

Effects of industrial development on wolverine (*Gulo gulo*) ecology in the boreal forest of northern Alberta

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Wolverine Project Progress Report – Winter 2014/2015



Birch Mountain field site in northcentral Alberta

PROJECT PARTNERS

- Alberta Conservation Association
- Alberta Environment and Sustainable Resource Development
- Alberta Fish and Game Association – Minister’s Special License
- Alberta Sports, Recreation, Parks & Wildlife Foundation
- Alberta Trappers Association
- Animal Damage Control
- Bildson Reality Ltd.
- Canadian Circumpolar Institute
- Daishowa-Marubeni International
- Dene Tha First Nation
- Environment Canada
- Husky Oil
- TD Friends of the Environment Foundation
- The Wolverine Foundation
- Tolko
- Rocky Mountain Wilderness Society
- Safari Club International – Northern Alberta Chapter
- Strategic Oil
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SUMMARY

Wolverines *May be at Risk* in Alberta but there are inadequate data available to accurately assess population status. There is interest by stakeholders (e.g., government, trappers, conservation organizations, resource extraction industries) in how industrial activities are impacting wolverine populations. The aim of our project is to model and predict the effects of industrial infrastructure and activity on wolverine ecology in the lowland boreal forest of northern Alberta. The aim of this report is to summarize data collected over two winter field seasons and to begin some exploratory data analyses. Our research takes place in the Birch Mountains of northcentral Alberta and in Rainbow Lake of northwest Alberta. The Birch Mountains are relatively undisturbed by industrial development whereas Rainbow Lake has high human use and development. At these two sites, we live-trap, radiocollar, and track wolverines to quantify wolverine movement, habitat selection, foraging, and density. As of April 2015, we have documented 44 individual wolverines in Rainbow Lake and 9 wolverines in the Birch Mountains. We have collected approximately 30,000 GPS points from 23 wolverines at 2-hour intervals. We performed some exploratory analyses using these data that will be detailed below. Male wolverines have greater movement rates than females and both sexes are more active during the day than at night. Wolverine movements across high-grade industrial roads and paved roads were 10-15x the normal median movement rate. We found a significant positive relationship between the density of roads in a wolverine's home range and their median movement rate. We found a significant increase in the movement rate of wolverines during timber harvest activities and also found wolverines were further from cutblocks during timber harvest. Wolverines in the lowland boreal appear to concentrate winter foraging on beaver, snowshoe hare, and moose. During the summer and winter, wolverine GPS clusters were more often found in wetland beaver habitats. We also found wolverine clusters were more likely in coniferous versus broadleaf forests. Wolverine dens were found in a timber slash pile, beaver lodge, tree root wad, and in down trees. We discuss our findings in relation to wolverine research from throughout their circumpolar range. The winter of 2015/2016 will be our final field season live-trapping and tracking wolverines in northern Alberta.

INTRODUCTION

Wolverine ranges and populations in North America are believed to be declining as a result of displacement from agriculture, urbanization, and industrial development (Ruggiero et al. 2007, Slough 2007). In Canada, wolverines are considered a species of *Special Concern* (COSEWIC 2014) while in Alberta wolverines *May be at Risk* (ESCC 2014). Both national and provincial assessments relate the paucity of data available to make accurate population assessments (wolverines are considered by the Alberta government to be Data Deficient) and the concern for how industrial activities (forestry, oil and gas, mining) might be impacting populations. Our primary research goals are to model and predict the effects of industrial development on wolverine distribution and movement along a gradient of industrial disturbance in northern Alberta. This report summarizes field data collected over the last two winter field seasons and begins some exploratory data analyses.

Industrial development is common throughout the lowland boreal forest of northern Canada as the region provides plentiful timber, oil, and gas resources. The resource extraction industry builds roads, pipelines, seismic lines, and camps to access and transport these resources to processing plants and markets. As of the 1990's, the density of linear features in northern Alberta averaged 1.8 km/km² (Schneider 2002). Researchers have shown linear features can alter the ecology of boreal wildlife species. For example, roads and seismic lines improve the hunting efficiency of wolves (McKenzie et al. 2012) and alter the distribution and abundance of deer, caribou, and moose (James et al. 2004, Bowman et al. 2010, Latham et al. 2011).

We lack a detailed understanding of how human developments impact wolverine populations. Potential effects of developments on wolverines, however, include increased competition from top predators (Bowman et al. 2010, Fisher et al. 2013, Khalil et al. 2013), increased mortality (Johnson et al. 2005), or displacement (Krebs et al. 2007, Koskela et al. 2013). Our research program principally focuses on displacement, or the distribution and movement of wolverines relative to industrial infrastructure and human use. Our research takes place in an ecosystem with greater infrastructure densities than have ever been reported in the wolverine literature. This facilitates testing of previously identified human development thresholds for wolverines (Carroll et al. 2001, Lofroth and Krebs 2007). Additionally, we know of no peer-reviewed literature that investigates the fine-scaled movement and habitat selection patterns of wolverines in industrial landscapes. These data would be paramount for anticipating how industrial development influence wolverine populations.

Displacement from industrial developments could reduce the amount of habitat available to wolverines and increase the energy that is needed to acquire resources. For example, Johnson et al. (2005) reported an 11-34% increase in the amount of poor and low-quality grizzly bear habitat because of resource extraction in the Northwest Territories. Roever et al. (2010) reported an increase in grizzly bear movement when near roads and numerous authors have reported the barrier effect of roads on wildlife movement (Dyer et al. 2002, Fahrig and Rytwinski 2009, Roever et al. 2010, Northrup et al. 2012). A loss of habitat connectivity and greater disturbance can translate to lower fitness levels for wildlife, such as reduced body condition, density (Ciarneillo et al. 2007), or reproductive output (Phillips et al. 2000). Researchers have experimentally shown a reduction in wolverine fecundity with reduced food availability (Persson 2005).

For this report, we intend to take an exploratory look at wolverine movement rates relative to season, roads, and timber harvest activities. Under the assumption that animal movement rates are low in high-quality habitat (Pyke 1984), we would predict that wolverine movement rates will be greater when wolverines are in areas of high human use and development. This will ultimately impact the ability of wolverine to optimally forage (Pyke et al. 1977). We will also investigate the distribution of wolverines relative to timber harvest activities and roads. As reported elsewhere with wolverines (May et al. 2006, Krebs et al. 2007, Koskela et al. 2013), we suspect that wolverines will avoid disturbances and human infrastructure, reducing the amount of suitable habitat.

