Spatiotemporal Patterns and Population Characteristics of Harvested Wolverine (*Gulo gulo*) in Yukon

by

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ABSTRACT

Wolverines (*Gulo gulo*) are harvested for fur in Yukon, Canada, but little is known about the sustainability of their harvest. In the absence of population data, harvest management relies on harvest data to assess the efficacy of regulations and harvest sustainability. I examined the spatiotemporal patterns of wolverine harvest in Yukon from 1988 to 2015. Overall, there was no significant trend in wolverine harvest over time, but harvest patterns varied regionally. Wolverine harvest was concentrated in southwestern Yukon, where estimated mean annual harvest rates remained high (>10%) over time, indicating that harvest is likely sustained by immigration from harvest refugia. In contrast, wolverine harvest in eastern and northern Yukon was relatively low, and estimated mean annual harvest rates (<6%) suggest sustainable local harvest. Only 13% of licensed trappers, and 16% of traplines, reported wolverine harvest in a given year, indicating that wolverine was not a focal species for many trappers. Wolverine harvest is likely affected by the overall fur trapping and trapline utilization trends. However, individual behavior among trappers varied, with a few trappers appearing to focus on wolverines (25% of total wolverines were harvested by 3% of trappers), demonstrating that individual trappers have disproportionate effect on wolverine harvest patterns. Consequently, trapper motivation may be an important factor in wolverine harvest dynamics, particularly at regional scales. Demographic data collected from harvested wolverines provide information on the vulnerability and variability of different sex and age cohorts to harvest, which in turn, may have implications for harvest sustainability. I assessed the variability of different sex and age classes of harvested wolverines among years, and within the trapping season (early vs. late winter). I also documented basic reproductive parameters (e.g., litter size, pregnancy rates), and examined the potential implications of harvest timing on reproductive females. The overall harvest was skewed toward males and young individuals. The sex ratio of harvested animals did not fluctuate during the study, but I observed variation in the age structure among years. The age structure also varied within the harvest season, with a greater proportion of adults harvested in late winter. Most (81%) adult females were reproductively active when they were harvested. The timing of gestation varied, with expected parturition from mid-February to late March. The prominence of young males in the harvest suggests source-sink dynamics, where populations in harvested areas may largely consist of dispersing animals from harvest refugia in surrounding areas. Harvest during late winter is likely to have a more significant impact on populations than in the early winter, due to increased harvest of adults and susceptibility of denning females to harvest in late winter.

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CHAPTER I: General Introduction

Wolverine (*Gulo gulo*) is an elusive, rarely observed carnivore that inhabits the tundra and boreal forest of the northern latitudes (Ruggiero *et al.* 2007). Wolverines are able to inhabit relatively unproductive ecosystems, surviving by opportunistic scavenging and hunting (Magoun 1985; Banci 1987; Lofroth *et al.* 2007; van Dijk *et al.* 2008b). They occur in naturally low densities and their home ranges are large (100 km^2 to > 1000 km^2; Banci and Harestad 1990; Banci 1994; Landa *et al.* 1998; Inman *et al.* 2012a). They can travel long distances for food, mates and dispersal (Gardner *et al.* 1986; Vangen *et al.* 2001). Wolverines may be sensitive to human disturbance (May *et al.* 2006; Krebs *et al.* 2007) and they require extensive secure areas to maintain viable populations (COSEWIC 2014). Wolverines have a low reproductive output (Magoun 1987; Persson *et al.* 2006), and thus, a low population growth capacity. These traits imply that wolverine populations are vulnerable to exploitation and habitat fragmentation (Kyle and Strobeck 2001; Ruggiero *et al.* 2007).

The historic range of wolverine contracted in the early 1900s, similar to other large carnivores, such as wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*), due to human land use changes, over-harvest and persecution (Abramov 2016). Conservation efforts in the last decades have revived populations in parts of their historic range in northern Europe, as management policies of large carnivores have changed (Linnell *et al.* 2001), and the importance of apex carnivores to entire ecosystem functions has recently become better understood (Estes *et al.* 2011; Khalil *et al.* 2014). Currently, large wolverine populations occur in Russia, Alaska and Canada. Smaller, or fragmented, populations occur in the northwestern contiguous United States, Fennoscandia, Mongolia and China (Abramov 2016). Climatically, the wolverine range is roughly delineated by areas with persistent winter snow cover, which presently fall largely within the boreal forest zone. The importance of persistent winter snow cover, and the potential impact of climate change on wolverine habitat, has received attention in recent years, but findings are inconclusive (Copeland *et al.* 2010; Brodie and Post 2011; McKelvey *et al.* 2011; Aronsson and Persson 2016; Webb *et al.* 2016).

Because of their rarity and vulnerability to exploitation and habitat fragmentation, wolverines are a conservation concern in several jurisdictions within their range (Landa 2007). Globally, wolverine conservation status was recently downlisted from Near Threatened to Least Concern (IUCN 2009; 2016) due to large populations that still remain in Russia and North America (Abramov 2016). However, the global population is assessed as 'declining' due to ongoing habitat fragmentation and harvest (Abramov 2016), particularly in Russia, where wolverine populations have declined over the recent decades due to overharvest and decline in prey (reindeer; *Rangifer tarandus*) populations (Landa 2007). In Canada, wolverines are assessed as 'Special Concern' due to limited population data, lack of recovery in its historic range in eastern Canada, habitat fragmentation, and potential impacts of climate change (COSEWIC 2014). Wolverine harvest is permitted in Russia, Alaska and western Canada, where large areas of unfragmented habitat with low human density still remain. Wolverines are harvested mostly for their fur, but also to protect livestock and game (Banci 1994; Landa *et al.* 1999; Bischof *et al.* 2012).

Unlike many other furbearer species, wolverines have an intrinsically low resiliency to harvest due to their low density and low reproductive output (Weaver *et al.* 1996; Banci and Proulx 1999). Wolverines are also susceptible to trapping because they travel widely and are readily attracted to bait (Hornocker and Hash 1981). In contrast, wolves, for example, are relatively resilient to harvest despite their large home ranges and low density, because their reproductive potential is high (Boitani and Mech 2003) and they are difficult to trap (Government of Yukon 2012). The sustainable harvest rate for wolves has been estimated at 35% of the fall population (Webb *et al.* 2009), whereas the sustainable harvest rate for wolverine has been estimated at below 10% (Weaver *et al.* 1996; Banci and Proulx 1999; Krebs *et al.* 2004). Consequently, careful management of wolverine harvest is required to ensure sustainability.

Various methods are used for assessing harvest sustainability. Common measures of harvest sustainability include demographic models of population growth, the Robinson & Redford surplus production models, and population trends through time (Weinbaum *et al.* 2012). These methods require reliable population data, which are often difficult or costly to obtain for species that occur at low density, and occupy remote and rugged landscapes. As a result, population estimates for wolverine in Canada are limited (COSEWIC 2014). In the absence of population data, harvest data can be used to inform harvest management. Monitoring harvest rates provides a temporal trend and can be used to compare different regions; however, the results may be ambiguous as the harvest effort is often unknown and harvest may be under-reported (Weinbaum *et al.* 2012; COSEWIC 2014). Monitoring the sex and age structure of harvested animals allows for a better assessment of harvest than a simple harvest rate, because harvest vulnerability typically varies among sex and age classes and certain sex-age classes are more valuable than others from the perspective of population persistence. For most species, the harvest of juvenile males is considered more sustainable than the harvest of breeding females (Whitman *et al.* 2003; Dalerum *et al.* 2008).

The survival rate of adult females is the dominant factor affecting population growth rates, and thus, sustainable harvest (Dalerum *et al.* 2008). The survival of breeding females is critical for species that have low reproductive output. For example, the sustainable harvest rate of adult female polar bears (*Ursus maritimus*) is typically <1.6% of the total population (Taylor *et al.* 1987). Restricting the harvest of females can be used as a management strategy for grizzly bears and polar bears (Taylor *et al.* 1987; Smith 1990; Case and Buckland 1998). The sustainable harvest rate of adult female wolverines has not been estimated; however, the influence of harvest sex ratio on population persistence has been demonstrated, with a stronger effect if the female proportion of harvest was high (Dalerum *et al.* 2008). Because wolverine trapping techniques are nonselective with respect to sex and age, conservative harvest strategies are required (Krebs *et al.* 2004). Wolverine harvest is typically male-biased, similar to other mustelids (King 1975; Banci and Proulx 1999; Fryxell *et al.* 2001). Regular monitoring of the harvest sex ratio, and restricting female harvest where needed, is recommended for wolverines (Dalerum *et al.* 2008).

Most harvest sustainability measures assume a closed population, or operate at localized scales (Weinbaum *et al.* 2012), which can lead to inaccurate conclusions, particularly for species with high dispersal capacities (Novaro *et al.* 2000), such as wolverine. Understanding the species' dispersal mechanism and distance, and barriers for dispersal, are critical for assessing harvest sustainability at an appropriate spatial extent. If local harvest pressure is high, and population viability depends on immigration from harvest refugia, then the spatial distribution and size of areas with and without harvest are important for successful dispersal between the populations (Novaro *et al.* 2000). Recent studies warn that harvest of wolverines may only be sustainable if adequate harvest refugia exist (Krebs *et al.* 2004; Golden *et al.* 2007a; Dalerum *et al.* 2008). Because wolverines require large home ranges and may respond negatively to human development, harvest refugia should consist of large areas of unfragmented landscape. Identification and protection of harvest refugia is important for harvest management of wolverines (Krebs *et al.* 2004), because human encroachment into wolverine habitat and over-harvest are the main threats to wolverine populations (Abramov 2016).

