphological adaptation of proportionally large feet compared to body size allows for a low body mass

to foot load ratio for lynx as compared to coyotes (Murray and Boutin 1991), giving lynx a seasonal advantage over other predators when snow limits access to areas where prey are abundant. Under stable conditions, this results in little or no competition during the winter when lynx hunt their main prey, snowshoe hares (*Lepus americanus*; Murray and Boutin 1991). Recently, with increased popularity of winter recreation (particularly snowmobiling), access to some deep snow landscapes have been altered. Multiple studies conducted on southern lynx populations (the outer periphery of lynx core distributions) have found that coyotes are not only using snow-compacted trails, but establishing themselves year-round in areas they previously used only seasonally (Murray and Boutin 1991, Koehler and Aubry 1994, Murray et al. 1995, Lewis and Wenger 1998, Bunnell et al. 2006). In regions of the intermountain west, coyotes can exploit areas of deep snow by using snow-compacted trails to travel and hunt in otherwise inaccessible winter terrain. In these areas, snowmobile activity and trail systems managed for winter recreation have created travel networks for coyotes (Bunnell et al. 2006), leading to a potential breakdown of spatial segregation between coyotes and lynx. Increased coyote presence and altered seasonal habitat use by both species could increase the potential for resource competition.

Competition between coyotes and lynx may occur via exploitation (indirect) competition, interference (direct) competition, or both. Exploitation competition between coyotes and lynx may be documented in an overlap of coyote and lynx diets where both species occur. Several studies (Todd et al. 1981, Todd and Keith 1983, Parker 1986, Quinn and Parker 1987, Murray et al. 1994, O'Donoghue et al. 1997, O'Donoghue et al. 1998, Patterson et al. 1998, Dumond et al. 2001) have identified snowshoe hares as a

major component of coyote winter diets in North America. O'Donoghue (1997) found when comparing coyote, lynx, and snowshoe hare densities in the Yukon, Canada, that lynx were more abundant where coyotes were less dense, rather than where hares were denser, suggesting interactions with coyotes may be more of a limiting factor for lynx population size than the availability of snowshoe hares. Litvaitis and Harrison (1989) suggested that in areas where coyote populations were increasing, they were reducing the prey availability for subordinate species, therefore reducing the carrying capacity for those species.

While biologists speculate that exploitation competition between coyotes and lynx may most likely be a concern during the fall (Aubry et al. 2000, McKelvey et al. 2000, Kolbe et al. 2007) and winter months (Bider 1962, Ozoga and Harger 1966, Murray et al. 1995, Buskirk et al. 2000, Bunnell et al. 2006), few studies have conducted multi-season dietary analyses to determine the variation of coyote diets in high elevation winter recreation areas. Furthermore, no studies have assessed variations in seasonal coyote diets within habitats used by lynx near the southern periphery of their range, aside from winter analyses conducted in western Montana (Kolbe et al. 2007). Where southern populations persist, lynx and snowshoe hares have been reported as scarce and patchily distributed (Murie 1940, Aubry et al. 2000, Hodges 2000, Squires and Laurion 2000), as well as susceptible to generalist predators because of habitat alterations and increased fragmentation (Ruggiero et al. 2000). This makes multi-season dietary analysis important for closing knowledge gaps and understanding dietary relationships between coyotes and lynx in their southern range. Documenting seasonal dietary shifts of coyotes would be useful to managers for determining when and where lynx are most likely to be impacted

by coyote utilization of similar prey items, and if increased coyote populations or snowmobile activity could be detrimental to lynx.

The objective of this study was to determine the seasonal variation and dietary diversity of coyote diets in high elevation terrain and to investigate if dietary overlap exists between coyotes and lynx within habitats where lynx reside in northwestern Wyoming. A secondary objective was to identify during which season(s) dietary overlap was occurring and, for coyote diets, determine whether specific prey items were correlated with snow depth. We hypothesized that coyote diets would reflect a generalist nature during all seasons with greater dietary diversity occurring during the spring and summer months when more prey species were available. We further hypothesized that if snowshoe hares occurred in coyote diets, they would peak in the fall and winter months when other prey items were less available. Similar to studies conducted in the northern part of their range (O'Donoghue et al. 1998), we hypothesized lynx diets would consist primarily of snowshoe hares with a small component of other small mammals, such as red squirrel (*Tamiansciurus hudsonicus*). Dietary diversity of lynx was expected to increase during the spring and summer months.

STUDY AREA

We conducted this study on the east and west sides of Togwotee Pass in northwestern Wyoming, located southeast of Yellowstone National Park and east of Grand Teton National Park. U.S. Highway 26 runs east to west crossing Togwotee Pass and was the only major highway located in the study area. The 512-km^2 study area was

characterized by extensive recreational trails and roads maintained year-round. Most of the study area was in Teton County, although a portion extended into Fremont County. The area was composed of the Bridger-Teton and Shoshone National Forests, plus some large, privately-owned ranches. Elevations ranged from 1,800 m 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 study season (December through April) averaged 226.6 cm in 2006, 149.40 cm in 2007, and 228.9 cm in 2008 (Natural Resources Conservation Service 2008).

Habitats varied between the east and west sides of the pass, with the eastern side classified as dry and the western side as wet. Plant communities on both sides included cottonwood (*Populus angustifolia*) riparian zones, interspersed with sagebrush (*Artemisia* spp.) uplands and willow (*Salix spp*.)-wetland communities at lower elevations. At intermediate elevations, aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were the dominant species. Whitebark pine (*Pinus albicaulis)*, spruce (*Picea engelmannii*), 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 were extirpated from Wyoming by the 1930's, they have since re-established as a result of the 1995 re-introduction efforts in Yellowstone National Park, with at least 4 packs residing near Togwotee as of July 2006 (U.S. Fish and Wildlife Service 2006). Other carnivores aside from coyotes and lynx

included cougars (*Puma concolor*), wolverines (*Gulo gulo),* grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), and pine martins (*Martes americana*). Ungulate species found in the study area included elk (*Cervus elaphus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and a few white-tailed deer (*O. virginianus*). Pronghorn antelope (*Antilocapra americana*) were in the study area during the snow-free season on the east side of the pass. Small mammals comprising the potential prey base for coyotes and lynx were snowshoe hares, red squirrels, Uinta ground squirrels (*Spermophilus armatus*), black-tailed jackrabbits (*Lepus californicus*), cottontail rabbits (*Sylvilagus spp*.), ruffed grouse (*Bonasa umbellus*), blue grouse (*Dendragapus obscurus*), northern flying squirrels (*Glaucomys sabrinus*), deer mouse (*Peromyscus maniculatus*), voles (*Microtus spp.*), gophers (*Thomomys spp*.), and various cricetid species.

The area was classified in 2008 as a lynx Critical Habitat Designation (U. S. Department of the Interior) because lynx have persisted historically and recently, although in relatively low numbers. This Wyoming Distinct Population Segment (DPS) is part of the Greater Yellowstone Area designation, encompassing 110,727 km^2 primarily composed of federal land. Although the area was considered marginal habitat because snowshoe hares were patchily distributed throughout the region, the area was considered to be genetically important for the overall lynx population (U.S. Department of the Interior 2008).

Hunting and trapping of coyotes was extensive throughout the study area. Past records from the U.S. Forest Service and Wyoming Department of Game and Fish

indicated predator removal has been occurring for several decades. Although trapping of lynx was prohibited in the region, local trappers have incidentally caught lynx while trapping for bobcats and coyotes (T. Krause, personal communication).

METHODS

We collected coyote scats opportunistically while backtracking individuals (see Chapter 3), and along designated routes surveyed every two weeks from August 2006 through June 2008. Scat collection routes encompassed approximately 45 km of roads and trails that were surveyed by walking, or driving. During the initial collection, only fresh scats were collected to ensure analysis would reflect seasonal prey consumption during a known time period, while old scats were cleared from the route to ensure they would not be collected at a later date. Because several predator species with similar fecal characteristics were present in the study area, only samples that measured 1.0-3.5 cm in diameter and 12.7-33.0 cm in length, and could positively be identified as coyote scat using track and sign criteria (Elbroch 2003) were collected. If there was any question by field personnel regarding species identification for a given scat, that scat was excluded from analysis.

Lynx scats were collected only during the winter months from October 2005 through April 2008. Scats were collected opportunistically while backtracking individuals later confirmed to be lynx through DNA analysis (McKelvey et al. 2006). Because of their scarcity, lynx scats were rarely detected during the spring, summer and fall without snow cover for tracking or other sign to confirm their presence. All lynx scats were

collected in the same spatial area as the coyote scats, and were collected and analyzed using the same procedures outlined for coyotes.

All scats were labeled with a reference number, date and Universal Transverse Mercator (UTM) location, then air dried, separated and analyzed by hand. Prey species were identified using reference guides for bone fragments and hair identification (Glass 1973, Adorjan and Kolenosky 1969, Moore et al. 1974, Elbroch 2006). Prey items were estimated by volume to the nearest 10%, with items <10% being excluded from analysis to avoid overestimation of small prey items (Martin et al. 1946, Weaver and Hoffman 1979). Results of scat analyses were presented as frequency of occurrence and percent occurrence. Frequency of occurrence was calculated by dividing the number of scats in which a food item is found by all scats in the sample. Percent occurrence was calculated by dividing the number of times one food item or prey species occurred in a sample of scats by the total number of occurrences of all food items found in that sample (Kelly 1991).

Scats were sorted by season and year to determine variations in prey occurrence for coyotes. Seasons were defined as: spring (1 Apr-30 Jun), summer (1 Jul-31 Aug), fall (1 Sep-30 Nov), and winter (1 Dec-31 Mar). Scats were not collected during all 4 seasons each year, but were collected for 2-3 seasons per year over the course of 3 years. Horn's similarity index (Horn 1966) was used to determine dietary overlap between coyotes and lynx. The Shannon-Weaver diversity index (Colwell and Futuyma 1971) was used to estimate dietary diversity of coyotes and lynx. A Student's t-test was used to compare differences in diversity by season between the two species.

We examined the variation of the main prey items (ungulates, rodents, snowshoe hare, whitebark pine seeds) in the coyote's diet in relation to snow depth using regression analysis for all months with available snow depth data. To provide a more complete account of monthly snow depth averages than was available from snow depth data compiled from backtrack data (Chapter 3), snow depth data used for analyses was obtained from the Bridger-Teton National Forest, Backcountry Avalanche Hazard and Weather Forecast historical weather data for the Rendezvous Bowl site (U.S. Forest Service 2008). Rendezvous Bowl was the closest site available to the study location, located 54 km southwest of our study area, at the same elevation and general aspect as our study area. Accumulated daily snow depths were averaged for each month.

RESULTS

We collected 470 coyote scats throughout the study area (winter: 224, spring: 103, summer: 92, fall: 50). We collected 24 lynx scats from 5 individuals near Togwotee Pass while conducting snow tracking during winter. All prey items found in lynx scats were also found in coyote scats (snowshoe hare, grass, red squirrel, coyote hair).

For all 3 years combined, mule deer was the predominant prey item by percent occurrence (20.1%) in coyote scats, followed by elk (12.5%), montane vole (12.0%), and snowshoe hare (8.0%). Occurrence of ungulates peaked in the winter (56.3% of all winter prey occurrences) and spring (44.9% of all spring prey occurrences). Occurrence of rodents peaked in the summer (69.4%) while lagomorphs, mainly snowshoe hare, peaked in the fall (24.7%) and spring (9.5%). Percent occurrence of snowshoe hare was highest

during the fall (22.1% of all fall occurrences) and least during the winter (3.5% of all winter prey occurrence). Red squirrel was primarily found during the summer (11.6% of all summer occurrences) and winter (7.3% of all winter occurrences) (Table 2.1).

Among coyote scats, percent occurrence of ungulates increased during the winter from 44.0% in 2007, to 65.5% in 2008, as did percent occurrence of rodents in the summer months from 65.7% in 2006, to 72.0% in 2007. Lagomorphs, however, showed a decrease in percent occurrence during the fall from 31.8% in 2006 to 13.8% in 2007. From winter 2006-2007 to winter 2007-2008, occurrence of snowshoe hares in coyote scats almost doubled from 2.7% to 4.1%. Percent occurrence of red squirrels increased during the summer months from 4.2% in 2006 to 22.4 % in 2007 (Fig. 2.1).

Of notable interest was a peak in the occurrence of whitebark pine seeds in coyote scats during the winter of 2006-2007 (Fig. 2.2). Snowfall was below average during that winter (Fig. 2.3), and ungulate prey occurrence in coyote scats was 21% less than during the winter of 2007-2008 (Fig. 2.1). Whitebark pine seeds were the second highest food item of all winter food occurrences, accounting for 15% of occurrences from 2006 – 2008. Of all winter food items, mule deer occurred most frequently, followed by whitebark pine seeds (15%), elk (14.6%), moose (10.8%), red squirrels (7.3%), voles (5.4%), and snowshoe hares (3.5%). Dietary diversity for coyotes was highest during the spring, followed by the fall, winter, and then summer (Table 2.1).

Of 24 lynx scats, there were a total of 27 prey occurrences. Snowshoe hares accounted for the majority of prey occurrences (85.2%), followed by grass (7.4%), red squirrels (3.7%), and coyote (3.7%). Horn's similarity index did not show significant dietary overlap between coyote and lynx diets during the winter (Table 2.2). Without a

sufficient number of scats collected during the fall months for lynx, we were not able compare the diet between the two species during the fall season. However, we hypothesize that the greatest potential for overlap would have occurred during the fall when occurrence of snowshoe hare peaked for coyotes, and secondarily during the spring when coyotes were still persisting in high elevation terrain but snow was limiting the prey species available. When comparing dietary diversity, coyotes showed a significantly greater dietary diversity than lynx during the winter ($t = 2.84$, $df = 210.62$, $P = 0.0049$; Table 2.2).

The monthly cumulative snow depth varied with an average monthly depth of 226.6 cm in 2006, 179.1 cm in 2007, and 228.9 cm in 2008; both 2006 and 2008 were above average snow years (Fig. 2.3, Natural Resources Conservation Service 2008). When comparing specific prey items (by percent occurrence) to daily snow depth averaged by month, there were significant correlations between two winter prey items found in the coyote's diet: moose ($r^2 = 0.693$, $df = 11$, $P = 0.040$) and snowshoe hare ($r^2 = -0.854$, $df = 11$, $P = 0.008$). A positive correlation existed between snow depth and moose, such that as snow depth increased the occurrence of moose in the diet of coyotes increased. A negative correlation was shown between snow depth and snowshoe hare, such that as snow depth increased the occurrence of snowshoe hare in the diet of coyotes decreased. There was not sufficient data to determine if correlations existed between prey items in lynx winter diets and monthly snow depth.

DISCUSSION

Coyote Food Habits

As expected, diversity indices indicated coyotes in our study area acted as generalist predators with high dietary diversity. Occurrence of snowshoe hare in coyote diets occurred primarily in the fall and rarely in the winter compared with other prey items. The shift in percent occurrence of snowshoe hares we documented was similar to findings by O'Donoghue et al. (1998) who reported coyote predation on hares declined by 90% during January, February, and March from higher levels observed in the fall. Staples (1995) found snowshoe hare occurrence in coyote scats was twice as prevalent during snow-free months. Our results showed occurrence of snowshoe hare remains in coyote scats to be at their lowest during the winter months, and occurrence of snowshoe hare in coyote scats decreased during winter months with deeper snow likely reflecting availability of other prey (e.g., ungulate carcasses) and decreased use of snowshoe hare (Fig. 2.2). In regards to percent occurrence of winter prey, our findings were similar to Kolbe et al. (2007) who found cervids to be the primary prey item detected through scat analysis and coyotes rarely preyed on snowshoe hare during the winter in Seeley Lake, Montana.

Our results differ from other studies conducted in nearby areas, but these studies were all conducted at lower elevations and prior to wolf recovery. Coyote diet studies conducted near Togwotee, including those in Jackson Hole (Murie, 1935, Weaver 1977, Wigglesworth 2000), Grand Teton National Park (Murie 1935), and Yellowstone National Park (Murie 1940), reported elk and voles to be the highest occurring prey items

in coyote scats. The high occurrence of mule deer and moose in our analysis suggests a difference in the availability of those species in the study area during the winter months from 2006 through 2008. Whether the higher occurrence of mule deer and moose in our dietary analysis are the result of direct predation of weakened animals impacted by harsh winter conditions or scavenging events from wolf kills is unknown. Coyotes have been shown to be more successful at killing ungulates in deep snow than in shallow snow (Ozoga and Harger 1966, Gese and Grothe 1995). Although wolves have recently established in the area, information regarding the effects of a trophic cascade in the higher elevations of this region have not been documented. However, during the course of the study, coyotes were documented scavenging on wolf kills of elk and moose on several occasions (J. Burghardt, unpublished data), possibly accounting for the high occurrence of moose in the coyote scats.

The high occurrence of mule deer compared to other ungulate species may reflect niche relationships between coyotes and wolves, snow depth, and/or proximity to elk feeding grounds. During the winter, the majority of elk that summer on Togwotee Pass migrate to feeding grounds outside the study area. Therefore, during the winter fewer elk remain in deep snow habitats as an available food source, thereby limiting encounter rates within our coyote territories and leaving mule deer as the dominant ungulate species available for predation. In northwestern Montana, Arjo (1998) found that during winter, scats from coyotes residing inside wolf territories contained more deer and lagomorphs than coyotes found outside wolf territories shortly after wolf colonization. Arjo (1998) speculated this could have resulted from increased coyote group sizes in the study area compared to previous years, which would have enabled them to hunt as a pack rather than

individually. Although coyote pack sizes were not quantified in our study, observations indicated coyotes travelled in groups consisting of >2 individuals. If coyote numbers within our study area were high compared to previous documentation because of wolf presence, and able to hunt as a pack rather than individually, this may account for the increase of mule deer in the coyote diet.

Coyotes have demonstrated prey switching when one resource becomes depleted from an ecosystem (Bartel and Knowlton 2004, Patterson et al. 1998). Prey switching may explain the importance of whitebark pine seeds during the winter of 2006-2007 when it accounted for 33% of winter occurrences, whereas in the winter of 2007-2008 it accounted for only 7%. The only substantial difference in prey consumption during those same winters was the occurrence of snowshoe hares, which nearly doubled in the year that whitebark pine seeds occurred less frequently. Profitability models predict that when a predator encounters a profitable prey at a high rate, less profitable items will be omitted from the diet. Profitability takes into account energy expenditure and risk required to locate and obtain prey (Krebs 1980). Being a low snow year, possibly during the winter of 2006-2007 coyotes were able to more readily access whitebark pine seed caches made by red squirrels which required lower energy and risk than in the following year when deep snow might have prohibited them from excavating up caches. Use of whitebark pine seeds by coyotes has not been previously documented and other predator species (particularly grizzly bears) in this ecosystem have been shown to rely on whitebark pine seeds (Kendall 1983, Mattson and Jonkel 1990). Coyote use of whitebark pine seeds could be important for managers to consider in future management plans.

In northwestern Montana, Kolbe et al. (2007) found snowshoe hares composed only a small proportion of coyote winter diets, and their predation rate of hares would be insufficient to meet the energetic needs of a coyote when few other resources were available. They concluded there was a lack of evidence to support exploitation competition between coyotes and lynx during the winter months. Our results showed similar findings with regards to the proportion of snowshoe hare found in the winter diet of coyotes. However, in our study area elevated occurrences of snowshoe hare in coyote diets during the fall and spring suggest those may be more critical times to evaluate potential exploitation competition between coyotes and lynx, especially in areas where snowshoe hare abundance is low. As competition is a reflection of prey abundance and diet breadth, measuring prey abundance and assessing snowshoe hare population status would be important considerations when exploring potential competition in the future. Another factor to consider is differences in predator dynamics between the two study areas. When comparing carnivore track surveys, while Kolbe et al. (2007) documented relatively few coyotes in his study area (0.67 coyotes/km) and an abundance of lynx (0.35/km), we documented an abundance of coyotes (2.88 coyotes/km) and few lynx (0.02/km). Therefore, even though snowshoe hare only accounted for only 8% of overall coyote diet, the number of snowshoe hares consumed by the higher density of coyotes in our study area could be substantial.

Finally, it should be mentioned that high track crossing rates of snowshoe hares by coyotes (see Chapter 3) could indicate a potential for future prey specialization or prey switching should other prey items become limited. Without long-term documentation of predation rates of snowshoe hare by coyotes and a thorough knowledge of snowshoe hare

population dynamics, distribution, and status in our study area, we cannot determine whether there would be a sufficient hare population to support the energetic needs of the local coyote population, thereby becoming an issue when considering exploitation competition between coyotes and lynx.

Lynx Food Habits

Similar to studies on lynx populations in other parts of their southern range, lynx from our study area showed a high occurrence of snowshoe hare in their winter diet (Koehler 1990, Parker et al. 1983), with low dietary diversity during the winter (Squires and Ruggiero 2007). This supports conclusions by Aubry et al. (2000) who suggested that regardless of geographic location, snowshoe hare are the dominant prey item for lynx. Aubry et al. (2000) also suggested a dominant occurrence of snowshoe hare within lynx scat is independent of local hare population status, such that if hare populations are low, while dependency on alternate prey may increase, lynx will continue to show a dominant dependency on their major prey (characteristic of their specialist nature). This would result in fewer individual lynx being supported by limited hare availability.

Our data lacked adequate sample size of scats during all the seasons, other than winter, to determine seasonal shifts in lynx dietary diversity. However, both Koehler (1990) and Parker et al. (1983) found the dependency on alternate prey items to be most during the summer months, regardless of snowshoe hare availability. Koehler (1990) found annually red squirrel was the second most frequently occurring prey item in lynx scats. During a study conducted in north-central Washington, scat analysis showed snowshoe hare accounting for 79% of the diet, and red squirrel accounting for 24 % (n =

29 scats; Koehler 1990). In the southern Canadian Rockies, one study documented 52% snowshoe hare and 30% red squirrel in lynx diets during the winter (frequency of occurrence), by investigating kill sites found during snow tracking (Apps 2000). Regardless, studies on lynx diet using scat analysis have shown winter as the season when lynx prey most heavily on snowshoe hare likely due to limited availability of alternate prey species (Aubry et al. 2000). Whether located in core habitats where conditions are ideal or on the outer periphery of suitable habitat, results continue to reveal this pattern (Aubry et al. 2000).