Overall, this report represents some preliminary and exploratory analyses from two winter field seasons in Rainbow Lake and the Birch Mountains of northern Alberta. The goals of this report are to: 1) present initial data on population estimates; 2) investigate the spatial ecology of wolverines in the boreal;

3) investigate wolverine response to roads and timber harvest; 4) investigate wolverine foraging and habitat selection; and 5) report on natal dens found in the boreal.

STUDY AREAS

Our field sites include Rainbow Lake of northwest Alberta and the Birch Mountains of northcentral Alberta (Figure 1). The center of the Rainbow Lake study area is the town of Rainbow Lake (119°28'18.705"W, 58°32'22.361"N). Our Rainbow Lake study site is approximately 2,380 km² in area (100% MCP around live-trap grid) and bounded by the Hay River to the south, the Hay-Zama Complex to the north, and the Chinchaga River to the east. The British Columbia border is an approximate study area boundary to the west.

Rainbow Lake is in the central mixedwood natural subregion, with pine (e.g., jackpine (*Pinus banksiana*)) and deciduous (e.g., aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*)) uplands and white spruce (*Picea glauca*)/balsam fir (*Abies balsamea*) lowlands. Lowland areas in Rainbow Lake have extensive bog and fen formations. The climate is characterized by long cold winters and short warm summers. Average annual temperature is -1.3°C with 414 mm of precipitation (Environment Canada, Climate Normals, 1971-2000). Average study area elevation is 500m. Topography in the study area is relatively flat except for narrow river valleys and an escarpment on the north extent of the study area. The landscape surrounding the town of Rainbow Lake has been developed by the oil, gas, and forestry industries since the 1950's. Developments include seismic lines, cutblocks, high-grade gravel roads (all-season), winter roads, pump jacks, processing plants, pipelines, and industrial camps.

The Birch Mountains (114°5'25.403"W, 57°9'21.219"N) is our second field site and is bounded to the north by the Panny River, the east by the Leige River, the south by the Wabasca River, and the west by an oil and gas field. They study area is approximately 2,280 km². The Birch Mountains is undeveloped except for ubiquitous seismic lines and serves as a low-disturbance control. The Birch Mountains are in the lower boreal highlands natural subregion and have similar tree species as those found

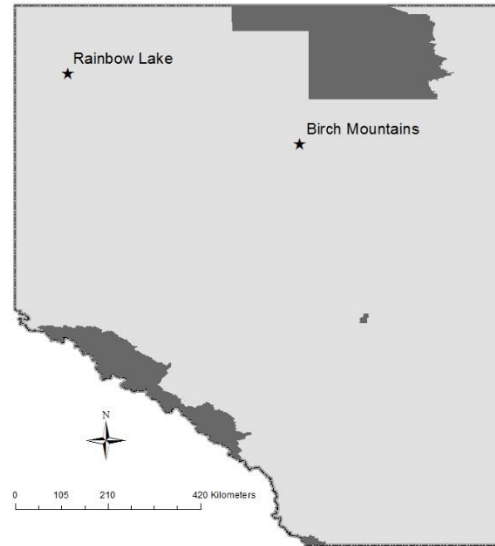


Figure 1. Our wolverine field research sites in northern Alberta. The Birch Mountains are relatively undisturbed by industry whereas Rainbow Lake is heavily developed.



High-grade gravel road near the Rainbow Lake oil and gas processing plant

in Rainbow Lake. However, the boreal highlands are characterized by colder winters and summers than the central mixed hardwood natural subregion. Elevations are approximately 500m.

FIELD METHODS

Our primary objective was to sample the movements and habitat selection of wolverines along a gradient of industrial development within Rainbow Lake and the Birch Mountains. To do this, we needed to live-trap and radiocollar wolverines. We established 14 log live-traps (Copeland et al. 1995) in Rainbow Lake in the summer and fall of 2013 for the winter of 2013/2014 live-trapping season. We established another 4 portable traps built of 4" x 4" timber later in the winter. These portable traps were built by members of the Alberta Trappers Association (ATA) and the Dene Tha First Nation. The Alberta Conservation Association (ACA) and the ATA established and maintained two run-poles on the western edge of our live-trapping grid during that first winter. In the winter of 2014/2015, we built an additional live-trap and established 6 run-poles throughout the Rainbow Lake study area. In total, we had 19 live-traps and 8 run-poles operational during the 2014/2015 live-trapping season. Live-traps and run-poles were spaced approximately 20 km and capture data used for a population estimate within a mark-recapture-resight framework (Figure 2).

The Birch Mountain field site had 8 run-poles operated by the ATA/ACA during the winter of 2012/2013 and 2013/2014. We did not begin live-trapping in the Birch Mountains until the winter of 2014/2015. During this first winter, we built 13 live-traps in the Birch Mountains and established 10 run-poles. Similar to spacing in Rainbow Lake, traps and run-poles were generally separated by 20 km.

Live-traps were baited with beaver and physically checked every 3-days by field crews. Trap status (open or closed lid) was monitored in real time with satellite trap transmitters. Run-poles were baited with beaver and checked and re-baited every 2-weeks. Unless an animal entered a live-trap during the evening, we were generally able to respond to triggered traps within a few hours of the animal going into the trap. Once captured, we immobilized wolverines with ketamine and dexdomitor. Once sedated, we removed the wolverine from the trap and weighed the animal, took tissue and hair samples, morphometric measurements, and attached an ear tag and GPS radiocollar programmed to record GPS locations at two hour intervals. We used both Iridium satellite and store-on-board radiocollars. Iridium collars sent GPS data daily via email.



Birch Mountain field site in northcentral Alberta.



Wolverine live-trap in Rainbow Lake. Traps are baited with beavers and equipped with satellite trap transmitters.

Other field activities included establishing and rotating a system of motion-sensor cameras used to quantify industrial traffic patterns throughout the Rainbow Lake field site. These data will be related to wolverine movement and habitat selection. We sampled high-grade, winter, and paved roads throughout our study area.

We investigated wolverine foraging habits by visiting GPS radiotelemetry clusters. We visited all clusters with ≥ 2 GPS points taken chronologically and within 200m of each other. We emphasized visiting smaller clusters as soon as conditions permitted (within 1-2 days of being created) so that sign (e.g., hair, bones, or scat) could easily be discovered. When conditions made visiting smaller clusters fruitless, we would visit

larger clusters where sign was more easily observable. Bed sites were discerned in the field by looking for melted snow where the wolverine had laid down. Dens were bed sites that were enclosed by some type of vegetation structure (e.g., under down willow or aspen, root wad). Dens found in the spring when females have kits were checked for evidence of kits being present. Natal dens were verified by listening for kits at the den or by documenting kits with motion-sensor cameras placed at dens. Cache sites were where the wolverine had dug up food items from the ground. We would verify these were caches by looking for evidence of the prey (e.g., bone, fur) either in the cache hole or in the immediate area of the hole. Predation sites were where we found an animal carcass but no evidence of dug up caches. Scavenge sites were where we found large prey we suspect the wolverine had not killed, but was instead killed by a larger predator. All of these features could be found at the same cluster (e.g., bed, cache, and scavenge site).

