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Potential Impacts of Coyotes and Snowmobiles on Lynx Conservation in the Intermountain West

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Abstract

*Researchers and managers have hypothesized that coyote (*Canis latrans*) incursions into deep snow areas, facilitated by packed trails created by snowmobiles, may negatively impact lynx (*Lynx canadensis*) populations through interference or exploitation competition. In response to this hypothesis, federal agencies have limited snowmobile use within potential lynx habitat. We used aerial track counts and ground tracking to compare coyote activity in deep snow areas with and without snowmobile trails on the Uinta Mountain Range of northeastern Utah, USA, and 3 comparable sites in the Intermountain West to test this hypothesis. Our analysis suggests that snowmobile trail presence is a good predictor of coyote activity in deep snow areas. Over 90% of coyote tracks observed in our study areas associated with a snowmobile trail were within 350 m of the trail. Snow depth and prey density estimates influenced whether a coyote returned to a snowmobile trail. Our results suggest that restrictions placed on snowmobiles in lynx conservation areas by land management agencies because of the potential impacts of coyotes may be appropriate.* (WILDLIFE SOCIETY BULLETIN 34(3):828–838; 2006)

Key words

Canada lynx, Canis latrans*, competition, coyote, Idaho, Intermountain West,* Lynx canadensis*, packed snow, snowmobile trails, track counts, Utah, Wyoming.*

The Canada lynx was listed under the Endangered Species Act in March 2000. The listing crystallized the need for better information documenting the extent to which coyotes use compacted snow routes created by winter recreation activities to access deep snow areas where they may negatively impact lynx populations through competition (Buskirk et al. 2000, Ruediger et al. 2000, U.S. Forest Service and U.S. Bureau of Land Management 2004).

Canada lynx have evolved morphological characteristics (large feet and long legs) providing them with a competitive advantage over other similarly sized carnivores (i.e., coyotes and bobcats [*Lynx rufus*]) in deep snow (Murray and Boutin 1991). Murray and Boutin (1991) and Litvaitis (1992) documented spatial segregation of lynx and coyotes during annual periods of deep snow. Recent advances in snowmobile technology and performance, along with increased trail grooming programs, have increased human activity and the amount of snow compaction in deep snow areas of the Intermountain West (Knight and Gutzwiller 1995, Buskirk et al. 2000). Buskirk et al. (2000) and Ruediger et al. (2000) reported that this increased activity coincided with a decrease in lynx populations. Several investigators (Bider 1962, Ozoga and Harger 1966, Keith et al. 1977, Murray and Boutin 1991, Koehler and Aubrey 1994, Murray et al. 1995, Lewis and Wenger 1998) reported observing coyotes using packed trails created by winter recreation activities (especially snowmobiling). They suggested this might negate the competitive advantages of lynx by providing coyotes and other carnivores with winter travel corridors into areas from which they were historically excluded during annual periods of deep snow.

Buskirk et al. (2000:94) hypothesized that the historical segregation of lynx and coyotes "may break down where human modifications to the environment increases access by coyotes to deep snow areas." Buskirk et al. (2000) and Ruediger et al. (2000) suggested that increased competition has contributed to the decline of lynx populations in the Intermountain West. In response to these concerns, Ruediger et al. (2000) recommended that federal agencies limit snowmobile use within potential lynx habitat. These steps were taken despite the fact that the hypothesized relationship between coyotes and snow-packed trails had never been quantified.

The objective of our study was to quantify the extent to which snowmobile trails may facilitate coyote access to potential lynx habitat during periods of deep snow. To accomplish this objective, we collected data designed to determine whether snowmobiles trails allow coyotes access to deep snow areas from which they would otherwise be excluded. Additionally, if snowmobile trails would facilitate coyote access into deep snow areas, we wanted to determine how large an area would be impacted.

Study Area

The study was conducted on 4 sites within the historic range of lynx located throughout the Intermountain West (Fig. 1; McKelvey et al. 2000). The primary study site encompassed the north and west slopes of the Uinta Mountain Range (UMR) of northeastern Utah, USA. The UMR is unique among western mountain ranges in its east–west orientation. The UMR extends from the Green River (below Flaming Gorge Reservoir) on its eastern border, west to the town of Kamas, Utah, where it joins the Wasatch portion of the Rocky Mountains (approx. 240 km). The UMR extends north to south from the Green River Basin in southwest Wyoming, USA, to the Uinta Basin of northeastern Utah (approx. 80 km). Elevations in the UMR range from 2,000 to >4,000 m and contain the highest peaks in Utah.

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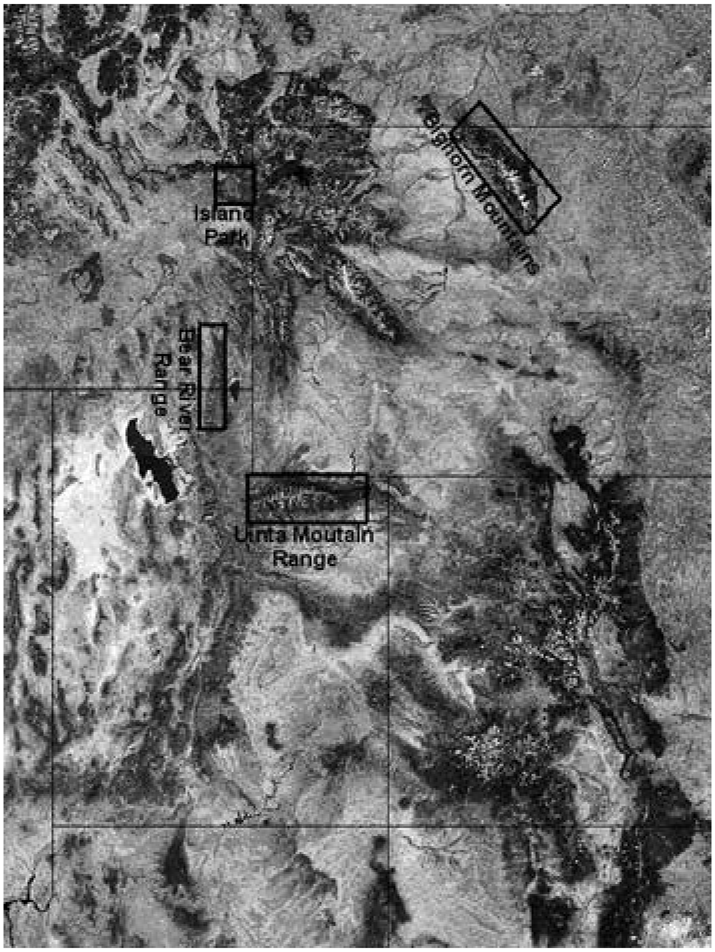

Figure 1. Study site locations in the Intermountain West for which the relationship between coyotes and snowmobile trails was quantified through ground tracking during winters 2000–2001, 2001–2002, and 2002–2003.

