

Human footprint, habitat, wolves and boreal caribou population growth rates



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Abstract

Apparent competition has been shown to play a key role in population declines of woodland caribou. The mechanism is based on the process of increased human footprint leading to increased moose and deer numbers, greater predator populations and subsequently higher predation rates on caribou. Yet, apparent competition among moose, deer and caribou is undoubtedly influenced by other factors such as climate change, fire, weather patterns, and may vary with natural landscape attributes (e.g., land cover type) that also affect ungulate abundance and distribution. To explicitly evaluate how spatial factors influence apparent competition, we initiated a project to examine how population growth rates of caribou relate to landscape attributes (e.g., degree of human disturbance; proportion of uplands versus wetlands), ungulate abundance, and wolf abundance. To accomplish this, we surveyed 6 large areas (4000-5000 km²) to estimate wolf density in landscapes that varied from almost no human footprint in the Northwest Territories (NWT), to intensive footprint in Alberta and British Columbia (BC). Pre-existing sources of information about the sampling areas included knowledge of moose density, caribou population growth rates (λ), and GIS mapping layers representing human footprint and land-cover type. Wolf densities ranged from 1.6/1000 km² in NWT to 15.6/1000 km² in northeast BC. With only 6 data points, results are necessarily preliminary, but we found an inverse relationship between wolf density and caribou λ . We also found that human footprint positively affected wolf density and negatively affected caribou λ . Land cover type (wetlands) negatively affected caribou λ . Even though data are very limited, our sampling design captured high variation in wolf densities, human footprint and land cover, which will facilitate future analyses once additional data are collected. By directly relating spatial factors to population parameters (e.g., growth rates and abundances), our approach provides an explicit assessment of the apparent competition hypothesis, the prevailing paradigm for explaining widespread declines of woodland caribou.

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Introduction

Apparent competition (Holt 1977) is considered to be the key mechanism explaining the decline of boreal caribou. In this case, the process of apparent competition involves increased abundance of moose and deer, causing numerical increase in predator populations, and the decline of caribou because they are less fecund and perhaps more vulnerable to predation compared to other ungulates. It is commonly reported that increased moose and deer abundance is directly caused by human disturbance to their habitat (hereafter 'human footprint') thereby linking human footprint to caribou decline (Schwartz and Franzmann 1991, Rempel et al. 1997, Serrouya et al. 2011). Yet the apparent competition between these ungulates and caribou is undoubtedly influenced by other non-disturbance factors such as climate change, weather patterns, or natural habitat attributes that also affect moose and deer abundance across the landscape.

To disentangle the degree to which human footprint contributes to caribou decline, several conditions must be achieved: 1) a study must include sufficient variability in human footprint and habitat conditions; 2) a reliable method is required to track the abundance (either relative or absolute) of wolves and their prey; and 3) Identifying the independent effects of footprint and habitat requires controlling for the possible confounding factors, either experimentally or statistically. The first condition is increasingly challenged by the advancing human footprint, but near-pristine conditions still exist in some parts of Saskatchewan and southern NWT.

Several approaches have been attempted to enumerate wolves in forested ecosystems, including intensive radio-collaring efforts followed by flights to count numbers within each pack (Latham et al. 2011), detecting tracks in defined survey units (Patterson et al. 2004), and complete censuses (van Oort and Bird 2011, Serrouya 2013). The radio-collaring approach has been successfully used in boreal forests, but is very expensive due to the need to radio-collar each pack and it usually takes several years to acquire the sample needed to obtain an estimate. In contrast, censuses where all habitats are covered may not be possible in the boreal forest where study areas are usually too large to cover in detail.

For this project, we had two primary objectives. The first was to pilot a cost-effective and accurate method to count wolves in the boreal forest. This methodological objective consists of three components: conducting a simulation analysis to guide survey intensity, applying the result of the power analysis with surveys in the field, and conducting a post-hoc assessment on the accuracy of the method. The second objective, which is more ecologically driven, is to address the relative influence of human footprint, climate, and natural habitat composition on the abundance of moose, wolves, and caribou. In this report we address both objectives, while recognizing that data are restricted to 6 survey areas across two winters (2015 and 2016).

Methods

Objective 1: Wolf Surveys

Study design and selection of Wolf Survey Units (WSU)

To ultimately evaluate the potential links between landscape attributes and populations of predator and prey, we delineated wolf survey units (WSUs) to maximize variation in the influence of habitat disturbance and encompass areas where recent estimates of caribou λ and moose density were available. As a consequence, WSUs were irregular in shape, but we attempted to minimize edge:area ratios when defining WSU boundaries. We defined relatively large WSU areas of approximately 4000 to 5000 km² to increase the probability of encountering and enumerating multiple resident packs in low density settings, and to minimize edge effects. During

the winters of 2014/15 and 2015/16, we delineated and surveyed the following six WSUs (Figure 1).

Hay River Lowlands (HRL). The HRL was the most northern WSU surveyed (60.8 °N), located west of Tathlina Lake in the NWT. The site (5571 km²) was largely comprised of wetlands (66 %) and upland coniferous forests (23 %), with minimal disturbance from human footprint (0.07 %; see *GIS – Human Footprint* below for a description of how disturbance was estimated). These disturbances were primarily old linear features (seismic) generally in advanced stages of natural regeneration. A small community (population < 50) at Kakisa Lake was noted on the eastern side of the WSU. Snowmobile activity was minimal to non-existent in this site during surveys. Evidence of recent forest fires were noted. HRL was surveyed from a base at Fort Providence. Fuel was transported from Hay River to the Fort Providence airstrip.

Fort Liard (FL). Located immediately east of Fort Liard and the Liard River in the NWT (population < 600), FL (4382 km²) is a northern WSU (60.4 °N) primarily comprised of coniferous upland forest (64 %) formed by a ridge running north up the center of the WSU. Wetlands (7 %) exist on the eastern part of the WSU. Human footprint was relatively low (0.6 %) although cabins and snowmobile activity were noted in the southern part of the site near the Muskeg River and near some of the southern lakes. FL was surveyed from a base at Fort Nelson, BC, with a cash of drummed fuel at the Fort Liard airstrip.

Calendar (CAL). Located in the northeastern corner of BC, CAL (59.8 °N) is a moderately disturbed WSU (1.3 %) comprised of coniferous forest (64 %) and wetlands (18 %), but during the survey much of the forest was observed to be black spruce and the wetland component may be higher. The roughly triangular site (4974 km²) was defined by the NWT border to the north, the Alberta border to the east, and the Petitot River to the southwest. Recent forest fire history was evident over large parts of CAL, especially in the northern part of CAL. The habitat disturbance was primarily caused by seismic cut lines throughout the WSU, but pipeline right of ways (ROW) were not uncommon, in addition to some unploughed and ploughed service roads. Pipelines and roads were more prevalent in the southern part of CAL. Outside of the oil and gas activity, human activity was not noted to be high. There were few cabins or snow-mobile routes noted. CAL was surveyed out of Fort Nelson, with a fuel cache positioned at the Helmut airstrip not far to the south of CAL.