ANALYSIS METHODS/RESULTS

Mark-recapture-resight data

We operated live-traps in Rainbow Lake during the winter of 2013/2014 from mid-November through mid-April for a total of 108 days or 579 trap nights. During this first winter field season, we captured 24 different wolverines (11 males and 13 females) in live-traps. In the winter of 2014/2015 traps were open for 1,007 trap nights. Over this period, we live-trapped 26 wolverines (14 males and 12 females). Of the 26 individual wolverine captured in the winter of 2014/2015, 15 were animals captured previously in the winter of 2013/2014. New captures included 7 males and 4 females. This brings the total number of wolverines live-trapped in Rainbow Lake to 33 animals (16 females and 17 males). We operated 6 run-poles in Rainbow Lake between 42 and 145 days. We documented 4 different wolverines at these run-poles not documented at live-traps. Additionally, we documented 7 different wolverines at live-traps that were never captured. This brings the total number of individual wolverines documented in Rainbow Lake to 44.

We built 13 live-traps in the Birch Mountains in December 2014 and January 2015, opening and baiting traps as they were built. Traps remained open until early-April 2015. We captured a single female wolverine over this short but intense trapping period. We documented another 4 wolverines at run-poles throughout the Birch Mountain field site. In the 2 years that run-poles operated in Rainbow Lake prior to last winter, 9 different wolverines were documented.

We used the Lincoln-Petersen method for an initial estimate of the population of wolverines in Rainbow Lake. We focused the estimate using mark-recapture data from live-traps during two sessions (winter 2013/2014 & winter 2014/2015).

The Lincoln-Petersen equation, $N = Kn/k$:

N : the number of animals in the population;

K : number of wolverines marked in winter 2013/2014 = 24;

n number of wolverines captured/sighted in the winter of 2014/2015 = 33; and

k : number of wolverines captured/resighted in winter 2014/2015 that were marked = 15.

Using the above equation, the population estimate was 52.8 animals (24x33)/15) in the Rainbow Lake study area. We intend to use spatially explicit capture-recapture (SECR) models to better estimate density based on 3 winters of mark-recapture-resight data. Figure 2. will be helpful in developing a spatially-explicit model. Lines connect the detectors (live-traps or run-poles) where individual wolverines have been captured. Animal IDs in boxes indicate the animal was only captured at a single detector. As can be seen, wolverines frequently are trapped or documented at multiple detectors, giving us a good understanding of their overall space use. Many of the animals that have only been captured a single time

are located at the outskirts of our trapping grid (Figure 2). Because of insufficient data, we have not yet estimated a population for the Birch Mountain study area.

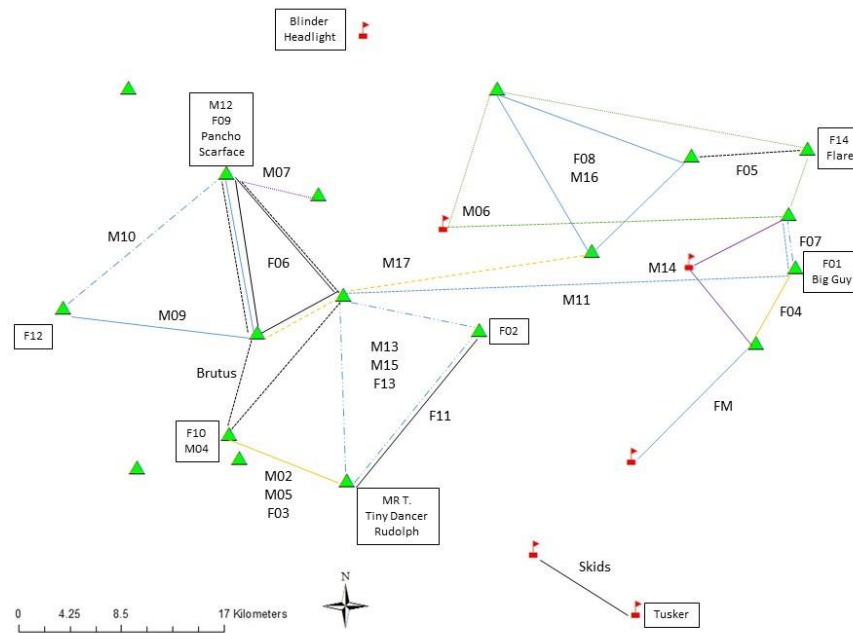


Figure 2. Live-traps (green triangles) and run-poles (red flags) at the Rainbow Lake field site. Animal names in boxes indicate the animal was only captured at a single trap/run-pole. Lines next to animal names indicate the detectors where the wolverine has been documented.

Wolverine movement

The following section explores the spatial ecology of wolverines at the Rainbow Lake field site. The 100% MCP for resident female wolverines was 319 km² (SD = 70, n = 9) and resident males was 753 km² (SD = 412, n = 6). We created step lengths (n = 17,039) from the approximately 29,000 GPS points collected from Rainbow Lake wolverines at two-hour intervals (Figure 3, 4). A step length is the euclidean distance between a GPS fix taken every two hours. We can see that a majority of wolverine step lengths are < 500 m (n = 9,426). Wolverine movements between 1 and 4 km's in a two hour period also are common (Figure 4).

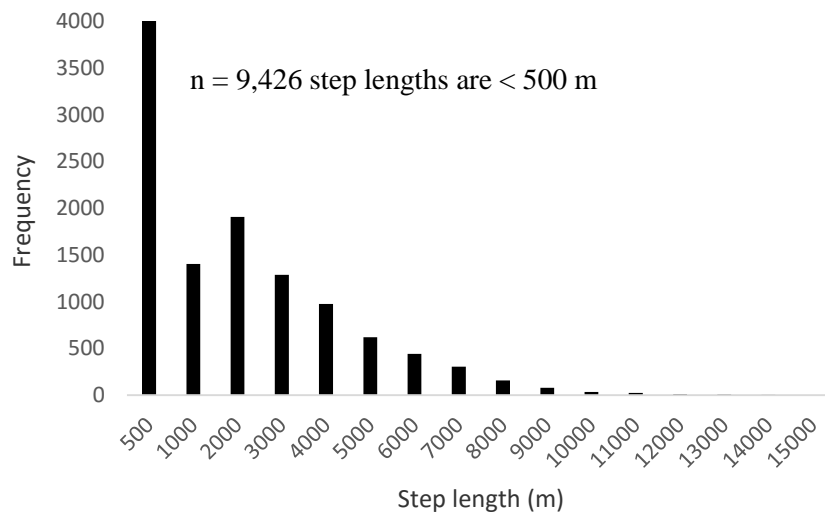


Figure 3. Wolverine (n = 22) step lengths (n = 17,086) from the Rainbow Lake field site.