The UMR is characterized by extensive lodgepole pine (*Pinus contorta*) forests at lower elevations, subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmanni*) forests at higher elevations, and alpine tundra at approximately 3,200 m in elevation. North and south slopes have several river drainages characterized by gentle riparian meadow bottoms. The High Uinta Wilderness Area occupies 186,155 ha in the center of the UMR. Average snow depth for the UMR on 1 February at the Hayden Fork SNOTEL station (elevation = 2,773 m) was 91 cm (Natural Resource Conservation Service 2003).

The other study sites included the Bear River Range (BRR) of northern Utah and southeastern Idaho, USA, the Island Park area (IP) of eastern Idaho, and the Big Horn Mountains (BHM) of northern Wyoming. The BRR is the northernmost extension of the Wasatch portion of the Rocky Mountains. The BRR extends from the Bear River in southern Idaho, USA, south 150 km to the Ogden River between Cache Valley to the west and Bear Lake valley to the east. Elevations on the BRR range between 2,000 and 2,900 m. The BRR was characterized by aspen forests (*Populus tremuloides*) giving way to lodgepole pine and subalpine fir forests at higher elevations. Average snow depth for the BRR on 1 February at the Bug Lake SNOTEL station (elevation = 2,423 m) was 104 cm (Natural Resource Conservation Service 2003).

The IP is a high mountain valley immediately west of Yellowstone National Park and south of the continental divide. The dominant feature of IP is the Henry's Fork of the Snake River that bisects the valley. The IP area is approximately 221,140 ha in size with elevations ranging from 1,800 to 2,500 m. The IP was dominated by lodgepole pine and had been heavily logged following mountain pine beetle (*Dendroctonus* spp.) outbreaks in the 1960s and 1970s. Average snow depth for IP on 1 February at the Island Park SNOTEL station (elevation = 1,917 m) was 109 cm (Natural Resource Conservation Service 2003).

The BHM extends from the Bighorn River in southern Montana, USA, south 150 km to U.S. Highway 16 and forms the eastern border of the Bighorn River Basin. Elevations on the BHM range from 2,000 to >4,000 m. The BHM were characterized by broad stands of lodgepole pine giving way to stands of subalpine fir and Engelmann spruce at higher elevations. Alpine tundra on the BHM began at approximately 3,050 m. Average snow depth on the BHM on 1 February at the Burgess Junction SNOTEL station (elevation = 2,402 m) was 130 cm (Natural Resource Conservation Service 2003). Only the ground-tracking method described below was used in the ancillary study sites.

Methods

Aerial Track Counts

We used aerial track-count data to compare coyote activity in deep snow areas with and without snowmobile trails to determine whether snowmobile trails allow coyotes to access deep snow areas from which they would otherwise be excluded. These counts ($n = 12$) were conducted with Utah highway patrol pilots and helicopters during the winters of 2001–2002 and 2002–2003 in the East and West Black's Forks drainages of the north slope of the UMR. We chose these drainages because the High Uinta Wilderness boundary crossed them approximately equidistant from the mouth and the top of the drainage. This assured that approximately half of the drainage would be without snowmobile trails (snowmobiles are illegal within the wilderness area). This made it possible to compare coyote activity levels from the lower section of the drainage (with snowmobile trials) to the upper section (without snowmobile trails). We conducted aerial track counts when skies were clear during the morning hours while the angle of the sun was casting shadows, making coyote trails easier to see and identify.

We started counts of coyote trails from known locations at the mouth of each drainage and recorded the number of coyote trails and an index of the level of snowmobile activity (single trails, braided trails, pavement-like trails) for each 1.85-km section (1 nautical mile) up the drainage until snowmobile trails ended. From this point, we recorded the number of coyote trails for each additional 1.85-km section up the drainage until tree-line. We conducted aerial track counts with a minimum of 3 people in the helicopter: an observer, a recorder, and the pilot each with specific responsibilities. The observer counted the coyote tracks and reported the level of snowmobile activity. The recorder recorded data from the observer and the pilot. The pilot maintained an altitude approximately 30 m above the ground and kept track of when each 1.85-km section was finished. The sections were