Fluctuations in the snowshoe hare cycle could alter lynx dependence on alternate prey items and shifts in seasonal dietary diversity, bringing about additional stress or increased competition. Unfortunately, evidence of any long-term cycle of snowshoe hares near Togwotee Pass is unknown. In addition, data on annual fluctuations in hare abundance and subsequent lynx diets and the role of prey population fluctuations is unknown. Recent evidence suggests that although patchily distributed, habitats currently exist that support snowshoe hare in the region (N. Berg, unpublished data), and could theoretically continue to support a lynx population in northwestern Wyoming (Squires and Laurion 2000). Similar to Squires and Ruggiero (2007), we found that although lynx may prey on alternate prey species, such as red squirrels, to supplement their diet, snowshoe hares continue to be the predominant food. The main question is if there is a sufficient prey base available, and if the dietary analysis shows a reliance on snowshoe hares, what other factors might be influencing the long-term population viability of lynx in this region.

Cougars, wolves and bobcats are other predators aside from coyotes that may influence lynx behavior and population viability in northwestern Wyoming. Cougars have been documented killing lynx during the late fall and early winter in western Montana (Squires and Laurion 2000). However, competition between cougars and lynx would most likely take place during the non-snow months in the form of interference competition, as snow limits cougar mobility and utilization of habitats used by lynx during winter (Buskirk et al. 2000). The increased presence of wolves has been suggested to have a potentially positive effect on lynx numbers, as wolf presence is thought to reduce the number of coyotes. Berger and Gese (2007) found coyote abundance in Jackson Hole, Wyoming, was being limited by competition with wolves. Although most researchers argue direct competition between wolves and lynx is unlikely due to variation in size and niche requirements, field personnel documented wolves chasing a lynx near Togwotee Pass, Wyoming. As of yet, there is little evidence to suggest either positive or negative impacts on lynx resulting from wolf establishment in the area. Alterations to ecosystem dynamics will likely continue to fluctuate for the next several years until the system stabilizes in the presence of wolves.

Bobcats and lynx are largely allopatric although there have been studies showing lynx population declines in areas where bobcat populations have increased (Parker et al. 1983, Hoving et al. 2003). Regardless, the relationship between lynx and bobcats is poorly understood. Characteristically larger and more aggressive than lynx, bobcats may be significant competitors of lynx, capable of both interference and exploitation competition (Buskirk et al. 2000). However, snowfall seems to be a factor influencing

distribution and niche use by bobcats (Parker et al. 1983), therefore limiting seasonal resource overlap with lynx in our study area.

Dietary Competition

Our data suggest there is little dietary overlap between coyotes and lynx in northwestern Wyoming. Exploitation competition between coyotes and lynx is difficult to ascertain without direct observations of interactions, or recording species responses to manipulated conditions in a controlled environment. The ability to classify competition between coyotes and lynx in a natural setting can only be achieved by identifying specific variables to determine the degree of overlap in resource utilization, thereby implicating whether coyotes could be considered detrimental to local lynx populations. Unfortunately, because coyotes are so adaptable and change their feeding habits depending on local conditions, determining cause and effect relationships are more likely dependant on annual fluctuations in prey. Several variables should be considered when trying to determine whether competition is truly occurring and outcomes resulting from that competition. In our study area, understanding how wolves will influence the system, what trophic cascades will occur, how snow compaction influences prey availability and coyote feeding behaviors, and documenting snowshoe hare population trends would assist in determining the long-term future viability of lynx populations in northwestern Wyoming.

MANAGEMENT IMPLICATIONS

Our results indicate coyotes were not competing with lynx for food during the winter in northwestern Wyoming from August 2006 through June 2008. Coyotes did persist in high elevations through the winter despite deep snow, and because coyotes have been shown to prey switch and alter their behaviors due to shifts in local dynamics (as demonstrated in their use of whitebark pine seeds), the possibility of future dietary overlap occurring in the winter should not be ruled out. Additionally, further information is needed to determine if dietary overlap is occurring between coyotes and lynx during the fall, as hypothesized, and if other types of competition are occurring (i.e., spatial or temporal avoidance, direct mortality). Dietary overlap in the fall between coyotes and lynx could indicate the potential for coyotes to utilize snowshoe hares more extensively during the winter months under favorable conditions. Evidence of avoidance behaviors by lynx or interference competition could be detrimental to lynx populations and require management actions. Future research efforts should focus on determining whether resource overlap is occurring between coyotes and lynx by investigating lynx habitat use compared to coyote presence and prey abundance. We also suggest continued monitoring of coyote diets and coyote habitat use in high elevation terrains to detect dietary shifts, determine changes to the ecosystem, and determine if future management changes are needed in core lynx areas for lynx population persistence.

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Table 2.1. Seasonal prey occurrence in coyote scats for winter (Dec-Mar), spring (Apr-Jun), summer (Jul-Aug), and fall (Sep-Nov), Togwotee Pass study area, Wyoming, 2006-2008.

SPECIES	Winter n (%)	Spring n (%)	Summer n (%)	Fall n (%)	Total n	Frequency of occurrence (%) n=470 scats, 650 occur.	Percent occurrence (%) n=470 scats, 650 occur.
Ungulates							
Mule deer	77 (29.6)	42 (21.9)	6 (5.0)	6 (7.8)	131	27.9	20.2
Elk	38 (14.6)	27 (14.1)	7 (5.8)	9 (11.7)	81	17.2	12.5
Moose	28 (10.8)	11 (5.7)	0 (0)	0 (0)	39	8.3	6.0
Pronghorn	0 (0)	0 (0)	1 (0.8)	0 (0)	1	0.2	0.2
Lagomorphs							
Snowshoe hare	9 (3.5)	17 (8.9)	9 (7.4)	17 (24.0)	52	11.1	8.0
Mountain cottontail	0 (0)	1 (0.5)	0 (0)	1 (1.3)	2	0.4	0.3
Small mammals							
Montane vole	14 (5.4)	17 (8.9)	37 (30.6)	10 (13.0)	78	16.6	12.0
Pocket gopher	0 (0)	14 (7.3)	26 (21.5)	11(14.3)	51	10.9	7.8
Red squirrel	19 (7.3)	8 (4.2)	14 (11.6)	5 (6.5)	46	9.8	7.1
Jumping mouse	5 (1.9)	13 (6.8)	1 (0.8)	3 (3.9)	22	4.7	3.4
Least chipmunk	6 (2.3)	5 (2.6)	3 (2.5)	0 (0)	14	3.0	2.2
Ground squirrel	1 (0.4)	7 (3.7)	3 (2.5)	1 (1.3)	12	2.6	1.8
Deer mouse	0 (0)	5 (2.6)	1 (0.8)	0 (0)	6	1.3	0.9
Other	1 (0.4)	1 (0.5)	1 (0.5)	0 (0)	3	0.6	0.5
Other mammals							
Coyote	3 (1.2)	3 (1.6)	1 (0.8)	0 (0)	7	1.5	1.1
Red fox	2 (0.8)	0 (0)	2 (1.7)	0 (0)	4	0.9	0.6
Other	2 (0.8)	6 (3.0)	0 (0)	0 (0)	8	1.6	1.4
Bird	1 (0.4)	0 (0)	0 (0)	0 (0)	1	0.2	0.2
Plant material							
Whitebark pine seeds	39 (15.0)	2 (1.0)	1 (0.8)	8 (10.4)	50	10.6	7.7
Other	14 (5.4)	12 (6.2)	8 (6.6)	6 (7.8)	40	8.5	6.2
Insect	0 (0)	1 (0.5)	0 (0)	0 (0)	1	0.2	0.2
Human garbage	1 (0.4)	1 (0.5)	0 (0)	0 (0)	2	0.4	0.3
Total occurrences	260	193	121	77	651		100.0
Total # scats	224	103	92	50	470	138.3	

Table 2.2. Indices of dietary diversity (Shannon's diversity index) and dietary overlap (Horn's similarity index) for coyotes and lynx by season, Togwotee Pass, Wyoming, July 2006 – June 2008.

	Shannon's Diversity Index			
Season	**Coyote**	**Lynx**	***P*-Value**	**Horn's Similarity Index**
Winter	0.72	0.41	0.0049	0.33218
Summer	0.67			
Spring	0.92			
Fall	0.89			
Overall	0.75			

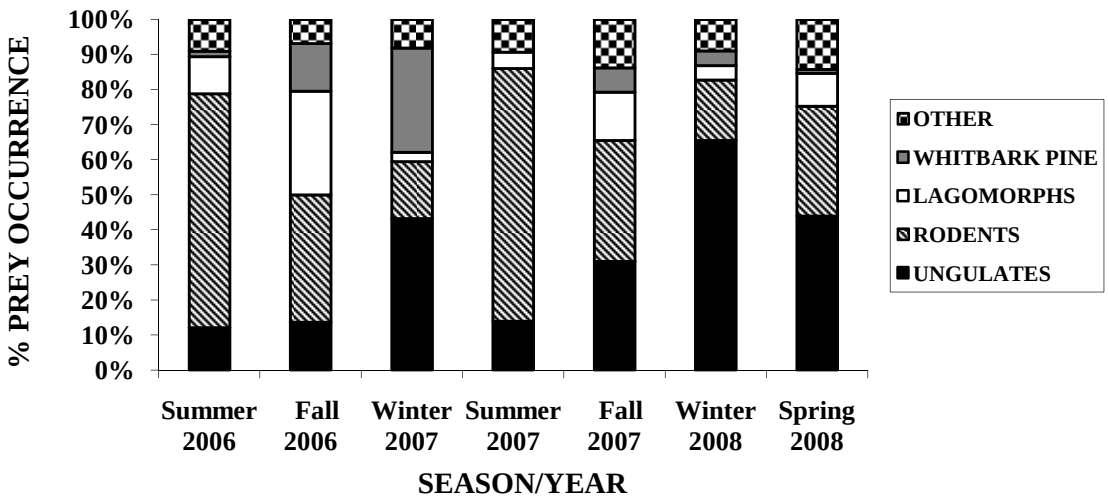

Fig. 2.1. Seasonal comparisons of major prey items among coyote scats, Togwotee Pass, Wyoming, 2006-2008.

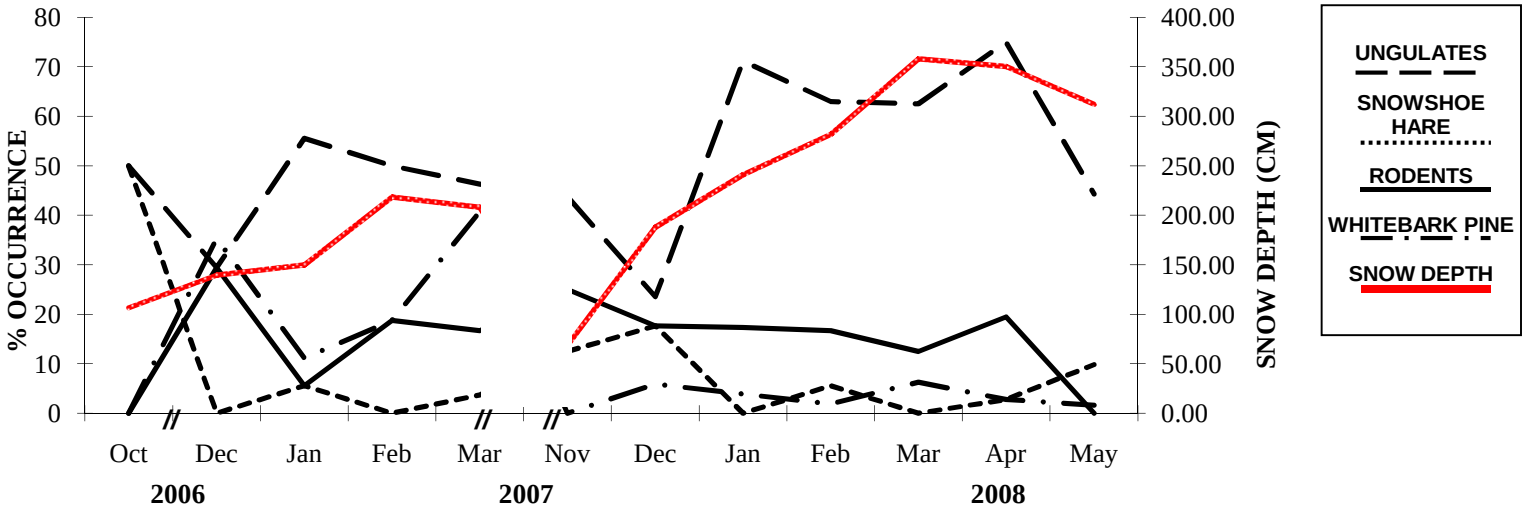

Fig. 2.2. Percent occurrence of food items found in coyotes scats and average daily snow depth (cm) by month and year on Togwotee Pass, Wyoming, October 2006 – May 2008. Months when scats were not collected denoted by //.

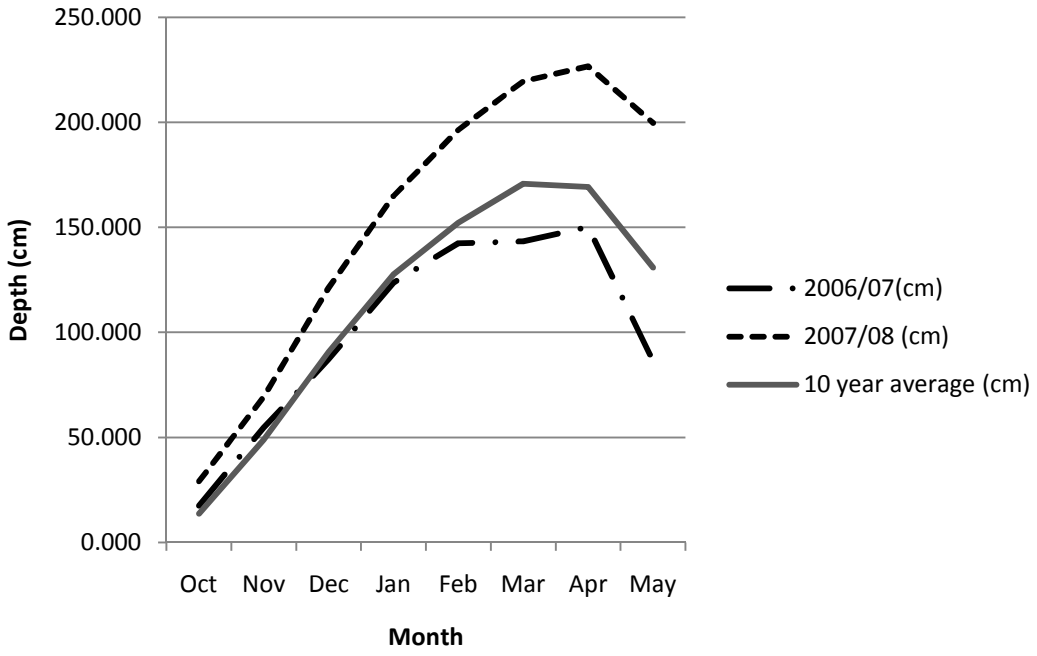

Fig. 2.3. Annual winter snow depth data (cm), October 1 through May 31 (2006-2008), and the 10-year average (1998-2008) snow depth for Togwotee, Wyoming.

CHAPTER 3

INFLUENCE OF SNOW COMPACTION ON COYOTE MOVEMENTS WITHIN LYNX HABITAT IN NORTHWESTERN WYOMING

ABSTRACT

Increased snowmobile traffic in habitats used by Canada lynx (*Lynx canadensis*) remains controversial due to the concern of coyote (*Canis latrans*) use of snow-compacted trails and the resultant potential for direct and indirect competition with lynx. Previous findings have suggested that coyotes require access to snow-compacted trails (created by snowmobiles and trail grooming practices) in order to exploit deep snow regions of the Intermountain West. Determining the variables influencing coyote use of snow-compacted trails to travel and hunt remains a priority for managers attempting to conserve lynx and their critical habitats. Information is particularly important for populations residing in the southern periphery of lynx range. During two winter field seasons from December 2006 through April 2008, we conducted winter backtracking of coyotes in northwestern Wyoming to determine how snow compaction and varying snow columns influenced coyote movements. Despite record snow depths, coyotes persisted in high elevation habitats used by lynx throughout the year. Coyotes accounted for 75% of all carnivore tracks encountered along surveys of groomed trails managed for snowmobile use. All (100%) coyotes backtracked used trails compacted by snowmobiles for some portion of their travel. During backtracking,

coyotes used trails compacted by snowmobiles an average of 34.5% of their travel distance for a mean distance of 149 m. Coyote exploitation of snow-compacted routes was directly related to the amount of snow compaction available. Coyotes traveled closer to compacted trails than randomly expected and selected shallower snow when traveling off snowmobile-compacted trails. Snowshoe hares were the predominant prey encountered by coyotes, with rates as high as 24.3 hares/km. Rodents, red squirrels, and snowshoe hares were encountered by coyotes more than randomly expected. Additionally, coyotes showed preferential use of snowmobile tracks in the presence of an ungulate kill. Distance traveled by coyotes was directly related to the level of snowmobile activity in the area, rodent encounter rates on compacted trails, and rodent encounter rates off compacted trails. In northwestern Wyoming, snow compaction resulting from winter recreation use appeared to have an influence on coyote movements during the winter.

INTRODUCTION

Conservation and management activities for Canada lynx (*Lynx canadensis*) populations in the contiguous United States (U.S.) have increased in an effort to enhance species recovery and protect critical habitats. Since their listing in 2000 (U.S. Department of the Interior 2000), investigations of the potential impacts to discrete subpopulations of lynx residing in various regions have been initiated. Determining appropriate management approaches to minimize adverse impacts and maximize species recovery is paramount for many land agencies managing areas with lynx habitat (U.S. Department of

Agriculture 2007). Concerns regarding the relationship between snowmobile activity and coyote (*Canis latrans*) presence within winter habitats used by lynx remain a focal point for many management agencies. Conflicting information suggest varying degrees of coyote dependence of snow-compacted trails, and therefore the potential for varying impacts of coyotes on local lynx populations. Regional differences in snow depth and supportiveness, terrain, recreation use (level and expanse), lynx density, availability of food, suitable habitat, and/or species dynamics may account for this observed variation in the dependence of coyotes using trails compacted by snowmobiles. Coyotes are one of the most successful generalist predators in North America and are known to be highly adaptive to human-modified environments (Toweill and Anthony 1988, Morey et al. 2007). In regions where seasonal activity is dictated by winter climates, coyotes alter their behaviors to negate the impacts of deep snow by using areas and habitats where snow is shallower and more supportive (Murray and Boutin 1991, Kolbe et al. 2007). Due to their high foot-load to body-mass ratio, coyotes on average have a greater sinking depth than lynx making travel and hunting in deep snow terrains more energetically expensive (Crete and Lariviere 2003). Lynx have specially adapted feet and a body type resulting in a lower foot-load to body-mass ratio, making travel and hunting on the snow analogous to non-snow conditions and giving them a competitive advantage over other predators such as bobcats (*Lynx rufus*) or coyotes during the winter (McCord and Cardoza 1982, Buskirk et al. 2000, Ruediger et al. 2000, Ruggiero et al. 2000). Therefore, although coyotes and lynx inhabit the same geographical areas, the two species occupy separate niches seasonally based on fluctuations in snow profiles, with coyote's primarily occurring in lower elevations with more supportive snow during the winter and lynx

occurring in higher elevations with deeper snow (Murray and Boutin 1991). Increased winter recreation use creates an increase of compacted snow surfaces, thereby providing an opportunity for coyotes to exploit deep snow conditions and utilize resources year round. In the Intermountain West, coyotes have been documented using snow-compacted routes to travel, hunt and persist in otherwise inaccessible winter terrain (Bunnell et al. 2006). Bunnell et al. (2006) suggest the continued use of snowmobiles may result in consistent compacted trails within lynx conservation areas which may have detrimental impacts to local lynx populations in the Intermountain West. Furthermore, they suggest minimizing or rotating compaction areas (thereby limiting potential impacts by coyotes) as an appropriate strategy to implement for management agencies concerned with protecting habitats needed to sustain lynx and their main prey, snowshoe hares (*Lepus americanus*).

The growing popularity of snowmobiles combined with recent technological advances has enabled greater access to backcountry terrain, expansion of trail grooming, and an increase in off-trail use by winter recreationists. In light of this, management has focused on determining if snowmobile use has the potential to influence system dynamics. The potential for competition between coyotes and lynx could emerge either as exploitation (indirect) or interference (direct) competition. Researchers have suggested increased competition between coyotes and lynx resulting from snow compaction would mostly occur during the fall (Aubry et al. 2000, McKelvey et al. 2000, Kolbe et al. 2007) and winter months, as coyotes have been shown to use snow-compacted paths to travel and hunt (Bider 1962, Ozoga and Harger 1966, Murray et al. 1995, Buskirk et al. 2000, Bunnell et al. 2006). Understanding how coyote behaviors are influenced by winter

recreation use (particularly their use of snow-compacted trails within habitats used by lynx in winter) is necessary for understanding how lynx populations might be impacted by current and future management plans in critical lynx habitat. The objective of this study was to document the influence of snow compaction created by snowmobiles on coyote winter movements in deep snow terrain. Data was collected in an effort to characterize this association and determine what variables influence coyote movements in areas occupied by lynx.

STUDY AREA

We conducted this study on the east and west sides of Togwotee Pass in northwestern Wyoming, located southeast of Yellowstone National Park and east of Grand Teton National Park. U.S. Highway 26 runs east to west crossing Togwotee Pass and was the only major highway located in the study area. The 512-km^2 study area was characterized by extensive recreational trails and roads maintained year-round. Most of the study area was in Teton County, although a portion extended into Fremont County. The area was composed of the Bridger-Teton and Shoshone National Forests, plus some large, privately-owned ranches. Elevations ranged from 1,800 m 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 study season (December through April) averaged 226.6 cm in 2006, 149.40 cm in 2007, and 228.9 cm in 2008 (Natural Resources Conservation Service 2008).