We binned wolverine step lengths into short and long distance movements (Table 1). During the evenings in both summer and winter, wolverines tend to have shorter step lengths that indicate resting or foraging. During the day, wolverines have an equal percentage of short and long-distance movements (Table 1).

Wolverine step lengths based on sex, season, and time of day are displayed in Table 2. We use the descriptive statistic median because step length data were positively skewed and had outliers. Included with medians are the 25th and 75th quartiles. Movement rates are representative of the distance traveled in a two-hour period. Male and female wolverines have greater movement rates in the summer than winter. Both sexes have greater movement rates during the day rather than night. Finally, male movement rates are greater than female movement rates (Table 2).

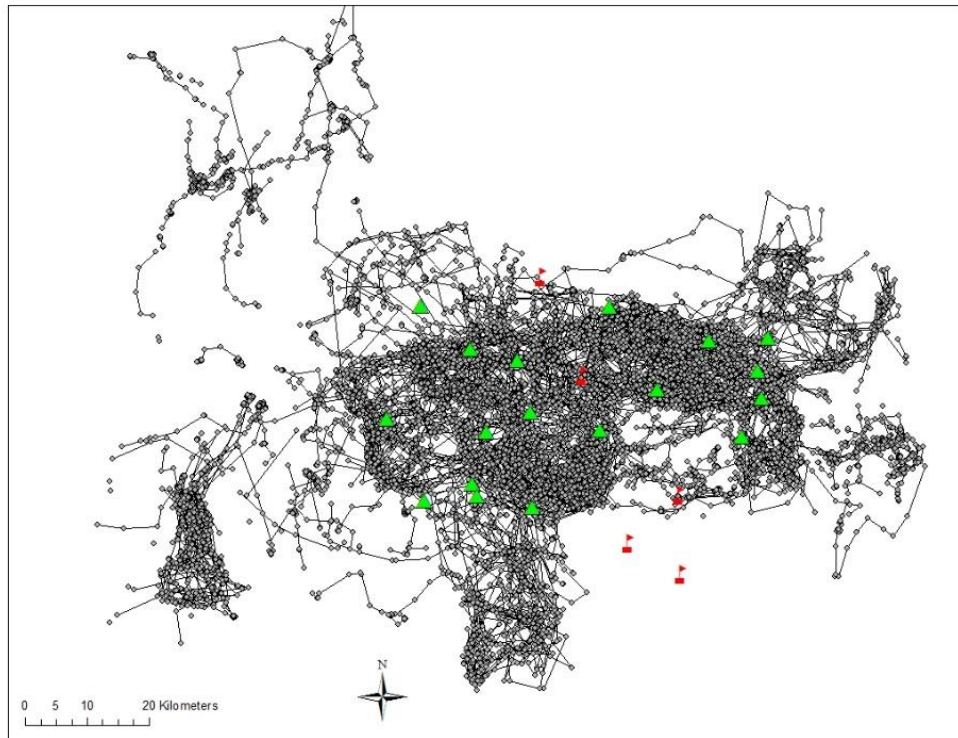


Figure 4. Wolverine ($n = 22$) GPS data and associated step lengths ($n = 17,086$) in the Rainbow Lake field site. Data were collected starting in November 2013 and are current through July 18, 2015. Green triangles represent live-traps and red flags represent run-poles.

Table 1. Wolverine step lengths binned into short and long distance categories.

Criteria	N step lengths, steps \geq 500 m	N step lengths, steps < 500 m	Total steps
Summer	3,155 (48%)	3,425 (52%)	6,580
Winter	4,638 (43%)	5,821 (57%)	10,189
Night summer	1,261 (42%)	1,741 (58%)	3,002
Day Summer	1,894 (52%)	1,684 (48%)	3,578
Night winter	2,079 (39%)	3,193 (61%)	5,272
Day winter	2,559 (49%)	2,628 (51%)	5,187

*Day is from 8:00 – 18:00; summer is from May 1 – October 31

Table 2. Wolverine step lengths based on season, sex, and time of day in Rainbow Lake, Alberta. We present step lengths as medians with the 25th and 75th quartile.

	Male (m)	N	Female (m)	N
Summer	462 (61, 2153)	4,004	406 (46, 1605)	2,576
Winter	189 (25, 2028)	6,423	131 (19, 1374)	4,036
Night summer	278 (45, 1624)	2,576	270 (30, 1445)	1,305
Day summer	633 (83, 2494)	2,307	557 (66, 1763)	1,271
Night winter	122 (19, 1434)	3,163	79 (14, 895)	2,109
Day winter	294 (34, 2668)	3,260	260 (29, 1892)	1,927

Wolverines, roads, and industrial development

This section explores the response of wolverines to industrial infrastructure and activities within the Rainbow Lake field site. Roads (high-grade, winter, paved) are one of the most ubiquitous industrial features in Rainbow Lake and are the focus of these summaries. The median density of roads at wolverine GPS locations in Rainbow Lake ($n = 27,518$) was 0.52 km/km^2 (0.00, 0.94), with a max used road density of 3.27 km/km^2 . Median road density at male GPS locations was 0.40 km/km^2 (0.00, 0.86) and median road density at female GPS locations was 0.64 km/km^2 (0.12, 1.00). The average road density within the 100% MCP of wolverines ($n = 20$) was 1.69 km/km^2 (SD = 0.559). We found a positive

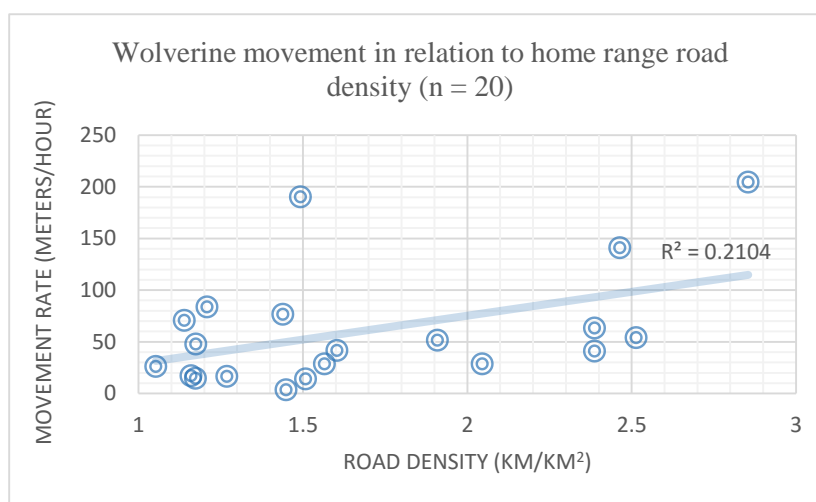


Figure 5. The relationship between wolverine step lengths and road density within the wolverine's 100% MCP. Movement rates are inclusive of movements in both summer and winter and were scaled to one hour. Animals include both resident and sub-adult wolverines.

