

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA National Wildlife Research Center - Staff
Publications

U.S. Department of Agriculture: Animal and Plant
Health Inspection Service

2012

Seasonal Variation of Coyote Diet in Northwestern Wyoming: Implications for Dietary Overlap with Canada Lynx?

Jennifer L. B. Dowd
Utah State University

Eric M. Gese
USDA/APHIS/WS National Wildlife Research Center, eric.gese@usu.edu

Follow this and additional works at: https://digitalcommons.unl.edu/icwdm_usdanwrc

Dowd, Jennifer L. B. and Gese, Eric M., "Seasonal Variation of Coyote Diet in Northwestern Wyoming: Implications for Dietary Overlap with Canada Lynx?" (2012). *USDA National Wildlife Research Center - Staff Publications*. 1125.
https://digitalcommons.unl.edu/icwdm_usdanwrc/1125

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Animal and Plant Health Inspection Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA National Wildlife Research Center - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

and

Eric M. Gese¹, U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, Department of Wildland Resources, Utah State University, Logan, Utah, 84322

Seasonal Variation of Coyote Diet in Northwestern Wyoming: Implications for Dietary Overlap with Canada Lynx?

Abstract

Exploitative competition through resource utilization may occur between coyotes (*Canis latrans*) and other carnivores. In the southern periphery of Canada lynx (*Lynx canadensis*) range, there is concern that increased snowmobile activity may enable coyotes to increase their movements into deep snow areas during the winter months, thereby potentially creating heightened resource competition with lynx, mainly for the lynx's main prey, snowshoe hares (*Lepus americanus*). We studied the seasonal variation of coyote diets and the dietary overlap between coyotes and lynx in a 512-km² 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. A total of 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 during the winter, accounting for 85.2% of all prey occurrences. Coyote use of snowshoe hares peaked in the fall (24.1% of all occurrences). We found little dietary overlap between coyotes and lynx during the winter months when lynx mainly fed on snowshoe hares and coyotes fed mostly on ungulates.

Key Words: Exploitative competition, resource competition, diet overlap

Introduction

Canada lynx (*Lynx canadensis*) were listed under the Endangered Species Act due to a lack of adequate management plans incorporating 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 was an 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. Coyotes (*Canis latrans*) have been recognized as a potential competitor with lynx (Buskirk et al. 2000, Ruediger et al. 2000). 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 (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). 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 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). These sympatric predators have coexisted because morphological differences allow them to occupy separate niches within an ecosystem and utilize different resources (Krebs 1978). In the

¹Author to whom correspondence should be addressed.
Email: eric.gese@usu.edu

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 (Murray and Boutin 1991, Litvaitis 1992, Crete and Lariviere 2003). With increased popularity of winter recreation (particularly snowmobiling), access to some deep snow landscapes have been altered. Studies conducted on southern lynx populations have found 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 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.

Competition between coyotes and lynx occurs via exploitation competition, interference competition, or both. Exploitation competition between coyotes and lynx may be documented in an overlap of coyote and lynx diets. Several studies (e.g., Todd et al. 1981, Parker 1986, Murray et al. 1994, O'Donoghue et al. 1998, Patterson et al. 1998) have identified snowshoe hares (*Lepus americanus*) as a major component of coyote winter diets in North America. O'Donoghue et al. (1997) found 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) found in areas where coyote populations were increasing, they were reducing the prey availability for subordinate species, therefore reducing carrying capacity for those species.

Although exploitation competition between coyotes and lynx may be a concern during the fall (Aubry et al. 2000, McKelvey et al. 2000, Kolbe et al. 2007) and winter (Ozoga and Harger 1966, Murray et al. 1995, Buskirk et al. 2000, Bunnell et al. 2006), few studies have conducted multi-seasonal dietary analyses to determine the variation of coyote diets in high elevation areas

with winter recreation. 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 alteration and increased fragmentation (Ruggiero et al. 2000).

Our objective was to determine the seasonal variation, dietary diversity, and dietary overlap of coyotes and lynx in high elevation terrain in northwestern Wyoming. A secondary objective was to identify during which seasons dietary overlap was occurring and, for coyote diets, determine whether specific prey items were correlated with snow depth. We hypothesized coyote diets would reflect a generalist nature during all seasons with greater dietary diversity occurring during the spring and summer 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 when other prey items were less available. Similar to studies conducted in the northern part of their range, we hypothesized lynx diets would consist primarily of snowshoe hares with a small component of other small mammals, such as red squirrel (*Tamiasciurus hudsonicus*) and dietary diversity of lynx would increase during the spring and summer.