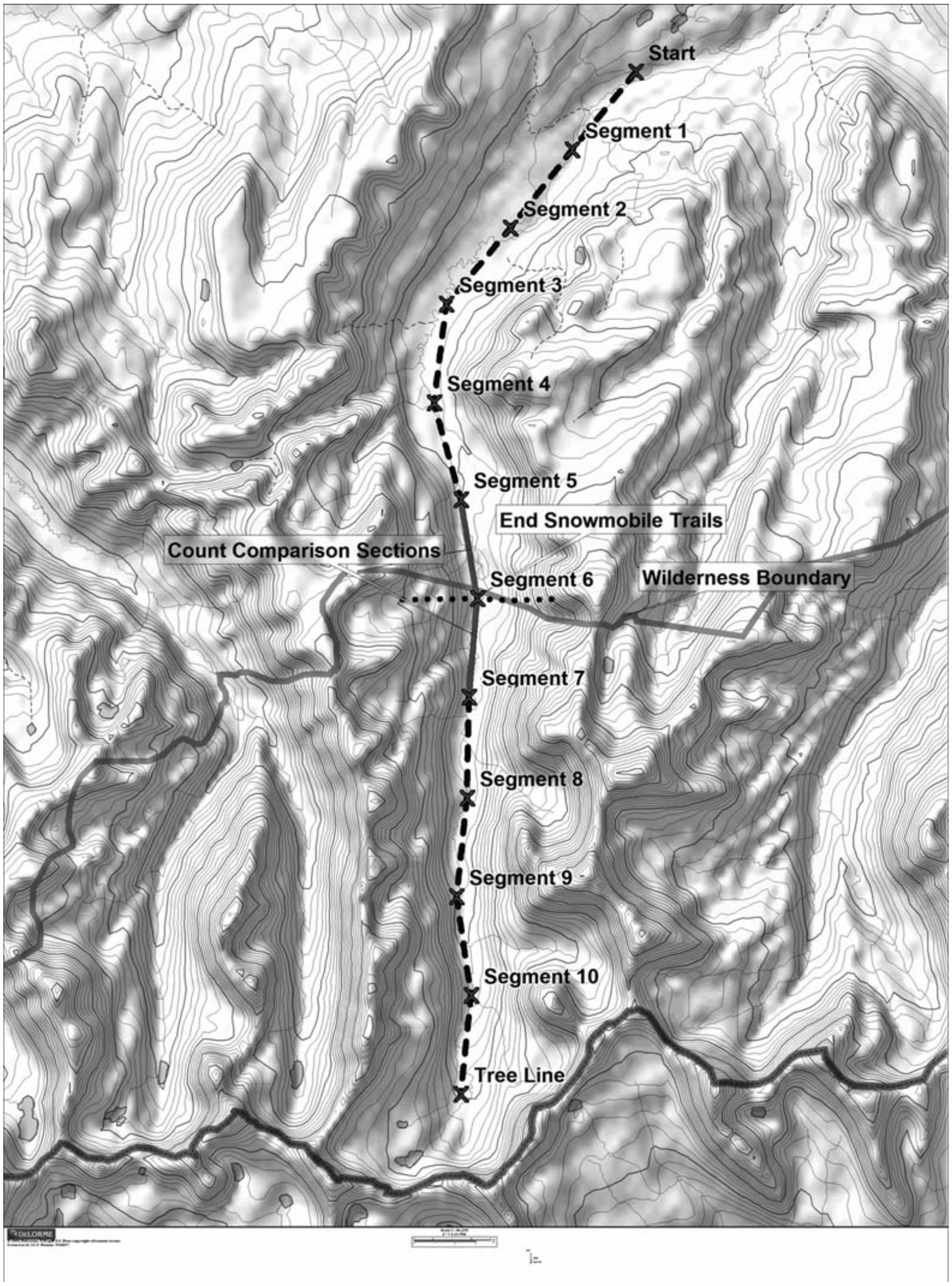

Figure 2. Diagram illustrating the method of data collection and areas compared in the within flight analysis of aerial track data collected during winters 2001–2002 and 2002–2003.

measured using the global positioning system onboard the aircraft. We used the same observer for each flight to limit potential variation associated with different observers.

We compared coyote trail counts for sections with and without snowmobile trails within and between flights. We made within-flight comparisons between 1.85-km sections below (with snowmobile trails) and above (without snowmobile trails) the point where snowmobile trails ended for each flight (Fig. 2). Between-flight comparisons were possible because snowmobile trails ended at different elevations for each flight. This allowed counts of coyote trails in sections that had snowmobile trails during some flights to be compared to counts for the same sections when snowmobile trails were not present (Fig. 3). To standardize the data, because flights occurred at various lengths of time following snowfall, we converted track counts per segment into the proportion of tracks counted for the entire flight prior to comparison.

Ground Tracking

We used ground tracking to quantify the area adjacent to snowmobile trails potentially impacted by coyotes and to quantify coyote behavior relative to the presence of snowmobile trails and local habitat and environmental parameters. In addition, we