Habitats varied between the east and west sides of the pass, with the eastern side classified as dry and the western side as wet. Plant communities on both sides included cottonwood (*Populus angustifolia*) riparian zones, interspersed with sagebrush (*Artemisia* spp.) uplands and willow (*Salix spp*.) -wetland communities at lower elevations. At intermediate elevations, aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were the dominant species. Whitebark pine (*Pinus albicaulis)*, spruce (*Picea engelmannii*), 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 were extirpated from Wyoming by the 1930's, they have since re-established as a result of the 1995 re-introduction efforts in Yellowstone National Park, with at least 4 packs residing near Togwotee Pass as of July 2006 (U.S. Fish and Wildlife Service 2006). Other carnivores aside from coyotes and lynx included cougars (*Puma concolor*), wolverines (*Gulo gulo)*, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), and pine martins (*Martes americana*). Ungulate species found in the study area included elk (*Cervus elaphus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and a few white-tailed deer (*O. virginianus*). Pronghorn antelope (*Antilocapra americana*) were in the study area during the snow-free season on the east side of the pass. Small mammals comprising the potential prey base for coyotes and lynx were snowshoe hares, red squirrels, Uinta ground squirrels (*Spermophilus armatus*), black-tailed jackrabbits (*Lepus californicus*), cottontail rabbits (*Sylvilagus spp*.), ruffed grouse (*Bonasa umbellus*), blue grouse

(*Dendragapus obscurus*), northern flying squirrels (*Glaucomys sabrinus*), deer mouse (*Peromyscus maniculatus*), voles (*Microtus spp.*), gophers (*Thomomys spp*.), and various cricetid species.

Hunting and trapping of coyotes occurred throughout the study area. Past records from the U.S. Forest Service and Wyoming Department of Game and Fish indicated predator removal had been practiced for several decades. Although trapping of lynx was prohibited in the region, local trappers have incidentally caught lynx while trapping for bobcats and coyotes (T. Krause, personal communication).

Snowmobiling was extensive during the winter, allowing riders to access approximately 966 km of groomed trails and 2.5 million acres of off-trail riding in and around the study area once snow conditions permitted (typically late October through May). Trail grooming operations typically began by mid-December with trails maintained through April 1 depending on snowfall. Wyoming's Continental Divide Snowmobile Trail (CDST) was considered one of the top trail systems in the west, contributing towards many of the 17,876 resident, 983 commercial, and 17,518 non-resident snowmobile permits purchased in the state from July 2007 through June 2008 (Wyoming Department of State Parks and Cultural Services 2008).

METHODS

Coyote Captures

We captured coyotes in the summer and fall using Victor #3 padded-jaw “soft-catch” leg-hold traps with attached tranquilizer tabs (Balser 1965) containing 600 mg propiopromazine. A variety of baits and lures were used to attract coyotes to the traps.

Traps were placed along roads, trails, and along forest edges near open meadows throughout the study area. Coyotes were also captured during winter by placing road kill 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 and the USDA/National Wildlife Research Center. Coyotes were trapped in a representative manner across the study area using all methods.

Carnivore Surveys and Snow Depth/Penetration Routes

To examine the variation of snow characteristics and predator use on different sites within the study area, we established 3 15-km routes for repeated surveying of carnivore tracks and snow depth/penetration measurements on machine-groomed snowmobiles trails (Fig. 3.1). Routes were established once snow became consistent and the trails were marked by Forest Service personnel. The three routes established within the study were called Flagstaff Loop (FSL), Squaw Basin Loop (SBL), and Sheridan Creek Loop (SCL). Routes were established in habitats known to be used by lynx in the winter and within the study area boundaries containing radio-collared coyotes, thereby documenting the variation in the snow column across the study area. Routes were distributed evenly across the study area and had to meet the standard criteria of 15 km of continuous groomed trail that received daily maintenance throughout the winter by local personnel. Along each survey route, 15 permanent snow stations were set up at 1 km intervals (Fig. 3.1), 10 m from the edge of the compacted trail, to document snow depth

and snow penetration. Depth was measured using an avalanche probe pole (marked in cm); penetration was measured (indexed) by dropping a 100 g brass weight from 1 m above the snow surface and measuring the distance penetrated below the snow surface (Kolbe et al. 2007).

Routes were surveyed using snowmobiles, every 2 weeks from December 2007 through April 2008. Personnel surveyed all routes simultaneously to ensure similar environmental conditions were measured. During surveys, each individual carnivore track encountered was identified to species and documented using a handheld Global Positioning System (GPS); locations were recorded using Universal Transverse Mercator (UTM) coordinates. Tracks of the same species that were encountered >100 m from a previously recorded track were recorded as an independent observation, but only if the tracks were not continuous along the groomed trail.

Coyote Backtracking

Radio-collared coyotes were backtracked during the winters of 2006-2007 and 2007-2008 using methods similar to those developed by Kolbe et al. (2007) at Seeley Lake, Montana. The purpose of backtracking individuals was to quantify the influence of snow compaction on coyote movements in an area where lynx, coyotes, and snowmobiles occur, and to allow for comparison to results from studies in geographically separate regions. In an effort to determine if various snow packs and differences in snow supportiveness would influence the dependence of coyotes on compacted trails for movement, we sampled individuals residing on the east, west, and continental divide of Togwotee Pass. Data collected during the backtracking of individuals was used to

determine the variance from random expectation of the distance a coyote would travel on or off of a snow-compacted trail and the influence of various environmental variables including the rate of prey and predator encounters, snow depth, snow supportiveness, and the distance a coyote traveled off of the nearest compacted snowmobile trail. Individual coyotes were selected randomly for backtracking using a computer generated randomization sequence (SAS Institute Inc. 1999) to avoid bias and ensure all coyotes were sampled randomly, yet equally. Once selected, coyotes were located by triangulation using $\geq$3 azimuths, and their position projected using LOCATE II (LOCATE, version 1.82, Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). Once the track location was verified, a starting location for the actual track was then used to generate a starting location for the control track. Control (random) tracks were created using digital layers from previously documented coyote tracks in a random direction and projection (or "spin"), 2-3 km distance from the actual start point of the individual being tracked that day (Fig 3.2). This procedure and projection distance were used to ensure sampling independence from the actual track and, for statistical purposes, to be used for comparing data collected from the actual coyote track to random tracks (Kolbe et al. 2007).

The direction and projection of random tracks were generated randomly using SAS (SAS Institute Inc. 1999), by creating a randomized sequence selected from values between 1 and 360 (representing degrees); one randomization sequence was created for the direction, and one for the projection. Before going into the field, the random track created for that day was overlaid onto a topographic map using ArcGIS (ESRI, Redlands, California) to ensure field personnel were capable of conducting a track survey in the

terrain where it had been randomly projected. If the random track had been projected in an avalanche path or dangerous/unattainable terrain, the track was reprojected to ensure safety of personnel, using a second set of projected numbers from the randomized sequence. If the terrain was considered acceptable, the random track layer was permanently saved onto a digital map, transferred to a handheld computer (Trimble GeoExplorer® series 3, Sunnyvale, California) and taken into the field. The only reason a track was ever reprojected was for safety reasons. Therefore ensuring random tracks were not projected in areas simply because they were easy to access or conduct track surveys in, eliminating potential surveyor bias of roads, terrain and snow compaction.

Backtracking began in the morning after night movements had taken place and before the snow column deteriorated. Both actual and random track surveys were conducted by teams of 2 field personnel, taking measurements and recording data for $\geq$3 km of tracking. Start locations were reached using skis and snowmobiles along pre-existing compacted trails to avoid additional compaction as much as possible within the study area. Teams communicated with radios to commence backtracking of actual and random tracks simultaneously. Using the GeoExplorer® handheld computer, all data was collected in digital format using a datasheet generated with the computer software GPS Pathfinder Office. At the start of each track, initial track information was recorded including observers, start time, start location, temperature, elevation, and a classification (high, medium, low) of snowmobile use in the area. Classifications of high, medium, and low levels of snowmobile use were determined by visually assessing the amount of terrain covered by snowmobile tracks within a 1 km buffer of the track. A high classification was used for terrain with snowmobile tracks covering >60% of the ground

area within the buffer zone; snowmobile tracks covering <10% of the area was considered low use; snowmobile tracks covering 11 - 59% of the area was considered medium use.

During the actual backtrack of a coyote, Pathfinder software recorded UTM locations every 5 seconds along a given track. Point locations were marked every time a habitat change was encountered, organizing the track into distinct but consecutive segments identified by habitat (Kolbe et al. 2007). Groomed trails were considered a distinct habitat type. Coyote travel distance on and off snow-compacted trails was documented by track segments with start and end points marking transitions within habitats. Prey track crossings and predator track crossings were identified as point locations, and identified by number and species every time a prey or predator's track crossed a coyote travel path. Snow depth was measured with every habitat change and every 200 m along the track using an avalanche probe (marked in cm) to measure from the snow surface to the ground. An index of snow penetrability was documented whenever the habitat changed and every 200 m along the backtrack by dropping a 100 g weight from 1 m above the snow surface and measuring the distance of penetration below the surface (Kolbe et al. 2007). All established snowmobile trails, including groomed trails and off-trail snowmobile tracks, within 1 km of both actual and random tracks were recorded for measuring coyote distance to the nearest compacted snowmobile trail. Tracks made by field personnel while conducting the survey were not recorded as these occurred after the coyote had traveled the actual route the previous night. All parameters were similarly measured along the random tracks.

Once the actual and random tracks were completed, data recorded on the Trimble units were downloaded and imported into GPS Pathfinder Office. Once imported, tracks were differentially corrected to enhance the location data quality and improve data integrity. Tracks were then smoothed to eliminate bounce or GPS scatter caused by canopy cover or varying topography which can influence location accuracy (DeCesare et al. 2005). All tracks were converted to ArcGIS files for analysis. Coyote travel distance to the nearest compacted snowmobile trail (Fig. 3.2) was determined by calculating a centroid point for each segment along a given coyote track and measuring the distance from the centroid point of each segment to the nearest compacted snowmobile trail using ArcGIS (Kolbe et al. 2007).

Statistical Analysis

To determine differences in snowpack across the study area for analysis of carnivore track encounters, we compared mean snow depth and penetration collected from the 15 snow survey stations along our 3 snow depth/penetration routes, by month. To detect trends in carnivore use of maintained snowmobile trails, we ran correlation analyses on carnivores encountered versus snow depth and snow penetration for each survey route individually and combined, by month. To determine if there was a relationship between the number of coyotes encountered compared to other predators as snow depth increased, we ran correlation analyses on percent coyote encounters (out of all predator species) versus snow depth and snow penetration for each survey route by month.

Backtrack data was compiled into track pairs by individual and date. Tracks were divided into “compacted” and “non-compacted” categories, then divided into segments (based upon habitat transition) to compute mean prey track encounters (per km), mean predator track encounters (per km), mean snow depth (cm), and mean snow penetration (cm). Snow depth and penetration measurements recorded every 200 m along both actual and random tracks were used to determine variations in the snow column across the study area for backtrack analyses. Once calculated for each segment, variables were averaged for compacted and non-compacted categories and the number of segments per track and mean segment distance were determined. The distance traveled on and off compacted trails was divided by the total track distance to determine percent use of snow compaction for each track pair.

To determine if coyotes were traveling closer to compacted trails during specific months throughout the winter, we compared distance from traveled coyote track to snow compacted trail by month and year for both random and actual tracks. Our sampling unit was defined as each track pair, consisting of one actual and one random coyote track for any given day. Snow depth and snow penetration were averaged for each track segment to produce an overall average for each track. Distance from the traveled coyote track to the nearest compacted trail was determined by calculating a distance for each segment on a given track and averaging those distances to produce a single mean distance for each track (Fig. 3.3). Distances to the nearest compacted trail of actual and random tracks were compared using a t-test.

To determine how snow depth and snow penetration encountered by coyotes influenced their use of snow-compacted trails, we ran correlation analyses by comparing

the percent that coyotes used compacted trails during actual backtracks, and the average snow depth encountered on compacted trails, average snow depth encountered off compacted trails, average snow penetration encountered on compacted trails and average snow penetration encountered off compacted trails for all tracks. Regression analyses were used to determine how each variable (snow depth on, snow depth off, snow penetration on, snow penetration off) influenced the percent use of snowmobile compacted trails by coyotes, and determine curve estimations for actual coyote backtracks.

To determine how large prey items influenced coyote movement, we compared the use of snow-compacted trails on all actual tracks containing ungulate kills to those where ungulate kills were not documented. Tracks were categorized by either presence (1) or absence (0) of an ungulate kill, as documented during actual coyote backtracks. A distance ratio was calculated by dividing the actual distance traveled by a coyote (using snow-compacted surfaces) by the shortest possible travel distance possible, projected from start to finish points. This distance ratio was then compared between tracks based on presence of ungulate kills using a t-test to determine whether coyotes preferentially use snowmobile trails when accessing large prey items rather than traveling the shortest direct distance.

A multi-response permutation procedure (i.e., MRPP; e.g., Mielke and Berry 2001) was used to test for differences in variable means between random tracks and the actual tracks used by coyotes. We used the procedure ‘mrpp’ implemented in the R library ‘vegan’ (R software, version 2.6.2; R Development Core Team 2008). MRPP’s test whether there is a significant difference between two or more groups of sampling

units, thus allowing us to compare variables from each track pair (actual and random) by day. This method is similar to a simple analysis of variance as it compares dissimilarities within and among groups. The MRPP algorithm first calculates all pairwise distances in the dataset, then permutates the sampling units and their associated pairwise distances, and recalculates these distances based on the permutated data. It ultimately evaluates whether these differences across permutated datasets are significantly different or not based on *P*-value statistics (Stevens and Oksanen 2009).

The MRPP was applied to a number of variables by calculating the means of each variable and assessing if they were significantly different between actual and random tracks for each variable of interest. We first investigated differences in those means for habitat-related variables: level of snowmobile use, snow depth, and snow penetration. Snowmobile use was classified as low, medium, or high, as described previously. To obtain a mean value of snowmobile use for both actual and random tracks, we transformed snowmobile use into an ordinal variable (i.e., 1, 2, 3, replaced low, medium, and high). We also tested for differences in prey-related variables: rate of encountering tracks left by rodents, red squirrels, snowshoe hares, and ungulates. Additionally, we examined predator avoidance using the rate of wolf track encounters along the actual and random tracks.

We were interested in understanding which factors (i.e., coyote identity, level of snowmobile use, snow depth, snow penetration, rodents, red squirrels, snowshoe hares, ungulates, and wolf track encounters) on and off the snowmobile tracks could explain the percentage of time coyotes spend on snowmobile tracks (i.e., '%Track'). To address this question, we used beta-regressions (Ferrari and Cribari-Neto 2004) via the 'betareg'

procedure implemented in the R library ‘betareg’ (R software version 2.6.2.; R Development Core Team 2008). Beta regressions can be implemented in situations where the dependent variable (%Track) is continuous and restricted to the unit interval 0-1, such as proportions or rates. The regression was modeled to be beta-distributed and called for 2 parameters: a mean and a dispersion parameter. The mean is linked, as in generalized linear models, to the responses through a link function (e.g., logit) and a linear predictor. Because some of the covariates of interest had the potential to be collinear (i.e., strongly correlated), we calculated a variance inflation factor (i.e., package ‘‘car,’’ procedure ‘vip’ in R version 2.6.0; R Development Core Team 2008) across covariates prior to model selection (Neter et al. 1996). A variance inflation factor <5 indicated a lack of colinearity.

The estimation procedure was performed by maximum likelihood thus providing log-likelihood information and allowing us to calculate Akaike’s Information Criterion ‘AIC’ (Akaike 1973) defined as follows: AIC = -2 * *log-likelihood* + 2 * *df*, where *df* stands for the number of degrees of freedom in the model. We also calculated Akaike model weights (w_i) to conduct model comparison and determine which model(s) served as the best approximation(s) to the data: $w_i = \exp(-0.5 * \Delta AIC) / \sum \exp(-0.5 * \Delta AIC)$, where ΔAIC stands for the difference in AIC values between the best performing model and the model of interest.

We based model selection on both AIC and *P* values. We first estimated a global model testing for additive effects of all of the covariates of interest. Second, we removed all covariates that did not have a significant effect on %Track ($P > 0.1$) and checked then whether AIC decreased or increased. If AIC values are positive, the smaller the value the better model fit, and vice versa for negative AIC value (the biggest negative value

corresponds to the best performing model). Third, we repeated the process until we found a model that provided the best AIC value and for which each covariate had a significant effect on the response variable %Track ($P \leq 0.1$).

RESULTS

Fifteen (4 F, 11 M) coyotes were captured and radio-collared from August 2006 through February 2008; 7 individuals were captured using leghold traps, 2 captured using snowmobiles, and 6 captured using net-gunning from a helicopter. 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. Three individuals were sampled during the first year (28.93 km of sample effort), while all 13 individuals were sampled during the second year (236.12 km of sample effort).

Carnivore Surveys

We completed 24 surveys for a total of 360 km of sampling from December 2007 through April 2008 on Flagstaff Loop, Squaw Basin Loop, and Sheridan Creek Loop. The variance in the snow column across the study area was represented by the snow depth and snow penetration measurements, with the east side of Togwotee (Sheridan Creek Loop) and continental divide (Squaw Basin Loop) showing a more dense, supportive snow profile, while the west side of Togwotee (Flagstaff Loop) showed a dryer, less supportive snow profile.

All three snow survey routes showed high coyote encounter rates suggesting continuous use by coyotes even in deep snow years (Table 3.1). Coyotes were the most

common predator encountered along groomed trails across all survey routes (Table 3.1), accounting for 75% of documented tracks (1,037 of 1,381) from December through April. Wolves were the second most commonly encountered predator (Table 3.1), accounting for 9.3% of documented tracks (129 of 1,381). Predator encounters were most frequent on the Flagstaff Loop transect located on the west side of Togwotee Pass, accounting for 56.5% of all predator track encounters from the three survey areas during the winter months; 33.6% of all predator tracks occurred on the Sheridan Creek Loop on the east side of Togwotee Pass and 9.8% of all predator tracks occurred on the Squaw Basin Loop directly on Togwotee Pass (Table 3.1).

Of the three survey routes, Squaw Basin Loop, located directly on Togwotee Pass, had the highest average snow depth (average snow depths: SBL = 144.77 cm, SCL = 97.37 cm, FSL = 91.86 cm), the lowest average snow penetration measurement (average snow penetration: SBL = 13.09 cm, SCL = 21.13 cm, FSL = 24.23 cm), and the lowest percentage of coyote encounters compared to all other predator encounters (SBL = 68.1%, FSL = 70.8%, SCL = 84.5%; Table 3.1). Wolves were the second most frequently encountered predator on the Squaw Basin Loop (15.3%), as were mustelids for the Flagstaff Loop (14.2%) and Sheridan Creek Loop (15.5%; Table 3.1).

There was a significant correlation between coyote track encounters and snow penetration measurements taken on the Flagstaff Loop ($r = 0.800$, $P < 0.05$). Ermine track encounters correlated with snow penetration measurements from the Squaw Basin Loop ($r = 0.745$, $P < 0.05$). When comparing percent occurrence of coyote track encounters compared to other predator track encounters, there was a positive correlation between coyote encounters and snow depth ($r = 0.991$, $P = 0.001$) on the Flagstaff loop. As snow

depth increased on the Flagstaff loop route, the percent of coyote track encounters compared to other predator track encounters increased. Additionally, there were negative correlations between coyote track encounters and snow penetration on Flagstaff loop (r = -0.985, *P* = 0.002) and Squaw Basin loop (r = -0.394, *P* = 0.020). As snow penetration decreased (i.e., the snow surface became more supportive) on both routes, coyote track encounters increased.

Backtracking

A total of 13 adult coyotes (4 F, 9 M) were backtracked 57 times for a total of 265.05 km of actual coyote backtracks during 2 winters, 2006-2007 and 2007-2008. An additional 278.54 km of random track surveys (n = 57 random tracks) were conducted during the same time period. We averaged 4.62 backtrack pairs per animal (range = 3-6, SD = 1.19); actual backtracks averaged a distance of 4.64 km in length (n = 57, range = 1.56-12.21, SD = 1.69) with 34.10 habitat transitions (track segments) per backtrack (range = 15-61, SD = 10.10). Coyotes remained within any given habitat for a mean distance of 0.138 km during actual backtracks (range = 0.001-1.149, SD = 0.120). Actual backtracks were conducted in areas that were most frequently categorized as medium snowmobile use areas (38.6%; 22 of 57 tracks) followed by low snowmobile use (35.1%; 20 of 57 tracks), and high snowmobile use (26.3%; 15 of 57 tracks).

Coyotes used trails compacted by snowmobiles for a portion of their track on 100% of all actual backtracks conducted (57 of 57 backtracks). For all actual backtracks combined, coyotes used snow-compacted trails an average of 34.5% (range = 0.02 – 86.68, SD = 23.02) of their travel distance, and when traveling on compacted trails they

traveled a mean continuous distance of 149 m per occurrence (range = 0.1-352, SD = 0.90; Table 3.2), with a mean overall distance of 1.5 km spent on compacted trails per backtrack. Coyotes used compacted trails on actual backtracks an average of 11.88 times per backtrack (range = 1-33, SD = 6.28; Table 3.2). This was more than 2x as often as found on the random tracks (mean use of compacted snow was 5.32 times on random tracks), and 3x higher for the distance traveled on a compacted trail than random (mean continuous distance traveled on compacted snow per occurrence was 59 m on random tracks). Coyotes traveled significantly closer to compacted trails than random expectation ($t = -2.236$, $df = 56$, $P = 0.030$), and selected shallower snow when traveling off compacted trails ($t = -3.909$, $df = 56$, $P < 0.001$).