Study Area

We conducted this study on the east and west sides of Togwotee Pass in northwestern Wyoming. The 512-km² study area was characterized by extensive recreational trails and roads maintained year-round. The area was composed of the Bridger-Teton and Shoshone National Forests, plus some large, privately-owned ranches. Elevations ranged from 1800 m to >3600 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 (2000 - 2400 m). Cumulative monthly snow depth for the winter study season (December-April) averaged 226.6, 149.4, and 228.9 cm during 2006, 2007, and 2008, respectively (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 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 1930s, they have since re-established as a result of the 1995 re-introduction efforts in Yellowstone National Park (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 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.

Methods

We collected coyote scats opportunistically while backtracking radio-collared individuals (Dowd 2010), and along designated routes surveyed every 2 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 1–3.5 cm in diameter and 12.7–33 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 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 (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 (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) determined dietary overlap between coyotes and lynx. The Shannon 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. Snow depth data used for analyses was obtained from the Bridger-Teton National Forest, Backcountry Avalanche Hazard and Weather Forecast historical weather data (U.S. Forest Service 2008). 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 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 (Figure 1).

Of interest was a peak in the occurrence of whitebark pine seeds in coyote scats during the winter of 2006-2007 (Figure 2). Snowfall was below average during that winter, and ungulate prey occurrence in coyote scats was 21% less than during the winter of 2007-2008 (Figure 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 spring, followed by the fall, winter, and then summer (Table 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). 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

TABLE 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	Percent occurrence (%) n = 470 scats
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							
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							
Insect	0 (0)	1 (0.5)	0 (0)	0 (0)	1	0.2	0.2
Human garbage							
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	

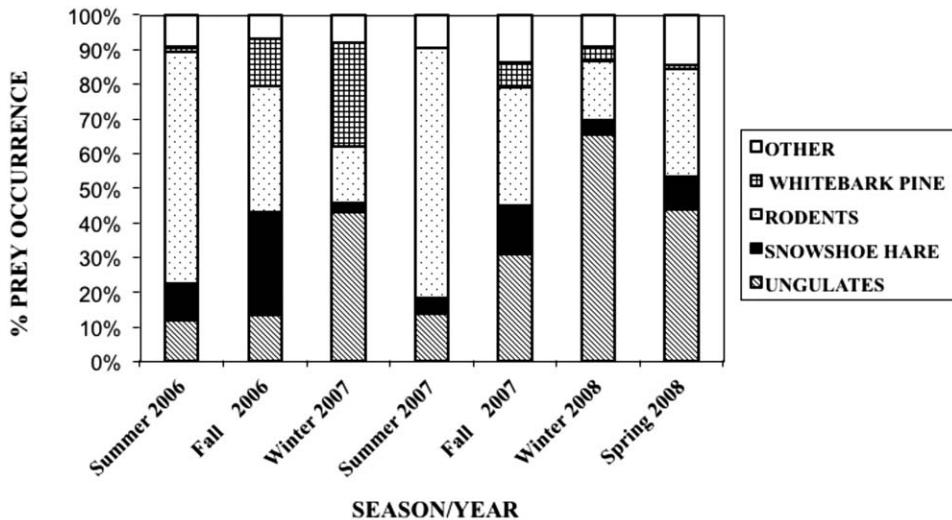


Figure 1. Seasonal comparisons of major prey items among coyote scats, Togwotee Pass, Wyoming, 2006-2008.