Wolverine is one of approximately 25 furbearer species harvested for fur in Canada (Fur Institute of Canada 2015). Historically, the fur trade was a significant economic industry and its impact on the cultural and social development of Canada was tremendous (Stabler 1990; Banci and Proulx 1999). Over the centuries, the global fur market has gone through volatile changes influenced by changing fashions, new textiles, fur farming and public anti-fur sentiment (McCandless 1985; Siemer *et al.* 1994; Banci and Proulx 1999). These factors, together with socio-economic changes (*e.g.,* urbanization, new economic sectors) have resulted in the decline of fur trapping activity. The majority of the present day fur trade is for domestic furs, which constitute two thirds of Canadian fur exports (Statistics Canada 2012). Approximately 500 wolverines are harvested annually in Canada for a total value of $125,000 (Statistics Canada 2010). Most animals are harvested in western Canada (British Columbia, Yukon and Northwest Territories); relatively few wolverines are harvested in Manitoba, Saskatchewan, Alberta and Nunavut. Wolverine pelts are highly valuable due to their rarity and frost-resistant quality, and they are some of the most expensive furs in the market. They are mostly used as a trim or ruff on parkas, or in taxidermy (Banci 1994).

Wolverines have been harvested in Yukon for centuries; initially for clothing and trade by indigenous people, later almost exclusively for the fur trade (McCandless 1985; Yukon Fish and Wildlife Management Board 2005). Until the fur market collapse in late 1940s, fur trapping was the principal means of self-support for Yukoners. It was the most important industry after mining

(McCandless 1985). The economic importance of fur trapping in Yukon has faded, similar to the rest of Canada, due to fast socio-economic changes in recent decades. However, it is considered a culturally important activity with potential to revitalize through focused support and strategy (Yukon Fish and Wildlife Management Board 2005). Trapping remains an important activity for indigenous people in Yukon and the value of this tradition cannot be easily measured by the market economy perspective. The relatively recent history of 'bush' lifestyle and fur trapping continue to provide a social identity and a source of pride for many Yukoners.

Present day fur trapping in Yukon is largely a recreational activity; with 10–20% of trappers considered full-time. Consequently, the harvest rates among trappers are uneven; the top 20% of active trappers harvest 60–80% of all furs (Yukon Fish and Wildlife Management Board 2005). Trapper motivations, and consequently, harvest effort, are likely related to several interacting variables, including the economics, perceived animal abundance, weather conditions and access (Stabler *et al.* 1990; Banci and Proulx 1999; Dorendorf *et al.* 2016). Fluctuations in trapping activity have been related to changes in pelt prices in some studies (Elsken-Lacy *et al.* 1999; Gehrt *et al.* 2002); but not in others (Robichaud and Boyce 2010; Hiller *et al.* 2011; Kapfer and Potts 2012). Wolverine fur has a higher pelt price than any other Yukon furbearer species (Yukon Fish and Wildlife Board 2005); thus, wolverines are highly desirable for trappers. However, wolverine abundance is naturally low and they are unlikely to be a primary species of interest to many trappers. Economically the most important furbearer species in Yukon are lynx (*Lynx canadensis*) and marten (*Martes americana*), which are relatively abundant and their furs are valuable and generally in high demand (Banci and Proulx 1999; Yukon Fish and Wildlife Management Board 2005).

Wolverine populations in Yukon are largely unknown. A population density of 5.6 wolverines/1000 km^2 was estimated in Kluane in southwestern Yukon (Banci 1987), and 9.7 wolverines/1000 km^2 in Old Crow in northern Yukon (Golden *et al.* 2007b). A crude population estimate for Yukon is 3500–4000 wolverines and it is considered stable based on the annual harvest numbers and trapper questionnaires (Slough 2007). In recent decades, Yukon Government has initiated the collection of two types of data specific to wolverine harvest: 1) fur sealing records, and 2) carcass collections. Mandatory fur sealing is required for all harvested wolverines since 1988. Fur sealing records include the harvest date and location of each animal. A wolverine carcass collection program was initiated in 2005 to obtain data on the sex and age structure, and other biological data, of the harvested animals. In the absence of population data, these datasets can inform the harvest management of wolverine and provide an initial assessment of harvest sustainability. Using these data on harvested wolverines, this thesis examines the temporal and spatial dynamics of wolverine harvest, and describes the population characteristics of harvested wolverines in Yukon.

In chapter II, I explore the temporal and spatial patterns of wolverine harvest over 27 years from 1988 to 2015 in Yukon. First, I explore temporal trends in the territorial wolverine harvest. Slough (2007) informally assessed wolverine harvest in Yukon as stable almost 10 years ago, and I will re-assess this statement based on territorial and regional trends. Second, I examine the time series of wolverine harvest in relation to other fur harvest metrics that may affect the harvest effort of wolverine, such as the number of licensed fur trappers, the harvest of other furbearer species, and pelt prices. I hypothesize that wolverine harvest is related to the overall trapping activity, particularly of lynx, because of its importance to Yukon trappers. I expect that pelt prices do not affect wolverine harvest, because wolverine are rare and their harvest is likely not an economic priority for trappers. Third, I summarize the spatial distribution of wolverine harvest and explore regional harvest trends. I expect that wolverine harvest is spatially heterogeneous and concentrated near human population centres. Finally, I assess the regional sustainability of harvest by estimating annual harvest rates and the amount of harvest refugia. I note regions with consistently >10 % estimated annual harvest rate as potentially unsustainable (Weaver *et al.* 1996; Banci and Proulx 1999; Krebs *et al.* 2004), and further assess their potential vulnerability to over-harvest based on harvest refugia in and around these regions.

In chapter III, I examine the population characteristics of harvested wolverines through necropsy of trapper-submitted wolverines over 8 years from 2006 to 2014. First, I determine the sex and age structure of harvested wolverines. These data provide information on the vulnerability of different sex and age classes to harvest, and how their vulnerability may fluctuate during the harvest season and among years. Because adult females are the most valuable members of the population from the perspective of population persistence, understanding when they may be most vulnerable to harvest is a key to establishing management practices that minimize their harvest. Second, I assess the reproductive status of harvested female wolverines. For breeding wolverines, I relate the timing of their harvest in relation to the stage of their pregnancy in order to assess the harvest incidences of gestating and denning females.

In Chapter IV, I highlight the key findings, and provide harvest management recommendations for harvest managers, as well as wolverine trappers.

Chapter III was written as a manuscript, and it is included in this thesis in manuscript format and length. All citations and references in this thesis are formatted according to the specifications of *Wildlife Research* journal.

CHAPTER II: Spatiotemporal Patterns of Wolverine Harvest in Yukon

Introduction

Wolverines are naturally rare, generally occurring in lower abundance than other northern carnivores even in optimal habitats (Quick 1953; Banci 1994). Due to naturally low productivity, the replacement of harvested animals may be slow. As a result, human-caused mortality of wolverines may be mostly additive, rather than compensatory, to natural mortality (Krebs *et al.* 2004), similar to other carnivores that typically occur in low density (Pöysä 2004; Cooley *et al.* 2008; Murray *et al.* 2010; Sparkman *et al.* 2011). Consequently, wolverines are susceptible to over-harvest. Wolverines are also vulnerable to habitat fragmentation and land use conflicts (Landa 2007). Growing human populations and demands for natural resources is resulting in expanding encroachment into previously undisturbed habitats (Goudie and Viles 1997). As a result of continued habitat fragmentation, associated increases in access to wolverine habitat, and harvest pressure, the global wolverine population is estimated to be declining (Abramov 2016).

Wolverines are harvested throughout most of their range in North America. Careful management is important for ensuring the sustainable harvest of this sensitive species. Understanding the spatial and temporal patterns of harvest is important for proper management of wolverine populations (Golden *et al.* 2007a). In the absence of population data, harvest management relies on harvest data to address sustainability and the efficacy of regulations. Spatial and temporal harvest trends may provide early warning signals of over-harvest, and thus prompt further study and adaptive regulatory changes.

In Yukon, wolverines range throughout the territory. They are classified as furbearers and big game, and they are harvested under territorial trapping and hunting regulations. Most wolverines are trapped; few wolverines are hunted annually. Wolverine is one of 14 furbearer species trapped in Yukon, and fur harvest is regulated spatially. Individual fur trappers must either hold the rights to a trapping concession (registered trapping concession; RTC) or act as an assistant trapper to the concession holder(s). The designation of RTCs encourages their holders to act as stewards and trap sustainably, but there is no quota for wolverine harvest.

Banci (1987) found that wolverine harvest in Yukon was strongly correlated with harvest effort (number of trappers), and that few trappers actively trap wolverines. Because wolverines are naturally rare, they are likely trapped opportunistically, and fluctuations in their harvest may be correlated to the harvest of other furbearer species, such as lynx (DeVink *et al.* 2011), which is the most important furbearer species in Yukon (Yukon Fish and Wildlife Management Board 2005). Wolverines may also be caught incidentally in traps set for lynx or wolf, because the habitat and equipment used for trapping these species are similar.