When averaged by track, coyotes crossed significantly more predator tracks on actual tracks than on random tracks (actual: mean = 5.82/km [range = 0-34.85, SD = 6.31]; random: mean = 3.09/km [range = 0-22.6, SD = 3.82]; $t = 3.052$, $df = 56$, $P = 0.003$). Although more tracks of prey were encountered on actual backtracks than on random tracks (actual: 11.27/km, range = 0-54.75, SD = 11.60; random: 9.96/km, range = 0-67.49, SD = 12.13), when analyzed by track it was not significant. Aside from coyotes, wolf tracks were the predominant large predator (coyote size or larger) crossed on both actual and random tracks, and were crossed at similar rates on both actual (mean = 0.35/km, range = 0-7.69, SD = 1.26) and random tracks (mean = 0.37/km, range = 0-9.36, SD = 1.52). Snowshoe hares (SSH) were the predominant prey tracks crossed on both actual and random tracks, with encounter rates as high as 24.26 SSH/km on actual tracks (mean = 5.83, range = 0-24.26, SD = 6.42) and 56.94 SSH/km on random tracks (mean = 5.77, range = 0-56.94, SD = 9.85). Grouse were the only prey item that were encountered

with marginal significance on actual tracks more than on the random tracks (t = 0.063, df = 56, $P = 0.063$).

While there appeared to be an inverse relationship between the overall percent that coyotes used compacted trails and snow penetration when plotted by month (Figure 3.3), statistical analyses did not reveal a significant correlation. However, when we regressed the percentage of compacted trails used by coyotes versus snow conditions (depth and penetration) on and off compacted trails by day, there was a significant relationship. However, only 20.3% of the variation in use of compacted trails was explained by the snow depth and penetration ($F = 3.31$, df = 2, $P = 0.017$; Table 3.3). Regardless, coyotes apparently increased their use of compacted trails as snow penetration off compacted trails increased (became less supportive), and as snow penetration on compacted trails decreased (became more supportive). Additionally, coyotes increased their use of compacted trails as snow depth both on and off compacted trails increased.

When comparing ratios between the mean distances of the shortest possible travel route and the actual travel route chosen by coyotes where ungulate kills were present, we saw a significant difference in the amount of use on compacted trails ($P < 0.0001$). The distance ratio was significantly higher in cases where there was an ungulate carcass (suggesting preferential use of snowmobile trails by coyotes in the presence of an ungulate kill), compared to a situation where there was no ungulate carcass. Coyotes preferred to meander along a compacted trail leading to a carcass rather than travel a more direct, but off trail, route of travel.

All habitat variables were significant with the exception of the mean level of snowmobile use between random and actual tracks (i.e., MRPP; Table 3.3, $P = 0.801$). This indicated snowmobile use did not explain coyote backtracks more than random expectation. Snow depth and snow penetration variables on the other hand indicated coyotes preferentially used shallower tracks where snow penetration (i.e., MRPP; Table 3.3, $P < 0.001$) and snow depth (i.e., MRPP; Table 3.3, $P = 0.005$) were lower than random expectation. Coyotes preferentially used tracks where red squirrel track encounters were higher than random expectation (i.e., MRPP; Table 3.3, $P < 0.001$), but where rodent and snowshoe hare track encounters were lower than randomly expected (i.e., MRPP; Table 3.3, rodents: $P = 0.04$, hares: $P = 0.012$).

Our beta regression models indicated coyotes were exploiting snow-compacted routes, with their use being directly related to the amount of snow compaction available. Because all variance inflation factors were <5 (Appendix A), our models did not present any serious issues concerning colinearity (Neter et al. 1996). The best performing model retained an effect of snowmobile use (i.e., low, medium, or high), an effect of the rodent track crossings on snowmobile trails, and the effect of rodent track crossings off snowmobile trails on the time spent by coyotes on snowmobile tracks '%Track' (Table 3.5; AIC = -28.6670, $df = 5$). The model explained 58.42% of the overall AIC weight (Table 3.5, $w_i = 0.5842$) and outperformed the following best models by only 0.7369 AIC points. The second best performing model was quite similar to the best performing model, only it did not include an effect of rodent abundance off the snowmobile tracks on %Track (Table 3.5, AIC = -27.9301, $df = 4$, $w_i = 0.4042$).

The best performing model indicated snowmobile use had a progressive negative effect on %Track (i.e., high use: β = -0.0252; CI: -0.2447 to 0.1943; P = 0.9084; medium use: β = -0.6791; CI: -0.9774 to -0.3808; P = 0.0228; low use: β = -0.0252; CI: -1.2496 to -0.6312; P = 0.0024). However, only lower and medium levels had a significant negative effect on %Track (Table 3.4, P = 0.0024 and 0.0228, respectively). The abundance of rodent tracks encountered on the snowmobile trails positively and significantly influenced the percentage of time a coyote spent on snowmobile trails (β =0.1545; CI: 0.0969 to 0.2121; p = 0.0073). In contrast, the number of rodent tracks encountered off the snowmobile trail had a significant negative impact on %Track (β = -0.4800; CI: -0.7707 to -0.1893; P = 0.0987).

DISCUSSION

The objective of this study was to determine if snow compaction created by snowmobiles influenced coyote movements, and therefore had the potential to facilitate competition between coyotes and lynx. While actual competition between these species would be difficult to quantify, the potential for competition could be better understood with a basic understanding of the possible species interactions and the impacts one species would have on another, assuming a high degree of resource overlap. Evidence suggested overlap and thus potential competition, including 1) coyotes remained in deep snow habitats (i.e., known lynx winter habitats) throughout the winter despite deep snow conditions, 2) coyote use of compacted snowmobile trails was directly associated with presence of a food source (demonstrated by preferential use in the presence of an ungulate kill) which demonstrated their ability to selectively target species and

preferentially use trails to facilitate access, and 3) coyote use of compacted snowmobile trails was directly related to the availability of groomed trails (as demonstrated by the correlation between use of snow-compacted trails and snowmobile use on the landscape classification). Overall, compacted snowmobile trails appeared to influence coyote winter movements in deep snow habitats. Although the levels of snow depth and penetration during which coyotes became dependant on snowmobiles to exploit deep snow conditions were not identified, the snow column (primarily snow supportiveness measured by penetration) appeared to be the primary variable enabling movements in deep snow habitats. Prey availability was also a likely influence driving coyote movement as documented on coyote backtracks, though predator presence may have altered coyote behaviors, as well as selection and utilization of available food sources.

Snow Surveys Stations and Coyote Encounters on Groomed Trails

Both coyote and lynx tracks were detected on groomed snowmobile trails during carnivore surveys over the course of the winter. All 3 snow survey routes showed a high coyote track encounter rate above all other predators, suggesting high use by coyotes even in deep snow years. While coyotes have been shown to shift territory use to lower elevations during the winter (Koehler and Hornocker 1991), this was not documented in our study. Instead, our findings were similar to Kolbe et al. (2007) who documented little change in the mean elevation of coyote backtracks during winter. Based on continuous monitoring of individuals using telemetry locations, we were able to determine that coyotes resided and persisted in their home ranges throughout the year and did not

demonstrate seasonal shifts due to deep snow. This was further demonstrated through our observations of high coyote use of managed snowmobile trails through all winter months, with an increase in coyote track encounters both in number and in composition of all predator track encounters as the winter progressed. Of the 3 routes, Squaw Basin Loop had the highest degree of snow supportiveness and the highest percent of coyote track encounters compared to other predators. There are several possible explanations for this high coyote track encounter rate: 1) the energetic trade-offs and the predators' ability to utilize resources in deep snow habitats; 2) adaptability to and the influence of recreation activities and disturbance; and/or 3) behavioral traits associated with movement patterns (e.g., coyotes selecting for road structure).

Energetic trade-offs become important in winter areas when harsh conditions mean high energetic costs and survival requires a balance of nutritional intake with energy expenditure. Predators must either adapt their behavioral patterns to utilize resources in deep snow habitats or shift their range to an area where food is more accessible and acquisition of resources less energetically expensive. Given the high encounter rate of coyote tracks on Squaw Basin Loop we could infer that either: 1) coyotes were capable of utilizing resources in deep snow habitats more effectively than other predators; 2) other predators were not capable of successfully utilizing resources in deep snow habitats; or 3) coyotes occurred at higher densities than other predators in the system (i.e. wolverine and lynx are both rare, but occurred at low densities). The high coyote presence indicated they had the means for survival during the harshest winter conditions in northwestern Wyoming. However, no obvious physical or known physiological adaptations explained their ability to persevere in deep snow more

successfully than other predators. Behavioral adaptations must therefore play a role in coyotes continued use of deep snow habitats.

Coyotes may be more adaptable and tolerant of disturbance caused by snowmobiles than other predators. Snowmobile trails are used frequently by people and constantly managed for daily use which may be a deterrent to less tolerant wildlife species. Coyotes, however, may adapt to these human-modified areas and use them to their advantage for traveling, hunting, and accessing desirable habitat patches. Coyotes are adept at exploiting urban environments (Grinder and Krausman 2001, Morey et al. 2007), therefore tolerance of snowmobile activity was a plausible explanation for their high prevalence in this winter recreation area.

The last plausible explanation to consider in regards to the high use of managed snowmobile trails by coyotes, suggested the association of specific behavioral traits with movement patterns, which could be demonstrated by the use of a road because of its structure. Kolbe et al. (2007) found coyotes in Seeley Lake, Montana, may have selected for road structure and location rather than the snow conditions on them. While Kolbe's theory is a plausible explanation in regions where snow conditions result in more supportive or unaltered travel conditions, it was not a likely explanation for what was encountered in our study area. We suggest this primarily because coyote travel patterns changed based on snow conditions (depth and supportiveness), and that coyotes in our study area traveled closer to snow-compacted trails than random expectation. We believe this behavior was a direct result of facilitated travel on compacted surfaces, several of which coincidentally were managed for winter recreation. Unfortunately, this is not something we were able to quantify in our study. Most likely, the high level of coyote

track encounters on the Squaw Basin Loop is not the result of a single cause, but rather a combination of the above mentioned variables as well as the degree of snow supportiveness demonstrated in that area. It is also possible other factors not considered in this dataset played a role in the high use of snowmobile trails by coyotes on Squaw Basin Loop (see Coyote backtracks below and Chapter 4). However, from our results, we suggest snow supportiveness was perhaps the most important influence (more so than snow depth) for determining where coyotes occurred during winter in our study area.

Additionally, coyotes were the only species having a higher track encounter rate with increased snow depth and decreased penetration, suggesting this response to snow conditions may be species specific. All other species (i.e., wolves and mustelids) showed decreased encounters, except for during a unique instance on Squaw Basin Loop during March 2008. During this month, we observed a dramatic increase in wolf track encounters, and a corresponding decrease in coyote track encounters (the lowest during the winter). We suspect the low occurrence of coyote tracks was due to high wolf presence that month, with a rebound in coyote presence once wolves vacated the area.

Although the percentage of coyote tracks encountered compared to other predators on Flagstaff Loop was not as high as Squaw Basin Loop (70.8% versus 84.5%), the abundance of coyote tracks recorded on Flagstaff Loop (555 of 1037) indicated variables in addition to snow depth and penetration may influence habitat selection during winter. The number of coyote tracks encountered on Flagstaff Loop accounted for 53.5% of all coyote track encounters across the study area. Other variables responsible for this may have included differences in habitat type, forest structure and canopy cover, disturbance (expanse of snowmobile use on the landscape and noise), habitat

fragmentation, species assemblage, prey availability, and/or carcass availability (see Chapter 4).

Coyote Backtracks

Prey and predator track crossings

Coyotes crossed more prey tracks and fewer predator tracks during actual backtracks while traveling on compacted snow than on random backtracks (Table 3.2). However, while coyotes still crossed fewer predator tracks while traveling on non-compacted surfaces during the actual backtrack, they crossed fewer prey tracks on non-compacted surfaces than on random backtracks (Table 3.2). While sufficient prey availability was likely enabling coyote persistence in the study area, predator avoidance may be dictating their use of non-compacted snow surfaces more than prey encounters.

Ungulates and red squirrels were the only prey species that showed a higher than expected track crossing rate on actual compacted versus random compacted coyote backtracks, suggesting selection of compacted trails may be more associated with those species than other prey (Table 3.2). Based on our winter diet analyses (Chapter 2), coyotes may be selecting travel paths based on ungulate presence; considered a highly desirable food source because of the high energetic yield. Although coyote predation on ungulates has been reported and success of taking down deer and elk was related to snow depth (Gese and Grothe 1995), killing of ungulates by coyotes is considered risky due to the possibility of injury and low success rates (Paquet 1992). Therefore, the association between coyote travel paths and ungulate presence was not likely due to direct killing by coyotes in our study area, rather this association could be coyotes using ungulates as a

food source through other means, such as exploiting kills made by other predators. Sign at predation sites indicated most ungulate carcasses encountered along coyotes backtracks were wolf kills, which were scavenged by coyotes. Scavenging of wolf kills can be advantageous to coyotes, provided they can exploit the kill while minimizing costs of gaining access and managing the direct risk posed by wolves (Atwood 2006). A variety of behavioral responses have been demonstrated by coyotes adjusting to the potential dangers posed by wolves when exploiting ungulate carcasses in areas recently occupied by wolves (Atwood and Gese 2007). Additionally, numeric superiority and the presence of dominant individuals from a pack can influence the success of coyotes displacing wolves and heighten acquisition of carcasses (Atwood and Gese 2007).

Extensive use of ungulate carcasses during winter may be more common in regions similar to our study area, characterized by high elevation and deep snow conditions, where species rely on a high return from prey to meet energetic needs. Additionally, snow may limit access to other prey species typically available in lower elevations. Although our study was conducted in habitats consisting of patchily distributed clusters of conifer forest widely disbursed in meadows and open woodland, coyotes were not often observed hunting voles or mice in meadows or open woodland areas during daylight hours. We believe this was due to snowmobile presence during daylight hours deterring coyotes from spending extended periods of time in open terrain. In addition, much of the open terrain had been compacted by snowmobiles, thereby altering surface snow conditions and making pouncing and digging for small mammals more difficult.

However, one potential benefit of altered snow surfaces was documented when multiple field observations revealed individual coyotes using compacted trails to network and navigate from one timbered patch to another. During several backtracks, coyotes used compacted trails to travel from one forested cluster to another where snow was shallower under trees and behaviors such as chasing, digging or hunting voles and mice occurred. This could possibly provide an ecological explanation for the association between coyote travel paths and red squirrel encounters. In addition, the association with red squirrel track crossings on actual compacted coyote backtracks could be explained if coyotes were selecting areas that have a high occurrence of red squirrels because of their association with squirrel middens located in whitebark pine habitats. Coyotes may have navigated to areas containing red squirrels, as they may have been more prevalent than other rodent species due to snow depth (as red squirrels remain active year round while several other species burrow in the winter), and therefore were a desirable prey item for coyotes. In addition, there were several instances when tracking coyotes in forested habitats when we observed coyotes digging in squirrel middens, therefore the association between coyote travel paths and red squirrel encounters was likely due to use of squirrel middens. Dietary analyses (Chapter 2) and coyote habitat use (Chapter 4) suggest coyotes were not targeting red squirrels themselves, but selecting habitats to access squirrel middens.

Coyote association with compacted trails

All backtracks conducted during the study showed use of compacted trails for some portion of the track. While coyote backtracks were most frequently documented in

areas with medium levels of snowmobile activity followed by low activity, we found that the more snowmobile tracks were present, the more they were used by coyotes indicating that coyotes were exploiting compacted routes, with their use being related to the amount of snow compaction available. It is possible that as winter progressed and snowmobile use increased (both in volume and extent) over the course of the winter that coyotes became acclimated to snowmobile presence and were less hesitant to use trails. It is also possible that as winter progressed, use of snow-compacted trails became necessary due to non-supportive snow conditions, in order to travel and access prey or habitat patches containing prey in deep snow habitats. Preferential use of snowmobile tracks by coyotes in the presence of an ungulate kill demonstrated their objective of using the least amount of energy possible to access prey.

We documented coyote use of compacted trails on every backtrack suggesting that even though coyotes are only using compacted trails an average of 34.5% of their overall track distance, there is a strong association between coyotes and compacted trails in our study area. Analysis of percent coyote use of snow compacted trails and snow depth by month, shows coyotes using snow compacted trails more during core winter months (January through March; Fig. 3.3). Use of compacted trails was less during December and April, when temperatures were higher, and snow was wetter and more compacted due to melting and freezing cycles. During these months, conditions were more similar to those typical of many areas where lynx and coyotes coexist, such as Kolbe et al. (2007) in Seeley Lake, Montana. Based on results from Kolbe et al. (2007), they were not able to conclude that “compacted snowmobile trails facilitated coyote movements” in their study area. We suggest this is likely due to snow conditions in

northwestern Wyoming being much drier and less supportive than those documented in Montana. Unlike Kolbe's findings, there were several instances during our study when coyotes used snow compacted trails almost exclusively over the course of a 3 km backtrack (Fig. 3.4).

Extensive use of compacted trails was not the only finding contradictory to those of Kolbe et al. (2007). In addition to coyotes using compacted snowmobile surfaces more than expected, we also found that the mean distance coyotes traveled from compacted trails was shorter on actual versus random tracks. It can therefore be implied that not only are coyotes associating their chosen travel path closer than expected to compacted trails, but that they are demonstrating other behaviors such as foraging and bedding closer than expected to compacted trails. While Kolbe et al. (2007) suggested coyotes can behaviorally adapt by selecting shallower and more supportive snow where they naturally occur to travel, hunt, and utilize resources rather than rely on snowmobile compacted surfaces, we further suggest that the level of behavioral adaptation needed in order to persist in such habitats is dictated by snow characteristics indicative of the geographical setting. Therefore, adaptations, behaviors and use of compacted surfaces will differ based on geographical location and ultimately, characteristics of the snow column. In our study area, we found that compaction from snowmobiles greatly facilitated movements and exploitation of deep snow habitats.

Relationships Between Coyotes, Snowmobiles, and Lynx

Critical habitat designations are geographic areas that have been identified by regional experts to contain specific physical and biological features that are essential for

the conservation of threatened or endangered species, and require special management considerations or protection to enhance species recovery until delisting occurs or the critical habitat designations are revised (U.S. Department of the Interior 2009). Mandated by the Department of the Interior to alter current forest practices and create plans that specifically address current and future threats to lynx, criteria specifying how to best identify these threats are still developing as new information becomes available regarding factors that may adversely modify designated habitats. Approximately 101,010 km² of federal, state and private lands have been classified in the contiguous U.S. as critical habitat for lynx.

Additionally, designations include some amount of boreal forest or similar "matrix" landscapes providing one or more of the following beneficial habitat elements for lynx: snowshoe hares for prey; abundant, large, woody debris that can be used for denning; and extended periods of winter snow conditions characterized by deep, fluffy snow. The 24,606 km² of designated critical habitat in the Greater Yellowstone Area (GYA) includes portions of Yellowstone National Park, Teton, Fremont, Sublette, and Lincoln Counties in Wyoming. The GYA is considered an important designation by serving as a potential corridor of connectivity between suitable habitats and lynx metapopulations in the Rocky Mountain region (U. S. Department of the Interior 2009). Still, much remains unknown about species assemblages, and predator-prey and predator-predator relationships within this designation. More information is needed to effectively manage this critical habitat to enhance species recovery.

Our study area provided insight on the relationships between compacted snowmobile trails and their influence on coyote movements in the southern periphery of

lynx range. While direct impacts from snowmobiles on individual lynx were not documented, potential impacts of a likely competitor, the coyote, due to their association with snow compacted trails were indicated.

While snowshoe hare could be an attainable food source and provide a supportable prey base, the repeated visitations to ungulate carcasses highlight the importance of this food source over the course of our study. This is not surprising as carcasses provide a high reward with low energy expenditure (especially if coyotes are using compacted trails to access a carcass), although it should be considered that while there may be a high payoff, there is still risk involved if coyotes are primarily scavenging ungulate carcasses from wolf kills. Therefore, relying on carcasses could be not only risky, but unpredictable as the nature of carcass availability; wolf presence and wolf tolerance of coyotes all have the capacity for abrupt change. Because of this, we suggest that while ungulate carcasses may possibly provide a substantial food source, it is not a reliable one. Rather, we suggest the likelihood that in the future, coyotes could be dependent on both the presence of ungulate carcasses and availability of snowshoe hare to meet energetic needs. Since we have shown that it is likely compacted trails facilitate access to prey, we are concerned with the association between coyotes and compacted trails, and what implications this may have on the local lynx population.

Understanding what role coyotes play in deep snow regions and how snowmobiles influence their behaviors can help us better manage habitats that support lynx and their prey. Management of timber harvests, recreation use, and species assemblages influencing lynx will all be necessary for successful recovery. While the designation of critical habitats by the federal government is a major step towards species

recovery and raising public awareness, it is less effective if we do not understand the underlying mechanisms influencing lynx population persistence. Because snow compaction resulting from winter recreation had an influence on coyote movements during the winter months in northwestern Wyoming, allowing the expansion of winter recreation within lynx critical habitat designations could be counterproductive to lynx conservation efforts.

MANAGEMENT IMPLICATIONS

In northwestern Wyoming, snow compaction resulting from winter recreation use appeared to influence coyote movements during the winter months. In addition to what direct impacts of snowmobiling may cause through disturbance, expansion of current winter recreation use areas may create persistent travel corridors that could be utilized by coyotes. Since coyote use of snow compacted trails was directly related to how much was available, coyote movements may be altered by limiting snow compaction. Further research should be conducted to determine whether the suggestions of Bunnell et al. (2006) to alter winter recreation use areas are practical and could be implemented successfully in areas where lynx conservation is a concern. Further research is also needed to determine direct influence of snowmobiles on lynx movements and population persistence.

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Table 3.1. Total number and percent of predator tracks, mean snow depth, and mean snow penetration recorded along 3 survey routes (Flagstaff Loop, Squaw Basin Loop, Sheridan Creek), Togwotee Pass study area, northwestern Wyoming, December 2007 through April 2008.