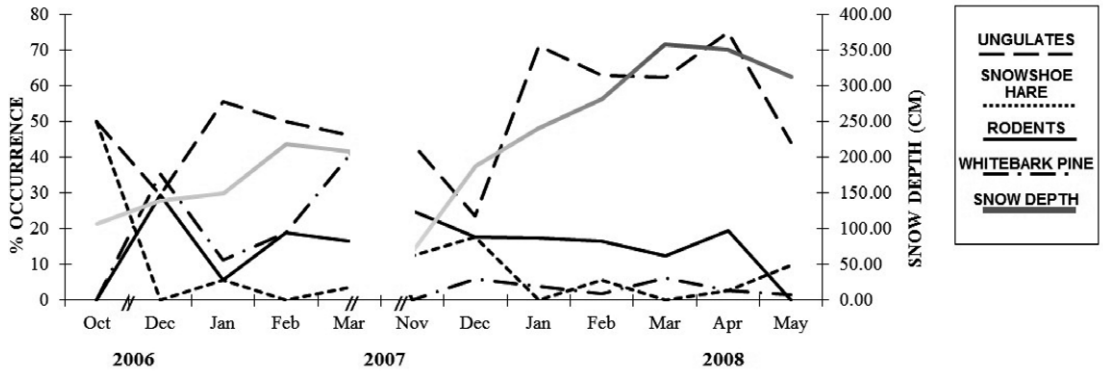


Figure 2. Percent occurrence of food items found in coyotes scats and average daily snow depth (cm) by month and year on Togwotee Pass, Wyoming, October 2006 – May 2008. Months when scats were not collected denoted by //.

TABLE 2. Indices of dietary diversity (Shannon diversity index) and dietary overlap (Horn’s similarity index) for coyotes and lynx by season, Togwotee Pass, Wyoming, July 2006 – June 2008.

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

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).

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 (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 were generalist predators with high dietary diversity. Occurrence of snowshoe hare in coyote diets occurred primarily in the fall and rarely in the winter. The shift in 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 (Figure 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 near 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 winter 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 (Ozoga and Harger 1966, Gese and Grothe 1995). Although wolves have recently established in the area, the effects of a trophic cascade in the higher elevations of this region have not been documented. During the study, coyotes were documented scavenging on wolf kills of elk and moose on several occasions.

The high occurrence of mule deer 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. 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.

Coyotes have demonstrated prey switching when one resource becomes depleted (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 occurrence during those same winters was the occurrence of snowshoe hares, which nearly doubled in the year that whitebark pine seeds occurred less frequently. Being a low snow year (2006-2007), possibly coyotes were able to more readily access whitebark pine seed caches made by red squirrels than during the following year when deep snow might have prohibited them from excavating caches. Use of whitebark pine seeds by coyotes has not been previously documented, whereas grizzly bears rely on whitebark pine seeds (Kendall 1983, Mattson and Jonkel 1990).

In northwestern Montana, Kolbe et al. (2007) found snowshoe hares composed only a small proportion of winter diets of coyotes, and concluded there was a lack of exploitation competition between coyotes and lynx during winter. Our results were similar 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 diet during the fall and spring suggest those may be more critical times for 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 their 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; Dowd 2010). 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.

Lynx Food Habits

Similar to studies on lynx in other parts of their southern range, lynx from our area showed a high occurrence of snowshoe hare in their winter diet (Koehler 1990, Parker et al. 1983), with low dietary diversity during 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).

Our data lacked adequate sample size of scats during all the seasons, other than winter, to determine seasonal shifts in lynx dietary diversity. 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. 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.

Dietary Overlap

Our data suggest that during the winter months 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 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 dependent on annual fluctuations in prey. Several variables should be considered when determining whether competition is truly occurring and outcomes resulting from that competition. In our 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. The increased presence of wolves may have a potentially positive effect on lynx numbers, as wolf presence may reduce the number of coyotes (Berger and Gese 2007). 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. As of yet, there is little evidence to suggest either positive or negative impacts on lynx resulting from wolf establishment in the area.

Conclusion

Our results indicate coyotes were not competing with lynx for food during the winter months 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, and if other types of competition are occurring (e.g., spatial or temporal avoidance, direct mortality). 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.

Acknowledgements

Funding and logistical support provided by the U.S. Department of Agriculture, Wildlife Services, National Wildlife Research Center, the U.S. Forest Service, Bridger-Teton National Forest, and Endeavor Wildlife Research Foundation. We thank P. Dowd, S. Dempsey, M. Greenblatt, S. Hegg, M. Holmes, M. Linnell, S. McKay and G. Worley-Hood for field assistance, and J. Bissonette, J. Squires, and J. Laundré for review of the manuscript.