Fur trapping and trapline utilization in Yukon fluctuate temporally and spatially. Concomitant with this, spatiotemporal patterns of wolverine harvest may be influenced by trapper motivations, which may fluctuate based on interacting factors, such as weather conditions, trapline accessibility, fuel prices, perceived animal abundance, and fur values (Ahlers *et al.* 2016). Weather conditions, fuel prices and access may be particularly important motivators for Yukon trappers, who typically must travel long distances to access and check their traplines. Adequate snow cover and solid ice on wetlands and waterbodies are critical for snowmobile travel, and early winter or spring snow conditions may have a significant impact on the length of effective trapping season. Fuel prices are typically high in northern communities, particularly outside

Whitehorse (Yukon Government 2016). In Alaska, which is similar to Yukon in terms of remoteness, >80% of wildlife harvesters reduced their subsistence trips in the last decade because of gasoline costs (Brinkman *et al.* 2014). Trapping activity may also be influenced by perceived animal abundance, with trappers increasing effort when animals appear abundant, in order to harvest more furs. Increasing effort when animals are abundant may also be a strategy by local trappers to control predator numbers (Daigle *et al.* 1998; Dorendorf *et al.* 2016). Wolverines are known to prey on reindeer, caribou and domestic sheep (Landa *et al.* 1997; 1999; Lofroth *et al.* 2000); however, predator control in Yukon has focused mostly on wolves (*e.g.* Hayes and Harestad 2000). Wolverine harvest may nevertheless be affected by wolf control because wolverines are readily attracted to bait and may be caught incidentally in wolf traps. In addition, wolf control may have an indirect negative impact on wolverines, via reduced scavenging opportunities (Koskela *et al.* 2013a).

With the exception of quota on marten in some RTCs, there are no restrictions on the volume of furs which may be harvested in Yukon from a given RTC; thus, there are no economic restrictions for fur harvest in Yukon. Fluctuations in market pelt prices may affect trapping effort, and thus harvest rates (Ahlers *et al.* 2016), but other studies indicate that economic motivations may have become weaker (Hiller *et al.* 2011; Kapfer and Potts 2012; Dorendorf *et al.* 2016). Wolverine pelt price is the highest among Yukon's furbearers ($289 ± 54 [SD] between 1988 and 2015). In comparison, the next highest pelts prices of wolf and lynx were $182 ± 51 and $164 ± 74, respectively, for the same time period. However, wolverine harvest by volume is low in comparison with most other furbearer species. Economically, the most important furbearer species in Yukon are lynx and marten, which are harvested in larger numbers (79% of annual average value of fur sales between 1970 and 2002). Wolverine harvest had the third highest annual value over this period; however, it was still relatively low compared to lynx and marten returns (> $230,000 annually each for lynx and marten; < $35,000 for wolverine).

Wildlife harvest is typically spatially heterogeneous and concentrated near settlements (Novaro *et al.* 2000; Siren *et al.* 2004; Robichaud and Boyce 2010). Such heterogeneity may be particularly pronounced in regions that lack road networks, and consequently, road access may create population sinks, whereas remote areas act as population sources (Laurence *et al.* 2006; Robinson *et al.* 2008). In Alaska, wolverine harvest is concentrated near settlements, roads and accessible drainages (Golden *et al.* 2007a); however, wolverine harvest in Alaska is not spatially regulated. In Yukon, the spatial regulation of fur trapping may have a smoothing effect on harvest patterns, but difficulty of access may reduce the utilization of remote traplines and concentrate effort near population centres. For example, wolf harvest in Alberta is spatially regulated, but the most active trapping areas were still within 400 km of the main human population centres (Robichaud and Boyce 2010).

The natural history characteristics of wolverine, such as low density and low reproductive output, contribute to a low resiliency to harvest, with their sustainable harvest rate estimated at < 10% (Weaver *et al.* 1996; Banci and Proulx 1999; Krebs *et al.* 2004). In addition, it has been suggested that wolverine harvest may only be sustainable if adequate harvest refugia exist (Krebs *et al.* 2004; Dalerum *et al.* 2008). Wildlife harvest refugia must be large enough to support reproduction with sufficient connectivity for successful dispersal into harvested areas (Novaro *et al.* 2000). Wolverines require large home ranges (100–1000 km^2) and their dispersal distances are high (60–500 km; Magoun 1985; Gardner *et al.* 1986; Banci 1987; Flagstad *et al.* 2004; Inman *et al.* 2012a). Thus, harvest refugia must be large enough to support wolverine home ranges and to permit effective dispersal between unharvested and harvested populations.

Identification of harvest refugia, particularly near heavily harvested areas, is important for ensuring that adequate spatial controls are in place to sustain harvest.

Evaluations of the spatiotemporal patterns of wolverine harvest have recently been conducted in Alaska, British Columbia and Alberta (Golden *et al.* 2007a; Lofroth and Ott 2007; Webb *et al.* 2013). This study constitutes the first evaluation of long term wolverine harvest patterns in Yukon, conducted through an examination of wolverine harvest data from 1988 to 2015.

In this chapter, I first examine the temporal patterns of wolverine harvest in Yukon with specific objectives to:

1. Summarize the annual wolverine harvest metrics (the number of wolverines harvested, the number of wolverine trappers, and the number of RTCs reporting wolverine harvest), and examine their relationships and temporal trends. Because most trappers are unlikely to target wolverines due to their rarity, I expect that relatively few fur trappers and RTCs report wolverine harvest in a given year.
2. Explore other factors that may affect the annual fluctuations in wolverine harvest, such as the number of licensed fur trappers, the harvest of other furbearers (lynx and wolf), and pelt prices. I expect that wolverine harvest relates to general fur trapping activity, indicated by annual trapping license sales. I also expect that wolverine harvest may relate specifically to the harvest of lynx and wolf, because their trapping techniques are similar to wolverine trapping, and wolverines may be harvested opportunistically or incidentally by lynx and wolf trappers. I do not expect wolverine harvest to be strongly related to pelt prices, because economic gains may not be an important motivator for many fur trappers.

Second, I explore the spatial distribution of wolverine harvest in Yukon with specific objectives to:

1. Establish the spatial distribution of wolverine harvest in RTCs across Yukon, and visually examine wolverine harvest in relation to roadways, because access may influence the trapping effort of wolverines. I expect that wolverines are harvested more frequently in RTCs near roadways, because road access in Yukon is highly limited.
2. Examine regional patterns of wolverine harvest over time in order to determine regional harvest status. Harvest trends may vary among regions due to differences in harvest effort, wolverine abundance, or both.
3. Examine wolverine harvest by region for negative feedbacks. I hypothesized that harvest success in one year may reduce harvest in the consecutive years, as a result of reduced wolverine abundance.

Finally, I assess the harvest sustainability of wolverines with specific objectives to:

1. Estimate annual harvest rates of wolverine for each region based on annual harvest numbers and a reference wolverine population density. Because wolverine populations are sensitive to over-harvest, regional annual harvest rates >10% may be unsustainable (Krebs *et al.* 2004). Although this method of estimating harvest rates is crude, this approach can provide a warning signal for potential overharvest in the absence of population data, and recommend additional assessments or regulatory actions at a regional scale.

2. Estimate the area of harvest refugia in each region. Harvested wolverine populations may depend on dispersing animals from unharvested areas for their persistence; thus, information on harvest refugia is useful for assessing harvest sustainability.

Methods

Study Area

Wolverines are legally harvested throughout Yukon, Canada. Yukon is approximately 482,000 km^2 with a population of 37,600 people (Yukon Bureau of Statistics 2016). The majority of people (~77 %) are located in the City of Whitehorse. Much of the territory is devoid of human infrastructure or access, and remains largely unfragmented by anthropogenic disturbance. Yukon has a rugged and complex topography, characterized by mountain ranges, plateaus, valleys and lowlands. The climate is subarctic continental, which is relatively dry. The annual precipitation ranges from 250 to 600 mm, which mostly falls as snow from October to May. The temperature varies seasonally, ranging from -15 to -30 °C in January and from 10 to 15°C in July. Much of Yukon is characterized by boreal forest in valley bottoms, and shrub communities and alpine tundra at and above the treeline, respectively (Smith *et al.* 2004).

The wolverine population size in Yukon has been estimated at 4380 (Banci 1987) and 3500–4000 resident animals (COSEWIC 2014), based on habitat suitability estimates and expert opinion. Harvest management is informed by harvest records and trapper questionnaires, which suggested a stable harvest (Slough 2007). Wolverine trapping season extends through the winter from 1 November to 10 March. Approximately 500 fur trapping licenses were sold annually in Yukon between 1988 and 2015. The number of licensed trappers is higher than the number of available trapping concessions because concession holders can have an unlimited number of assistant trappers (but typically only 1 or 2) and group concessions typically have multiple trappers (typically 6–8).