Snow survey route	Total predator tracks	% coyote tracks	% wolf tracks	% mustelid encounters	Mean snow depth (cm)	Mean snow penetration (cm)
Flagstaff	781	0.71	0.13	0.14	91.9	24.2
Dec	62	0.26	0.37	0.31	51.0	40.1
Jan	82	0.56	0.23	0.13	78.2	29.5
Feb	150	0.69	0.15	0.16	95.8	20.5
Mar	233	0.75	0.12	0.13	108.4	20.6
Apr	254	0.85	0.04	0.11	199.1	12.4
Squaw Basin	163	0.68	0.15	0.13	144.8	13.1
Dec	3	0	0	1.00	88.9	33.2
Jan	17	0.41	0	0.53	108.9	22.2
Feb	56	0.96	0	0	123.9	10.1
Mar	49	0.31	0.51	0.14	153.6	17.5
Apr	38	0.92	0	0.08	168.8	17.5
Sheridan	439	0.85	0	0.15	97.4	21.1
Dec	37	0.70	0	0.30	57.1	34.0
Jan	67	0.75	0	0.25	82.5	25.2
Feb	82	0.83	0	0.17	101.0	16.0
Mar	143	0.83	0	0.17	113.3	17.5
Apr	110	0.99	0	0.01	128.2	17.5

Table 3.2. Comparisons between compacted and non-compacted track portions from actual (265.05 km) and random (278.54 km) coyote tracks recorded in the Togwotee Pass study area, northwestern Wyoming, 2006 – 2008.

	Actual tracks		Random tracks	
Variable	**Compacted**	**Non-compacted**	**Compacted**	**Non-compacted**
Total distance traveled (km)	85.94	179.58	34.07	244.47
Mean % distance of track	34.52	65.56	13.17	86.86
Mean snow depth (cm)	78.6	91.4	76.9	104.4
Mean penetration (cm)	11.9	19.3	10.6	20.2
# segments/track	12	22	5	20
Mean travel distance/segment (km)	0.124	0.105	0.078	0.206
Distance to snowmobile trail (m)	0	142.5	0	238.6
Predator track crossings	5.38	3.61	6.30	4.87
Wolves/km	0.53	0.19	0.11	0.19
Prey track crossings	12.74	12.18	5.31	16.56
Rodents/km	0.68	0.27	0.85	0.49
Red squirrels/km	2.60	3.10	1.54	3.22
Snowshoe hares/km	4.78	6.54	12.66	5.73
Ungulates/km	1.65	2.26	0.15	0.72

Table 3.3. Regression analysis for percent distance coyotes use a snow compacted trail versus snow depth on compacted trails, snow penetration on compacted trails, snow depth off compacted trails, and snow penetration off compacted trails, for all actual tracks (total distance = 265 km) in the Togwotee Pass study area, northwestern Wyoming, 2007-2008.

Variables	B	Std. Error	Beta	t	P
Snow depth (compacted)	0.396	0.124	0.705	3.197	0.002
Snow penetration (compacted)	-1.357	0.492	-0.440	-2.758	0.008
Snow depth (non-compacted)	-0.405	0.169	-0.511	-2.393	0.020
Snow penetration (non-compacted)	0.831	0.413	0.305	2.011	0.050

Table 3.4. Multi-response permutation procedure testing for differences in variable means between actual tracks (265 km) and random tracks (279 km) in northwestern Wyoming, 2007-2008.

Variables	Actual track	Random track	P
Snowmobile use*	20(L) / 22(M) / 15(H)	14(L) / 27(M) / 16(H)	0.801
Snow depth (cm)	85.018	99.265	0.005
Snow penetration(cm)	15.594	17.231	< 0.001
Rodents/km	0.471	0.574	0.004
Red squirrels/km	2.850	2.685	< 0.001
Snowshoe hares/km	5.657	10.375	0.012
Ungulates/km	1.958	0.488	0.077
Wolves/per km	0.360	0.171	0.379

* Snowmobile use L: low, M: medium, H: high.

Table 3.5. Model selection results for beta regression models testing for the effects of various covariates on the amount of time spend by coyotes on snowmobile tracks (i.e., %Track), northwestern, Wyoming, 2007-2008.

Model definition	df	*AIC	ΔAIC	exp(-0.5*ΔAIC)	*Wi
%track ~ Snowmobile use + Rodent encounters/on tracks + Rodent encounters/off tracks	5	-28.6670	0.0000	1.0000	0.5842
%track ~ Snowmobile use + Rodent encounters/off tracks	17	-27.9301	0.7369	0.6918	0.4042
%track ~ All covariates	4	-19.7438	8.9232	0.0115	0.0067
%track ~ Rodent encounters/on tracks	1	-19.0951	9.5719	0.0083	0.0049

*AIC stands for Akaike's Information Criterion. AIC = -2 * *log-likelihood* + 2 * *df*, where *df* stands for the number of degrees of freedom in the model (Akaike 1973).

*w_i = exp (-0.5 * ΔAIC) / ∑ exp (-0.5 * ΔAIC), where ΔAIC stands for the difference in AIC values between the best performing model and the model of interest.

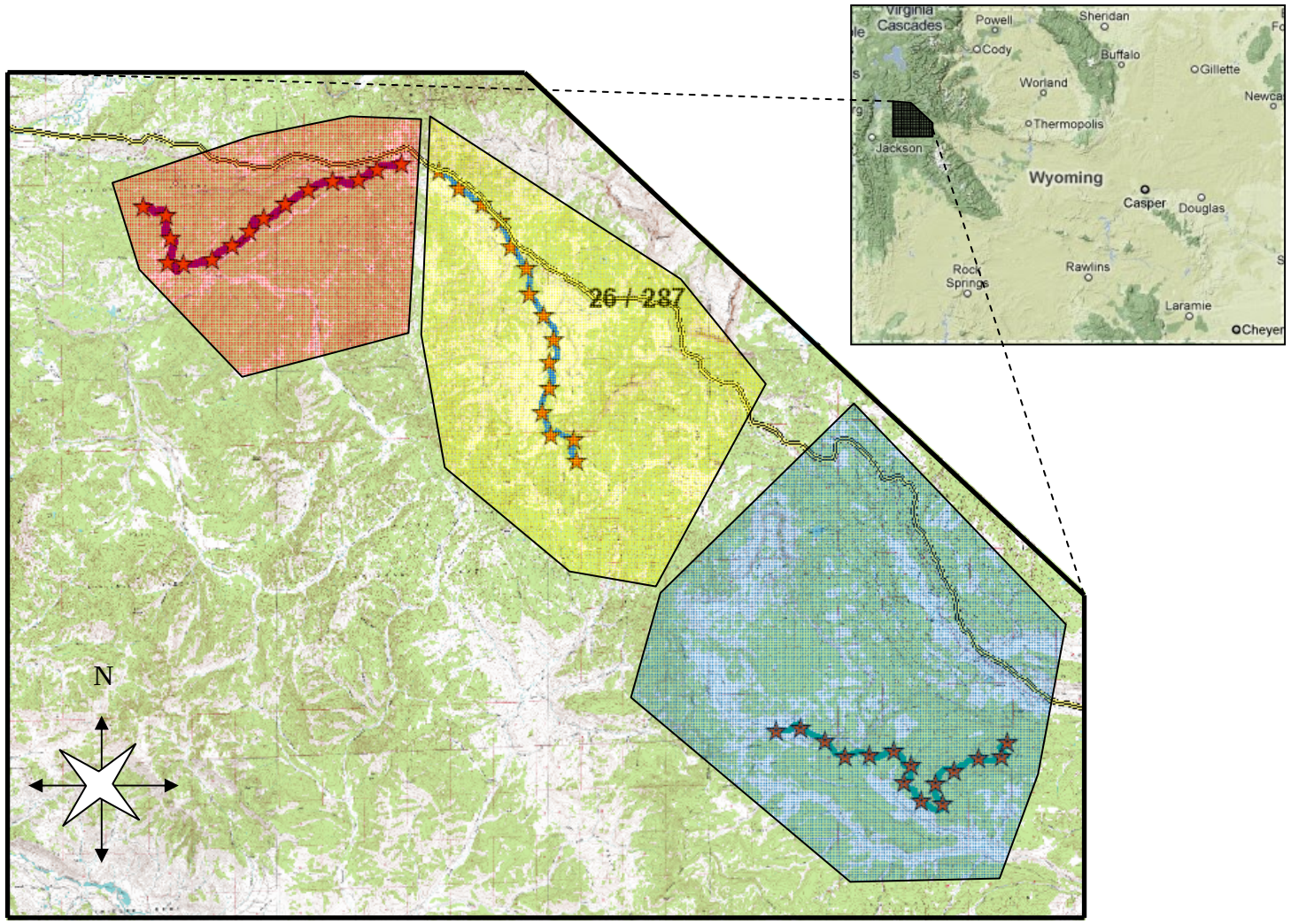


Fig. 3.1. Togwotee Pass study area showing survey routes and coyote backtracks distributed on the west side, east side, and continental divide.

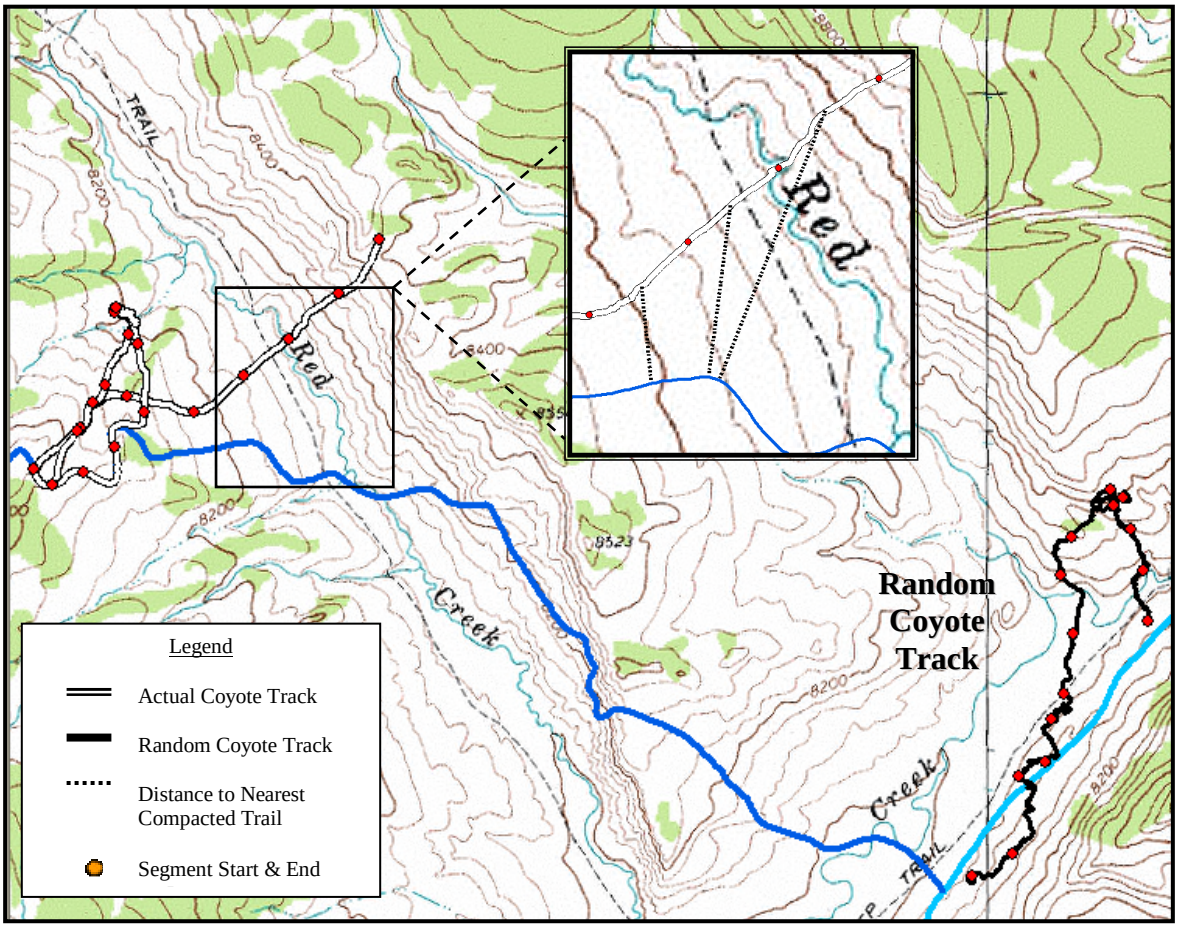
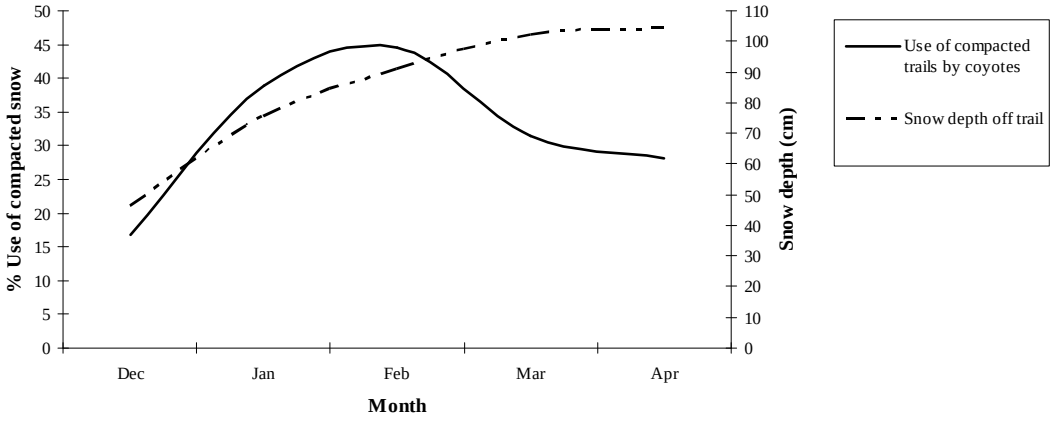


Fig. 3.2. Comparison of an actual and random coyote track documented on 15 February 2008, Togwotee Pass, Wyoming. Inset shows how distance to nearest compacted trail was calculated, by finding the centroid point for each segment within a given track and measuring the distance (m) to the nearest groomed snowmobile trail.

(A)



(B)

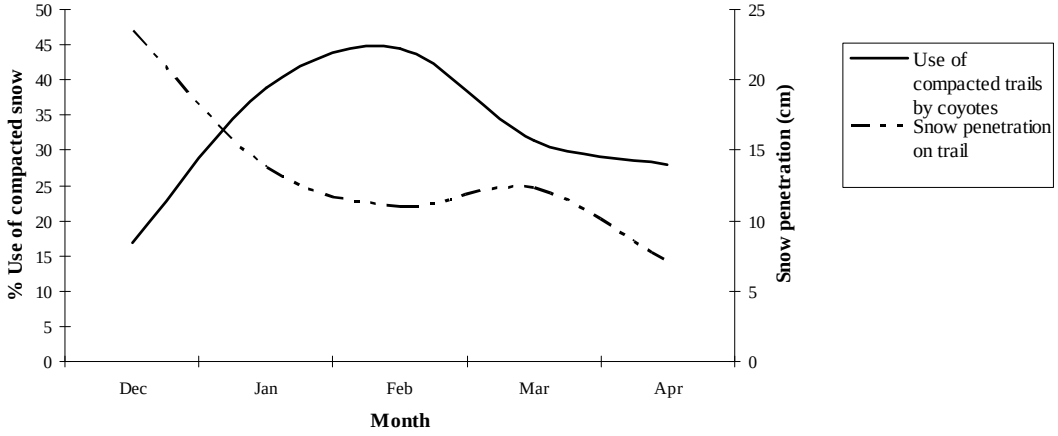
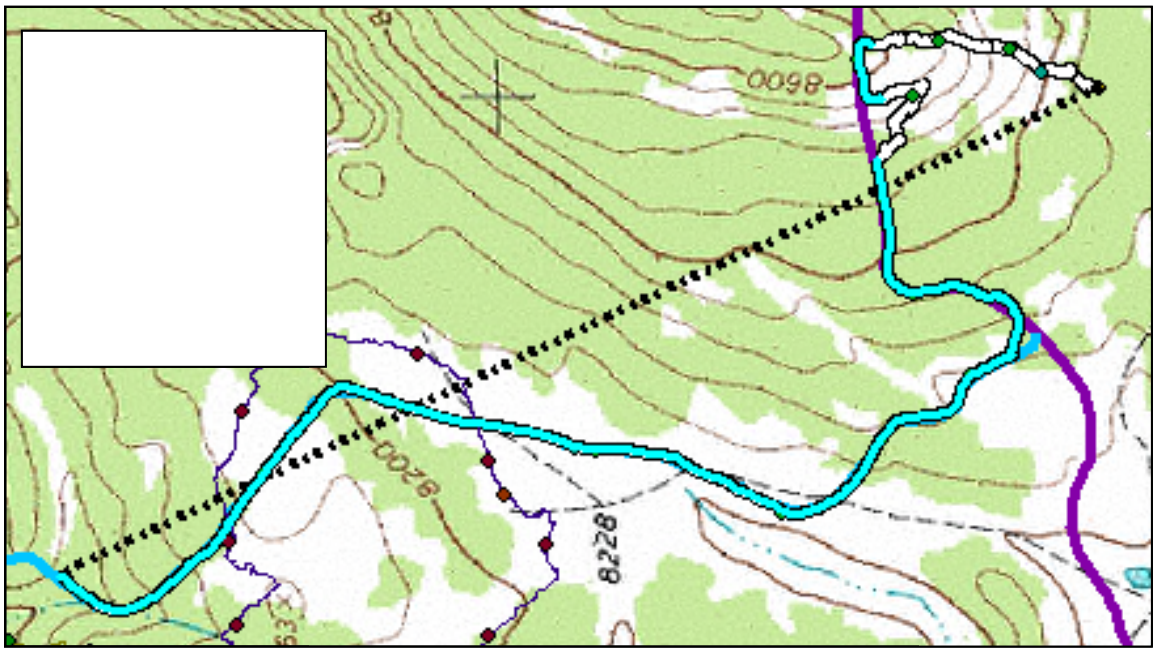


Fig. 3.3. Percent use of compacted trails by coyotes in relation to (A) snow depth off the compacted trail, and (B) snow penetrability on the compacted trail, for each winter month, December 2007 through April 2008, northwestern Wyoming.

(A)



(B)

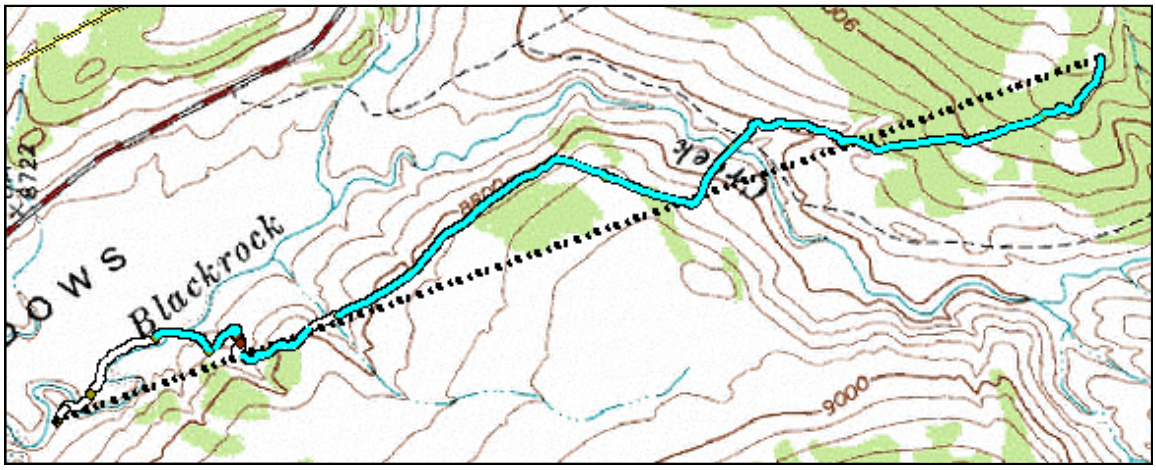


Fig. 3.4. Examples of coyote travel paths in the presence of snow compacted trails: (A) Male coyote 05 on 4 January2008, and (B) Male coyote 15 on 3 April 2008, northwestern Wyoming, 2007-2008.

CHAPTER 4

SPATIAL RELATIONSHIPS BETWEEN HABITAT USE AND SNOW CHARACTERISTICS: HOW COYOTES USE THE LANDSCAPE IN DEEP SNOW TERRAIN

ABSTRACT

In the last century, coyotes (*Canis latrans*) have not only 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 extremely deep snow habitats, we studied coyote space use patterns in deep snow landscapes to examine behavioral adaptations which enable them to use high elevation terrain during the winter. We examined the influence of snow depth, snow penetrability, canopy cover, and habitat, as well as the rates of prey and predator track encounters, on coyote travel distance in high-elevation terrain in northwestern Wyoming. We backtracked 13 radio-collared coyotes for 265.41 km during the winters of 2006-2007 and 2007-2008. Using the backtracking data from actual coyotes and 259.11 km of random travel paths, we compared coyote habitat use and availability on the landscape. Coyotes used specific habitats differently than was available on the landscape. Open woodlands were used for the majority of coyote travel distance (25.6%), followed by mixed conifer (21.2%) and closed stand spruce fir (9.6%). Prey track encounters peaked in closed stand, mature Douglas-fir (DF2; 109.0/km, n = 2) followed by 50-150-year-old Lodgepole Pine stands (LP1; 46.8/km, n = 95) and 0-40-year-old regeneration Lodgepole Pine stands (LP0;

41.1/km, n = 25). Groomed trails represented the habitat type with the most significant variation between use and availability on the landscape (12.0% used versus 0.6% available). Beta regressions and generalized linear models (GLM's) indicated that coyote use of habitats with dense (>50%) canopy covers increased as snow penetration increased (became less supportive), rates of red squirrel track encounters increased, and rates of rodent track encounters increased. Additionally, results suggested that coyotes spent more time within habitats containing tracks of ungulates (deer, elk, and moose). This, partnered with convoluted travel patterns within these habitats, suggested coyotes used habitats characterized by higher canopy cover to hunt. Conversely, use of habitats with dense canopy covers decreased as snow depth increased, and coyotes demonstrated more direct travel patterns within habitats characterized by less dense (0-10%) canopy cover and lower snow penetration (more supportive). This suggested coyotes used these habitats characterized by low canopy covers to travel, likely reflecting the difficulty of coyotes to travel in less supportive snow. Results indicated coyotes remained present throughout the winter and seemed to effectively use resources despite deep snow conditions. The high use of groomed trails associated with coyote habitat use could be a concern for managers where coyote presence might alter system dynamics.