Literature Cited

- Adorjan, A. S., and G. B. Kolenosky. 1969. A Manual for the Identification of Hairs of Selected Ontario Mammals. Research Report 90, Research Branch Ontario Department of Lands and Forests, Toronto, Canada.
- Apps, C. D. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 351-372.
- Arjo, W. M. 1998. The effects of recolonizing wolves on coyote populations, movements, behaviors and food habits. Ph.D. dissertation, University of Montana, Missoula.
- Aubry, K. B., G. M. Koehler, and J. R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 373-396.
- Bartel, R. A., and F. F. Knowlton. 2004. Functional feeding responses of coyotes, *Canis latrans*, to fluctuating prey abundances in the Curlew Valley, Utah, 1977-1993. *Canadian Journal of Zoology* 83:569-578.
- Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology* 76:1075-1085.
- Bunnell, K. D., J. T. Flinders, and M. L. Wolfe. 2006. Potential impacts of coyotes and snowmobiles on lynx conservation in the intermountain west. *Wildlife Society Bulletin* 34:828-838.
- Buskirk, S. W., L. F. Ruggiero, and C. J. Krebs. 2000. Habitat fragmentation and interspecific competition: implications for lynx conservation. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 83-100.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-576.
- Crete, M., and S. Lariviere. 2003. Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology* 81:1808-1814.
- Dowd, J. L. B. 2010. Coyote diet and movements in relation to winter recreation in northwestern Wyoming: implications for lynx conservation. M.S. Thesis, Utah State University, Logan.
- Elbroch, M. 2003. *Mammal Tracks and Sign: a Guide to North American Species*. Stackpole Books, Mechanicsburg, Pennsylvania.
- Elbroch, M. 2006. *Animal Skulls: A Guide to North American Species*. Stackpole Books, Mechanicsburg, Pennsylvania, USA.
- Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133:36-43.
- Hodges, K. E. 2000. Ecology of snowshoe hares in southern boreal and montane forests. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 163-206.
- Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist* 100:419-424.

- Kelly, B. T. 1991. Carnivore scat analysis: an evaluation of existing techniques and the development of predictive models of prey consumed. M.S. Thesis, University of Idaho, Moscow.
- Kendall, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. *International Conference of Bear Research and Management* 5:166-173.
- Koehler, G. M. 1990. Populations and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68:845-851.
- Koehler, G. M., and M. G. Aubry. 1994. Lynx. In L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski (editors), *The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western United States*, U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-254, Washington, D.C. Pp. 74-98.
- Kolbe, J. A., J. R. Squires, D. H. Pletscher, and L. F. Ruggiero. 2007. The effect of snowmobile trails on coyote movements within lynx home ranges. *Journal of Wildlife Management* 71:1409-1418.
- Krebs, J. R. 1978. Optimal foraging: decision rules for predators. In J. R. Krebs and N. B. Davies (editors), *Behavioral Ecology: An Evolutionary Approach*, Blackwell Scientific Publications, Oxford. Pp. 23-63.
- Lewis, L., and C. R. Wenger. 1998. Idaho's Canada lynx: pieces of the puzzle. Idaho Bureau of Land Management, Technical Bulletin 98-11, Boise, Idaho, USA.
- Litvaitis, J. A. 1992. Niche relations between coyotes and sympatric Carnivora. In A. H. Boer, (editor) *Ecology and Management of the Eastern Coyote*, University of New Brunswick Wildlife Research Unit, Fredericton, New Brunswick, Canada. Pp. 73-85.
- Litvaitis, J. A., and D. J. Harrison. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. *Canadian Journal of Zoology* 67:1180-1188.
- Martin A. C., R. H. Gensch, and C. P. Brown. 1946. Alternative methods in upland gamebird food analysis. *Journal of Wildlife Management* 10:8-12.
- Mattson, D. J. and C. Jonkel. 1990. Stone pines and bears. In W. C. Schmidt and K. J. McDonald (compilers), *Proceedings - Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High Mountain Resource*. United States Forest Service General Technical Report INT-270. Pp. 223-236.
- McKelvey, K. S., Y. K. Ortega, G. M. Koehler, K. B. Aubry, and J. B. Brittell. 2000. Canada lynx habitat and topographic use patterns in north central Washington: a reanalysis. In L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 307-336.
- McKelvey, K. S., J. V. Kienast, K. B. Aubry, G. M. Koehler, B. T. Maletzke, J. R. Squires, E. L. Lindquist, S. Loch, and M. K. Schwartz. 2006. DNA analysis of hair and scat collected along snow tracks to document the presence of Canada lynx. *Wildlife Society Bulletin* 34:451-455.
- Moore, T. D., L. E. Spence, and C. E. Dugnonle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Bulletin No. 14, Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- Morey, P. S., E. M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area. *American Midland Naturalist* 158:147-161.
- Murie, A. 1940. Ecology of the coyote in the Yellowstone. *Fauna of the National Parks of the United States*, Bulletin No. 4, U.S. Department of the Interior, U.S. Government Printing Office, Washington, D. C., USA.
- Murie, O. J. 1935. Food habits of the coyote in Jackson Hole, Wyoming. U.S. Department of Agriculture Circular 362:1-24.
- Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia* 88:463-469.
- Murray, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by Canada lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology* 72:1444-1451.
- Murray, D. L., S. Boutin, M. O'Donoghue, and V. O. Nams. 1995. Hunting behavior of a sympatric felid and canid in relation to vegetative cover. *Animal Behavior* 50:1203-1210.
- Natural Resources Conservation Service. 2008. SNOTEL data network. <<http://www.wcc.nrcs.usda.gov/snotel/snotel.pl?sitenum=822&state=wy>>. Accessed December 2008.
- O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80:150-162.
- O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79:1193-1208.
- Ozoga, J. J., and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. *Journal of Wildlife Management* 30:809-818.
- Parker, G. R. 1986. The seasonal diets of coyotes, *Canis latrans*, in northern New Brunswick. *Canadian Field Naturalist* 100:74-77.
- Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. *Canadian Journal of Zoology* 61:770-786.
- Patterson, B. R., L. K. Benjamin, and F. Messier. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. *Canadian Journal of Zoology* 76:1885-1897.