We found a positive

correlation between the step length of adult and sub-adult wolverines and road density within their home range ($r(20) = 0.21$, $p = 0.04$) (Figure 5). This relationship was more significant when only resident wolverines were included ($r(15) = 0.49$, $p = 0.003$) (Figure 6).

Wolverines regularly crossed both high-grade gravel roads and paved highways within our Rainbow Lake study site. We documented 1,556 crossings of high-grade industrial roads. Median step length across high-grade roads was 4.38 km (2.76, 6.64) and 63% of high-grade road crossings occurred during the day. Wolverine crossings of Highway 58 (paved) 306 times. Median step length across Highway 58 was 6.16 km (3.81, 9.07) and 68% of crossings occurred during the day.

Because of timber harvest, there was a surge in human use of the Rainbow Lake field site in the second winter field season (2014/2015). This presented the opportunity to investigate wolverine movement

before and during timber harvest. There is no planned timber harvest occurring in Rainbow Lake in the winter of 2015/2016. The local timber company (Tolko) provided us with polygons of their harvest units, as well as the start and end dates of harvest operations. Additionally, Tolko provided data on the frequency and timing of logging trucks leaving each compartment. For this exercise, we divided the landscape into 3 different units, with each unit encompassing cutblocks that shared general timber harvest start and end dates. Start dates ranged from November 30 – December 30, 2014 and end dates ranged from March 11 – March 20, 2015. Each unit was a 100% MCP of all cutblocks within that unit. We buffered each unit by 5 km (approximate 95th percentile wolverine movement distance) and identified GPS data points within these buffered units that coincided temporally with dates before and during harvest.

We found a 9% decrease in step lengths < 500 m during timber harvest activities (Table 3). We have evidence of a significant increase in the median step length of male wolverines during the day ($t(1,766) = 4.91$, $p < 0.001$, t-test assuming unequal variances) and night ($t(1,502) = 2.88$, $p = 0.002$) during timber harvest (Table 4). Females also had a significant increase in step length during timber harvest in both day ($t(1,043) = 1.56$, $p = 0.06$) and night ($t(836) = 3.34$, $p < 0.001$). Overall, we see a larger effect on male wolverines than female wolverines as a result of timber harvest activities (Table 4).

We investigated the distribution of wolverine locations before and during timber harvest activities relative to cutblocks and industrial infrastructure (Table 5). We found that wolverines were significantly further from cutblocks during timber harvest activities when compared with before ($t(1,161) = 3.82$, $p < 0.001$, t-test assuming unequal variances). Wolverine locations did not significantly change their proximity to high-grade roads during timber harvest. We have evidence of wolverine using areas of lower road density during timber harvest but this result was insignificant (p -value > 0.1) (Table 5).

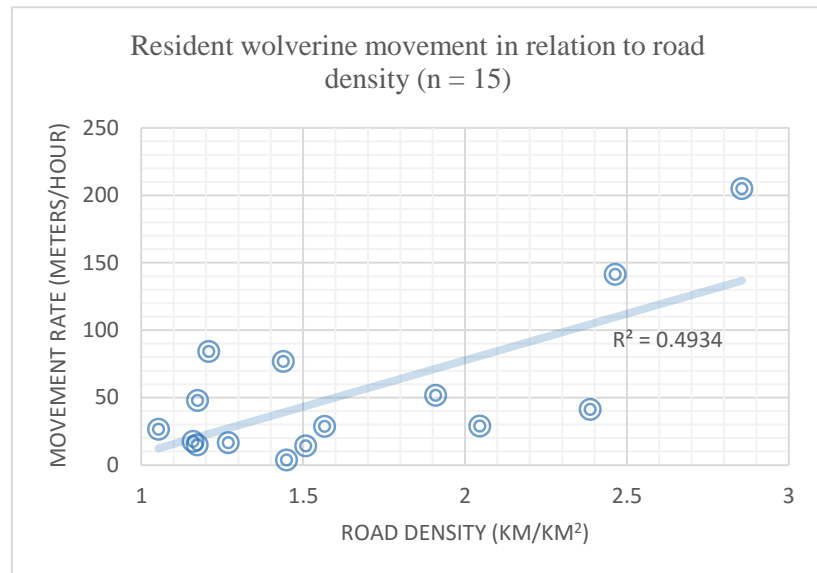


Figure 5. The relationship between wolverine step lengths and road density within the wolverine's 100% MCP. Movement rates are inclusive of movements in both summer and winter and were scaled to one hour. Animals include only resident wolverines.

Table 3. Short and long wolverine step lengths before and during timber harvest activities.

Criteria	Before	%	During	%
N step lengths < 500 m	2,274	69	1,661	60
N step lengths ≥ 500 m	1,023	31	1,112	40

Table 4. Wolverine step lengths before and during timber harvest activities.

	Day (male)*	Night (male)*	Day (female)*	Night (female)*
Before (n)	749	714	478	935
Median (m)	44.34	18.50	50.51	24.06
25 th	3.82	1.52	4.40	3.72
75 th	595.42	412.78	910.17	222.94
During (n)	1,036	792	900	466
Median (m)	158.59	51.39	58.78	38.85
25 th	14.88	0.00	7.80	5.30
75 th	1655.86	905.27	846.33	608.04

*indicates a significant t-test result ($p \leq 0.05$)

Table 5. Wolverine distribution before and during timber harvest. Values displayed are medians and quartiles.