Clarke (CLK). The moderately disturbed CLK (58.5 °N), was located immediately southeast of Fort Nelson, where oil and gas industrial activity has created many seismic cut lines, pipeline right of ways (ROW), and roads (disturbed habitat = 2.7 %). The 5161 km² site encompassed part of the Fort Nelson River along its southwestern edge and the Fontas River along its southern edge. The WSU extended north of these rivers to the approximate latitude of Fort Nelson, and was comprised largely of upland coniferous or broadleaf forests (60 %) and wetlands (25 %). Outside of oil and gas activity (seismic lines, roads, pipelines and some production plants), this WSU encompasses Highway 97 and Fort Nelson (population < 4000), situated near the northwest corner of CLK. Snowmobile activity was observed at this WSU. CLK was surveyed out of Fort Nelson.

Chinchaga (CHIN). Immediately south, and overlapping slightly with CLK is the CHIN WSU (58.0 °N). With the Sikanni Chief River along its western boundary, and the Fontas River within its northern boundary, this WSU was defined by the Chinchaga RRA (Resource Review Area), a region where oil and gas tenuring has been suspended. Like CLK, CHIN (3414 km²) was dominantly comprised of upland conifer and broadleaf forest (51 %), but had a higher component of wetlands (43 %). Recent forest fires were also evident in parts of CHIN. Human disturbance (1.7 %) was typified by oil and gas impacts (seismic lines, pipeline ROW, and roads) in addition

to some logging. Snow-mobile activity was relatively rare within CHIN. CHIN was surveyed out of Fort Nelson.

Cold Lake (CL). CL (55.7 °N) was a relatively large (7271 km²) square-shaped site located immediately north of the Cold Lake Air Weapons Range in northern Alberta. This WSU was the most southerly and easterly surveyed to date and contained the greatest level of human disturbance (7.5 %), including on-going human activity observed during the survey. Coniferous forest covered 41 % of the WSU, the remaining parts being largely comprised of wetland (24%) and broadleaf forest (16 %). CL was surveyed out of the Primrose Airstrip and a nearby camp.

Parker (PK). PK was a small WSU (752 km²) near Fort Nelson that we surveyed in 2015. Data from this WSU were not considered for analysis as the WSU was too small for estimating wolf density. One wolf pack consisting of 6 wolves was estimated during this survey (Serrouya et al. 2015a).

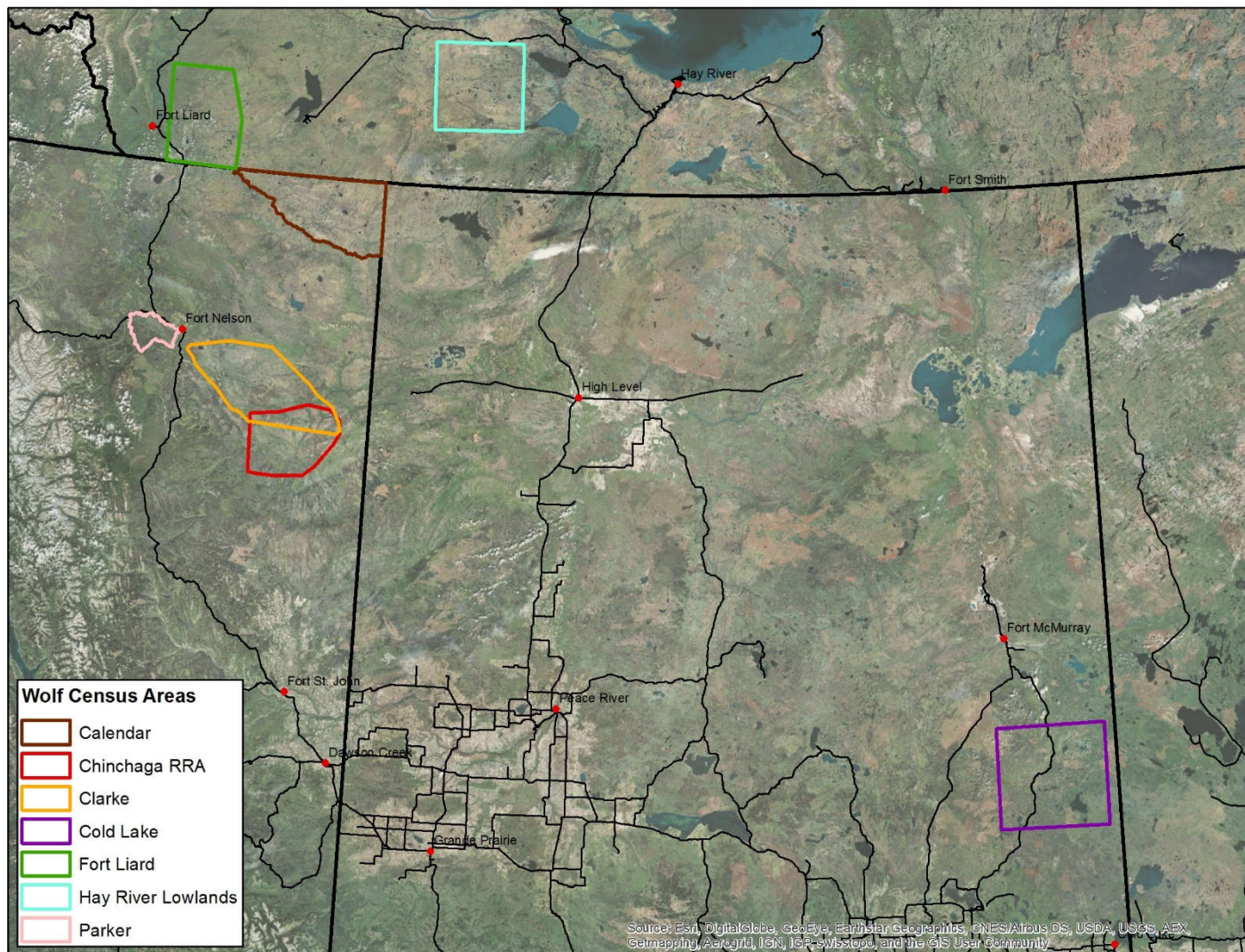


Figure 1. Map showing the six WSUs that were surveyed in two winters (2014/2015 and 2015/2016).

Field surveys: wolf census counts

We estimated wolf density by conducting complete aerial census counts within each WSU. These counts were performed by flying transects in winter when wolf packs can be detected by tracks in the snow. Aerial transects constituted the search phase of the surveys. Once wolf tracks were encountered, these track networks were surveyed in order to achieve pack size and location data. We designed these surveys carefully in order to maximize wolf track encounters, maximize wolf track detection, and to minimize counting errors. These three considerations are detailed below.