- Ruediger, B., J. Claar, S. Gniadek, B. Holt, L. Lewis, S. Mighton, B. Naney, G. Patton, T. Rinaldi, J. Trick, A. Vandehey, F. Wahl, N. Warren, D. Wenger, and A. Williamson. 2000. Canada lynx conservation assessment and strategy. U.S. Forest Service, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, and U.S. National Park Service, Missoula, Montana, USA.
- Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. Ecology and conservation of lynx in the United States. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RMRS-GTR-30WWW.
- Squires, J. R., and T. Laurion. 2000. Lynx home range and movements in Montana and Wyoming: preliminary results. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires (editors), *Ecology and Conservation of Lynx in the United States*. University Press of Colorado, Boulder. Pp. 337-349.
- Squires, J. R., and L. F. Ruggiero. 2007. Winter prey selection of Canada lynx in northwestern Montana. *Journal of Wildlife Management* 71:310-315.
- Staples III, W. R. 1995. Lynx and coyote diets and habitat relationships during a low hare population on the Kenai Peninsula, Alaska. M.S. Thesis, University of Alaska, Fairbanks.
- Todd, A. W., L. B. Keith, and C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. *Journal of Wildlife Management* 45:629-640.
- Toweill, D. E., and R. G. Anthony. 1988. Coyote foods in a coniferous forest in Oregon. *Journal of Wildlife Management* 52:507-512.
- U.S. Fish and Wildlife Service. 2006. Number of wolves and packs in Wyoming, summer 2006, outside Yellowstone National Park. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- U.S. Forest Service. 2008. Bridger-Teton national forest backcountry avalanche hazard and weather forecast, historical weather data. <<http://www.jhavalanche.org/data.php>>. Accessed December 2008.
- Weaver, J. L. 1977. Coyote-food base relationships in Jackson Hole, Wyoming. M.S. Thesis. Utah State University, Logan.
- Weaver, J. L., and S. W. Hoffman. 1979. Differential detectability of rodents in coyote scats. *Journal of Wildlife Management* 43:783-786.
- Wigglesworth, R. R. 2000. Habitat use, diet, social organization, and seroprevalence of disease in coyotes (*Canis latrans*) in Grand Teton National Park and suburban/agricultural areas of northwest Wyoming. M.S. Thesis, University of Wyoming, Laramie.

Received 9 February 2012

Accepted for publication 9 May 2012