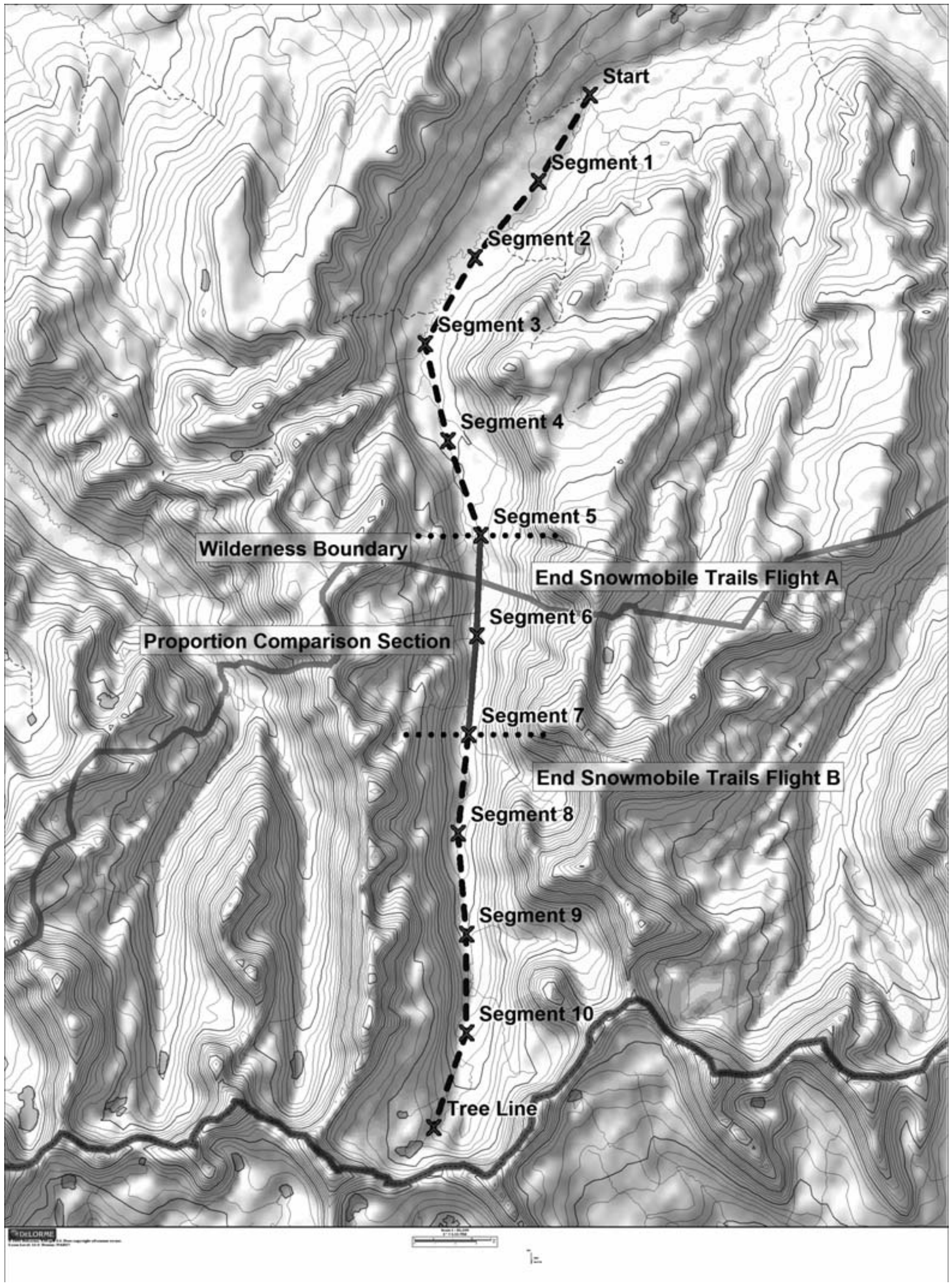

Figure 3. Diagram illustrating the method of data collection and areas compared in the between flight analysis of aerial track data collected during winters 2001–2002 and 2002–2003.

compared habitat and environmental variables between study sites to quantify differences and analyze the response of coyotes to snowmobile trails in relation to geographic environmental variation. We conducted ground tracking throughout each study site not related to the aerial track counts described above.

We located coyote trails by following existing snowmobile trails until we observed a coyote trail entering and following or following and leaving the snowmobile trail. After we located an initial coyote trail, we measured the snowmobile trial distance to each subsequent coyote trail using a snowmobile odometer. We then followed coyote trails until one of the following destinations or origins was determined: 1) snowmobile trail, 2) carrion carcass (e.g., big game, livestock, etc.), 3) bed or resting site, 4) ski or snowshoe trail, 5) bare slope, or 6) trail lost. We recorded the destination as unknown if after 600–800 m the coyote trail showed no sign of returning to a snowmobile trail or reaching another discernable destination or origin. We recorded the direction of travel (toward or away from the snowmobile trail where it was located) for all coyote trails of unknown destination or origin. For each coyote trail, we collected the following data: 1) trail type (single foot prints, feet dragging between steps, or chest pushing through snow), 2) number of snowshoe hare and red squirrel

Table 1. Summary of model selection parameters used to determine the best-fit model for the analysis of aerial track count data collected in the Uinta Mountains during winters 2001–2002 and 2002–2003.

Comparison	Model[a]	AIC_c	ΔAIC_c	Normalized AIC_c weight
Within flight	T, E, T*E	27.3	0	1.0
Within flight	E	44.5	17.2	<0.001
Within flight	T, E	47.7	20.4	<0.001
Within flight	T	51.5	24.2	<0.001
Between flight	T	17.9	0	1.0
Between flight	T, E	32.2	14.3	<0.001
Between flight	T, E, T*E	42.8	24.9	<0.001
Between flight	E	52.9	35	<0.001

[a] T = Presence of snowmobile trails, E = Elevation.

tracks (tracks/m) intersected (adjusted for time since last snowfall), 3) total distance off the snowmobile trail, 4) maximum distance from a snowmobile trail (0–50 m, 50–100 m, etc.), 5) time since last snowfall, 6) group size (single, pair, family group), and 7) habitat conditions.

We recorded habitat and environmental parameters along the coyote trail at random points between distances of 100–200 m, 300–400 m, and 500–600 m. At each habitat point, we recorded the following information: 1) snow depth and snow hardness, 2) tree density (T^2 method; Krebs 1999), 3) diameter at breast height (dbh) for the trees in the density measurement, 4) tree-stand age structure (even, uneven, mixed), 5) stand species composition, and 6) percent of trees with limbs at snow level. Snow hardness was determined by measuring the penetration depth of a #7 lead sinker dropped from 60 cm above snow level.

Statistical Analysis

We conducted statistical analyses with the aid of SAS® (SAS Institute 2001) and MINITAB® (Minitab, Inc. 2000). We compared aerial counts of coyote trails within each flight using a paired *t*-test of the trails counted 1.85 km above and below the end of snowmobile trails. In addition, we applied mixed models to the data with the number of trails counted as the dependent variable and elevation and presence of snowmobile trails as independent variables. We used elevation in the models as a surrogate for increasing snow depth because it was impossible to land the helicopter to measure snow depths with the designated wilderness. We included flight and drainage in the models as blocking variables. In addition, we compared aerial counts of coyote trails between flights using a paired *t*-test of the proportion of trails counted in given sections of each drainage with and without snowmobile trails present. We also compared aerial counts of coyote trails between flights using mixed models, but with the addition of repeated measures with unstructured covariance. We again used proportion of coyote trails counted as the dependent variable with elevation and the presence of snowmobile trails as independent variables. We included elevation as a repeated measure because the mean elevation for each comparison (with and without snowmobile trails present) was identical (Fig. 2). We included drainage and flight as a blocking variable in all models. The dependent variable (proportion of coyote trails counted) was subjected to arcsine square-root transformation for both models prior to analysis to better meet assumptions of normality and homogeneity of variance. We selected combinations of elevation and the presence of snowmobile trails (Table 1) as candidate models a priori to analysis and we used Akaike's Information Criterion, adjusted for small sample sizes (AIC_c), for model selection and we used normalized AIC_c weights to estimate the effect size of the independent variables (Anderson et al. 2000). In addition, we used linear regression to compare the average proportion of coyote trails per 1.85-km segment and the average proportion of flights with snowmobile tracks in each 1.85-km segment (Figs. 4, 5).