N = 4,060	Before
Distance to cutblock (km)*	0.84 (0.38, 1.55)
Road density (km/km ²)	0.38 (0.00, 0.81)
Distance to high-grade (km)	2.90 (1.59, 6.99)
n = 3,436	During
Distance to cutblock (km)*	0.96 (0.52, 1.62)
Road density (km/km ²)	0.33 (0.00, 0.80)
Distance to high-grade (km)	2.91 (1.45, 8.16)

*indicates a significant t-test result ($p\text{-value} \leq 0.05$)

Foraging and natal dens

Our goal in this section was to summarize our wolverine cluster data and present field observations of wolverine caching behaviour. We have visited 118 GPS clusters over the course of 2-winter field seasons. The most frequent occurrence at GPS radiotelemetry clusters were beds (Table 6). We often found beds at sites where wolverines were scavenging or had made a kill. On numerous occasions, however, we did find beds without any identifiable prey items nearby ($n = 52$). Beds were generally small clusters of 2-3 GPS points and were often under thick spruce or fallen trees. For example,

one wolverine frequented a den that was protected underneath down alder and willow. Another wolverine denned under aspen trees felled by a beaver.

We found fairly equal evidence of wolverine predation and scavenging events at GPS radiotelemetry clusters (Table 6). Predation events were primarily of beaver, snowshoe hare, and grouse. Scavenging events were wolf and hunter killed ungulates such as moose or caribou. At beaver predation sites ($n = 8$), the wolverine accesses the lodge through digging out the vent or ambushes the beaver when it is on-land felling trees and eating bark. We documented 7 clusters associated with predation events on snowshoe hare, with multiple hare carcasses found at these clusters. Overall, clusters with identifiable prey remains indicated that moose, beaver, and snowshoe hare were important prey items for wolverine in winter, although ungulate (e.g., moose, unknown) was the most prevalent (Figure 7). There were 53 clusters we visited that had no obvious evidence of prey items (e.g., beds, dens). At these locations, scats were again predominantly comprised of beaver, moose, and snowshoe hare, although beaver and snowshoe hare were most prevalent (Figure 9).

We documented 30 caching events at GPS radiotelemetry clusters. The characteristics of cache sites varied greatly. We documented 11 caches in wetland type areas, with three on the upland edge of a pond and 8 in the cattails and willow. We documented 5 caches in bogs and 4 caches in structures created by the beaver, with 2 in a lodge, 1 in a dam, and 1 under felled aspen trees.

Of the 16 females we have captured in live-traps, we have documented 11 lactating. We found 4 wolverine dens in 4 different types of structures, including, a spruce tree root wad, a timber slash pile, a beaver lodge, and a system of fallen black spruce trees within a bog. Three out of the four females moved their kits after we discovered their dens. We believe both our activities and wet conditions within dens from snowmelt drove den abandonment.

Wolverine denning appears to commence in late-February and early-March. Our radiocollars are unsuccessful in acquiring satellites for GPS fixes when females are within dens and therefore the daily ratio of successful to unsuccessful fixes offers a rough estimate of the initiation of denning. F7 denned within a slash pile and her GPS data indicated she had her kits March 7, 2015. F4 denned in a beaver lodge and her GPS data indicated she had her kits on approximately February 26, 2015. We believe F3 had her kits on February 23, 2015 but we were unable to verify a reproductive den. Similarly, the female we caught in the Birch Mountains was lactating and likely had her kits on March 10, 2015 but we were unable to verify a natal den.

Overall, we have only been able to verify the successful rearing of a single offspring. F8 had two kits at her den in March 2014 but we only observed a single kit with F8 at the live-traps over the summer of 2014. We believe that M16 is her surviving offspring (captured in March 2015) because they are often found together at live-traps and because M16's GPS data is exclusively within F8's home range. We believe that M6 is the father of M16, although this will need to be verified with DNA data.



A beaver lodge dug out by wolverines in Rainbow Lake.

Table 6. Activities at wolverine GPS radiotelemetry clusters

Site type	Sample size	% occurrence
bed	52	37
den	6	4
natal den	4	3
cache	30	22
predation	25	18
scavenge	22	16

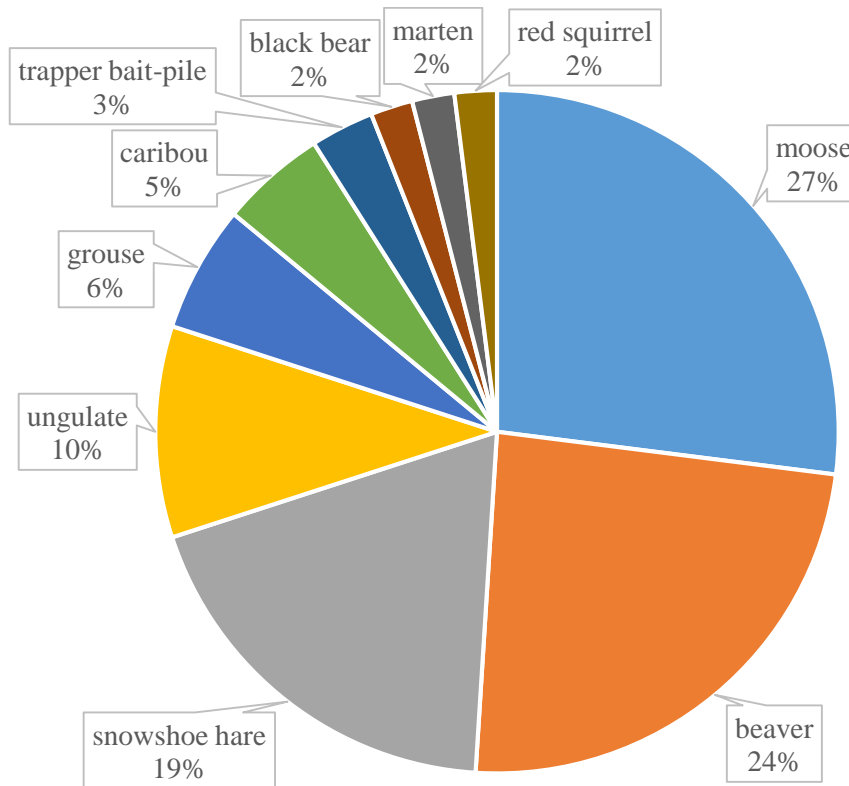


Figure 7. The occurrence of confirmed prey at wolverine GPS radiotelemetry clusters (n = 62)