Temporal Patterns of Harvest

I obtained wolverine harvest data from the fur sealing records collected by Yukon Government from 1988 to 2015. Mandatory fur sealing is required for all harvested wolverines, regardless of end use (sale/personal use) or trapper status (First Nation/non First Nation). Each fur sealing record includes the harvest date, trapper name and RTC. These data indicate only legal harvests, and does not include information on unsuccessful attempts to harvest wolverine or the amount of trapping effort. I summarized the annual data for the number of wolverines harvested, the number of trappers that harvested wolverines and the number of RTCs reporting wolverine harvest. I used regression methods to describe trends in time series of these wolverine harvest metrics from 1988 to 2015.

To examine factors that may affect wolverine harvest, I summarized the annual data for several metrics related to fur trapping activity in Yukon, including the number of licensed fur trappers, lynx harvest, lynx pelt price, wolf harvest and wolf pelt price (Environment Yukon, unpublished data). I adjusted the pelt price data for inflation based on the 2014 consumer price index for Canada (Statistics Canada). I examined the relationships among the harvest metrics using correlation analysis, further evaluated their significance with linear regression techniques, and ranked the models using Akaike Information Criterion (AIC). To assess potential lagged effects of pelt price on wolverine harvest, I used cross-correlation analysis to investigate the relationship between stationary time series of wolverine harvest and pelt price (*sensu* Robichaud and Boyce 2010). Because pelt prices fluctuate, trappers do not know the price of their furs prior to the trapping season. Instead, trappers may use price trends from previous year(s) to predict current year's prices and adjust their trapping effort accordingly. I compared annual wolverine harvest to current and previous year's pelt prices. I also compared wolverine harvest to current and previous year's pelt prices for lynx, because lynx is economically the most important furbearer in Yukon and its pelt price may affect trapper effort.

Prior to analyses, I confirmed normality of the response variable (annual wolverine harvest) with the Shapiro-Wilk normality test ($W = 0.956$; $P = 0.30$). I confirmed stationarity of the response variable with autocorrelation function (ACF), which showed no evidence of temporal autocorrelation, which were within the 95% confidence intervals. I used program R (version 3.2.4) for all analyses.

Spatial Patterns of Harvest

I created a spatial dataset of annual wolverine harvest in each RTC from 1988 to 2015, using ArcGIS (ESRI version 10.3.1). Currently, 376 RTCs cover most of the land area in Yukon (95%; approximately 455,000 km^2). The size of an RTC varies from 15 to 35,404 km^2, with a median size of 612 km^2. In order to demonstrate how wolverine harvest frequency relates to access, I created a map of RTCs reporting wolverine harvest in relation to roadways, and inspected their patterns visually.

I used ecoregions to define spatial units for regional analyses. Ecoregions are ecologically distinctive areas that take into account biophysical and climatic conditions at a regional scale (Environment Yukon 2016; Smith *et al.* 2004). Yukon has 25 ecoregions that range in size from approximately 1000 km^2 to 50,000 km^2 with each ecoregion including between 0 to 75 RTCs (Fig. 1). To examine regional wolverine harvest patterns over time, I summarized wolverine harvest in 5-year time periods from 1990 to 2015 (1990–1995, 1995–2000 and so on). For each 5-year time period and ecoregion, I calculated the mean annual harvest density (number of wolverines/1000 km^2) to account for the size differences among ecoregions. I also calculated the mean annual number of RTCs that reported wolverine harvest, in order to compare wolverine trapping effort among ecoregions. In GIS, I created mean annual harvest density maps for each 5-year time period to better understand spatiotemporal patterns of wolverine harvest. I defined 5 harvest density classes for wolverine harvest: very high ($\geq$ 1 wolverine/1000 km^2), high (0.60-0.99 wolverines/1000 km^2), medium (0.30-0.59 wolverines/1000 km^2), low (0.01-0.29) and none (0 wolverines/1000 km^2).

I examined temporal patterns of harvest in ecoregions in time series of annual harvest from 1988 to 2015. I inspected each time series for temporal autocorrelation with an autocorrelation function (ACF) to determine whether wolverine harvest in one year is affected by the harvest in previous year(s). I calculated the ACF over 8 annual time lags.

Harvest Sustainability

I assessed wolverine harvest sustainability in each ecoregion using two measures: 1) an estimation of mean annual harvest rate; and 2) an estimation of area without wolverine harvest (harvest refugia), in each 5-year time period. I estimated mean annual harvest rates based on mean annual number of wolverines harvested and a reference population size estimate. The wolverine population size reference is based on estimates from two regions in Yukon: 5.6 wolverines/1000 km^2 in Kluane in southwestern Yukon (Banci 1987), and 9.7 wolverines/1000 km^2 in Old Crow in northern Yukon (Golden *et al.* 2007b). The former estimate is for the number of resident wolverines (based on radio telemetry), whereas the latter estimate includes the whole population (based on snow tracking). A high proportion of non-resident animals are expected in harvested wolverine populations, because vacant areas created by the removal of resident animals may be filled by dispersing animals, which are typically young males that may remain in the transient population for extended periods of time, even years (Magoun 1985; Inman *et al.* 2012a). Thus, the density of 9.7 wolverines/1000 km^2 may better account for transient animals available for harvest. However, I calculated two harvest rate values based on the two population estimates, in order to provide a reasonably conservative range of values. For comparison, in adjacent jurisdictions wolverine densities were estimated at 7-21 wolverines/1000 km^2 in arctic Alaska (Magoun 1985), 6.5 wolverines/1000 km^2 in northern British Columbia (Lofroth and Krebs 2007) and 6.8 wolverines/1000 km^2 in west-central Alberta (Fisher *et al.* 2013).

I estimated the percent area without wolverine harvest for each ecoregion and time period, in order to represent potential harvest refugia. I included areas that are not designated as RTC (permanent harvest refugia), and those RTCs that reported no wolverine harvest during the 5-year period (temporal *de facto* harvest refugia). I also report the total area (km^2) of potential harvest refugia, because the size of harvest refugia is important for wide-ranging species, such as wolverine.

Results

Temporal Patterns of Harvest

Over the 27 year study period (1988–2015), 3552 wolverines were harvested in Yukon. The annual harvest was 132 ± 31 wolverines (SD), and ranged from 65 to 201 animals per year. The annual wolverine harvest in Yukon varied from year to year, but there was no significant trend over time (β = -0.45, SE = 0.78, r^2 = 0.01, P = 0.57). Total annual wolverine harvest was closely related to the number of RTCs reporting wolverine harvest in a given year (β = 2.15, SE = 0.24, r^2 = 0.76, P < 0.001 (Fig. 2). A mean of 2.3 ± 0.28 wolverines were trapped annually in each RTC, where wolverine harvest occurred, with no significant trend over time (β = -0.001, SE = 0.007, r^2 = 0.001, P = 0.86). The mean annual harvest density ranged from 0.02 to 13.35 wolverines/1000 km^2 among RTCs that reported some wolverine harvest (mean 0.86 ± 1.44 wolverines/1000km^2). No wolverine harvest was reported in 81 trapping concessions during the study period (Fig. 3). Wolverines were harvested at least once during the study period in 293 RTCs, which represents 78% of all RTCs. However, on those RTCs, where wolverine harvest occurred, wolverines were generally not harvested every year; an average of only 58 (16%) RTCs reported wolverine harvest in a given year.

Relatively few trappers harvested most of the wolverines, with 25% of all wolverines in 1988–2015 harvested by the top 3% wolverine trappers (Table 1). The mean annual harvest by most trappers (82%) was ≤ 2.3 wolverines, and most trappers (80%) harvested wolverines from only one RTC. Only 6% of trappers harvested wolverines from ≥ 3 RTCs. The top 6 trappers harvested wolverines from multiple RTCs (n = 27) over 8 to 27 years, indicating that relatively small number of RTCs resulted in most of the harvest. Trappers that regularly harvested a large number of wolverines did so by intensively harvesting different RTCs in different years; sustained harvest of wolverines was not maintained in any RTC. Single season harvest volumes in some RTCs were exceptionally high (>10 wolverines), and translated to harvest densities of 7 – 23 wolverines/1000 km^2.

To examine factors that may affect the annual harvest effort of wolverine, I summarized annual data for the number of licensed trappers, lynx harvest, wolf harvest, and the pelt price of wolverine, lynx and wolf (Appendix 1.). Wolverine harvest, and the number of RTCs reporting wolverine harvest, were significantly correlated with lynx harvest (r = 0.45 and r = 0.56, respectively) and the number of licensed trappers (r = 0.45 and r = 0.72 respectively; Table 2.). A significant correlation (r = 0.74) was also evident between lynx harvest and licensed trappers. Models for the lynx harvest and the number of licensed trappers were also the top ranking models based on AIC (Table 3.). There was no significant relationship between wolverine harvest and wolf harvest (r = 0.02). I found no correlation between wolverine harvest and current wolverine pelt price (r_{25} = 0.235, P = 0.24), or previous year's pelt price (r_{24} = 0.045, P = 0.82).

Similarly, I found no correlation between wolverine harvest and current lynx pelt price (r_{25} = 0.018, P = 0.93) or previous year's lynx pelt price (r_{24} = 0.120, P = 0.56).