We used analysis of variance (ANOVA) and Tukey's pairwise comparisons to identify differences in 1) continuous behavioral

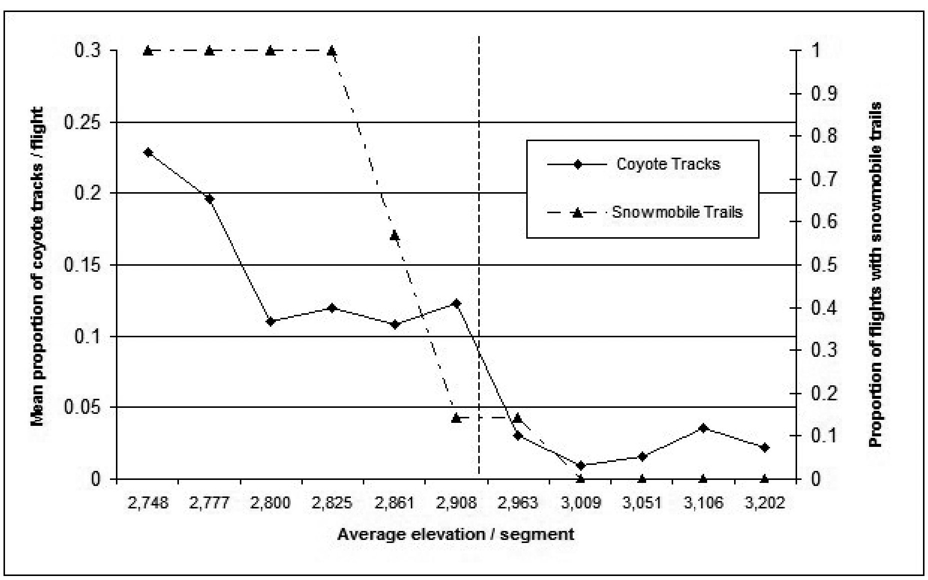

Figure 4. Mean proportion of coyote trails (left *y*-axis) compared to the proportion of flights with snowmobile trails present (right *y*-axis) for each 1.85-km section of the East Black's Fork Drainage for data collected during winters 2001–2002 and 2002–2003. The vertical dotted line indicates the approximate location of the High Uintas Wilderness boundary.

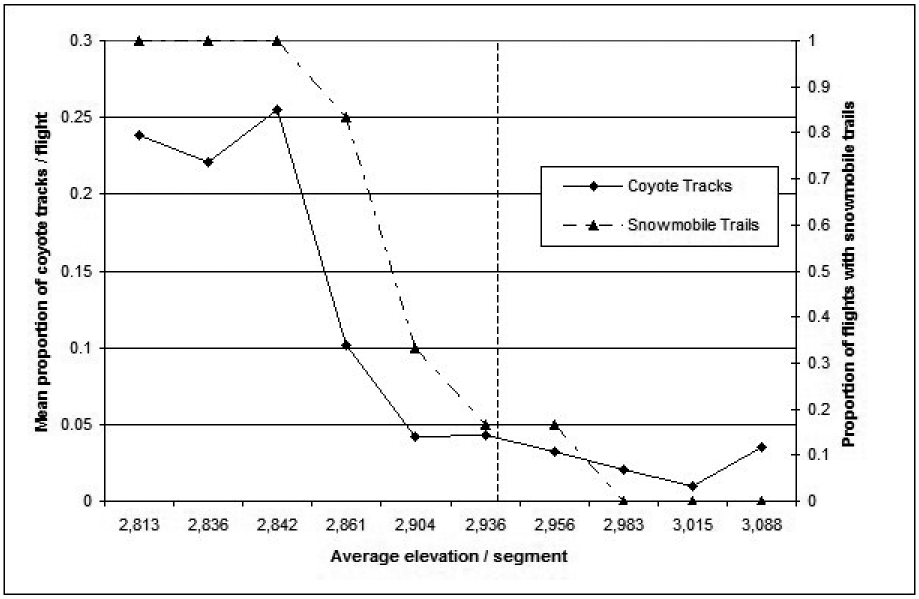

Figure 5. Mean proportion of coyote trails (left *y*-axis) compared to the proportion of flights with snowmobile trails present (right *y*-axis) for each 1.85-km segment of the West Black's Fork Drainage for data collected during winters 2001–2002 and 2002–2003. The vertical dotted line indicates the approximate location of the High Uintas Wilderness boundary.

variables (distance traveled off snowmobile trails, snowmobile trail distance between coyote trails), 2) habitat parameters (snow depth, snow hardness, tree density, tree dbh, percent of trees with limbs at snow level), and 3) prey-base variables (snowshoe hare tracks/m, red squirrel tracks/m, and total prey/m) between study sites for ground-tracking data. We transformed variables not meeting the assumptions of ANOVA using either natural-log or square-root transformations to meet test assumptions. We used chi-square tests to analyze differences in categorical variables (destination, track type, maximum distance from snowmobile trail (0–50 m, 50–100 m, etc.), tree-stand age, and tree-stand species composition) between study sites. We used a 2-sample *t*-test to compare the distance between coyote trails using groomed and ungroomed snowmobile trails within the UMR as an index of use. In addition, we separated ground-tracking data into 2 groups: coyote trails that did, or did not, return to a snowmobile trail. We then used logistic regression to identify habitat and environmental variables (i.e., snow depth and hardness) that most significantly discriminated between the 2 groups. We applied these analyses to the UMR and to all sites combined. Sample sizes at comparative sites were not adequate for individual analysis.