INTRODUCTION

Carnivore persistence in deep snow habitats is reliant on their ability to maximize energetic trade-offs (Poulle et al. 1995, Crete and Lariviere 2003, Zub et al. 2009). Ultimately, 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 Lariviere 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 often necessary for a species to effectively travel, hunt, and exploit resources within such deep snow habitats, as demonstrated in species such as Canada lynx (*Lynx candensis*) and snowshoe hare (*Lepus americanus*; Murray and Boutin 1991, Lesage et al. 2001, Murray and Larivière 2002).

Coyotes (*Canis latrans*) have expanded their geographic range in the last century by moving further north and east in North America and south through Mexico into Central America (Bekoff 1982, Reid 1997, Bekoff and Gese 2003). In addition, coyotes have expanded on a local scale into certain habitats which previously contained few coyotes (e.g., Grinder and Krausman 2001, Bunnell et al. 2006, Morey et al. 2007). While coyotes originally evolved as cursorial predators in the south-west and plains region of the United States and Canada (Moore and Parker 1992), coyotes have recently been documented thriving in a variety of habitats including large cities (Howell 1982, Martin 1999, Morey et al 2007), forested landscapes (Tremblay et al. 1998, Crete et al. 2001), and remote high elevation mountain ranges (Bunnell et al. 2006, Chapter 2). Understanding the role that behavioral and morphological traits play in enabling coyotes to demonstrate this wide level of environmental plasticity and opportunistic flexibility may assist in management of coyotes as well as other species affected by their presence.

Coyote encroachment of deep snow habitats is a concern because of their association with snow compacted trails (Bider 1962, Ozoga and Harger 1966, Keith et al. 1977), and possible competition with lynx (*Lynx canadensis*; Murray and Boutin 1991, Koehler and Aubrey 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 have suggested that geographically distinct regions differing in snow profile, predator communities, and expanse of snow compaction resulting from snowmobile use could results in different findings (Bunnell et al. 2006, Chapter 3). Human altered landscapes can influence resource availability and use (Andelt and Mahan 1980, Mattson et al. 1987, Shargo 1988, Mattson et al. 1992, Craighead et al. 1995, Grinder and Krausman 2001, Gibeau et al. 2002, Beckmann and Berger 2003) therefore changing species behaviors and ecosystem dynamics depending on the adaptive responses (morphological and behavioral) of the species involved. While specialized species may have difficulty adjusting to habitat changes influenced by humans, generalist species usually thrive (Toweill and Anthony 1988, Morey et al. 2007). Consequently, these changes would not only affect predator-predator dynamics, but also predator-prey dynamics and possibly the flora associated with those habitats (Litvaitis and Harrison 1989, Ripple et al. 2001, Hebblewhite et al. 2005). Coyotes, being a highly successful opportunistic predator, would likely succeed over other predators in such modified environments.

Canids may demonstrate a higher level of energetic tolerance in response to deep snow than their prey species (Crete and Lariviere 2003). Some behavioral traits known to

facilitate coyote success in deep snow habitats include their ability to 1) select travel paths with shallower, more supportive snow than is generally available (Murray and Boutin 1991, Kolbe et al. 2007); 2) travel at slow, steady speeds to cover large areas and increase their chance of prey encounters (Lima 2002); 3) demonstrate flexibility in prey selection and feeding habits (Patterson et al. 1998, Bartel and Knowlton 2004); and 4) hunting in groups to acquire larger prey (Gese and Grothe 1995). Several 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 looked at 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 landscape use. Although a recent study has 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 landscape use by coyotes in high elevation terrain characterized by long winters and deep snow to determine what variables influenced coyote use of deep snow habitats, and to understand what drives year round persistence under presumably unfavorable conditions. Therefore, 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 snow supportiveness), canopy cover, habitat type, prey track encounter rates, and predator track encounter rates influenced coyote travel distance in different

habitats. We predicted that 1) due to available habitat types and the lay of the land, habitat use by coyotes would reflect availability on the landscape, 2) the distance spent within different habitats would depend on snow depth and supportiveness (i.e., cost of locomotion) and prey availability (i.e., energy intake), and 3) coyote behavioral traits would be reflected in their use of various habitats based on movement patterns (i.e., groomed trails would be used for travel to cover distance and access desirable habitats, where timbered habitats with high canopy cover would be used for hunting). Ultimately, this research may provide insight towards understanding how coyotes use the landscape, what enables them to do this, and how their presence could influence other species within the ecosystem.

STUDY AREA

We conducted this study on the east and west sides of Togwotee Pass in northwestern Wyoming, located southeast of Yellowstone National Park and east of Grand Teton National Park. U.S. Highway 26 runs east to west crossing Togwotee Pass and was the only major highway located in the study area. The 512-km^2 study area was characterized by extensive recreational trails and roads maintained year-round. Most of the study area was in Teton County, although a portion extended into Fremont County. The area was composed of the Bridger-Teton and Shoshone National Forests, plus some large, privately owned ranches. Elevations ranged from 1,800 m 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 study season (December through April) averaged 226.6 cm in 2006, 149.40 cm in 2007, and 228.9 cm in 2008 (Natural Resources Conservation Service 2008).

Habitats varied between the east and west sides of the pass, with the eastern side classified as dry and the western side as wet. Plant communities on both sides included cottonwood (*Populus angustifolia*) riparian zones, interspersed with sagebrush (*Artemisia* spp.) uplands and willow (*Salix spp*.) -wetland communities at lower elevations. At intermediate elevations, aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) were the dominant species. Whitebark pine (*Pinus albicaulis),* spruce (*Picea engelmannii*), 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 were extirpated from Wyoming by the 1930's, they have since re-established as a result of the 1995 re-introduction efforts in Yellowstone National Park, with at least 4 packs residing near Togwotee as of July 2006 (U.S. Fish and Wildlife Service 2006). Other carnivores aside from coyotes and lynx included cougars (*Puma concolor*), wolverines (*Gulo gulo),* grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), red foxes (*Vulpes vulpes*), and pine martins (*Martes americana*). Ungulate species found in the study area included elk (*Cervus elaphus*), moose (*Alces alces*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and a few white-tailed deer (*O.*

virginianus). Pronghorn antelope (*Antilocapra americana*) were in the study area during the snow-free season on the east side of the pass. Small mammals comprising the potential prey base for coyotes were snowshoe hares (*Lepus americanus*), red squirrels (*Tamiasciurus hudsonicus)*, Uinta ground squirrels (*Spermophilus armatus*), black-tailed jackrabbits (*Lepus californicus*), cottontail rabbits (*Sylvilagus spp*.), ruffed grouse (*Bonasa umbellus*), blue grouse (*Dendragapus obscurus*), northern flying squirrels (*Glaucomys sabrinus*), deer mice (*Peromyscus maniculatus*), voles (*Microtus spp.*), gophers (*Thomomys spp*.), and various cricetid species.

Snowmobiling was extensive during the winter, allowing riders to access approximately 966 km of groomed trails and 2.5 million acres of off-trail riding in and around the study area once snow conditions permitted (typically late October through May). Trail grooming operations typically began by mid–December with trails maintained through April 1 depending on snowfall. Wyoming's Continental Divide Snowmobile Trail (CDST) was considered one of the top trail systems in the west, contributing to many of the 17,876 resident, 983 commercial, and 17,518 nonresident snowmobile permits purchased in the state from July 2007 through June 2008 (Wyoming Department of State Parks and Cultural Services 2008).

METHODS

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 below, Coyote Backtracking). 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). Cover types used a two-letter code paired with a number to classify a continuous patch, where the two letters represented an abbreviation of the dominant tree species and the number represented the age of the trees currently in the stand, or the time since the last disturbance (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, 3 = 300+ years old. A 2-letter abbreviation lacking an attached number represented a cover type that was a climax stand, often starting to show signs of other species co-dominating in the understory, multi-aged trees, and woody debris on the ground. Specific cover types documented 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 (Appendix B).

Coyote Captures

We captured coyotes in the summer and fall using Victor #3 padded-jaw "soft-catch" leg-hold traps with attached tranquilizer tabs containing 600 mg propiopromazine. A variety of baits and lures were used to attract coyotes to the traps. Coyotes were also

captured 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 (Barrett et al. 1982, 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 and the USDA/National Wildlife Research Center.

Coyote Backtracking

Radio-collared coyotes were back-tracked during the winter months of 2006-2007 and 2007-2008 using methods developed by Kolbe et al. (2007) at Seeley Lake, Montana. The purpose of backtracking individuals was to document microhabitat use and spatial patterns on snow-compacted routes and non-compacted terrain (i.e., areas not used by snowmobiles). Data collected during the backtracking of individuals was used to determine how extrinsic factors (prey track encounter rates, predator track encounter rates, snow depth, snow penetration, canopy cover, and habitat type) influenced the distance a coyote traveled within a given habitat.

Individual coyotes were selected randomly for backtracking using a computer generated randomization sequence (SAS Institute Inc. 1999) to avoid bias and ensure that all coyotes were sampled equally. Once selected, coyotes were located by triangulation using ≥ 3 azimuths, and their position projected using LOCATE II, version 1.82 (Nova Scotia Agricultural College [NSAC], 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 control travel path. Control paths, or “random travel paths” were

created 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 (Chapter 2). This procedure and projection distance were used to ensure sampling independence from the actual travel path and, for statistical purposes, to be used for comparing data collected from the actual coyote travel path to random travel paths (Kolbe et al. 2007).

The direction and projection of random travel paths were generated randomly using SAS (SAS Institute Inc. 1999), by creating a randomized sequence selected from values between 1 and 360 (representing degrees); one randomization sequence was created for the direction, and one for the projection. Before going into the field, the random travel path created for that day was overlaid onto a topographic map using ArcGIS (Environmental Systems Research Institute (ESRI), Redlands, California) to ensure field crews were capable of conducting a travel path survey in the terrain where it had been randomly projected. If the random path had been projected in an avalanche path or dangerous/unattainable terrain, the path was reprojected to ensure the safety of the field crews, using a second set of projected numbers from the randomized sequence. If the terrain was considered acceptable, the random travel path layer was permanently saved onto a digital map, transferred to a handheld computer (Trimble GeoExplorer® series 3, Sunnyvale, California) and taken into the field. The only reason a travel path was ever reprojected was for safety reasons. This ensured that random paths were not projected in areas simply because they were easy to access or conduct travel path surveys in, eliminating potential surveyor bias of roads, terrain and snow compaction.

Backtracking began in the morning after night movements of coyotes had occurred and before the snow column deteriorated. Both actual and random path surveys were conducted by teams of 2 field personnel, taking measurements and recording data for ≥ 3 km of tracking. Start locations were reached using skis and snowmobiles along preexisting compacted trails to avoid additional compaction as much as possible within the study area. Using a Trimble GeoExplorer, all data was collected in digital format using a datasheet generated with the computer software GPS Pathfinder Office, version 3.0 (Trimble Navigation Limited, Westminster, Colorado, USA). At the start of each travel path, initial track information was recorded including observers, start time, start location, ambient temperature, and elevation. Teams communicated with radios to commence backtracking of actual and random paths simultaneously.

During each actual or random travel path, pathfinder software recorded locations every 5 seconds along any given travel path. Point locations were marked every time a habitat change was encountered, organizing the travel path into distinct but consecutive segments identified by habitat (Kolbe et al. 2007). Canopy cover was recorded within each habitat using a densiometer to rank canopy closure into 4 categories: 0-10%, 11-39%, 40-69%, and 70-100% canopy cover. Prey and predator track crossings were identified at point locations by number and species every time a set of animal tracks crossed a coyote travel path. Snow depth was measured with every habitat change and every 200 m along the travel path using an avalanche probe (marked in cm) to measure from the snow surface to the ground. Snow penetration was documented 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. Once imported, travel paths were differentially corrected to enhance the location data quality and improve data integrity. Travel paths were then smoothed to eliminate bounce or GPS scatter caused by canopy cover or varying topography which can influence location accuracy. All travel paths were converted to ArcGIS files for analysis.

Statistical Analysis

Habitat selection

Due to the scale of our study and the inadequacy of GIS layers currently available for the area, coyote habitat use was measured 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 between habitats. Unequal variances led to the use of a nonparametric Krukston-Wallis test in (SPSS version 10.0.5, SPSS Incorporated, Chicago, Illinois, USA) 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.

Biological covariates of interest

The covariates we hypothesized to be most important in determining how coyotes used the landscape included habitat characteristics (e.g., habitat cover 'HAB', canopy cover 'CC'), snow characteristics (e.g., snow depth 'SD', snow penetration 'SP'), predator track encounters (e.g., wolf 'WF'), and prey track encounters (e.g., snowshoes hares 'SSH', red squirrels 'RS', grouse 'GR', rodents 'ROD', ungulates 'UNG'). 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 densities 'TotPrey', in an attempt to save 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 version 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 colinearity, and vice versa. All the analyses below were conducted in R version 2.10.1 (R Development Core Team 2010).

Influence of snow characteristics, prey, and predators on distance traveled

Distance traveled within various habitats allowed to examine movement patterns (convoluted use versus straight line use) and understand behaviors associated with how coyotes used habitats. To understand which factors (i.e., habitat characteristics; snow characteristics, small [rodents, leporids and avian sp.] and large [ungulates] prey species, total prey, and predators) 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 (Fig. 4.1).

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 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. We believe that 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, snow characteristics, and as a function of both predator and prey encounter rates.

To address this, we used beta-regressions (Ferrari and Cribari-Neto 2004) via the 'betareg' procedure implemented in the R library 'betareg'. Beta regressions can be implemented in situations where the dependent variable (LRATIO) is continuous and restricted to the unit interval 0-1, such as proportions or rates. The regression was

modeled to be beta-distributed and called for 2 parameters: a mean and a dispersion parameter. The mean is linked, as in generalized linear models, to the responses through a link function (e.g., logit) and a linear predictor.

We used the function ‘qsreg’ in library ‘fields’ to conduct a robust spline regression between LRATIO and any significant covariate of interest; we then applied the ‘lowess’ function in library ‘stats’ (Becker et al. 1988) to draw weighted polynomial regressions between LRATIO and these covariates in order to graphically assess the direction and strength of the relationship between significant explanatory variables and LRATIO.

Habitat use based on variables encountered within 4 levels of canopy cover

Because habitats are categorical data and could not be quantified, we assessed coyote habitat use by comparing variables (snow characteristics, prey encounters and predator encounters) documented along actual coyote travel paths to a habitat serogate (canopy cover) within 4 levels: 0-10%, 11-39%, 40-69%, and 70-100%. Based on the classification system used for habitat types and not only differences in canopy cover characteristic of those habitats, but variations in snow characteristics, prey dynamics and predator dynamics demonstrated by canopy cover, we were able to use canopy cover to demonstrate what coyotes selected based on variables encountered. To determine differences in canopy cover use by coyotes, we analyzed the use of various canopy cover ‘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’, in an attempt to save some degrees of freedom. 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%, CC = 4 if > 69%). We used generalized linear models ‘GLM’ (Dobson 1990; package ‘MASS’, procedure ‘glm’) to model the effects of various covariates on a coyote’s choice of canopy cover levels (CC).

We also used robust spline regression and weighted polynomial regressions to study the relationship between canopy cover (CC) and any significant covariate of interest (see section above ‘Effect of snow characteristics, prey, and predator densities on distance traveled’ for a full description of the methods).

Model selection

For both beta regressions and generalized linear models, we used Akaike’s Information Criterion corrected for small sample size, AICc (Akaike 1973) defined as AICc = -2 * *log-likelihood* + 2 * *df*, where *df* stands for the number of degrees of freedom in the model. We also calculated Akaike model weights (w_i) to compare models and determine which model(s) served as the best approximation(s) to the data: $w_i = \exp(-0.5 * \Delta AICc) / \sum \exp(-0.5 * \Delta AICc)$, where $\Delta AICc$ stands for the difference in AICc values between the best performing model and the model of interest.

We based model selection on both AICc and *p*-values. We first estimated a global model testing for additive effects of all of the covariates of interest. Second, we removed all covariates that did not have a significant effect on either LRATIO or CC ($p > 0.05$) and checked then whether AICc decreased or increased. If AIC values are positive, the smaller the value the better model fit, and vice versa for negative AIC value (the biggest negative value corresponds to the best performing model). Third, we repeated the process until we found a model that provided the best AICc value and for which each covariate had a significant effect on the response variable of interest ($P \leq 0.05$). Finally, we considered biologically meaningful interactions between the covariates retained as part of the best performing model. If AICc improved, we considered the interaction model as the best performing model.

For each estimated parameter (β_i) that appeared in the best approximating model(s), 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) to discuss the significance of each covariate effect on the response variable (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.

Backtracking

A total of 59 coyote travel paths were followed for a combined distance of 265.43 km, from 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).

Habitat selection and use

We compiled a ranking system based on how habitats were used and assessed how we hypothesized they should be used under isolated conditions taking into account a single variable. 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 4.1).

Coyotes used open woodlands for the majority of their travel distance (25.6%), followed by mixed conifer (21.2%) and closed-stand spruce-fir (9.6%; Table 4.1). Prey encounters peaked in closed canopy, mature douglas fir (DF 2; mean = 109.0/km, n = 2) followed by dense, young lodge pine (LP1; mean = 46.8/km, n = 95), recently burned lodgepole pine (LP0; mean = 41.1/km, n = 25), climax stand lodgepole pine (LP; mean = 37.9/km, n = 3), and even-aged closed stand spruce fir (SF1; mean = 36.8/km, n = 100; Table 4.1). Wolf track crossings were most frequent in open woodland (OW; mean = 1.4/km, n = 337), aspen conifer (AC; mean = 1.1/km, n = 35) and 300+ year successional

forest lodgepole pine (LP3; mean = 1.0/km, n = 33; Table 4.1). 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 groomed trail (GT; mean = 42.2 cm, n = 95), mature whitebark pine co-dominated with spruce, fir and lodgepole (WB3; mean = 49.0 cm, n = 3) and mature to over-mature whitebark pine (WB; mean = 59.0 cm, n = 1; Table 4.1). The most supportive snow was also on groomed trails (GT; mean = 4.92 cm, n = 95) followed by mature to over-mature whitebark pine (WB; mean = 8.0 cm, n = 1) and aspen (AS; mean = 16.6 cm, n = 8; Table 4.1). The greatest travel distance ratio was encountered in groomed trail (GT; mean = 0.70, n = 95; Table 4.1), 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; mean = 0.63, n = 3) and open woodlands (OW; mean = 0.61, n = 337) had the next highest distance ratios (Table 4.1).

When comparing habitats encountered on our control paths to actual coyote backtracks, there were three habitat types that were not encountered on both datasets: 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 (38.18%) followed by mixed conifer (20.85%), young spruce-fir (SF0 = 9.14%) and closed-stand spruce-fir (SF1 = 8.53%; Table 4.1). Almost all of the top ten ranking habitats used by coyotes were also in the top ten habitats available across the

landscape (Table 4.1). The only major discrepancy when comparing availability to use by coyotes was with respect to groomed trails (GT). According to our random paths, groomed trail was only available 0.65% of the time, while it ranked third in coyote use, accounting for 12.04% of their travel distance, meaning that proportionally, they used GT 18.5 times more than available (Table 4.1). This is notably higher than any other habitat comparison encountered on the landscape.

We further assessed this by running a Kruskall-Wallis test which indicated a significant difference in distance covered between the control (random distance) and the treatment (actual distance), both across habitats ($x^2 = 154.39$, $df = 16$, $P < 0.001$) and between habitats (Table 4.2.). While coyotes were shown to use habitats aspen conifer (AC), groomed trail (GT), closed canopy lodgepole pine (LP2), 300+ year successional lodgepole pine (LP3), climax spruce fir (SF) and even-aged close stand spruce fir (SF1) more than what was available on the landscape, only GT ($x^2 = 38.13$, $P < 0.001$), LP2 ($x^2 = 4.17$, $P = 0.041$) and WB3 ($x^2 = 3.15$, $P = 0.076$) were considered significant (Table 4.2). Conversely, aspen (AS), closed canopy mature douglas fir (DF2), climax stand lodgepole pine (LP), young, dense lodgepole pine (LP1), open woodland (OW), recently disturbed spruce fir (SF0) and mature to over-mature whitebark pine (WB) were used by coyotes less than what was available on the landscape, although only LP1 ($x^2 = 7.93$, $P = 0.005$) and SF0 ($x^2 = 5.35$, $P = 0.021$) were significant (Table 4.2).

Effect of snow characteristics, prey, and predator encounters on distance traveled

We did not experience any issues with colinearity when running our models to assess the effect of variables on distance traveled by coyotes and coyote selection of habitats with differences in canopy cover. All variance inflation factors were < 5 (Appendix C; Neter et al. 1996). Due to low encounter rates (n = 2), we pooled DF2 habitats with MC to increase sample size, leaving us with 17 habitats for analysis. The best performing model retained an effect of all the covariates tested (HAB, CC, SD, SP, SSH, RS, GR, ROD, UNG, WF) on LRATIO (Table 4.3, AICc = -496.214, df = 10). The model explained 38.4% of the overall AIC_c weight (Table 4.3; $w_i = 1$), and performed as well as the next best performing model that explained 37.3% of the weight ($w_i = 0.373$) and only retained covariates that had a significant effect on LRATIO, as well as interaction terms: model 'CC + SP + UNG + CC*UNG + SP*UNG' (Table 4.3). We discussed only the latest model since the top model retained all covariates, including some that had no significant effect on LRATIO (Table 4.4).