Spatial Patterns of Harvest

Those RTCs that reported frequent wolverine harvest (wolverines harvested during ≥ 15 harvest seasons during 1988–2015) were located near roadways in Yukon (Fig. 4). Conspicuous patterns in the spatial distribution of wolverine harvest by ecoregion, during 1988–2015, were evident (Fig. 5). More wolverines were harvested in southwestern Yukon than eastern and northern Yukon. No wolverine harvest was reported for several ecoregions in far northern Yukon; however, unreported subsistence harvest by local First Nations may have occurred. As expected, the total harvest in each ecoregion was significantly related to the number of RTCs in each ecoregion (β = 8.8, SE = 1.2, r^2 = 0.78, P < 0.001). The largest number of wolverines harvested (n = 713) originated from Southern Lakes ecoregion, which has the largest number of RTCs (n = 75). These RTCs are also smaller on average than those in other ecoregions (mean size 388 ± 262 km^2 [SD]; Table 4). Consistent wolverine harvest occurred in 16 ecoregions, which I used for further analyses of the spatiotemporal patterns of harvest.

Temporal correlograms for ecoregions indicated that the change in wolverine harvest in consecutive years, or the other time lags evaluated, were not autocorrelated in most ecoregions (ACF values within ± 0.385; 95% CI; Appendix 2), except in Southern Lakes ecoregion, where a negative autocorrelation at lag 1 was significant (ACF -0.545; Fig. 6.). A significant autocorrelation suggests that increased harvest in one year is related to a decrease the following year, or vice versa.

Wolverine harvest density was consistently high in western Yukon, in the area roughly delineated by the Shakwak and Tintina Trenches, in Klondike Plateau, Wellesley Lake, Ruby-Nisling Ranges, Yukon Plateau Central, Southern Lakes, Yukon Stikine Highlands and Pelly Mountains ecoregions (Fig. 7–11.). The mean annual harvest density was the highest in southwestern Yukon in all 5-year time periods (> 0.59 wolverines/1000 km^2), whereas harvest density remained low in eastern and northern Yukon (0.0–0.29 wolverines/1000 km^2). Overall, harvest densities were lowest in 1995–2000 and highest in 2010–2015 (Fig. 7–11.). The mean annual harvest density over all time periods and ecoregions was 0.37 ± 0.26 (SD) wolverines/1000 km^2. Most ecoregions did not exhibit a significant trend in mean annual harvest density over time (Fig. 12–15.). A statistically significant trend was evident in Wellesley Lake and Ruby-Nisling Ranges, where harvest increased over the consecutive 5-year time periods from 1990 to 2015 (β=0.13, SE=0.06, $P = 0.05$; $\beta = 0.7$, SE = 0.23, $P < 0.01$, respectively; Fig. 15.), and McQuesten Highlands and Yukon Plateau North where harvest decreased ($\beta = -0.37$, SE = 0.13, $P < 0.01$; $\beta = -0.33$, SE = 0.09, $P = 0.001$, respectively; Fig. 13.). The highest mean annual harvest densities occurred in Ruby-Nisling Ranges, Southern Lakes and Wellesley Lake (0.94, 0.89 and 0.74 wolverines/1000 km^2, respectively). The lowest harvest densities occurred in North Ogilvie Mountains, Hyland Highland, MacKenzie Mountains and Selwyn Mountains (0.09, 0.14, 0.15 and 0.17 wolverines/1000 km^2, respectively).

Harvest Sustainability

I estimated the mean annual harvest rate (% of population harvested) in each 5-year time period for 16 ecoregion that reported at least one wolverine harvest annually (Table 5). Most ecoregions (*n* = 11) had consistently low estimated harvest rates (1–6%). None of the ecoregions in eastern or northern Yukon had annual harvest rate estimates > 10%, which I used as an approximation of potential overharvest (Weaver *et al.* 1996; Banci and Proulx 1999). Harvest rates >10% were estimated for 3 ecoregions in southwestern Yukon over more than one time period, including Ruby-Nisling Ranges, Wellesley Lake and Southern Lakes. The estimated annual harvest rates were particularly high in the recent 15 years in Ruby-Nisling Ranges (11–24%).

For 14 ecoregions with consistent harvest, I estimated the percent area and total area without harvest for each 5-year time period. I was not able to estimate unharvested area for the two large group trapping areas (RTC 405 and RTC 401 [Old Crow Basin / Davidson Mountains ecoregion]), because the actual areas that are harvested within these large group RTCs are unknown. The mean percent area without wolverine harvest among ecoregions over all time periods was 62 ± 16% (SD). The mean percent area without wolverine harvest initially increased in 1995–2000 and then decreased in subsequent time periods (59 ± 15% in 1990–1995; 66 ± 13% in 1995–2000; 63 ± 13% in 2000–2005; 62 ± 19% in 2005–2010; and 57 ± 14% in 2010–2015). The percent area and total area without wolverine harvest among ecoregions and time periods varied (Fig. 16–18.). The largest mean percent area without wolverine harvest were in northern Yukon (North Ogilvie Mountains and Mackenzie Mountains; 78% and 75%, respectively), in southwestern Yukon in Yukon-Stikine Highlands (76%), which has a large proportion of its area formally protected, and in eastern Yukon (Liard Basin; 73%). The smallest percent area without wolverine harvest were in western Yukon (Klondike Plateau 43%; Ruby-Nisling Ranges 48 %; Wellesley Lake 50% and Southern Lakes 51%; Fig. 19). The total area without wolverine harvest varied among ecoregions and time periods (range 883–37,204 km^2). Total area without wolverine harvest was highest in the large ecoregions in northern Yukon (32,058 km^2 in North Ogilvie Mountains and 25,034 km^2 in Mackenzie Mountains), and smallest in the small ecoregions in southwestern Yukon (2,170 km^2 in Wellesley Lake and 5,101 km^2 in Yukon-Stikine Highlands; Fig. 16–18), which also have some of the highest harvest rates.

Discussion

This was the first study in Yukon to examine wolverine harvest since the 1980s, and the first study to date to examine wolverine harvest in the context of harvest management and sustainability in Yukon. This work is important because wolverine is considered vulnerable to over-harvest, which is one of the main threats to wolverine populations worldwide. Because wolverines are harvested without quota in Yukon, understanding and monitoring the threats to harvest sustainability are important for advancing management of this species.

Temporal Patterns of Harvest

My results indicate that wolverine harvest in Yukon has been relatively stable over the last three decades. Temporal analyses did not reveal an overall increasing or decreasing trend in harvest data. The annual harvest related strongly to the number of traplines reporting wolverine harvest, and the mean annual number of wolverines taken per trapline remained steady.

Wolverine harvest was positively related to lynx harvest and the number of licensed trappers. In general, fluctuations in wolverine harvest reflect changes in wolverine trapping effort, which likely follows the overall fur trapping activity and trapline utilization patterns in Yukon. Wolverine harvest was not significantly correlated with the pelt price, despite the high value of wolverine pelts. Because wolverine pelt price has remained relatively steady over the years, there may have been insufficient opportunity to determine whether this affects trapper motivation to harvest wolverines. Regardless, the natural low density of wolverines likely limits the annual economic gains to most trappers.

Contemporary fur trapping in many regions in North America is considered largely a recreational activity. Fewer trappers are actively setting traps and the mean age of trappers has increased (Yukon Fish and Wildlife Management Board 2005; Zwick *et al.* 2006; Dorendorf *et al.* 2016). Trapper motivations, and the time and effort spent on trapping, likely vary in Yukon among user groups (*e.g.,* subsistence vs. outdoor recreation, First Nation vs. other), external factors (*e.g.,* economic or environmental conditions) and their interactions (Stabler *et al.* 1990; Daigle *et al.* 1998; Banci and Proulx 1999; Yukon Fish and Wildlife Management Board 2005; Zwick *et al.* 2006; Brinkman *et al.* 2014; Dorendorf *et al.* 2016). Wolverine harvest in Yukon appears to be mostly an irregular activity (but a regular activity to a few trappers) as only approximately 13 % of licensed trappers harvested a wolverine in a given year. In the Yukon fur trapping community, wolverines are often considered a "bonus" species, whose harvest numbers increase with increased trapper activity, but they are too sparsely distributed on the landscape to be a primary target (Yukon Department of Environment 2008). My study largely confirms this. The majority of trappers harvested wolverines infrequently, and when they did, it was in low numbers (1–2 wolverines). However, a few trappers harvested a disproportionately high number of wolverines, indicating focused wolverine trapping behavior. Four broad types of trapper behaviour became apparent in the data: 1) short term/low volume trappers that harvested 1 or 2 wolverines only once or twice in one concession; 2) long term/low volume trappers that harvested 1 or 2 wolverines regularly in one concession; 3) short term/high volume trappers that harvested many wolverines once in one concession; 4) long term/high volume trappers that harvested many wolverines frequently, but in different concessions. The majority of trappers belonged to the first two categories that could be described as opportunistic or conservative wolverine trappers, whereas the minority of trappers in the last two categories could be described as intensive or focal wolverine trappers. The Yukon Trapper Education program, which is a mandatory training program for new trappers, encourages trappers to harvest wolverines conservatively in order to sustain the local wolverine population, and most wolverine trappers appeared to practice stewardship on their traplines. In contrast, focal wolverine trappers likely harvested wolverines intensively on one trapline, and then moved into different traplines in the following years. The exceptionally high single-season harvest volumes of 7–23 wolverines/1000 km^2 in some RTCs indicate that wolverine densities may have been locally high.