Results

The mean number of coyote trails encountered in 1.85-km segments below ($\bar{x} = 3.0$, SE = 0.38) and above ($\bar{x} = 1.4$, SE = 0.65) the point where snowmobile trails ended differed ($t = 3.07$, $P = 0.005$). Comparison of mixed models used to analyze differences in the within-flight aerial trail counts (Fig. 2) identified the full model containing elevation, presence of snowmobile trails and the interaction as the best model (AIC_c weight = 1.0). This model fit the data an order of magnitude better than the other 3 models (Table 1). For between-flight comparisons, the mean proportion of coyote trails encountered in segments with ($\bar{x} = 0.35$, SE = 0.05) and without ($\bar{x} = 0.10$, SE = 0.02) snowmobile trails present also differed ($t = 5.62$, $P < 0.001$). Comparison of mixed models used to analyze differences in the aerial trail counts between flights (Fig. 3) identified the model containing only the presence of snowmobile trails as having the best fit (AIC_c weight = 1.0). This model also fit the data an order of magnitude better than any of the other 3 models (Table 1). For both sets of models, as elevation increased the presence of snowmobile trails and coyote trails decreased, with coyote trails being less frequent in the absence of snowmobile trails. Linear regression comparing the mean proportion of coyote trails and the mean proportion of flights with snowmobile trails present for each 1.85-km segment had r^2 (adjusted) values of 86.4% and 67.4%, respectively, for West and East Black's Forks drainages (Figs. 4, 5). The mean proportion of coyote trails in the segments of the East Black's Fork Drainage when snowmobile trails were present averaged 0.41 (SE = 0.07) compared to a mean proportion of 0.11 (SE = 0.03) when snowmobile trails were absent. In the West Black's Fork Drainage, the mean proportion of coyote trails when snowmobile trails were present was 0.28 (SE = 0.06) compared to a mean proportion of 0.08 (SE = 0.02) when snowmobile trails were absent.

ANOVAs of continuous habitat variables between study sites identified snow depth ($P < 0.001$), snow hardness ($P < 0.001$), tree dbh ($P = 0.006$) and percent of limbs at snow level ($P = 0.003$) as habitat variables that differed between study sites. All prey variables (snowshoe hare tracks/100 m [$P < 0.001$], red squirrel tracks/100 m [$P < 0.001$], and total prey tracks/100 m [$P < 0.001$]) also differed between study sites (Table 2).

Chi-square comparisons of categorical habitat variables between study sites identified age structure of tree stands ($P < 0.001$), species composition of tree stands ($P < 0.001$), species composition of trees in the T^2 density measurement ($P < 0.001$), and height of trees limbs above snow level for trees in the T^2 density measurement ($P < 0.001$) differed between study sites (Table 3). The ANOVA and chi-square comparisons of variables

Table 2. Mean comparisons of continuous habitat variables measured in association with winter coyote trails at 4 study sites in the Intermountain West during winters 2000–2001, 2001–2002, and 2002–2003.

Variable	UMR[a] 2001	UMR[a] 2002	BMR[a]	BRR[a]	IP[a]	ANOVA P value	Significant Tukey's comparisons
Snow depth (cm)[b]	$n = 54$	$n = 107$	$n = 33$	$n = 30$	$n = 29$	<0.001	UMR 01–BMR
	$\bar{x} = 66$	$\bar{x} = 60$	$\bar{x} = 92$	$\bar{x} = 77$	$\bar{x} = 78$		UMR 02–BMR
	SE = 3.3	SE = 3.0	SE = 4.0	SE = 4.3	SE = 6.3		UMR 02–BRR
							UMR 02–IP
Snow hardness (penetration depth [cm])	$n = 54$	$n = 107$	$n = 33$	$n = 30$	$n = 29$	<0.001	UMR 01–UMR 02
	$\bar{x} = 18.9$	$\bar{x} = 15.4$	$\bar{x} = 12.0$	$\bar{x} = 12.3$	$\bar{x} = 14.9$		UMR 01–BMR
	SE = 1.0	SE = 0.82	SE = 0.45	SE = 1.06	SE = 0.92		01–BMR
Tree density no./10 m[2 b]	$n = 51$	$n = 99$	$n = 33$	$n = 28$	$n = 29$	0.596	None
	$\bar{x} = 130$	$\bar{x} = 173$	$\bar{x} = 194$	$\bar{x} = 113$	$\bar{x} = 115$		
	SE = 39.7	SE = 35.9	SE = 52.0	SE = 24.6	SE = 26.2		
Tree dbh (cm)[c]	$n = 50$	$n = 97$	$n = 33$	$n = 28$	$n = 29$	0.006	UMR 01–IP
	$\bar{x} = 17.6$	$\bar{x} = 15.8$	$\bar{x} = 15.9$	$\bar{x} = 12.6$	$\bar{x} = 11.3$		
	SE = 1.3	SE = 1.0	SE = 1.2	SE = 1.4	SE = 1.4		
% limbs at snow level	$n = 34$	$n = 96$	$n = 33$	$n = 28$	$n = 29$	0.003	UMR 02–BRR
	$\bar{x} = 52$	$\bar{x} = 41$	$\bar{x} = 41$	$\bar{x} = 56$	$\bar{x} = 54$		
	SE = 4.2	SE = 2.4	SE = 4.0	SE = 4.5	SE = 4.4		
Snowshoe hare tracks/100 m (adjusted for time since last snowfall)[c]	$n = 46$	$n = 88$	$n = 30$	$n = 25$	$n = 25$	<0.001	UMR 02–BMR
	$\bar{x} = 1.5$	$\bar{x} = 1.0$	$\bar{x} = 2.5$	$\bar{x} = 3.1$	$\bar{x} = 0.7$		UMR 02–BRR
	SE = 0.26	SE = 0.13	SE = 0.51	SE = 0.72	SE = 0.26		BMR–IP
							BRR–IP
Red squirrel tracks/100 m (adjusted for time since last snowfall)[c]	$n = 46$	$n = 88$	$n = 30$	$n = 25$	$n = 25$	<0.001	BMR–All
	$\bar{x} = 0.6$	$\bar{x} = 0.8$	$\bar{x} = 2.4$	$\bar{x} = 0.5$	$\bar{x} = 0.4$		
	SE = 0.10	SE = 0.17	SE = 0.53	SE = 0.22	SE = 0.12		
Total prey tracks/100 m (adjusted for time since last snowfall)[c]	$n = 46$	$n = 88$	$n = 30$	$n = 25$	$n = 25$	<0.001	UMR 01–BMR
	$\bar{x} = 2.1$	$\bar{x} = 1.7$	$\bar{x} = 5.0$	$\bar{x} = 3.5$	$\bar{x} = 1.1$		UMR 02–BMR
	SE = 0.32	SE = 0.22	SE = 0.84	SE = 0.82	SE = 0.28		BMR–IP

[a] UMR = Unita Mountain Range, BMR = Bighorn Mountain Range, BRR = Bear River Range, IP = Island Park.
[b] Data subjected to a natural-log transformation.
[c] Data subjected to a square-root transformation.

associated with coyote behavior in relation to snowmobile trails failed to identify any differences between study sites (Table 4, Figs. 6, 7).