1. **Maximizing wolf track encounters.** Encounter rates increase with the time since previous snowfall and with survey intensity. In order to minimize track confusion (see below), we relied on the latter to maximize encounter rates; that is, we opted to increase search effort, and minimize time since previous snowfall. In a previous report, we described a simulation-based sensitivity analysis conducted on wolf collar GPS data, which we performed to optimize the spacing of aerial transects used to encounter wolf tracks shortly after a snow storm, when there are relatively few tracks on the landscape (3-km spacing; see Serrouya et al. 2015a). After field experience, we were satisfied with 3-km transect spacing, finding it to be a practical search-effort intensity that commonly provided multiple opportunities to encounter tracks from individual packs. For this report we repeated the simulation with higher-resolution wolf collar data to achieve a more realistic assessment of the efficacy of 3 km transect spacing (see *Validation* below).
2. **Maximizing wolf track detection.** Detection rates were maximized in our choice of transect flight paths (see below). Detection was also maximized by surveying under ideal snow tracking conditions, which generally occur when there is a deep (> 40 cm) snowpack covering 100% of the study site, when recent snow storms have deposited soft surface snow to maximize track visibility, when there have been minimal wind effects to erase fresh tracks, and when lighting conditions were bright, or lightly filtered. These conditions were met in most cases (see *Results*).
3. **Minimizing track confusion.** The primary step taken to minimize track confusion was to conduct surveys as soon as possible following a snow storm event, when there were relatively few fresh tracks that were clearly distinguishable from old tracks and tracks from other species. We noted old wolf tracks during surveys as they alert us to wolves in the area, but these observations did not interrupt our search flights, and did not contribute to wolf density estimates. By attempting surveys shortly after storms, we were able to avoid the following tracking issues: (1) tracks from multiple packs merging (i.e., keeping pack tracks isolated); (2) tracks from single packs superficially appearing as tracks from more than one pack (e.g., when a single track linking two distant areas of activity is missed in the timber); and (3) tracks obliterated by tracks from other species (e.g., caribou).

Aerial surveys were conducted with a Bellanca Scout and/or a Cessna L-19 Super Mountaineer Bird Dog. The pilots and the biologists were highly experienced with conducting aerial wolf surveys. The crew navigated via GPS enabled devices (e.g., iPad) containing digital georeferenced survey maps delineating survey grids (3 km cell size). We treated the 3-km grid lines as the dividing lines between parallel 3-km wide corridors, which we surveyed via meandering flight lines (Figure 2). The flight paths included occasional looping to re-examine tracks, and considerable meandering to survey over habitat that was optimal for maximizing detections (e.g., by flying over open areas such as frozen lakes, roads, seismic lines, wetlands, etc., and avoiding heavily timbered areas). Tracklogs and coordinates of wolf sign were recorded using hand-held GPS units (Garmin Map76csx). In all surveys, we advanced across the WSU progressively (e.g., from east to west, or north to south etc.) so that wolves previously counted

were unlikely to be counted twice as a result of movements from surveyed regions into regions of the WSU not yet surveyed. Additionally, we counted and recorded coordinates for all observations of moose, caribou, and evidence of wolf kills.

We estimated wolf pack sizes and attempted to quantify the degree of certainty associated with each estimate. A minimum wolf pack size was an objective count derived from tracking evidence such as clear splitting of tracks, from tracking the animals on a shallow snow surface such as lake ice, where individual wolf tracks could be separated, or from visual observations of the pack. We also recorded an upper estimate when the total group size was thought to be greater than the minimum count. These more subjective estimates were established on the observers' opinion based on the overall amount of sign, circumstances, and tracking conditions. In some cases only minimum counts were possible (e.g., if three wolves were seen at the edge of timber, and no other evidence of pack size was observed). During this survey and from our past experience, upper estimates have been validated on numerous occasions where tracking led to a visual observation of the pack. In these instances, upper estimates were most often accurate to within 1 wolf.

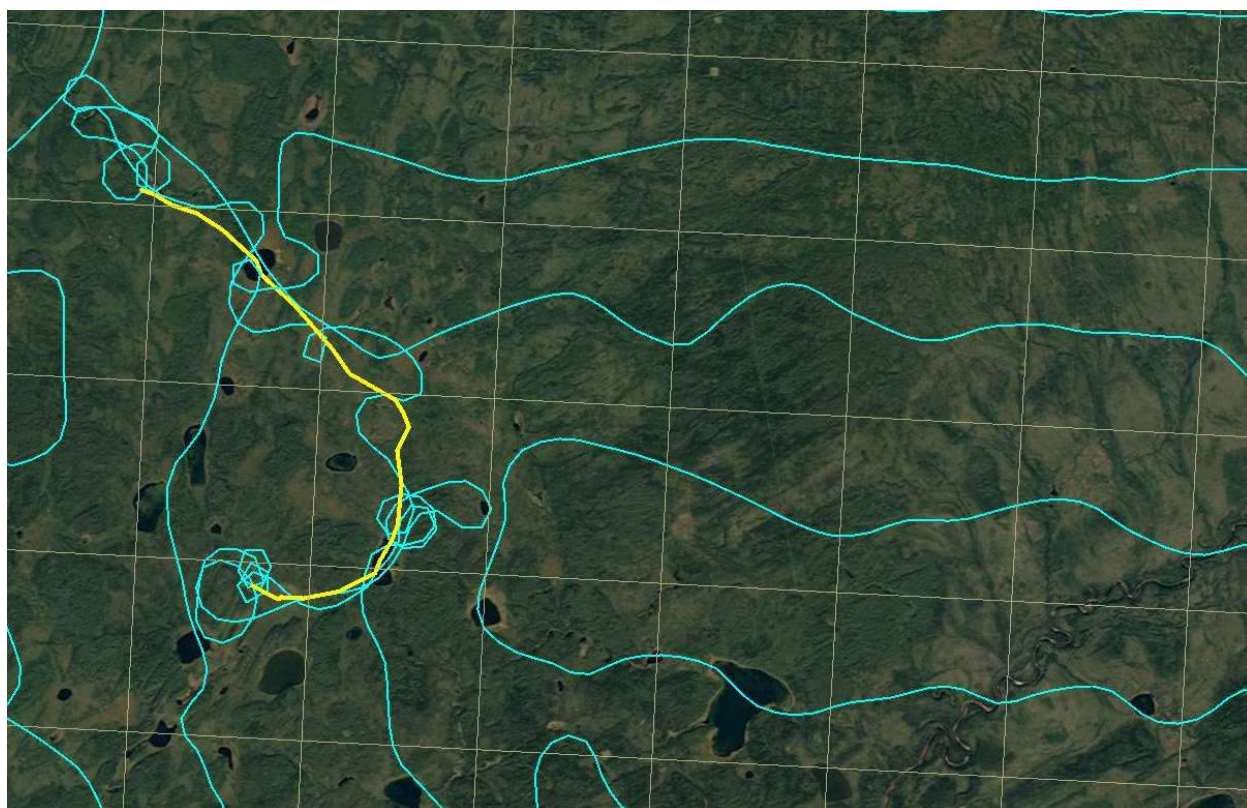


Figure 2. Example of survey flight paths during the Fort Liard WSU. The 3 km grid guided the survey flight paths (blue), which were allowed to meander within the 3 km cells in order to maximize detections (e.g., flying over lakes etc.). When wolf tracks were encountered, these were tracked. In this image, a wolf track network is illustrated as a solid yellow line. The pack had travelled from the north, and a partially eaten moose kill was located at the southern end, where a pack was observed. In this case, the track was first encountered towards the end of the day in poor lighting during a south bound transect (second column from left), with plans to investigate the following day. During the north-bound transect (third from left) on the following day, the fresh wolf track was encountered again independently, and then the fresh wolf track network was explored before continuing with encounter transects. Note that even in this relatively short track network, there was a chance of track encounter and detection in five cells.