Fur trapping activity in Yukon, based on trapping license sales, declined sharply in the early 1990s, stabilized at lower levels until the late 2000s, and has increased since then. My analyses of annual harvest density in 5-year time periods appears to align with this pattern, as the wolverine harvest density was the lowest in 1995–2000 and increased in subsequent time periods. The highest annual harvest densities occurred in the most recent time period of 2010–2015. However, a small number of trappers harvested most of the wolverines, and their influence on harvest patterns is disproportionately high as a result. For example, only two trappers harvested 37% of wolverines in Ruby-Nisling Ranges, and two different trappers harvested 82%

of wolverines in MacKenzie Mountains, in 2010–2015. Thus, both the number of wolverine trappers, and individual trapper behavior, may affect spatiotemporal harvest patterns on a regional scale. A specific study on trapper motivations (opportunistic versus focal wolverine trappers) would be valuable for improving the understanding of their effect on the spatiotemporal patterns of wolverine harvest.

Spatial Patterns of Harvest

The wolverine harvest in Yukon is concentrated in southwestern Yukon, particularly in Southern Lakes and Ruby-Nisling ecoregions. The harvest densities were consistently high in southwestern Yukon, and consistently low in eastern and northern Yukon during all time periods. The spatial heterogeneity of harvest may be explained by regional differences in wolverine abundance, harvest effort, or a combination. While wolverine ranges throughout Yukon, their abundance likely varies spatially based on habitat suitability. Wolverines are habitat generalists, highly mobile and opportunistic in their feeding habits (Banci 1987; Magoun 1985; Lofroth *et al.* 2007; van Dijk *et al.* 2008); thus, they can occupy a diversity of habitats that support scavenging or hunting opportunities. Several species of ungulates and other prey, such as snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), arctic ground squirrel (*Urocitellus parryii*) and other small game, are common throughout Yukon. Their abundance likely varies spatially and temporally based on species-specific habitat requirements, population fluctuations (*e.g.* the snowshoe hare cycle) and seasonal movement patterns (*e.g.* caribou migrations). The main diet items for wolverine in Yukon are ungulates (moose [*Alces americanus*] and caribou) and snowshoe hare (Robitaille *et al.*, unpublished data). Caribou density, on a coarse scale, is relatively similar in all regions of Yukon, except for the north where migratory caribou may seasonally occur at high densities. Coarse scale moose density in southwestern Yukon is generally similar or lower than in eastern and central Yukon (Environment Yukon, unpublished data). Snowshoe hare density fluctuates throughout Yukon in 9–10 year cycles but regional densities are similar (Krebs *et al.* 2014; Powell *et al.* 2013). Thus, it is unlikely that food abundance contributes to high wolverine abundance in southwestern Yukon relative to other regions, although food abundance is likely locally heterogeneous across the landscape.

Despite being habitat generalists, certain habitat characteristics may be important to the biology of wolverines. Denning female wolverines may prefer rugged high elevation subalpine habitats (Magoun and Copeland 1998), in order to protect their offspring from male wolverines and other predators, such as wolves, that tend to use lower elevation habitats (Lofroth *et al.* 2000). Female wolverines typically dig their dens in snow in late winter (Magoun and Copeland 1998; Pulliainen 1968), and persistent spring snow cover is potentially important for their reproductive success (Copeland *et al.* 2010). Snow typically persists longer in high altitudes. However, wolverines appear to be relatively abundant and successfully breeding in areas where spring snow cover is irregular (Aronsson and Persson 2016) and where the landscape is largely flat, such as northern Alberta (Webb *et al.* 2016). It is unlikely that high elevation habitats and spring snow cover are limiting factors in Yukon, because snow persists until late spring in most areas, particularly in subalpine or alpine habitats, which are commonly available in most ecoregions. Thus, it is unlikely that ruggedness and spring snow cover explain high wolverine harvest densities in southwestern Yukon relative to other regions. However, without accurate data on wolverine trapping effort, attempts to explain spatial harvest patterns by potential differences in wolverine abundance is difficult.

The relatively high wolverine harvest density in southwestern Yukon may be explained by trapping effort. A large number of RTCs report harvest in the southwest, compared to other regions. RTCs in southwestern Yukon are more numerous and smaller than those in other regions (harvested ecoregions in southwestern Yukon include approximately 45% of all RTCs but only approximately 20% of total land area), indicating that the harvest pattern might be due to higher densities of trappers in the landscape. The majority of human population is also located in western Yukon in the communities of Whitehorse, Dawson and Haines Junction, and their populations have steadily increased over recent years, (Yukon Bureau of Statistics 2016). In contrast, eastern and northern Yukon is less populated, and the population in the main community, Watson Lake, has decreased over the years (Yukon Bureau of Statistics 2016). Road access in Yukon is limited and large areas are remote, making access to traplines difficult. Frequently harvested RTCs appear to align near roads, which are mostly located in western Yukon.

Mean annual harvest densities of wolverine were relatively low and appeared stable over time in most ecoregions. However, relatively high annual harvest densities (> 0.59 wolverines/1000 km^2; > 10% estimated harvest rates) occurred in all harvested ecoregions in the southwest during the most recent time period of 2010–2015. Currently, approximately 50% of RTCs in southwestern Yukon report wolverine harvest, indicating space to grow within the current regulatory framework. However, the current harvest levels may impact wolverine populations in Southern Lakes ecoregion, because years of high wolverine harvest were followed by a decreased harvest, indicating potential harvest-related decrease in wolverine abundance.

Harvest Sustainability

The estimated mean annual harvest rates were low (1–5%) in ecoregions located in northern and eastern Yukon, through all 5-year time periods. At these harvest rates, wolverine populations may remain stable even without immigration (≤ 6%; Krebs *et al.* 2004). In addition, large proportions of the area (> 50%) in northern and eastern ecoregions were unharvested, and these areas were large in size (> 10,000 km^2 and up to 38,000 km^2), presumably capable of maintaining viable wolverine source populations. Light harvest, combined with large extents of land without harvest (refugia), support harvest sustainability in these regions. Further, adjacent areas in Alaska and Northwest Territories are mostly undeveloped and remote, presumably maintaining population connectivity. The lack of genetic structure between wolverine populations in northern Alaska and Northwest Territories supports this claim (Kyle and Strobeck 2001; Tomasik and Cook 2005). Because much of eastern and northern Yukon is remote and individual RTCs are large in size, regional overharvest in near future is unlikely. However, future land use activities may increase the utilization of remote RTCs by creating access. Minimizing road access to pristine, remote areas is likely the most important land use planning tool for maintaining extensive *de facto* harvest refugia.

High mean annual harvest rates (> 10%) were observed solely in ecoregions located in southwestern Yukon; particularly, Ruby-Nisling Ranges exhibited high estimated mean annual harvest rates (11–24%) in the last 15 years. Adjacent ecoregions of Wellesley Lake and Southern Lakes also exhibited high harvest rates (>10%). The sustained high harvest rates may be supported by dispersing animals from unharvested areas within and around these ecoregions. Banci (1987) estimated a population density of 5.6 wolverines/1000 km^2 for this region. If the population density estimate is accurate, the harvest rates currently experienced in this area would not be possible without a significant immigration of wolverines from unharvested areas.

Dispersing animals are typically young males, and they are often harvested more than other sex and age classes (Magoun 1985). I show in Chapter III that young males dominate the wolverine harvest in Yukon. Transient wolverines may sustain the wolverine harvest, particularly in southwestern Yukon, where harvest rates appear to exceed local wolverine productivity. Monitoring of demographic rates is traditionally used to evaluate sustainability of harvest, but because wolverine populations in harvested areas may display source-sink dynamics, harvest refugia should be considered for wolverine and other highly mobile carnivores (McCullough 1996, Novaro *et al.* 2001; 2005; Stoner *et al.* 2013). It is possible that many harvested species can tolerate high harvest rates as a result of a heterogeneous distribution of harvest pressure (Novaro 1995; Novaro *et al.* 2000). For sensitive species, such as wolverine, harvest refugia may be crucial for the sustainability of harvest (Krebs *et al.* 2004).

Few studies illuminate what constitute adequate wolverine harvest refugia, although harvest refugia are considered possibly the single most important landscape planning mechanism for the conservation of wolverine populations. Krebs *et al.* (2004) postulate, based on estimated growth rates and decline rates in unharvested and harvested populations, that refugia need to cover twice as much similarly productive wolverine habitat as harvested areas, particularly in regions where wolverine populations are isolated (typically in the southern extent of wolverine range where habitat is fragmented), and that in continuous populations, such as those in northwestern Canada and Alaska, a system of spatial controls of trapped and large untrapped areas may ensure long-term persistence of wolverine.