Logistic regression identified total prey ($P = 0.08$, odds ratio = 0.03) and snow depth ($P = 0.11$, odds ratio = 1.17) as the only variables discriminating between coyote trails that returned to a snowmobile trail ($n = 82$) and those that did not ($n = 53$) on the UMR (Concordance = 63.5%). When the same analysis was applied to all sites combined, snow depth ($P = 0.04$, odds ratio = 1.16) and total prey ($P = 0.07$, odds ratio = 0.08) were again the only variables discriminating between coyote trails that returned to a snowmobile trail ($n = 141$) and those that did not ($n = 73$; Concordance = 61.9%).

Discussion

Our results support the hypothesis that the presence of hard-packed trails has the potential to break down the spatial segregation of lynx and coyote populations during annual periods

Table 3. Chi-square comparisons of categorical habitat variables measured in association with winter coyote trails at 4 study sites in the Intermountain West during winters 2000–2001, 2001–2002, and 2002–2003.

Variable	Categories	χ^2	P value
Track type[a]	Single foot print, feet dragging between steps–chest pushing through snow	7.3	0.06
Age structure of tree stands[b]	<3 age classes, >3 age classes	36.9	<0.001
Species composition of tree stands	Lodgepole pine, subalpine fir–Engelmann spruce, aspen–conifer, mixed conifer	58.9	<0.001
Species composition of trees in the T[2] tree-density measurement	Lodgepole pine, subalpine fir, Engelmann spruce, aspen, dead	183.7	<0.001
Height (cm) of tree limbs above snow level	0, 0–50, >50	63.8	<0.001

[a] "Feet dragging between steps" and "chest pushing through snow" categories were combined because the chest pushing through snow category did not have a minimum sample of 5 for some sites.
[b] Even- and mixed-age structure categories were combined to create the <3 age-class category because the even-age category did not have a minimum sample of 5 for some sites.

Table 4. Mean comparisons of continuous coyote behavior variables measured in association with winter coyote trails at 4 study sites in the Intermountain West during winters 2000–2001, 2001–2002, and 2002–2003.

Variable	UMR[a] 2001	UMR[a] 2002	BMR[a]	BRR[a]	IP[a]	ANOVA *P* value	Significant Tukey's comparisons
Distance to destination (m)[b]	$n = 46$ $\bar{x} = 217$ SD = 217	$n = 91$ $\bar{x} = 211$ SD = 218	$n = 30$ $\bar{x} = 224$ SD = 273	$n = 25$ $\bar{x} = 243$ SD = 219	$n = 25$ $\bar{x} = 192$ SD = 197	0.496	None
Snowmobile trail distance between coyote tracks (km)[c,d]	$n = 55$ $\bar{x} = 1.5$ SD = 1.9		$n = 29$ $\bar{x} = 1.1$ SD = 1.3	$n = 22$ $\bar{x} = 1.8$ SD = 2.3	$n = 15$ $\bar{x} = 1.3$ SD = 1.6	0.816	None

[a] UMR = Unita Mountain Range, BMR = Bighorn Mountain Range, BRR = Bear River Range, IP = Island Park.
[b] Data subjected to a natural-log transformation.
[c] Data subjected to a square-root transformation.
[d] Limited to sampling events that took place within 48 hr of snowfall.

of deep snow (Buskirk et al. 2000, Ruediger et al. 2000). In our study, coyotes required the presence of packed trails to exploit areas of deeper snow. Elevation was negatively correlated with coyote use. Although lynx also will use packed trails, their morphological adaptations enable them to also travel on top of unpacked snow. Coyote behavior, relative to snowmobile trails, was consistent among study sites in spite of significant differences in habitat and environmental conditions. All continuous and categorical habitat and environmental variables measured along coyote trails, with the exception of tree density, differed significantly between study sites (Tables 2, 3). However, none of the variables measuring coyote behavior relative to the presence of snowmobile trails differed significantly between study sites (Table 4, Figs. 6, 7). This indicates that, at all study sites, environmental conditions (snow depth and hardness) were above a threshold wherein they dictated coyote behavior, forcing them to use packed trails. We believe this also suggests that coyotes were able to satisfy basic needs despite differences in habitat conditions (Table 2). Our interpretations were supported by the logistic regression analysis identifying snow depth and prey availability as the variables best discriminating between coyote trails that returned to snowmobile trails and those not returning.

Documentation and quantification of coyote invasions into deep snow areas of the Intermountain West lends increased legitimacy

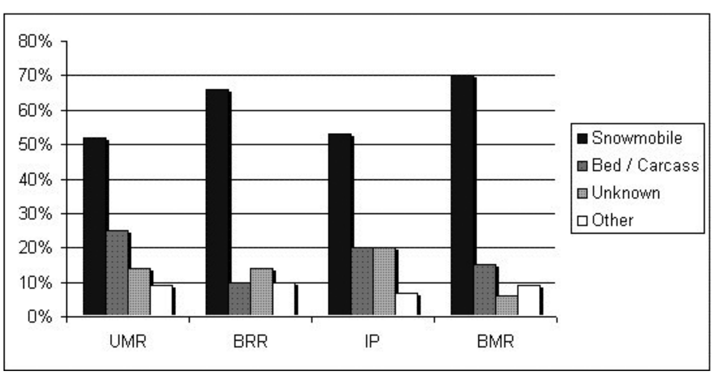

Figure 6. Comparison of the destinations/origins of coyote trails leaving, or entering and following, snowmobile trails for 4 sites in the Intermountain West during winters 2000–2001, 2001–2002, and 2002–2003. UMR = Uinta Mountain Range, BRR = Bear River Range, IP = Island Park, BMR = Bighorn Mountain Range.

to their potential impacts on lynx conservation as discussed by Buskirk et al. (2000), and Ruediger et al. (2000). Potential impacts can be classified as either habitat loss–fragmentation and competition. The impacts of interspecific competition can be further divided into exploitation and interference competition.