Validation

We validated our choice of 3-km transect spacing using newly available data from GPS-collared wolves captured within our study region ($n = 12$). Collars were programmed to record location coordinates every 5 minutes during winter. Using high resolution data was desirable because wolves frequently punctuate long distance movements with periods of substantial non-directional movements; for example, back and forth movements localized within in an area such as a kill site. Using the same simulation procedures described by Serrouya et al. (2015a), we ran simulations to assess probability of coming within 200 m of fresh tracks after 1 to 5 days since last snowfall. Although we considered two factors in the 2015 simulation (transect spacing and the window of time that empirical wolf movements would encompass), here we only considered the 3 km scenario, and only modulated the window of time (1 to 5 days).

For each iteration within the simulation, a temporary 'study area' was defined by the range of latitude and longitude in the wolf's GPS locations. We selected a random longitude within this area and then populated the entire area with simulated north-south transects spaced 3-km apart. Similarly, a random start date was selected within the temporary 'study period' for when wolf data was available. All wolf locations within the specified time window, beginning with the start date, were extracted and plotted on the GIS. The number of crossings that occurred across the simulated transect was tabulated for each wolf and time period. This process was repeated 50 times for each collared wolf ($n = 600$ simulations total).

To further validate our methodology, our plan in 2016 was to conduct census counts in areas where wolves were already tagged with GPS/VHF collars (primarily CL, but also CLK), which could then be used to assess rates of detection error. Unfortunately, this plan was implemented under very poor survey conditions in 2016 (see CL survey results below). No sightability correction was applied to our estimates due to the low sample size of collared packs ($n = 1$ in BC) or the poor survey conditions encountered in Alberta (CL).

Objective 2: Evaluating the Links between Landscape Attributes and Populations of Predator and Prey

Data: deriving variables for pilot analyses

In this report, we present pilot analyses of the first available data. Below we describe the variables considered in this first exploration of the dataset.

Land Cover

To characterize land cover across all survey units, we used Land Cover, circa 2000 vector data obtained from Natural Resources Canada (NRC 2009). These data are based on classified Landsat 5 and Landsat 7 ortho-images spanning all provinces and territories. Polygons representing contiguous land cover are classified into one of 44 categories. Within our survey units, only 19 categories occurred. We converted the vector data to rasters (cell size 240-m) then collapsed the 19 categories into five land cover classes that were *i*) biologically relevant to wolves, moose and caribou, and *ii*) aligned with our ultimate objective of evaluating how broad-scale natural habitat composition influences the distribution and abundances of these animals (Table 1). For these latter analyses, we calculated the proportion of each land cover class within each survey unit.

Table 1. Classification of land cover types used to evaluate how broad-scale natural habitat composition influences the distribution and abundances of wolves, moose and caribou. Land cover types were developed from Land Cover, circa 2000 vector data (NRC 2009).

Land Cover Type	Land Cover circa 2000 Class
Wetlands	Bryoids, Wetland Treed, Wetland Shrub, Wetland Herb
Coniferous Forest	Coniferous Dense, Coniferous Open, Coniferous Sparse
Broadleaf / Mixedwood Forest	Broadleaf Dense, Broadleaf Open Broadleaf Sparse, Mixedwood Dense, Mixedwood Open
Shrub / Meadow	Shrub Tall, Shrub Low, Herb
Other	Water, Exposed Land, Rock, Cloud Shadow

To assess the influence of natural ecological variability on predator and prey populations, we initially focussed on the relative proportion of wetland and conifer habitat within each WSU as these were the leading habitat types in each WSU. A strong negative correlation between these two variables, however, caused us to focus our pilot analysis on the wetland cover because it is redundant to include to correlated variables in statistical analyses. Wetland was one of the leading land cover types, and was highly variable among WSUs.

Human Footprint

Human footprint was estimated from Landsat 2008-2010 imagery that was digitized for human disturbance and obtained from Environment Canada (published 2013; downloaded August 2015). Footprint was expressed as a proportion of each WSU. Footprint polygons included features such cut blocks, well pads, mines, built up areas/settlement, oil and gas facilities and other unknown clearings. Linear features were converted to polygons using buffer widths modified from estimates provided by Dickie et al. (2016). Dickie measured a sample of widths from various linear features types using spot imagery (1-m resolution). We assigned widths to pipelines (20 m), transmission lines (37 m), seismic lines (10 m), roads and railway (30 m), airstrip (100 m), and unknown (50-100 m). All footprint polygons were merged and dissolved to eliminate overlap. Note that our estimation of footprint differs from estimates contained within the federal *Recovery Strategy for the Woodland Caribou* (*Rangifer tarandus caribou*), *Boreal population, in Canada* (Canada 2012) – and other caribou literature (e.g., Sorensen et al. 2008) – in that no buffers are applied to the footprint data.

Moose Density

Moose density estimates were provided by provincial/territorial agencies and the BCOGRIS. These data were only available for four of the WSUs and were not included in the pilot analysis at this time.

Wolf Abundance

We estimated wolf abundance using data from our wolf surveys. Note that these estimates could include edge packs recently in the WSU, and exclude edge packs not recently in the WSU. Time since snowfall is expected to increase the inclusion of edge packs. We attempted to control for this factor by surveying shortly after snowfall but recognize that a covariate of time since snowfall could potentially be used to statistically control for this variability. We did not include a statistical correction for time since snowfall due to small sample size, but we note that the effect is likely to be small given the substantial size of the WSUs and the relative consistency of our survey timing relative to snowfall history. Compared to the variability in wolf abundance observed among WSUs (our objective to measure), this source of error must be small. Because we believe that our

maximum wolf counts were more realistic than the minimum wolf counts, we analyzed upper estimates of wolf counts, converted into a density of wolves per 1000 km² based on the size of the WSUs.

Growth Rates of Caribou Populations

Caribou population growth rates were obtained from the Government of the NWT, the BCOGRIS, and from the literature (Hervieux et al. 2013). When more than one caribou lambda value was available for a WSU, we used the highest lambdas to represent the populations, under the assumption that this measure had higher biological relevance (struggling populations typically have consistently low lambdas whereas more viable populations likely experience low and high lambdas). However, for a subset of analyses, we also used the geometric mean of caribou lambda values from the past 5 years (2011-2015), though the sample size of lambda values was highly unequal among ranges ($n = 1 - 5$), so results should be viewed with caution. The correlation between the maximum lambda value and the geometric mean lambda was 0.64.