Availability of adequate harvest refugia is particularly important in southwestern Yukon, due to relatively high wolverine harvest densities, potentially increasing harvest trends, and the concentration of human population, which is increasing. In the most recent time period (2010 – 2015), the amount of unharvested area was 6,611 km^2 in Ruby-Nisling Ranges (35%), 1,468 km^2 in Wellesley Lake (34%), and 4,743 km^2 in Yukon-Stikine Highlands (71%). If considered in isolation, the first two ecoregions would be unlikely to support sustained high annual harvest rates, with only 35% of their area as temporal harvest refugia, whereas a large section of Yukon-Stikine Highlands is permanently protected. All three ecoregions are located adjacent to an extensive, continuous protected area consisting of Kluane National Park and Game Sanctuary (27,554 km^2), Tatshenshini-Alsek Provincial Park (9,580 km^2), Glacier Bay National Park (13,045 km^2) and Wrangell - St. Elias National Park (19,700 km^2). This massive protected area, in addition to temporal *de facto* harvest refugia within the harvested ecoregions, has likely acted as wolverine population sources for the harvested areas. On the other hand, Southern Lakes and Yukon Plateau Central are not located near extensive protected areas, and they likely rely on temporal *de facto* harvest refugia to sustain harvest. In the most recent time period (2010–2015), the amount of unharvested areas was 16,459 km^2 in Southern Lakes (57%) and 11,011 km^2 in Yukon Plateau Central (53%). Even though unharvested areas constituted just over half of the total area in these ecoregions, their size appear large enough to maintain wolverine source populations. However, their distribution within the ecoregions is fragmented and their existence subject to annual change depending on trapper activity. These ecoregions may become vulnerable to wolverine over-harvest, if trapper activity, and consequently, wolverine harvest pressure, increases.

Controlling temporal *de facto* harvest refugia in regions that experience high annual harvest rates may be an effective management tool for wolverine harvest (*e.g.* through rotating temporary closures; Squires *et al.* 2007), in order to allow new occupation and successful breeding in previously harvested areas. Time to reoccupation is largely unknown and likely depends on surrounding wolverine density. A study of unharvested wolverine populations in Sweden (Aronsson 2009) found that it usually took less than a year for female territories to be reoccupied after the death of a resident female, and that the vacated areas were occupied by new individuals (typically daughters of the deceased female), rather than absorbed by neighboring territories. Territorial inheritance likely reduces the time to reoccupation, but it may increase the time to next reproduction within the vacated territory, if the new occupants are young. Female wolverines become reproductively mature by 2 years of age (Banci and Harestad 1988), but prime reproduction age is not reached until about 4 years old (Persson 2005; Rauset *et al.* 2015; Chapter III in this thesis). Territorial inheritance has not been documented for males. However, reoccupation of vacant territories in harvested populations may be faster if the local population is able to supply new territory holders (assuming that some breeding females survive and reproduce), than if it depends on immigration from more distant populations.

Consistently low harvest densities in most parts of Yukon suggest a sustainable harvest on a territorial scale. Wolverine harvest levels could potentially grow; for instance, in the early 2000s, wolverine harvest was approximately 70% of 1980s harvest levels, and 35% of the historic highs, which occurred in the 1920s (Department of Environment 2008). However, the sustainability of historic harvest levels is largely unexamined. Banci 's (1987) examination of wolverine harvest during 1952 –1982 did not indicate wolverine population declines during that time, but she reported a very high number of traplines without wolverine harvest (76–94%). Yukon experienced severely reduced fur harvest levels after a period of very high fur prices in the 1980s. Subsequent reductions in harvest levels were assumed to be related to reduced trapper activity rather than long term animal population declines, because they applied to all furbearer species (Department of Environment 2008). However, if fur prices increased significantly, furbearer harvest levels could increase again.

Continued monitoring of wolverine harvest patterns is particularly important if trapper activity continues to increase. Harvest data collection and monitoring is critical for wolverine because population data are lacking. A more detailed assessment of harvest sustainability, supported by field studies of wolverine populations and productivity, is recommended in southwestern Yukon, particularly if harvest pressure on wolverine continues to increase. Further, the potential cumulative effects of climate change and land use activities, particularly with respect to wolverine denning habitat, are largely unknown and may warrant further study, in order to develop appropriate conservation strategies for wolverine populations in Yukon.

Table 1. Wolverine (*Gulo gulo*) harvest by individual trappers in Yukon during 1988–2015. Most trappers (79%) harvested <10 wolverines over the study period. A few trappers (*n* = 18), representing 3% of all trappers, harvested 25% of all wolverines.

Wolverine harvest volume by individual trappers	Number of individual trappers	Annual harvest volume by an individual trapper (mean)	% of total harvest volume	% of individual trappers
> 50	6	2.6 – 11.1 (4.7)	12	1
30 – 49	12	1.8 – 6.2 (2.9)	13	2
10 – 29	90	1.4 – 14.0 (2.8)	42	17
3 – 9	176	1.0 – 7.0 (1.9)	25	33
1 – 2	246	1.0 – 2.0 (1.1)	9	46

Table 2. Pearson's Product-moment correlations between wolverine (*Gulo gulo*) harvest metrics and the number of licensed trappers, lynx (*Lynx canadensis*) harvest, wolf (*Canis lupus*) harvest and their pelt prices in Yukon during 1988–2015. Strong correlations ($P < 0.05$) are indicated in bold font.

	Wolverine harvest	RTCs*) reporting wolverine harvest	Licensed trappers
RTCs*) reporting wolverine harvest	**0.87** ***(p<0.001)***		
Wolverine pelt price	0.23 *(p=0.24)*	0.03 *(p=0.89)*	
Licensed trappers	**0.45** ***(p=0.02)***	**0.72** ***(p<0.001)***	
Lynx harvest	**0.46** ***(p=0.01)***	**0.56** ***(p=0.002)***	**0.74** ***(p<0.001)***
Lynx pelt price	0.02 *(p=0.93)*	0.14 *(p=0.48)*	**0.44** ***(p=0.02)***
Wolf harvest	0.02 *(p=0.94)*	0.08 *(p=0.68)*	-0.13 *(p=0.53)*
Wolf pelt price	0.11 *(p=0.60)*	0.04 *(p=0.84)*	-0.11 *(p=0.58)*

* Registered Trapping Concessions.

Table 3. Linear regression models for annual wolverine (*Gulo gulo*) harvest in Yukon during 1988–2015. Models are ranked from lowest to highest Akaike's Information Criterion (AIC). Significant models are indicated in bold font ($P < 0.05$; $\Delta AIC < 2$).

Model	R^2	β	SE	P	AIC	ΔAIC
Lynx harvest	0.216	0.035	0.013	**0.01**	260.98	0
Licensed trappers	0.199	0.149	0.060	**0.02**	261.55	0.57
Wolverine pelt price	0.055	0.135	0.149	0.94	266.00	5.02
Wolf pelt price	0.011	0.065	0.122	0.60	267.23	6.25
Lynx pelt price	0.000	0.000	0.008	0.93	267.52	6.54
Wolf harvest	0.000	0.012	0.112	0.24	267.52	6.55

Table 4. Yukon ecoregions, registered trapping concessions (RTCs), and total wolverine (*Gulo gulo*) harvest during 1988–2015. Highlighted regions (n = 16) had some wolverine harvest annually, and these regions were used for further spatiotemporal analyses of wolverine harvest.

Ecoregion	**Area (km^2)**	**Number of RTCs**	**Mean size of RTC (km^2)**	**Total wolverine harvest (1988-2015)**
Yukon & Tuktoyuktuk Coastal Plain	12084	-	-	NA*)
Peel River Plateau & Fort McPherson Plain	22281	-	-	NA*)
British-Richardson Mountains	19490	-	-	NA*)
Old Crow Basin & Davidson Mountains a)	20430	1	20430	114
Eagle Plains	21985	-	-	0
North Ogilvie Mountains	41171	7	2661	96
MacKenzie Mountains	33480	16	2092	148
McQuesten Highlands	25457	27	942	188
Klondike Plateau	36968	33	1120	349
Yukon Plateau North	28992	33	906	189
RTC 405 b)	35404	1	35404	236
Selwyn Mountains	24054	14	1718	119
Pelly Mountains	34613	40	865	343
Yukon Plateau Central	20710	45	460	270
Ruby-Nisling Ranges	19059	30	635	468
Wellesley Lake	4349	6	725	81
St. Elias Mountains	15162	1	840	10
Mt. Logan	12392	-	-	0
Yukon-Stikine Highlands	6676	8	544	78
Yukon Southern Lakes	29129	75	388	713
Liard Basin	14675	23	638	78
Hyland Highland	17753	12	1479	69
Muskwa Plateau	642	1	642	0

a) Includes the harvest from group trapping concession (RTC 401) for the community of Old Crow.

b) Group trapping concession (RTC 405) extends over Yukon Plateau North and Selwyn Mountains, but it is treated separately in our analyses due to its large size.

*) Wolverine harvest marked as 'NA' in the Ecoregions in northern Yukon indicates unknown wolverine harvest due to potential unreported subsistence harvest by northern First Nations.

Table 5. Mean annual wolverine (*Gulo gulo*) harvest rate (%) estimates in harvested ecoregions in Yukon averaged over 5-year time periods from 1990 to 2015. Highlighted cells indicate time periods when harvest rates were ≥ 10%.