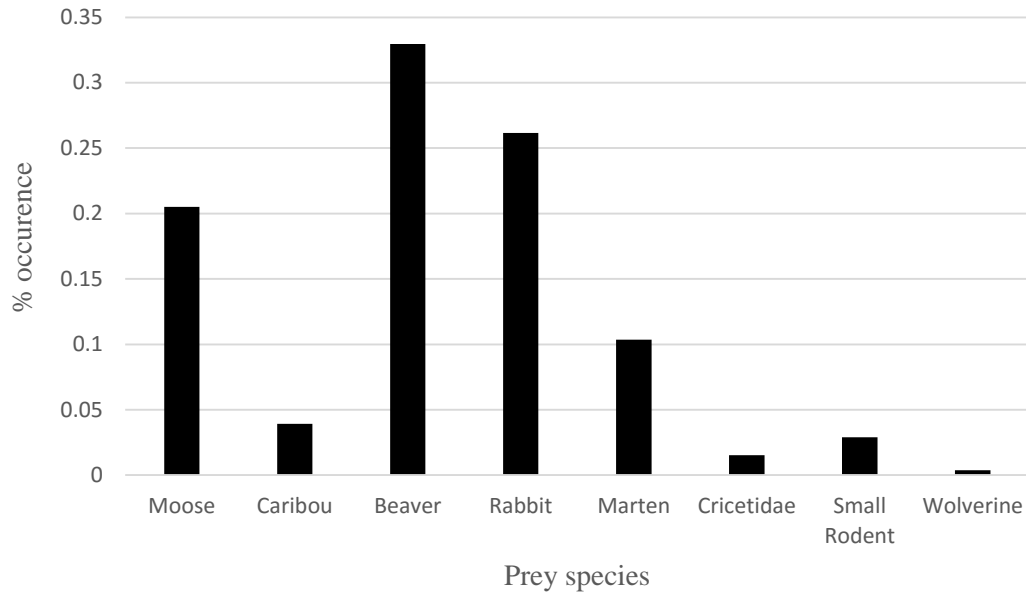


Figure 8. Percent occurrence of hair within scats collected at GPS clusters without identifiable prey remains nearby ($n = 69$ scats at 52 GPS clusters).

GPS clusters and habitat selection

Using the cluster algorithm created for investigating cougar kill sites by Knopff et al. (2008), we designated wolverine GPS clusters, or concentrations of GPS points that are related both spatially and temporally, for 22 wolverines. Of the 28,898 GPS data points we collected for wolverines at two-hour fix in Rainbow Lake, 20,830 points were associated with a GPS cluster. From these points, the algorithm



A beaver lodge used by wolverine F04 for denning. Photo captured in March 2015.

identified 4,890 GPS clusters, with 2,316 clusters initiated during the day (starting time of GPS cluster) and 2,574 initiated during the evening. The median amount of time a wolverine was at a cluster was 5 hours, and the number of days a wolverine spent at a cluster ranged from 1-9.

As an exploratory exercise, we used cluster data within a resource selection function (RSF) that compared habitat at wolverine GPS clusters to random locations. We used conditional mixed effects logistics regression with individual animal ($n = 22$) as the random effect. Each cluster (designated “1” in the RSF) was paired with 10 random locations (designated “0” in the RSF) within a 5 km (95th percentile movement distance of a wolverine) circle of the cluster location. We modeled 6 variables we felt would best explain where wolverines find food

in the boreal (Table 8). As this is an exploratory exercise, we simply evaluate the relative strength of each variable from the full model based on p and z -values. Wolverine GPS clusters in the summer were more likely to be found in bogs, wetlands, and coniferous forests, but not in broadleaf forests. In the winter, wolverine GPS clusters were more likely found in coniferous forests and near to open water.

Table 8. Wolverine GPS cluster locations (designated as “1” in the RSF) relative to random locations (“0”). Each cluster was paired with 10 random locations within a 5 km buffer of the cluster.

Summer clusters (n = 2,148)				
Variable	β	SE	Z-value	P-value
Distance to open water	-0.000	0.000	-0.67	0.503
Bog	0.353	0.077	4.58	0.000
Wetland (marsh, fen, swamp)	0.111	0.066	1.68	0.092
Distance to streams	-0.000	0.000	-1.60	0.110
Coniferous forest	0.382	0.057	6.69	0.000
Broadleaf forest	-0.314	0.072	-4.34	0.000
Winter clusters (n = 2,463)				
Variable	β	SE	Z-value	P-value
Distance to open water	-0.000	0.000	-2.10	0.036
Bog	-0.041	0.081	-0.50	0.614
Wetland (marsh, fen, swamp)	0.066	0.055	1.20	0.229
Distance to streams	-0.000	0.000	-0.63	0.530
Coniferous forest	0.211	0.053	3.97	0.000
Broadleaf forest	0.034	0.057	0.60	0.548

DISCUSSION

We have completed two winter field seasons radiocollaring and tracking wolverines in northern Alberta. The winter of 2015/2016 will be our final field season in the Birch Mountains and Rainbow Lake. We have had an unexpected level of success live-trapping ($n = 33$) and documenting ($n = 44$) individual wolverines in Rainbow Lake. Although we have only captured a single wolverine in the Birch Mountains, based on activity in the region, we are confident that our sample will increase after this final winter. These data will be critical for comparing wolverine ecology along a gradient of industrial activity represented at both field sites.

Wolverines and industrial development

The fact that a large wolverine population exists within Rainbow Lake was a bit of a surprise to us based on prior research about the effects of human developments on wolverine occurrence (e.g., May et al. 2006, Fisher et al. 2013). Roads are the most ubiquitous human created feature on the Rainbow lake landscape and are positively correlated with the occurrence of wells and other industrial infrastructure. Therefore, much of our analyses focused on the effects that roads have on wolverines. Wolverines in Rainbow Lake were using habitats with a median road density of 0.52 km/km^2 (0.00, 0.94) ($n = 22$ wolverines). The average density of roads within their home range was 1.69 km/km^2 ($SD = 0.559$). For comparison, the best known average density of roads within wolverine home ranges in the lowland boreal forest of Ontario was 0.43 km/km^2 ($n = 7$ wolverines, Dawson et al. 2010). For alpine wolverines, Carroll et al. (2001) reported that the probability of wolverine occurrence drops considerably above a road density of 1.5 km/km^2 and Lofroth and Krebs (2007) reported that wolverine density was only negatively affected above a 2.0 km/km^2 threshold. We had 10 wolverines with a home range road density greater than 1.5 km/km^2 and 5 wolverines with home range road density greater than 2.0 km/km^2 . These data provide evidence that wolverines can occur at much greater road densities than previously thought.