Ecological Pilot Analysis

The ultimate objective of our study is to compare the relative importance of human footprint vs. natural habitat (in this report amount of wetland habitat) for influencing both wolf density and caribou lambda. To that end, we present preliminary analyses that make comparisons among WSUs. Ideally, the analyses would be stratified by trophic levels, i.e., land cover type and human footprint would be used to predict moose density, which in turn would be used to predict wolf density, and finally wolf density would be used to predict caribou population growth. However, moose density estimates did not exist within each of our WSUs at the time of writing and we therefore did not consider moose in this report, but rather used land cover covariates to directly predict caribou population growth rates (*sensu* (Wittmer et al. 2007, Sorensen et al. 2008).

The amount of wetland habitat and human footprint in the WSUs were estimated as proportions (0 to 1) of each WSU, and thus transformed using the logit function:

$$\ln(p/(1-p))$$

where p is the proportion of the WSU classified as wetland or human footprint.

We evaluated inter-relationships among the four primary variables of interest (wetland, human footprint, wolf density, caribou lambda) using Pearson correlation matrix. We further explored univariate and bivariate relationships between the two primary predictors (wetland and footprint) and the two primary response variables (wolf density and caribou lambda). These linear regressions were fit with Gaussian linear models. We emphasize that results from these analyses should be viewed as preliminary and that all regressions presented in this report have low sample sizes.

Results

Wolf survey details

Details and results from the wolf surveys and supporting information for the WSUs are summarized in Table 2 and Table 3.

CAL was the first site to be surveyed (January 28 - February 3, 2015). Good lighting and snow tracking conditions were observed following a snow storm that ended on January 25.

CHIN was surveyed shortly after CAL (February 9 - 15, 2015) following a snow storm on February 6. Lighting conditions were suboptimal during the survey (overcast/dark) but snow tracking conditions were good. Because the survey was interrupted by poor lighting conditions and some

wind, it took place over an extended period of time, and the snow tracking became increasingly challenged by extensive track networks.

Two attempts were made to survey HRL. The first attempt was made in November, 2015. The weather forecast, which was initially ideal, was soon downgraded after the survey was underway. As an assurance measure to salvage data, survey transects were spaced out to half density, but we soon called off the survey due to poor weather including low cloud, fog, wind, and eventually a full storm. About 60% of HRL was surveyed during the first attempt. The wolf survey was successfully completed two months later (February 14 – 17, 2016) but the survey area was shifted to the northwest, closer to Fort Providence, to include an area with more radio collared caribou. The survey was conducted under ideal conditions following a snow storm on February 9, with minor interruption caused by poor lighting and some wind. Despite the relatively long time since most recent snowfall, the snow surface was largely untracked, so track confusion was not an issue.

Following a snow storm on December 11, CLK was surveyed on 14 - 18 December, 2015. We experienced moderate tracking conditions and the lighting was low-angle.

FL was surveyed on 25 – 30 January, 2016, following a snowfall on 19 January. We experienced good snow throughout the survey, although poor lighting and wind hampered survey progress.

In 2016, northern Alberta received very low snowfall and experienced warm temperatures. The best opportunity to survey CL was after a snowfall that ended on the night of February 16. We initiated the survey on February 20, completing it in three days. Snow conditions were highly variable, and generally poor. In some parts of the study area, snow cover was nearly absent or patchy (Fig. 6), whereas in other parts, there was as much as 40 cm of fresh snow. Overall this survey was conducted under poor detection and tracking conditions. Bright sunny lighting conditions were experienced and daytime temperatures were well above zero. Further, we were denied access to the Cold Lake Air Weapons Range, so had to shift the survey area substantially further north on short notice.

Table 2. Details regarding the timing and effort of wolf surveys completed during the winters of 2014/15 and 2015/16. The PK survey was not included in analyses. A wolf survey at HRL was attempted twice; here only details of the successful second attempt are presented.

WSU	Last Snow	Start Date	Airtime Hours	Survey Hours	End Date
PK	2015-01-31	2015-02-04	5	4	2015-02-04
CAL	2015-01-25	2015-01-28	28.6	19.9	2015-02-03
CHIN	2015-02-06	2015-02-09	27.9	20.8	2015-02-15
CLK	2015-12-11	2015-12-14	22.25	19.4	2015-12-18
CL	2016-02-15	2016-02-20	31	27.3	2016-02-22
FL	2016-01-19	2016-01-25	25.3	16.3	2016-01-30
HRL	2016-02-09	2016-02-14	20.4	16	2016-02-17

Table 3. Data summary at six Wolf Survey Units (WSU). Due to incompleteness, moose data were not analyzed in this report. Wolf density is calculated using the maximum estimates made during surveys.

WSU	Caribou Lambda (Year)	Geometric mean Lambda (n)	Collared Wolf Packs	Year of Wolf Survey	Number of Packs	Min. Count	Max. Count	Wolf Density (/1000km ²)
CAL	2015	1.07 (1)	-	2015	5	32	35	7.0
CHIN	2015	0.84 (1)	-	2015	8	52	61	15.6
CLK	2015	0.95 (1)	1/1	2015	6	32	38	7.4
CL	2015	0.82 (5)	3/6	2016	16	66	74	9.9
FL	2015	0.98 (5)	-	2016	4	21	23	5.3
HRL	2010	0.87 (2)	-	2016	2	8	9	1.6

Wolf survey simulations and validation

Using 5-minute winter GPS wolf collar data from the Cold Lake area (Dickie et al. 2016), our simulation using 3 km transect spacing estimated that wolves would be detected 81% of the time with only one day of fresh tracks, assuming 100% detection within 200 m of the transect line. This rapidly improved with time; 99% detection rate was estimated with two days of fresh tracks, a 100% detection rate with additional time.

During the CLK survey, there was only one collared pack (with three collared members). This pack was detected by the survey, but was double-counted by the survey team; backtracking had failed to link the distant regions of wolf activity.

During the CL survey 3 out of 6 wolf collared packs were clearly detected based on GPS data. No VHF signals were ever heard. One of these packs provided GPS collar locations that showed unequivocal confirmation that we counted them, but their VHF signal was not detected; other VHF beacon on the other two detected packs was heard after the packs had been located via the survey. An additional 3 GPS collars were not counted during the survey. The first of these was detected, but mistakenly discarded as being old tracks that were exceptionally hard to follow in very poor intermittent snow conditions. A second collar was malfunctioning – giving poor GPS records, and may have been compromised in the VHF as well. The third gave GPS locations within 1 km of a pack we tracked; this collar was programmed at 2 locations per day, and we suspect that the tracks we detected were associated with this animal. In general, there was low confidence that the VHF signals were reliable as indicated by one collar that recorded concurrent GPS locations where we found tracks, and by a lack of signals detected in general.

Ecological Pilot Analysis

Wolf density was highest in CHIN (15.6 wolves/1000 km²), followed by CL, CLK, CAL, FL, HRL (1.6 wolves/1000 km²; Table 3). Caribou lambdas were highest in FL (1.2), followed by CAL, HRL (all above 1), CLK, CL, and CHIN (0.84).