The potential for exploitation competition has been illustrated by studies that identified snowshoe hares as a major component of coyote winter diets (Todd et al. 1981, Todd and Keith 1983, Parker 1986, Murray et al. 1994, O'Donoghue and Boutin 1997, O'Donoghue et al. 1998, Patterson et al. 1998, Dumond et al. 2001). Similarly, a study of coyote winter diets in the UMR identified snowshoe hares and red squirrels as the 2 most common items in coyote diets after carrion (Shirley 2004). O'Donoghue et al. (1998), Todd et al. (1981), and Keith et al. (1977) found when snowshoe hares were at high densities, coyote predation rates were greater than those of lynx until snow depth limited coyote mobility.

Although coyotes are one of the most ecologically flexible of North American carnivores, in situations were prey is limited, coyotes behave as specialists (Murray et al. 1994, O'Donoghue and Boutin 1997). This increases the level of exploitation competition between coyotes and lynx during the time of year when prey is most scarce (Apps 2000). The potential for exploitation competition to negatively impact lynx populations is particularly high on the southern portion of lynx distribution where snowshoe hare population densities often are below the minimum density believed to be required to sustain lynx populations (Ruediger et al. 2000). For example, Litvaitis and Harrison (1989) found a negative correlation between bobcat and coyote populations during a period of increasing coyote populations, which they attributed to exploitation competition. Although not covered in the empirical results of this research, others have documented the potential of interference competition, dependent on the relative and numerical and population densities of the competitors, between lynx and coyotes (Murray et al. 1994, O'Donoghue et al. 1995, O'Donoghue 1997). In addition, several studies have demonstrated interference competition between coyotes and bobcats, and in all cases coyotes dominated the interaction. Anderson (1986), Jackson (1986), Toweill (1986), Fedriani et al. (2000), and Gipson and Kamler (2002) all reported instances of coyotes killing bobcats. However, it is important to recognize that both lynx and bobcats have been documented

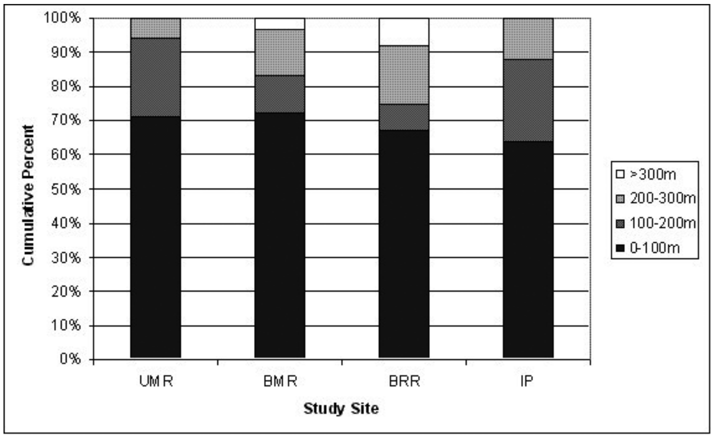

Figure 7. Maximum distance coyotes traveled from a snowmobile trail compared between 4 sites in the Intermountain West during winters 2000–2001, 2001–2002, and 2002–2003. UMR = Uinta Mountain Range, BRR = Bear River Range, IP = Island Park, BMR = Bighorn Mountain Range.

killing coyotes, but this seems more rare. In addition, expanding coyote populations have been implicated in the decline of bobcat populations in the western United States (Knowlton and Tzilkowski 1979). It is logical to assume that coyotes would dominate interspecific interactions with lynx similar to bobcats.

Management Implications

Our findings have important implications for lynx conservation in the Intermountain West. First, coyote impacts are predictable across a broad range of high-elevation deep-snow conditions in the presence of snowmobile trails. Second, because >90% of coyote trails stayed within 300 m of a snowmobile trail (Fig. 7), the area impacted by coyotes in deep-snow areas is directly related to the spatial arrangement of snowmobile trails.

The results of this study appear to validate the recommendations of Ruediger et al. (2000) and steps taken by land management agencies to limit the 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). We documented and quantified the putative invasions of coyotes into lynx winter habitat but did not directly measure competition between the 2 species. Although circumstantial evidence suggests the existence of competition, in the Intermountain West the topic merits further investigation. This will require simultaneous evaluation of sympatric coyote and lynx populations to identify and quantify the actual extent of exploitation and interference competition.

Our results also suggest coyotes require persistent trails to exploit an area during periods of deep snow. For example, in the East Black's Fork drainage, 76% of coyote trails were confined to sections of the drainage that had snowmobile trails present at least 60% of the time (Fig. 4) and in the West Black's Fork Drainage 81% of the coyote trails were counted in sections that had snowmobile trails present at least 80% of the time (Fig. 5).

Thus, management agencies attempting to limit coyote access to lynx winter habitat may be able to do so by making different areas open to snowmobiles on a rotating basis. Given the assumptions listed below, we hypothesize that if areas of lynx habitat were open to snowmobiling on a rotating rather then continual basis, coyote invasions could be greatly reduced because the presence of snowmobile trails would no longer be persistent. If this hypothesis is correct, coyote invasions into lynx habitat could be reduced and management agencies could avoid permanently closing, to winter recreation, areas designated as lynx habitat. Our hypothesis is based on the following assumptions: 1) closed areas are large enough to encompass entire home ranges, precluding coyotes from simply shifting activity within established home ranges, 2) areas are closed often enough and long enough so that the presence of snowmobile trails is perceived by coyotes as being unreliable, and 3) closures are effective at eliminating snowmobile use (i.e., enforcement). This hypothesis could be tested with the cooperation of state and federal management agencies and local snowmobiling associations. Based on our findings, we recommend management agencies follow the recommendations of the Lynx Conservation Assessment and Strategy for limiting snow compaction in potential lynx habitat.

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