Industrial roads appear to increase wolverine movement rates. Median wolverine step length when crossing high-grade and paved roads are 10-15x greater than the overall median wolverine step length from the Rainbow Lake study area. Additionally, we found a positive relationship between the density of roads in a wolverine's home range and their movement rates. Two different explanations can be made from these data: 1) wolverine movement rates increase near roads because wolverines are disturbed; and 2) wolverines are using roads as movement corridors. We would suggest that an adequate explanation incorporates both ideas. Whether a wolverine uses a road as a movement corridor is likely reliant on the level of human use. The majority of wolverine road crossings occur during the day when human use of the Rainbow Lake landscape is greatest. We believe that wolverines running along high-traffic high-grade roads and paved roads during the day is highly unlikely, especially for multiple kilometers, as the probability of encountering a vehicle is extremely high. This gives support to the idea of roads displacing wolverines. However, wolves have been shown to move along roads in areas of low road density (James and Smith 2000, Whittington et al. 2005). Grizzly bears use roads more during the evenings when human use is low (Roever et al. 2010). Wolverines in Rainbow Lake might have these same patterns, such that they use roads as movement corridors in areas of low road density or during the evening when human use of the landscape is at a minimum. Fine-scale movement data (e.g., 10 minutes fix rates) from Rainbow Lake might allow us to better disentangle this question.

The tendency for wolverines to cross roads during the day when human use is highest increases the risk of mortality from vehicle collisions. In the Zama City region of northern Alberta (Fort and High Level Districts), 9 different wolverines were killed by industrial vehicles over the winters of 2013 and 2014 (September to April). We do not believe that any wolverines in our study area were hit by vehicles even though there was increased vehicle traffic in 2014/2015 because of timber harvest activities. We did have a wolverine killed by wolves and a female wolverine was shot by game wardens for being a nuisance in the town of Rainbow Lake. Anecdotally, wolverines appear to regularly be nuisances within industrial camps and towns in northern Alberta. This also has been reported in the Northwest Territories (Johnson et al. 2005). Management of attractants and highway speeds are ways to reduce wolverine mortality in industrial landscapes.

We present evidence that wolverines are impacted by timber harvest activities. Wolverines decreased short movements associated with feeding or resting, increased movement, and used areas further from cutblocks when these metrics were compared before and during timber harvest. The effect size for male wolverines was greater than for females, which may indicate that males travel more and are more prone to regularly detect disturbances and be displaced. Other researcher have found that wolverines avoid clearcuts and have speculated this is to avoid predation risk (Hornocker and Hash 1982). Selection against areas of timber harvest was greatest for female wolverines in British Columbia (Krebs et al. 2007). Our current results are likely related to direct displacement from human activity. It might follow that moose, deer, and wolves increase their use of recently logged areas in Rainbow Lake in the years to come because of increased food abundance (as suggested by Bowman et al. 2010). In this situation, it is likely that wolverines would select against these recently logged areas to avoid predation risk (as suggested by Krebs et al. 2007).

Overall, we present mixed evidence on the effects of industrial disturbance on wolverine ecology. Timber harvest and areas of high-road density appear to displace wolverines. A loss of habitat and increased energetic expenditure because of industrial activity can offset the optimal foraging balance (Pyke et al. 1977) and have important ramifications on wolverine fitness. For example, timber harvest occurs when females are provisioning to fuel lactation. An increase in energy use or a reduction in available habitat during this time might impact a female's ability to reproduce successfully (Persson 2005). However, we also suspect that industrial roads with low human use offer wolverines travel corridors that they can utilize to efficiently move across the landscape while foraging. These low-cost movements could positively impact a wolverine's energy balance. The robust population of wolverines in Rainbow Lake would suggest that industrial development, such as that found in Rainbow Lake, has fairly minimal effects on wolverine populations.

Wolverine foraging and habitat selection

Our use of Iridium GPS radiocollars, combined with excellent access into wolverine habitats because of industrial roads, has allowed us to visit wolverine GPS clusters soon after they are created. These data are important for understanding wolverine diet and habitat selection patterns. Many of the smaller clusters we visit are wolverine beds with no discernable evidence of prey nearby. These beds are excellent sources of wolverine scat that are not heavily biased by nearby carcasses. At these clusters, and in declining magnitude, we found beaver, snowshoe hare, and moose. Smaller clusters are also where we find evidence of wolverine predation events on smaller prey or where we find wolverine caches. Larger clusters are generally beaver kills or wolf killed moose.

The general consensus in the literature is that wolverines are scavengers of large ungulate carcasses during winter (Banci 1981, Magoun 1987, Koskela et al. 2013, Inman and Packilia 2015). However, winter wolverine diets in British Columbia were comprised of an equal proportion of smaller prey, such as porcupine and marmot, and moose, caribou, and mountain goat carrion (Lofroth et al. 2007). We found a similar pattern, with the occurrence of beaver, snowshoe hare, and moose (or unknown ungulate) to be in fairly equal proportion in the wolverine's diet. These data give credence to wolverines as efficient hunters in winter. Interestingly, the importance of snowshoe hare in the wolverine's diet gives support to the idea that wolverine populations might cycle with snowshoe hare (Bulmer 1975).

We lack field observations of summer wolverine foraging but we suspect that beaver are an important component from our RSF analysis. This relationship seems logical considering that: 1) beavers are more susceptible to wolverines in the summer than winter because they are out of their lodges foraging (Baker et al. 2005); and 2) if wolves prey switch to beaver in the summer from moose in the winter (Latham et al. 2013), the availability of carcasses for wolverines is likely reduced, forcing them to seek other foods. The reduced ability of beaver habitat to explain cluster distribution in the winter relative to the summer is likely related to an increase in the breadth of the wolverine's diet in winter.

There was strong selection for bogs by wolverines in summer. Bogs are often in close proximity to other wetlands (fens, swamps, marshes, open water) and so some beaver predation events might take place in bogs. We also suspect that wolverines are caching beaver in bogs in the summer for use in the winter. We have found numerous dug out beaver caches in bogs in winter that the wolverine likely created the prior fall or summer. The high acidity (Vitt et al. 1994) and insulation provided by bogs likely preserves much of these meats for later use, similar to the role that scree fields and snow plays in wolverine caching in alpine environments (Inman et al. 2012). In addition, the wolverine's use of bogs might be tied to hunting for rodents such as shrews and voles (Larsen 1982). Summer foraging observations are important for understanding these habitat associations.

The lowland boreal wolverine's niche appears to be bogs, wetlands, and coniferous forests. This is apparent both from our cluster analysis and from many other RSFs not reported here. Selection for these low-productivity boreal habitats is analogous to the alpine wolverine's selection of high-elevation tundra and treeline areas (Inman et al. 2012). The top predator that most often shares boreal wolverine habitats, the wolf, often follows ungulate species that select upland habitats such as broadleaf forests (James et al. 2004, Bowman et al. 2010, Koskela et al. 2013). This spatial separation likely reduces interactions between the two species and, therefore, increases wolverine survival.

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