The correlation matrix showed increasing correlations between human footprint, wolf density and caribou lambda, while the amount of wetland habitat had less correlation with the other three variables (Figure 3 Left). Because of strong negative correlation between conifer and wetland components in the WSUs, we only considered wetland as a measure of habitat type hereafter. None of the four univariate linear regressions in Figure 3 were statistically significant (all $P > 0.1$). Results were similar whether the maximum caribou lambda value was used, or if the geometric mean lambda value was used (Figure 3). However, the correlation between wolf density and caribou lambda was strongest when the maximum caribou lambda value was considered.

The regression predicting wolf density was not improved by combining the two predictors (wetland and footprint; all terms NS). Conversely, the regression predicting caribou lambda strengthened when both these predictors were included (wetland and footprint; adj. $R^2 = 0.92$, both effects $P < 0.01$, residual df = 3; Figure 4, Appendix 1).

The negative relationship observed between caribou lambda and wolf density approached statistical significance (adj. $R^2 = 0.43$, $P = 0.09$; Figure 5).

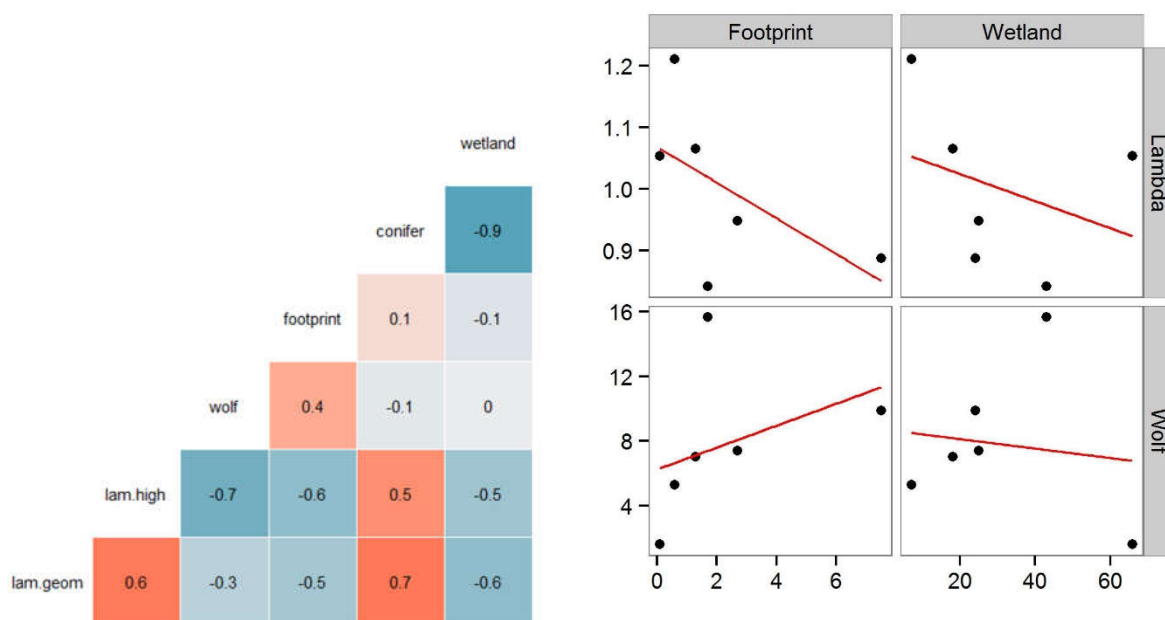


Figure 3. (Left) Pearson correlation coefficients among six ecological variables for the WSU: “lambda” is the highest recorded caribou population growth rate at each site, whereas lam.geom is the geometric mean lambda value from 2011-2015, though some ranges only had 1 or 2 lambda values. “Wolf” is the maximum density of wolves estimated from our surveys, “footprint” is the percent of the site areas that has been cleared by human disturbance (e.g., seismic lines, right of ways, forestry), and “wetland” is the percent of the sites mapped as wetland habitat (primarily acidic bogs). (Right) Relationships plotted between the amount of wetland habitat and human footprint with wolf abundance and caribou lambda.

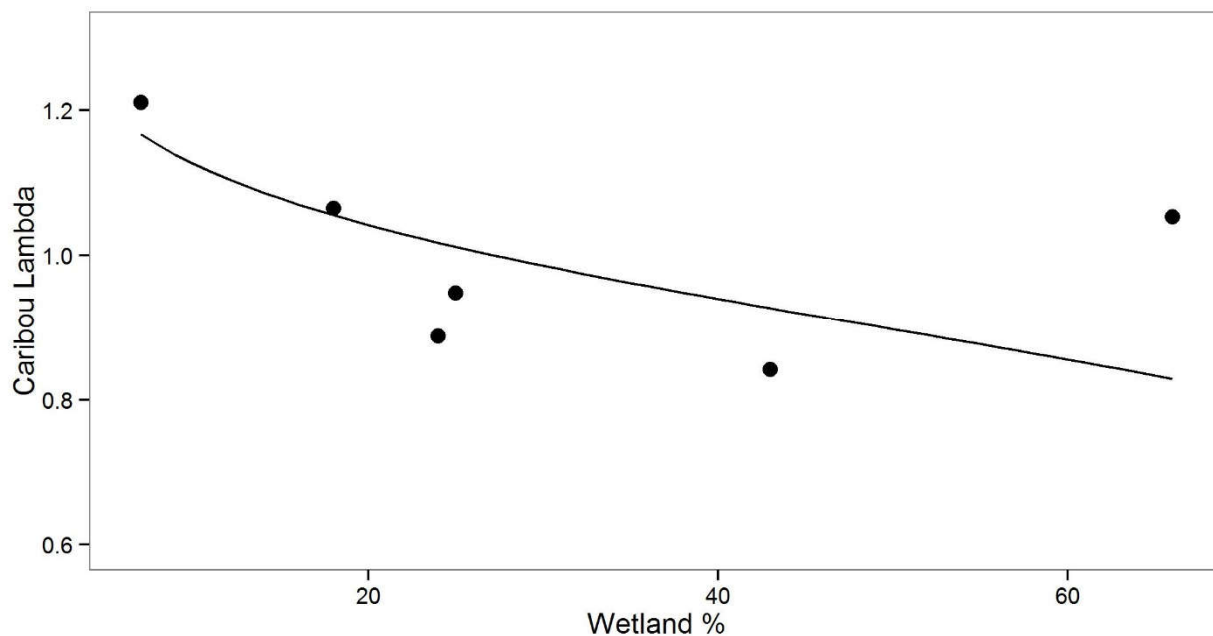


Figure 4. Results from a multi-variate general linear model examining the combined effect that the amount of wetland and the size of human footprint have on caribou population lambda (i.e. the maximum annual caribou lambda observed in each range over the last 5 years). The fitted line assumes the average observed value of human footprint. Data and model predictions are back-transformed to proportions.