The best performing model indicated that canopy cover 'CC', snow penetration 'SP', and ungulate encounter rate 'UNG' all had a significant effect on 'LRATIO'. Canopy cover negatively influenced the LRATIO, meaning that as canopy cover increased, the distance ratio increased. This result indicated that coyotes covered less distance (compared to the shortest possible distance) in habitats with dense canopy cover (Table 4.5., β_{CC} = -0.431, *95% CI*: -0.472 to -0.390, *z-test value* = -10.551 $P < 0.001$). Similarly, snow penetration had a negative influence on the distance ratio, suggesting that coyotes would tend to cover more distance in locales where snow penetration is low

compared to the shortest possible distance (Table 4.5; β_{SP} = -0.024, *95% CI*: -0.027 to -0.022, t = -9.721, P < 0.001). Ungulate encounter rates negatively affected the distance ratio as well, but to a lesser extent (Table 4.5; β_{UNG} = -0.006, *95% CI*: -0.009 to -0.003, t = -2.093, P = 0.036). This indicated coyotes tended to cover less distance (spend more time) in areas with ungulates (deer, elk, moose) than needed, however the effect was very weak. The same model also retained interactions between canopy cover and ungulate encounter rates, and between snow penetration and ungulate encounter rates, but those were not significant (Table 4.5).

The smooth regression between LRATIO and CC showed that the distance ratio gets larger as the snow gets deeper (Fig. 4.2A) indicating that coyote cover more distance in deep snow, probably reflecting the difficulty for them to move in high snow penetration locales. The relationship between LRATIO and log-transformed ungulate encounter rate 'log(UNG)' was flat and centered on 1, since encounters were mostly 0 (89.5% of observations), therefore very little inference can be made on this particular result (Fig. 4.2B). Lastly, the relationship between CC and LRATIO demonstrated that as canopy cover increased, the distance ratio decreased, indicating that coyotes covered less distance in 'closed' habitats (thick cover), and more distance in open habitats.

Habitat use based on variables encountered within 4 levels of canopy cover

The best performing model retained an effect of snow depth (SD), snow penetration (SP), red squirrel encounters (RS), and rodent encounters (ROD) (Table 4.6; AICc = 2197.084, *df* = 4). The model explained 48.3% of the overall AIC_c weight (Table

4.6; w_i = 0.483). The rest of the weight (39.8%) was explained by a similar model that only retained 3 of the 4 covariates, and rejected rodent encounters (Table 4.6; w_i = 0.398). The best performing model indicates that snow depth 'SD' had a significant but weak negative effect on canopy cover (Table 4.7; β_{SD} = -0.002, *95% CI*: -0.002 to -0.001, *z*-test *value* = -3.438, *P* = 0.001), whereby the deeper the snow, the larger the preference for low canopy cover habitats (Fig. 4.3A). Snow penetration had the opposite effect on habitat use (Table 4.7; β_{SP} = 0.017, *95% CI*: 0.015 to 0.018, *z*-test *value* = 9.528, *P* < 0.001), such that as snow penetration increased, the use of habitats where canopy cover was dense increased (Fig. 4.3B). Rate of red squirrel track encounters had a significant effect on canopy cover as well, whereby the higher the encounter rate, the larger the preference for dense canopy covers (Table 4.7.; β_{RS} = 0.003, *95% CI*: 0.002 to 0.004, *z*-test *value* = 4.386, *P* < 0.001; Fig. 4.3C). Rodent track encounter rate was retained as part of the model but was not significant (β_{ROD} = -0.001, *95% CI*: -0.002 to 0.000, *z*-test *value* = -1.542, *P* = 0.123; Fig. 4.3D). We also considered biologically meaningful interactions between significant covariates. However, they did not improve model fit, thus we did not present such model for the sake of conciseness.

DISCUSSION

Coyote Habitat Use versus Availability

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

cases, coyotes used specific habitats more or less than were randomly available. Significant differences in distance spent both between habitats and within habitats indicate that landscape use was not random. Significantly more use of GT, LP2 and WB3 suggested that these habitats had desirable traits for coyotes.

The fact that coyotes used groomed trails for a high proportion of their travel distance compared to availability on the landscape (12.0% versus 0.6%) suggests 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 4.1), we suspect the reason for high use of groomed trails compared to availability could be contributed to a low predator encounter rate, low mean snow depth and low mean snow penetration (of which GT received '1' rankings for all aforementioned variables). The combined influences of these variables suggested groomed trails presented a habitat where coyotes will experience minimal threat from other predators and low resistance to winter travel.

Additionally, groomed trails (GT) received a relatively high ranking for prey encounters (6 out of 18), showing that coyotes averaged 29.0 prey encounters/km (n = 95). Although other habitats ranked higher in prey encounters, it should be considered that because of low snow depth and high level of supportiveness in this habitat, coyotes could potentially cover more distance in a shorter time, expending less energy and encountering more prey due to temporal constraints than compared to other habitats. It is also possible, based on the distance ratio (which shows coyotes are 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 (see Chapter 2). Overall, groomed trails had the most high-ranking desirable traits for any habitat encountered suggesting that it could be the best habitat for minimizing energy expenditures and maximizing returns.

While snow depth appeared to be noticeably low in WB3 habitats and could provide the primary explanation for why coyotes used this habitat significantly more than availability (i.e., ease of travel), it should also be mentioned that diet analyses (Chapter 2) indicated a high presence of whitebark pine seeds in the diet of coyotes during certain months of the year. It is likely the stand structure and maturity of these trees (their ability to produce cones), combined with low snow depths (making access to seed caches more available), that coyotes spent more time in this older habitat than younger whitebark pine habitats could reflect the presence of whitebark pine seeds in coyote diets. Whitebark pine seeds have been shown to be an important food source for several bird and mammal species including black bears, grizzly bears and red squirrels (Mattson and Reinhart 1997). If coyotes were able to utilize 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 if they are 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 (Appendix 4.1). As for SF0, it is possible that a high predator encounter rate (wolf encounters = 1.01/km) could account for the difference in use versus availability (Table 4.2).

Despite habitat availability and the general expectation that coyotes demonstrate high use of meadows and grasslands because if provides desirable conditions for hunting (high detection rates and capture rates of prey occur in these habitats; Gese et al. 1996*b*), we were surprised by the high percent use of open woodland compared to other habitats by coyotes in our study area. Although coyotes used open woodlands less than were available on the landscape (use = 25.6%, n = 337; availability = 38.2%, n = 666)., we hypothesized that coyote use of this habitat would be significantly less than available due to the 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), hindered movement in deep snow (Crete and Lariviere 2003) and limited availability of small prey due to snow cover (Wells and Bekoff 1982, Halpin and Bissonette 1988). Coyotes were rarely observed in the open during daylight hours in winter (Burghardt, unpublished data). Since most of our backtracks were conducted on animals after night movements took place, we highlight the need for understanding coyote movements on a temporal scale to understand how coyotes use the landscape compared to other predators and prey within our study area. We believe coyote use of open woodland habitats

remained high primarily due to availability of snow compacted trails through this habitat (Chapter 2).

Coyote Travel Distance within Habitats

As we hypothesized, distances traveled within habitats were related to snow supportiveness, suggesting that the cost of locomotion influenced distance traveled within more energetically expensive habitats. Coyotes traveled further and straighter within habitats that had more supportive snow, while coyote travel paths were more convoluted in habitats with less supportive snow. Canopy cover also had this affect on coyote travel distance, indicating that coyotes traveled less distance (had a more convoluted travel path) within habitats having higher canopy covers. Essentially this indicates 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 further on more supportive snow when snow depths increased) supported this assumption, suggesting that coyotes changed their behaviors to minimize energy expenditure in the presence of deeper snow.

Although the association was weak, coyotes spent more time traveling in habitats with higher ungulate encounters possibly due to either 1) ungulates were spending more time in closed canopy habitats and this association was a parallel event, or 2) coyotes were occasionally selecting habitats that contained ungulates because it increased their chance of an encounter (perhaps a response to carcass presence). While there was insufficient data to test our second hypothesis, the association with habitats with higher ungulate encounters may reflect an attempt to more effectively encounter ungulate

carcasses. Winter is stressful on ungulates especially during periods of deep snow (Murie 1940). During such time, ungulates become more vulnerable to death or predation. In Yellowstone National Park, Gese et al. (1996*a*) found as snow depth increased, coyotes spent less time actively traveling and hunting and more time feeding on ungulate carcasses and resting. We encountered several instances during coyote backtracks where coyotes had been feeding on ungulate carcasses and these influenced their travel path (Chapter 2). Possibly the association of travel distance within segments and the presence of a carcass represented a similar response. Using habitats with low canopy cover to travel may also enable coyotes to access desirable habitats (containing carcasses or prey) more efficiently. If coyotes were regularly utilizing large prey such as carcasses, their need for constantly hunting of small prey would not be as crucial, and excessive expenditure of energy during the winter could be avoided.

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. 1996*b*). 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 hunting strategies for acquiring prey (Gese et al. 1996*a*). In this regard, forested habitats could be advantageous to coyotes in our study area, as dense canopy covers yield 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. (1996*b*) have 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 where demonstrated by coyotes hunting in forested habitats. However, this data was obtained from an area where snow compaction and persistent human disturbance was not an issue during prey acquisition in open terrains.

While sight has been accepted as the primary sense involved in coyote predation (Wells 1978), recognition and pursuit of prey such as leporids, ungulates and rodents may be hindered in forested habitats. The importance of olfactory and auditory senses should not be overlooked as methods for locating and acquiring food items by coyotes utilizing forested habitats, especially with regards to carcass utilization. Often in dense vegetation, sight alone would be prohibitive for prey acquisition. The use of all senses to increase efficiency in locating prey would be important for coyotes to maintain a balance between energy expenditure and intake.

Since habitat use was measured as a function of distance rather than time, we compared coyote use within habitats using movement patterns rather than temporal comparisons. Coyotes used habitats characterized by dense canopy cover to hunt during

the winter months as illustrated by the convoluted travel patterns while in forested habitats. While this could be interpreted as maneuvering around debris or seeking out more supportive snow within habitats, the observation of predation attempts and digging sites primarily in forested habitats partnered with the following of prey tracks supported our interpretation of hunting behavior (Burghardt, unpublished data). Additionally, coyotes preferred habitats with denser canopy cover as red squirrel encounter rates increased. While coyotes have been documented to prey on red squirrels, they have been shown to prefer other small mammal species over red squirrels, especially snowshoe hares (O'Donoghue et al. 1998). However, red squirrels are known to show a high association with whitebark pines and stash seeds in middens, which become important food sources for other wildlife species such as bears (Mattson and Reinhart 1997). As mentioned above, coyotes used WB3 habitats, which were characterized by dense canopy covers, more than available due to the presence of whitebark pine seeds (Chapter 3). Because of the association of red squirrels with whitebark pine, the selection of high canopy covers with an increase of red squirrels may not be due to red squirrel presence, but rather through association with whitebark seeds and middens.

Coyotes have been shown to use compacted trails to negate the impacts of deep snow (Murray and Boutin 1991, Murray and Lariviere 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 is likely due increased expenditures in dense habitats where snow is 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.

Implications for System Dynamics

Coyotes in our study area demonstrated versatility to deep snow conditions based on documented habitat use, behaviors associated with that use, and rates of prey encounter along coyote travel paths. During the course of our study, coyotes appeared to be abundant (Chapter 2), effectively used deep snow habitats, and maintained high performance levels (i.e., physical condition observed at time of capture) despite a light, non-supportive snow column. Whether coyote presence in these deep snow habitats may impact other species in the ecosystem is unknown. Knowledge of predator dynamics and how preys influence the behavioral responses of multiple predator species within a system can facilitate a greater understanding of potential impacts from a single species. The information we have provided regarding coyote habitat use in deep snow terrain could be useful for managers concerned with coyote presence in high elevation ecosystems. For example, analyses of coyote habitat use could be insightful to their use of whitebark pine habitats. Diet analyses showed coyote use of whitebark pine seeds to occur late fall and early winter (Chapter 3). Grizzly bears in the Greater Yellowstone

Ecosystem are particularly reliant on seed caches as a dietary source during the spring (March – May) and fall (September – November; Craighead and Craighead 1972). While seed caches may be limited during certain years, coyote use of this resource could impact grizzly populations relying on them for prehibernation nutrition.

Coyote use of groomed trails (for travel) and use of forested habitats (for hunting) during the winter could pose possible ecological implications. Coyote use of groomed trails within deep snow regions may create competition with other species, such as lynx, by enabling coyotes access to a broader variety and expanse of habitat patches. When considering access to and use of forested habitats, it should be highlighted that forested habitats provide some of the best concealment and quality habitat for snowshoe hares (Litvaitis et al. 1985). Snowshoe hares are a major food item found in coyote diets throughout North America (Parker 1986, Crete et al. 2001). In one study conducted in the boreal forests of Alberta, Canada, coyote densities were strongly related to snowshoe hare densities (Todd, Keith and Fischer 1981). Research conducted in our study area recorded a high density of snowshoe hares/ha (Berg 2010), demonstrating that although coyotes did not select for habitats containing snowshoe hares, they have been known to specialize on various species under optimal conditions. The cyclic phenomenon for which snowshoe hares are widely recognized results from both bottom up and top down effects, ultimately dependant on habitat quality and the abundance of winter browse balanced with predation (King and Schaffer 2001). However, with no prior knowledge of cyclic trends in this region, it is hard to know how coyotes could influence snowshoe hare and other species associated with their presence.

Further research should be conducted in this region to determine habitat use by coyotes without the presence of groomed trails. If we know whether coyote presence in high elevation terrain is primarily the result of groomed trails, we would have a better understanding of how to manage coyotes and conserve species influenced by their presence. We suspect that in their absence, locomotion costs would increase and coyotes might not be able to use the landscape as effectively, which could minimize their presence and impacts to the system.

MANAGEMENT IMPLICATIONS

The high use of groomed trails associated with coyote habitat use could be a concern for managers where coyote presence might negatively alter ecosystem dynamics. The high use of groomed trails by coyotes compared to availability on the landscape suggested that increased availability to routinely groomed trails could increase their use of these networks substantially, and utilize resources within forested habitats connected by these networks. Limiting the expanse of groomed trail systems, their proximity to conservation areas and/or predictability of their establishment on the landscape may help minimize coyote encroachment. In order to fully understand the potential influences of coyote presence in deep snow ecosystems, future work is needed to determine sequential spatial patterns for predictive modeling and temporal relationships with other species located in the system.

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Table 4.1. Habitat use by coyotes from actual backtrack data in the Togwotee Pass study area, northwestern Wyoming, winters 2006-2007 and 2007-2008. 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.

Habitat type	Habitat use (%)	Habitat availability (%)	Prey encounters	Predator encounters	Snow depth (shallowest to deepest)	Snow Pen. (most to least supportive)	Ratio (start @ lowest ratio = most to least hunting)
Assumption:			**Maximizing**	**Avoidance**	**Select for shallow**	**Select for supportive**	**Select for distance**
OW (Open Woodland)	(1) 25.63	(1) 38.18	(16) 10.57	(18) 1.35	(16) 97.60	(4) 16.89	(16) 0.61
MC (Mixed Conifer)	(2) 21.28	(2) 20.85	(6) 34.51	(13) 0.29	(12) 90.63	(13) 21.22	(6)0.43
GT (Groomed Trail)	(3) 12.04	(13) 0.65	(8) 29.00	(1) 0.00	(1) 42.23	(1) 4.92	(18) 0.70
SF1 (Spruce-Fir Closed Stand)	(4) 9.63	(4) 8.53	(5) 36.83	(1) 0.00	(10) 88.57	(17) 24.02	(2) 0.36
LP2 (Lodgepole Pine 150-300 yrs)	(5) 6.48	(6) 3.37	(13) 22.55	(14) 0.58	(7) 81.62	(6) 17.79	(8) 0.44
SF0 (Spruce-Fir Open Canopy)	(6) 4.95	(3) 9.14	(11) 23.62	(15) 1.01	(14) 91.25	(11) 20.39	(8) 0.44
LP1 (Lodgepole Pine 50-150yrs)	(7) 4.58	(5) 5.80	(2) 46.77	(1) 0.0	(6) 81.02	(8) 19.89	(13) 0.52
LP3 (Lodgepole Pine 300+ w/spruce)	(8) 4.04	(7) 2.65	(10) 24.58	(16) 1.03	(9) 82.40	(15) 22.70	(4) 0.41
SF (Spruce-Fir Climax w/WBP)	(9) 3.95	(8) 2.57	(14) 18.20	(1) 0.00	(5) 80.09	(16) 23.08	(3) 0.37
AC (Aspen/Conifer)	(10) 3.69	(9) 1.91	(12) 22.66	(17) 1.05	(11) 89.00	(10) 20.06	(12) 0.50
LP0 (Lodgepole Pine 0-40yrs)	(11) 1.57	(10) 1.90	(3) 41.08	(1) 0.00	(17) 103.99	(7) 19.48	(15) 0.54
WB3 (Pole to Mature)	(12) 0.68	(16) 0.43	(9) 26.06	(1) 0.00	(2) 49.03	(12) 21.14	(1) 0.29
WB2 (Mature, codominance)	(12) 0.68	(14) 0.63	(15) 15.91	(1) 0.00	(13) 91.17	(18) 24.73	(7) 0.43
AS (Aspen, all age)	(14) 0.55	(11) 1.47	(7) 29.48	(1) 0.00	(8) 81.75	(3) 16.56	(14) 0.53
WB1 (Whitebark Pine, pole)	(15) 0.16	(18) 0.00	(17) 5.95	(1) 0.00	(18) 110.00	(14) 22.00	(10) 0.49
LP (Lodgepole Pine 300+ Climax)	(16) 0.11	(15) 0.61	(4) 37.88	(1) 0.00	(15) 97.17	(5) 17.00	(17) 0.63
DF2 (Douglas fir, Closed, Mature)	(17) 0.09	(12) 0.86	(1) 108.09	(1) 0.00	(4) 75.50	(9) 20.00	(5) 0.42
WB (All whitebark, overmature)	(18) 0.01	(17) 0.24	(18) 0.00	(1) 0.00	(3) 59.00	(2) 8.00	(10) 0.49

Table 4.2. Kruskall-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.

	RANDOM			ACTUAL				
Habitat	Mean	SE	*n*	Mean	SE	*n*	χ^2	*P*
AC	0.160	0.109	31	0.286	0.354	34	1.537	0.215
AS	0.127	0.084	30	0.181	0.139	38	1.005	0.316
DF2	0.171	0.072	13	0.121	0.025	2	1.416	0.234
GT	0.038	0.042	47	0.339	0.450	94	38.128	0.000
LP	0.317	0.220	5	0.094	0.110	3	2.689	0.101
LP0	0.164	0.118	30	0.166	0.129	25	0.014	0.906
LP1	0.173	0.120	87	0.128	0.110	95	7.927	0.005
LP2	0.237	0.160	37	0.223	0.261	77	4.171	0.041
LP3	0.254	0.198	27	0.325	0.448	33	1.361	0.243
MC	0.250	0.231	216	0.254	0.266	222	1.346	0.246
OW	0.149	0.097	666	0.202	0.268	337	0.554	0.457
SF	0.416	0.397	16	0.338	0.563	31	1.815	0.178
SF0	0.239	0.170	99	0.196	0.197	67	5.346	0.021
SF1	0.230	0.206	96	0.256	0.247	100	0.022	0.881
WB	0.123	0.062	5	0.033	---	1	0.771	0.380
WB2	0.232	0.250	7	0.164	0.110	11	0.018	0.892
WB3	0.093	0.065	12	0.245	0.236	7	3.150	0.076

Table 4.3. Model selection results for beta regression models testing for the effects of habitat characteristics (habitat type ‘HAB’, 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’), total prey tracks crossed as a substitute for both small (rodents, ungulates and avian sp.) and large (ungulate) prey track crossing rates (‘TotPrey’), and predator (wolf ‘WF’) track crossing rate on distance covered by coyotes ‘LRATIO’.

Model Definition	AICc	ΔAICc	exp(-0.5*ΔAICc)	w_i
‘LRATIO’ ~ Habitat + Canopy Cover + Snow Depth + Snow Penetration + Snowshoe Hare + Red Squirrel + Grouse + Rodent + Ungulate + Wolf	-496.214	0.000	1.000	0.384
‘LRATIO’ ~ Canopy Cover + Penetration + Ungulate + Canopy Cover*Ungulate + Penetration*Ungulate	-496.153	0.061	0.970	0.373
‘LRATIO’ ~ CC + PEN + UNG	-493.665	2.549	0.280	0.107
‘LRATIO’ ~ HAB + CC + SD + SP + TotPrey + WF	-492.468	3.746	0.154	0.059
‘LRATIO’ ~ CC + PEN	-491.614	4.600	0.100	0.039
‘LRATIO’ ~ CC + PEN	-491.614	4.600	0.100	0.039

Table 4.4. Results pertaining to the best performing beta regression model testing for the effects of habitat characteristics(habitat type ‘HAB’, 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’. The shaded rows correspond to the covariates that had a significant effect on LRATIO.

	β estimates	SE	*lower*	*upper*	*Z*-value	*P*-value
Intercept	0.706	0.092	0.614	0.798	7.681	<0.001
HAB	-0.015	0.016	-0.031	0.001	-0.923	0.356
CC	-0.423	0.041	-0.464	-0.381	-10.272	<0.001
SD	0.000	0.001	0.000	0.001	0.379	0.705
SP	-0.024	0.002	-0.027	-0.022	-9.797	<0.001
SSH	0.000	0.001	-0.001	0.001	0.305	0.761
RS	0.001	0.001	0.000	0.002	0.837	0.402
GR	0.004	0.007	-0.003	0.011	0.537	0.592
ROD	-0.001	0.001	-0.002	0.000	-0.884	0.377
UNG	-0.002	0.001	-0.003	0.000	-1.355	0.175
WF	-0.002	0.003	-0.005	0.002	-0.492	0.623

Table 4.5. Results pertaining to the best performing beta regression model testing for the effects of habitat characteristics (canopy cover 'CC'), snow characteristics(snow penetration 'SP), prey track crossing rates (ungulate 'UNG'), and predator track crossing rates on the distance covered by coyotes 'LRATIO'. The shaded rows correspond to the covariates that had a significant effect on LRATIO.