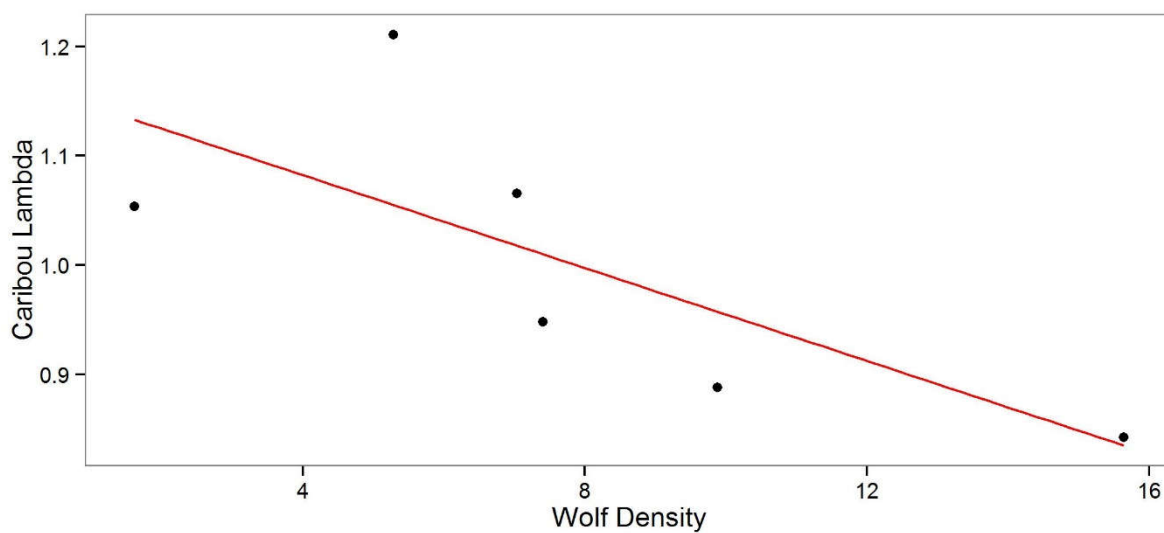


Figure 5. Potential negative relationship between wolf density (/km²) and caribou lambda (i.e. the maximum annual caribou lambda observed in each range over the last 5 years).

Discussion

There are numerous studies that have examined relationships between human footprint, ungulate populations, wolf densities and the growth or decline of caribou (Wittmer et al. 2007, Sorensen et al. 2008, Serrouya et al. 2011). The cause of widespread decline of caribou in North America has been explained by theoretical models (Weclaw and Hudson 2004, Serrouya et al. 2015b) and examined via empirical study (Bergerud and Elliot 1986, Seip 1992, Latham et al. 2011). Apparent competition (Holt 1977) attempts to explain the decline of some caribou populations by predator abundance, which in turn is indirectly mediated by habitat alteration (human footprint) via increases to populations of alternate ungulate prey (e.g., moose or deer). Apparent competition mediated by human footprint predicts that the decline of caribou varies at the scale at which predator density varies; regions with high footprint have large predator populations and strong caribou decline, whereas caribou populations will be more stable or growing in pristine regions where there are few other ungulates to sustain wolves. Despite decades of interest in this model, the linkage between human footprint, wolf density and caribou decline remains poorly tested at this most relevant scale, i.e., among broad regions that encompass differing densities of caribou and wolves.

The boreal caribou system is ideal for examining landscape-level variability. First of all, the strong decline in boreal caribou warrants investment towards understanding the role that human footprint plays in their decline. Second, the boreal forests forms one of the largest and most uniform biomes in Canada; hence, the geographic extent of study is almost unlimited, even for a study of such scale as ours (i.e., with 5000 km² sampling locations). Third, human footprint is increasing in the boreal system due largely to oil and gas developments in northeast BC, Alberta, and Saskatchewan. It was our goal to conduct a landscape level study examining the intertwined variabilities in caribou population growth, wolf density, human footprint and other natural predictors (e.g., latitude, habitat type).

Wolves have remarkable abilities to disperse and colonize, and their populations can likely respond rapidly to changing habitat conditions and prey densities. We therefore expect variability in wolf density across landscapes, where variation in habitat type – natural or not – amounting to variability in habitat suitability for these carnivores, is evidenced by the variability in their population density (e.g., low historic lag). Yet, despite expectations of measureable variability, quantitative assessment to detect variation in wolf density across landscapes is a challenging task – especially in forested environments (Patterson et al. 2004). Overcoming the challenge of assessing wolf densities is a task that is central to our study. Information on caribou population growth, human footprint, variability in boreal forest habitat types, and some data on moose abundance are available over vast regions of the boreal forest – but empirical data describing ecological correlates of wolf density remain scarce, and wolf density data is lacking in our study area (but see (Latham et al. 2011, Hervieux et al. 2014).

Counting Wolves

The boreal forest has low topographic relief, and while there is variability in upland versus lowland habitat types, there are almost no barriers to wolf movements. To assess wolf density, we conducted census surveys at each WSU, and given the uniform nature of the habitat, we utilized transect-based flight paths during the search and detect part of the census. We originally conducted a simulation to inform our decisions on transect spacing using GPS location data from collared wolves, where a single GPS location was recorded once per day during the winter (Serrouya et al. 2015). This former analysis indicated that transect spacing affected detection rates, but detection rates for all transect spacing improved dramatically as tracks on the landscape (time since snowfall) accumulated. To be conservative, we selected 3 km transects, a relatively narrow spacing distance. While improved detections were observed for shorter spaced transect

designs, our experience conducting wolf surveys, and the scale of our sampling areas gave us reason to avoid tighter transect layouts. We should note that detections would be greater than predicted by the fact that true detection opportunities would be greater than predicted by the simulation due to the tortuosity of wolf tracks that was not accounted for in the simulation, and because the aerial search paths freely meander between transects rather than following the transect lines. This method was chosen primarily to optimize detections by flying over open habitats where available, but at the same time, it increased the search intensity (flight distance per km²). Having chosen a census method, interest in validating the method became an important goal.

In 2016, we attempted to validate our census methods via two avenues. First, we acquired new GPS data from boreal wolves tracked by collars that recorded their coordinates every 5 minutes during winter. When we re-ran the simulation using a 3-km transect spacing, we found that detections quickly increased to 100% when two or more days of tracks were available on the landscape. This result validated the 3 km transect spacing, essentially indicating that our search is thorough enough to fly over tracks from all wolves on the landscape. As such, we conclude that our basic search/detect phase of the aerial census is valid, and unlikely to cause issues with counting errors.

The second avenue for validating our method was to compare the detections made during our census counts, with knowledge of true wolf presence determined via VHF collars. Unfortunately, this avenue was a largely unsuccessful test in 2016 because the one WSU where many wolves were collared had very poor snow conditions (Figure 6). Nonetheless, despite snow tracking conditions being unacceptable, we were able to detect 3 out of 6 collars in the area. This result provides an estimate of wolf detection rates achieved under sub-optimal conditions, and detection rates are expected to be much higher under normal working conditions.

During the CLK survey, we had another opportunity to assess our detection rate using wolf collar data. In this case the survey crew did not assess collar presence using VHF signals, rather, the GPS locations were examined during the survey track window, after the survey had been completed. In that case, the pack was detected, but was counted twice by mistake. Examination of the flight path showed only a single opportunity to link the two regions of wolf tracks; this track was missed, either because it was obscured when they were difficult to see (e.g., under canopy, or poorly defined in snow), or due to observer error (e.g., observers looking wrong direction or species identification mistakes).

Counting errors are unavoidable, but need to be assessed so that we have a better understanding of our data quality. We recognize several types of counting errors including (1) edge effects, (2) pack count false negatives, (3) pack count false positives, and (4) pack size enumeration errors.

Edge effects are minimized by surveying large areas, and are expected to vary as a function of time since snowfall. Shortly after a snowfall subsides, fresh tracks will be found in the WSU from approximately half of the pack territories straddling the WSU boundary. As time progresses, additional edge packs will enter the WSU until the number of packs is saturated. Typically this latter state needs to be avoided, as the abundance of tracks make differentiating wolf packs very confusing, leading to both false negative and false positive errors. Avoiding wolf corridors when drawing WSU boundaries (e.g., rivers) helps to minimize edge effects. Our approach to dealing with edge effects has been to use relatively similar shaped and sized WSUs and to be consistent with timing of the census following snowfall. This approach largely controls for the issue, but we recognized that there is likely an interaction that involves wolf density.



Figure 6. Poor snow-tracking conditions at Cold Lake (CL), 2016. This photo exemplifies how the probability of track detection is obscured by snow quality. Where the snowpack covered the ground, tracking was decent, however large parts of the snowpack in the CL WSU was broken by ground cover vegetation, making detection of tracks – and tracking wolves highly problematic.

Pack false negatives occur when packs are missed. Our simulation shows that false negatives are unlikely to be attributed to surveys not crossing wolf tracks. Rather, false negatives are likely when wolves have been working a timbered area, when snow tracking conditions are poor, or when observers make errors. There is little that can be done to deal with the former issue other than recognizing that it exists (underestimates in timbered landscapes). Conducting wolf surveys during ideal tracking conditions largely avoids the second issue, although we recognize it will be an issue on occasion due to poor lighting, localized wind effects etc. Observer error can be minimized by pairing experienced biologists with an experienced pilot as much as possible. In the boreal surveys, days are short in winter, so observer fatigue is less of an issue.

Interestingly, our experience in the CLK WSU showed that missing tracks can actually lead to pack false positives. This occurred because a wolf track linking two highly tracked areas was missed at the one location where the survey crew flew over the wolf trail. We do not know what the habitat was like, but it is to be expected that tracks were invisible to the crew. This error is best avoided by attempting to find and track all entry and exit points to wolf track networks – ideally all tracks are followed until the tracks are no longer fresh, at one end, and wolves are found, at the other end. Currently, we have documented when wolves are observed for each track network, but we have not been recording whether older tracks were identified as the origins of the fresh tracks. This may help assess the quality of the observations, although admittedly, there is only so much time that can be spent attempting to figure out confusing sets of tracks. As stated

earlier, working shortly after snowstorms end is likely one of the best approaches to assuring wolves are not double-counted as the track networks will be smaller, and less confusing.

Pack size enumeration errors are likely the least important error. Pack size is more fluid over the course of a winter, with deaths of some pack members, and the possibility of floater wolves forming temporary alliances with packs. Pack size has less ecological significance than the number of packs (killing units), and differences in food handling time between smaller and larger packs is offset by scavengers (Vucetich et al. 2004). Although we have not documented this, our counts from tracks are repeatedly validated when wolf packs are eventually observed, and this feedback has indicated that our maximum estimates are reasonably accurate. This source of validation could be considered in future surveys.

It should be remembered that, as per a Poisson distribution, counting errors increase with the size of the counts. In areas such as the HRL, where wolf density is very low, we expect counting errors (e.g., of number of packs and total numbers of wolves) to be very small, and therefore expect the range of possible outcomes to always portray a low wolf density. As wolf density increases, so does the potential for counting errors, resulting in a larger error term. We do not know the mathematical coefficient of how count error relates to wolf density, but we suggest that recognizing this principle gives credence to the assumption that we are able to correctly classify low density WSUs, and that WSUs where high densities are recorded are very unlikely to have a low density in truth. A conceivable outcome that is misleading is where a high density region appears to have low densities due to survey errors, but this will be balanced out by the opposite situation. Under this logic, we suggest that although the sampling is not perfect, the gradients in wolf density being observed likely mirrors true gradients among the WSUs, primarily because we will always be able to correctly assess low wolf densities.

Ecological Results

It is of course too early to draw any conclusions from our study given the limitations of our dataset; however, even with only six data points, the data are showing potential for statistically significant and ecologically interesting results. To this end, our results showed what we believe are encouraging data regarding the relationships between wolf density and caribou lambdas, and when wetland and human footprint were regressed against caribou lambdas. Results were generally consistent with expectations, where higher levels of footprint and wolves were correlated with lower caribou population growth. Footprint also coincided with higher wolf abundance. Natural habitat (wetland) and footprint were both correlated with caribou population growth rates, but inferring relative magnitude (a primary objective of this study) between the two factors is tenuous with only 6 data points. The negative association between caribou lambda and wetlands is likely because wetlands included treed and non-treed habitats. Future analyses will include how sensitive the results are to grouping the EOSD landcover categories. These results, if supported by a more robust dataset that includes moose abundance data, will provide unique empirical evidence supporting the model of apparent competition. We recognize that it would only take one new data point to disrupt any of these relationships (see Appendix 1). We present the data as pilot analyses to exemplify the types of analyses we hope to perform when additional data are available. Our primary goal with subsequent sampling is to sample low disturbance areas in more southerly latitudes (i.e. Saskatchewan), because currently our design pertaining to footprint is confounded with latitude.

Recommendations

We are highly encouraged by our results so far, and see value in continuing with this study. Below we summarize some of the targets and improvements for future sampling:

- Increase sample size;

- Survey WSUs with high disturbance at more northerly latitudes;
- Survey WSUs with low disturbance at more southerly latitudes;
- Survey WSUs with collared wolves to validate detection rates;
- Use VHF to assess false negative, and if possible, GPS data to assess double counting;
- Conduct dedicated VHF telemetry flight right after the survey;
- Record when fresh tracks are linked to old tracks;
- Incorporate more moose density data; and
- Assess whether forest fire (burn) data is available to include as a potential predictor.

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Appendix 1. The high significance of a two-variable general linear model on 6 data points is an unusual result, generally indicating strong biological effects; however, given the low sample size, our model deserves exceptionally high caution and deserves more detailed examination. Below is a graph showing how caribou population growth (lambda) is affected by the percentage of wetland habitat and the percentage of human footprint, both displayed in the logit scale which was used when fitting the two-variable general linear model. WSUs are labelled. The model estimate line shows the intercept predicted for average footprint values. Human footprint values are displayed by the colour of the points, and it can be seen that points further from the model prediction have more extreme footprint values. CL and HRL were clearly high influence data points in the two-variable model, which greatly reduced the residual variation by including footprint. This result can be easily upset by the addition of more data, which we strongly advise before considering the results as conclusive.