	β estimates	SE	*lower*	*upper*	*Z*-value	*P*-value
Intercept	0.697	0.052	0.645	0.748	13.444	<0.001
CC	-0.431	0.041	-0.472	-0.390	-10.551	<0.001
SP	-0.024	0.003	-0.027	-0.022	-9.721	<0.001
UNG	-0.006	0.003	-0.009	-0.003	-2.093	0.036
CC*UNG	0.001	0.002	-0.001	0.003	0.439	0.661
SP*UNG	0.000	0.000	0.000	0.000	1.383	0.167

Table 4.6. Model selection results for generalized linear models testing for the effects of snow characteristics (snow depth, snow penetration), prey (snowshoe hare, red squirrel, grouse, rodent, deer, elk, moose; or total prey), and predator (wolf) track crossing rates on habitats used by coyotes with varying canopy cover 'CC'.

Models	AICc	ΔAICc	Exp (-0.5*ΔAICc)	w_i
CC ~ Snow Depth + Snow Penetration + Red Squirrel + Rodent	2197.084	0.000	1.000	0.483
CC ~ Snow Depth + Snow Penetration + Red Squirrel	2197.471	0.387	0.824	0.398
CC ~ Snow Depth + Snow Penetration + Snowshoe Hare + Red Squirrel + Grouse + Rodent + Ungulate + Wolf	2200.619	3.535	0.171	0.083
CC ~ Snow Depth + Snow Penetration + Red Squirrel + Rodent + Snow Depth*Red Squirrel + Snow Penetration*Red Squirrel + Snow Depth*Rodent + Snow Penetration*Rodent	2202.915	5.831	0.054	0.026
CC ~ Snow Depth + Snow Penetration + Total Prey + Wolf	2206.178	9.094	0.011	0.005
CC ~ Snow Depth + Snow Penetration + Total Prey	2206.548	9.464	0.009	0.004

*AIC stands for Akaike's Information Criterion. AIC = -2 * *log-likelihood* + 2 * *df*, where *df* stands for the number of degrees of freedom in the model (Akaike 1973).

Table 4.7. Results pertaining to the best performing generalized linear model testing for the effects of snow characteristics (snow depth ‘SD’, snow penetration ‘SP’), prey track crossing rates (red squirrel ‘RS’, rodent ‘ROD’), and predator track crossing rates on canopy cover ‘CC’ selection by coyotes.

	β estimates	SE	*lower*	*upper*	*Z*-value	*P*-value
Intercept	0.290	0.051	0.239	0.342	5.646	<0.001
SD	-0.002	0.000	-0.002	-0.001	-3.438	<0.001
SP	0.017	0.002	0.015	0.018	9.528	<0.001
RS	0.003	0.001	0.002	0.004	4.386	<0.001
ROD	-0.001	0.001	-0.002	0.000	-1.542	0.123

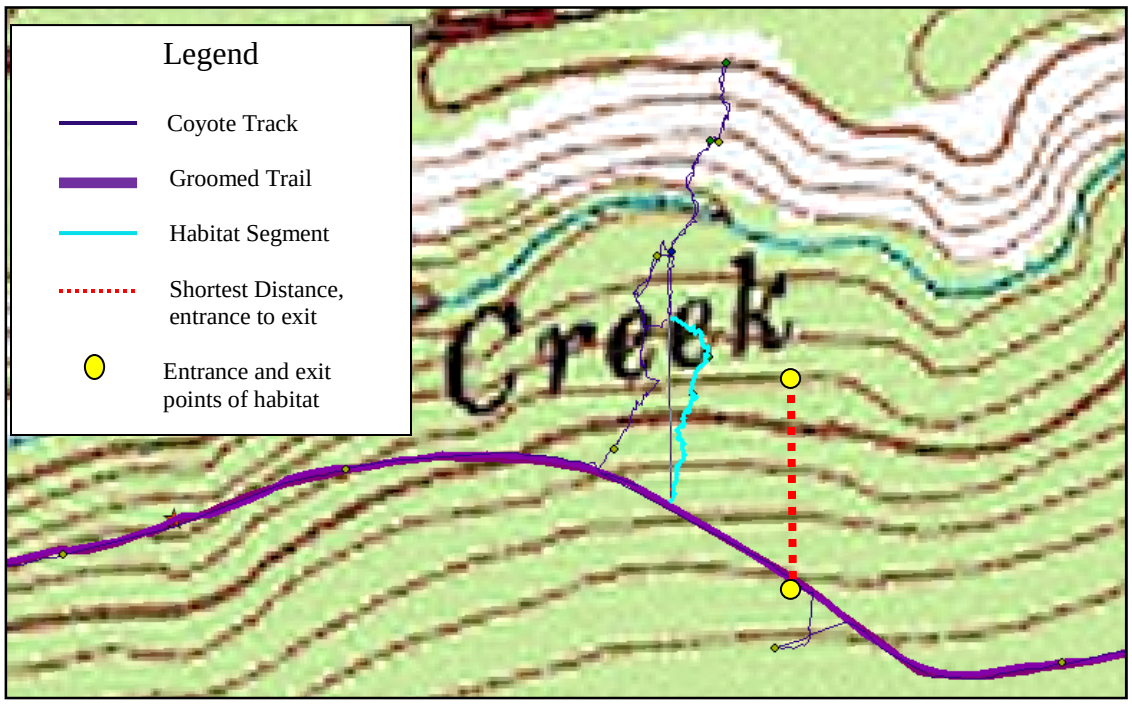

Fig. 4.1. Example of a coyote travel path and shortest distance measurement within different habitat types in northwestern Wyoming, 2007-2008; data collected on coyote F06 on 8 January 2008. Entrance and exit points for each distinct habitat were marked as point locations along the travel path. Distance ratio was calculated by comparing the actual travel distance to the shortest distance measurement.

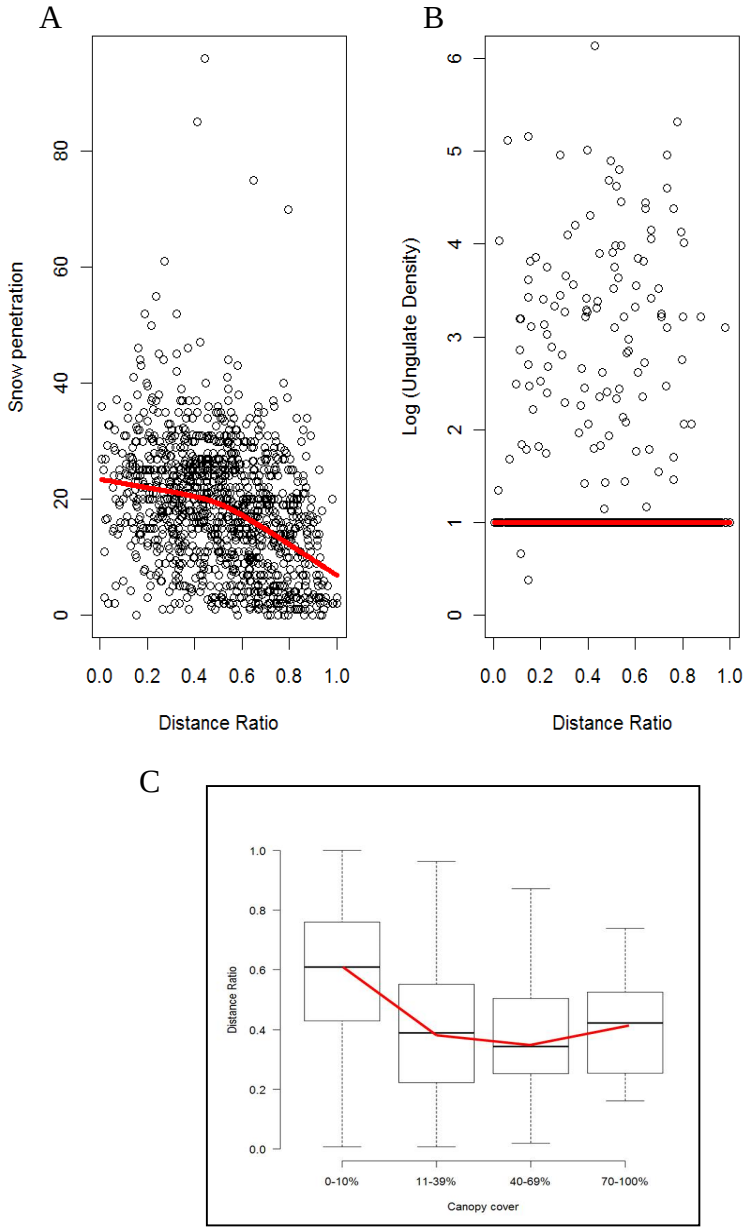

Fig. 4.2. Relationship between the distance traveled by a coyote (LRATIO) and the biological covariates of interest retained as part of the best performing model ('CC + PEN + UNG + CC*UNG + PEN*UNG'); relationship between A) LRATIO and snow penetration, B) LRATIO and UNG (ungulate density, log transformed), and C) LRATIO and canopy cover in northwestern Wyoming, 2006-2008.

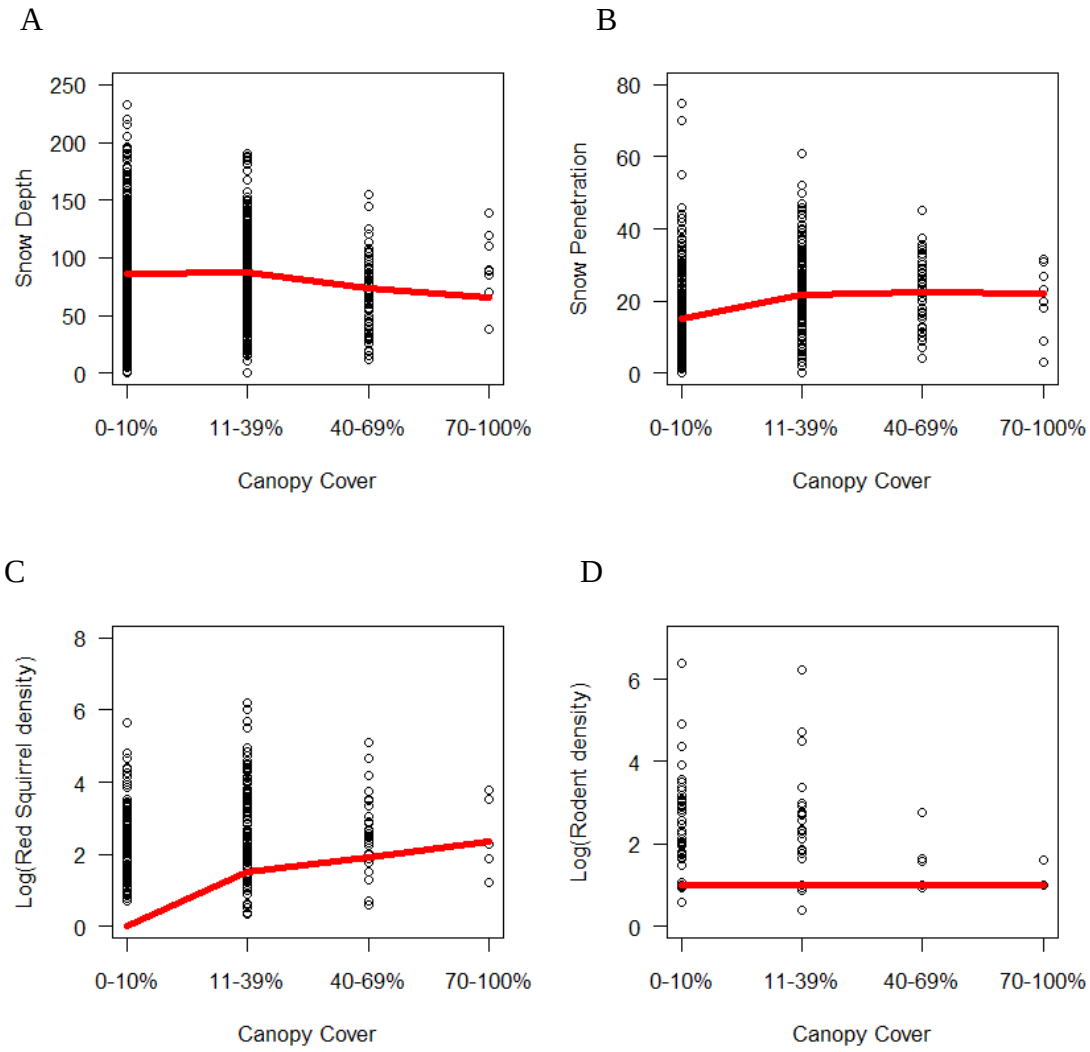

Fig. 4.3. Relationship between canopy cover (CC) and the biological covariates of interest retained as part of the best performing model, relationships between canopy cover and A) snow depth, B) snow penetration, C) red squirrel encounter rates, and D) rodent encounter rates, northwestern Wyoming, 2006-2008.

CHAPTER 5

CONCLUSION

Flexibility in resource utilization (Patterson et al. 1998, Bartel and Knowlton 2004) and adaptability to human altered landscapes (Toweill and Anthony 1988, Morey et al. 2007) by coyotes (*Canis latrans*) are two attributes that give them an advantage over other predators inhabiting similar geographic regions. Coexistence of coyotes and Canada lynx (*Lynx Canadensis*) has been attributed to variation in seasonal habitat selection, resource partitioning and niche differentiation because of physiological adaptations allowing lynx to remain in deep snow terrain and effectively utilize seasonal resources (Murray and Boutin 1991). Snow compaction resulting from winter recreation is an example of a human modification that could inadvertently cause a breakdown of spatial segregation, altering seasonal species distributions and possibly facilitating increased interactions between coyotes and lynx (Buskirk et al. 2000, Bunnell et al. 2006).

In northwestern Wyoming, snow compaction influenced coyote movements in habitats suitable for supporting lynx and their main prey, snowshoe hare (*Lepus americanaus*), resulting in exploitation of deep snow areas and year round persistence. Increased presence of compacted trails showed increased use by coyotes, suggesting the more snowmobile compacted trails available, the more they will be utilized by coyotes. Although a lack of dietary overlap was documented between the two species, snowshoe hares had one of the highest coyote encounter rates of all prey species, suggesting a potential use by coyotes under favorable conditions. This is further supported by our

findings that coyote use of forested habitats (where snowshoe hares were most prevalent) was not only high in ranking of which habitats were used, but also their use of forested habitats was primarily associated with travel patterns suggesting hunting behavior. Use of open areas was primarily associated with travel.

In Seeley Lake, Montana, Kolbe et al. (2007) suggested that although coyotes used compacted snowmobile trails more often than expected the influence of snowmobile trails appeared to be minimal on coyote movements and foraging success. Despite similar data collection methods and procedures, our results were not consistent with these findings. This was likely due to a regionally specific response resulting from differences in snow conditions, predator and prey densities, carrion availability, and differences in maintenance/use patterns for winter recreation. We suggest perhaps the most important variable to consider when assessing the potential for competition between coyotes and lynx during the winter is snowpack. Unlike Seeley Lake, Montana (Kolbe et al. 2007), the snowpack in northwestern Wyoming would not allow coyotes unhindered use of travel corridors and foraging areas in the absence of snow compaction. Similar to results found by Bunnell et al. (2006) in the Intermountain West, we suggest that coyotes in northwestern Wyoming likely required snow compacted trails to persist and effectively utilize resources in deep snow areas.

Dietary analyses conducted on coyotes in northwestern Montana (Arjo 1998) found high use of ungulates and rodents and low use of lagomorphs and vegetation to be an effect of wolf presence. Although wolf presence and influence on coyote dietary behaviors were not quantified in our study, the recent establishment of wolves on

Togwotee Pass may account for the high use of ungulates and low use of snowshoe hares during the winter. Based on snowshoe hare encounter rates documented on coyote backtracks, we expected to see a higher percent occurrence of snowshoe hare in our winter diet analysis. The high use of ungulates in our diet analysis and significantly higher encounter rate compared to random expectation indicated coyotes were selecting for habitats containing ungulates (most likely scavenging ungulate carcasses).

Preferential use of habitats by coyotes compared to availability on the landscape suggested coyotes were selecting habitats because of desirable features encountered within each habitat, such as on snow characteristics, prey encounters, predator encounters, and their ability to either hunt or travel efficiently. Ultimately, coyote use of habitats during the winter should be such that they minimize energetic expenditures and maximize energetic intake. The most dramatic difference in habitat use versus availability documented in our study area was that of groomed trails, which coyotes used approximately 18X more than available on the landscape. This is not surprising as the high level of supportiveness on groomed trails would greatly reduce locomotion costs associated with travel in deep snow, making travel conditions ideal for coyotes. However, it is reasonable to assume that were more groomed trails available on the landscape, coyote use of groomed trails versus availability would remain similar to our findings, meaning as the availability of groomed trails increased, coyote use of groomed trails would increase. This provides insight for management agencies considering expansion of groomed trail practices and potential impacts to ecosystem dynamics influenced by coyotes.

Overall, lack of dietary overlap but high use of snow compacted trails during our study suggested that rather than exploitation competition, interference competition between coyotes and lynx may be a concern during the winter. While we speculate exploitation competition is more likely during the fall, the lack of dietary overlap during the winter indicates a lack of exploitation competition with regard to prey use during the winter. While interference competition demonstrated through avoidance behaviors or aggressive acts may be hard to quantify, further information is needed to directly compare the relationship between coyote and lynx distributions within winter recreation use areas. The extensive use of deep snow terrain by coyotes in our study area, their significantly higher use of snowmobile trails and their closer proximity to snow compacted trails than randomly expected show that a relationship exists between coyotes and winter recreation, but does not directly measure the response by lynx other than provides implications for potential conservation concerns.

Direct monitoring of both species to better understand the extent of spatial resource partitioning and overlap would provide much needed insight to further understand what relationships exist between coyotes, lynx, and winter recreation. While we believe management of coyotes in high elevation terrain will depend on regulation and expanse of snowmobile use areas, the level of management needed will depend on regionally specific dynamics, variation of the snow column and geographical characteristics. Additionally, we suggest future research focus on comparing coyote behaviors in snowmobile use areas to non-use areas, identifying a threshold by which

snow compaction becomes necessary for coyote persistence in deep snow areas, and the influence of wolf presence on both species.

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APPENDICES

Appendix A. Generalized variance inflation factors (GVIF) for all covariates of interest collected in northwestern Wyoming, 2007-2008. Values inferior to 5 indicate a lack of colinearity between covariates.

Covariates	GVIF	df
Coyote identity	2.2883	1
Snowmobile use	2.2577	2
Snow depth/on track	4.1253	1
Snow penetration/on track	2.9866	1
Rodent encounters/on track	1.5623	1
Red squirrel encounters/on track	2.2501	1
Snowshoe hare encounters/on track	1.3369	1
Ungulate encounters/on track	2.7306	1
Wolf encounters/on track	3.3145	1
Snow depth/off track	4.0049	1
Snow penetration/off track	2.5945	1
Rodent encounters/off track	1.5134	1
Red squirrel encounters/off track	3.3479	1
Snowshoe hare encounters/off track	2.3031	1
Ungulate encounters/off track	2.5455	1
Wolf encounters/off track	3.8501	1

Appendix B. Vegetation Classification on the northwestern Wyoming study area, 2006-2008.

Dominant tree species (Overstory)	Cover type code	Classification Description
Aspen/Conifer	AC	Aspen-dominated stand with a substantial conifer understory.
Aspen	AS	Stands of all ages when aspen dominates.
Douglas Fir	DF0	Recently burned; 0-40 years old. Seedling to sapling stage
	DF2	Closed-canopy with mature trees, overstory largely intact; understory consists of small to medium subalpine fir, or lodgepole pine; forest floor covered with herbaceous vegetation; 150-300 years old.
	LP0	Recently burned; 0-40 years old. Seedling to sapling stage
	LP1	Very dense, even aged stand of young pole-sized trees; understory of small trees nonexistent. Forest floor vegetation sparse; 50-150 years old
Lodgepole Pine	LP2	Closed-canopy with overstory largely intact; understory consists of small to medium Engelmann spruce, subalpine fir, or lodgepole pine; forest floor covered with herbaceous vegetation; 150-300 years old.
	LP3	Canopy ragged, consisting predominately of lodgepole pine but containing some spruce, fir and whitebark pine; understory consists of small to large spruce and fir; forest floor has appearance of climax spruce-fir stand; successional forest; 300+ years old
	LP	Climax Stand of lodgepole pine beginning to break up; understory lodgepole and whitebark pine. Multi-age stand. Dry soils. Spruce and fir cannot grow on these sites. 300+ years old.
	GT	Any trail that is maintained by trail grooming practices during the winter
	MC	Conifer stand where no one species dominated in the main canopy or density. Mature Douglas fir may be present (Ex: mature but sparse Douglas fir with denser spruce/fir understory).
Groomed Trail	OW	Open areas such as meadow, sagebrush, willow or open woodland areas
Mixed Conifer	SF0	Recently disturbed wet sites dominated by Engelmann spruce and subalpine fir; canopy closure not year achieved.
Open Woodland	SF1	Even-aged closed stands; over/understory dominated by spruce and fir; whitebark pine often a component.
Spruce/Fir	SF	Climax Stands dominated by spruce and fir in both over- and understory. Lodgepole and doug fir may be an insignificant component; whitebark pine may be a significant component at higher elevations.
	WB0	Recently burned, near timberline, whitebark dominates reproduction.
	WB2	Pole to mature size; overstory largely intact; understory small to medium spruce, subalpine fir and whitebark seedling; 100- stand type; above 8,600 ft.
Whitebark Pine	WB3	Mature whitebark co-dominant with spruce, fir, lodgepole; understory dominated by spruce and fir; whitebark I seral in this stand type; above 8,600ft.
	WB	Mature to over-mature whitebark; nearly all reproduction is whitebark

Appendix C. Variance inflation factors 'VIF' for all covariates of interest, northwestern Wyoming, 2006-2008. Values inferior to 5 indicate a lack of colinearity between covariate.

Covariate	Abbreviation	VIF
Habitat type	HAB	1.124
Canopy cover	CC	1.146
Snow depth	SD	1.135
Snow penetration	SP	1.128
Snow shoe hare density	SSH	1.315
Red squirrel density	RS	1.476
Grouse density	GR	1.028
Rodent density	ROD	1.172
Ungulate density	UNG	1.073
Wolf density	WF	1.044