Ecoregion	Wolverine population estimate (a range)*	Harvest rate estimate (%; a range)				
		1990-1995	1995-2000	2000-2005	2005-2010	2010-2015
Old Crow Basin & Davidson Mountains	114-198	3 - 4	3 - 5	2 - 4	0 - 1	2 - 4
North Ogilvie Mountains	230-399	1 - 2	1 - 2	0 - 1	1 - 2	0 – 1
MacKenzie Mountains	187-325	2 - 3	1 - 2	3 - 5	0 - 1	2 – 3
McQuesten Highlands	143-247	4 - 8	2 - 4	3 - 4	1 - 3	2 - 3
Klondike Plateau	207-359	5 - 8	2 - 4	4 - 7	4 - 7	3 - 6
Yukon Plateau North	162-281	3 - 6	3 - 5	2 - 3	2 - 3	2 – 4
RTC 405	198-343	2 - 4	3 - 5	3 - 5	2 - 4	2 – 4
Selwyn Mountains	135-233	2 - 3	2 - 3	1 - 2	1 - 3	3 - 5
Pelly Mountains	194-336	4 - 7	4 - 6	4 - 7	3 - 5	3 - 6
Yukon Plateau Central	116-201	8 - 13	2 - 4	4 - 7	3 - 6	7 - 12
Ruby-Nisling Ranges	107-185	6 - 10	7 - 12	11 - 19	11 - 19	14 – 24
Wellesley Lake	24-42	1 - 2	7 - 12	12 - 21	10 - 17	8 - 13
Yukon-Stikine Highlands	37-65	6 - 10	2 - 4	4 - 7	4 - 7	6 - 11
Yukon Southern Lakes	163-283	10 - 18	9 - 15	9 - 15	10 - 17	8 - 14
Liard Basin	82-142	1 - 2	3 - 4	2 - 3	2 - 4	3 - 5
Hyland Highland	99-172	1 - 2	2 - 4	2 - 3	0 - 1	1 - 2

*) Based on wolverine population estimates of 5.6 wolverines/1000km^2 (Banci 1987) and 9.7 wolverines/1000km^2 (Golden *et al.* 2007b) in Yukon, and adjusted to the area size of each region.

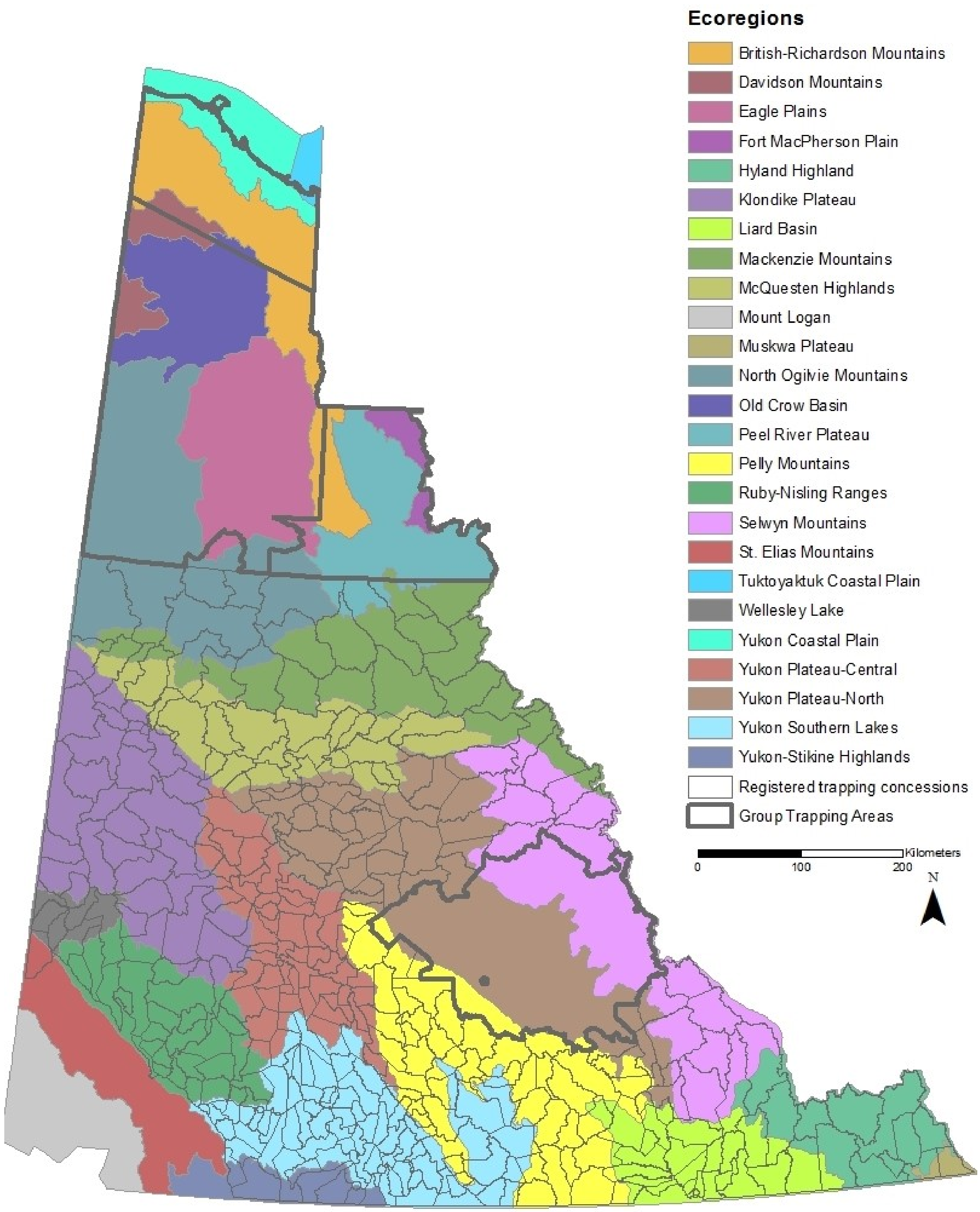

Figure 1. Ecoregions and Registered Trapping Concessions (RTCs) in Yukon.

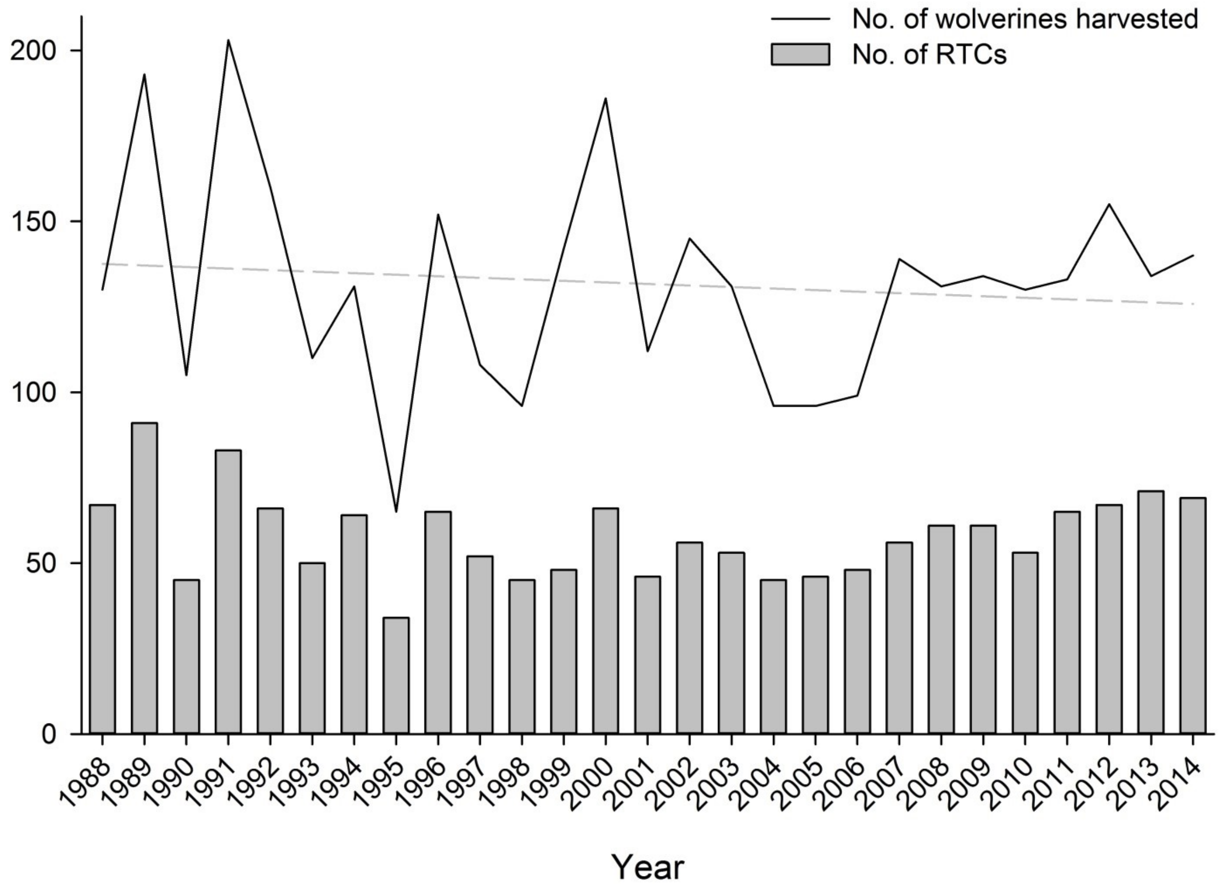

Figure 2. Annual wolverine (*Gulo gulo*) harvest and total number of Registered Trapping Concessions (RTCs) reporting wolverine harvest in Yukon from 1988 to 2015.

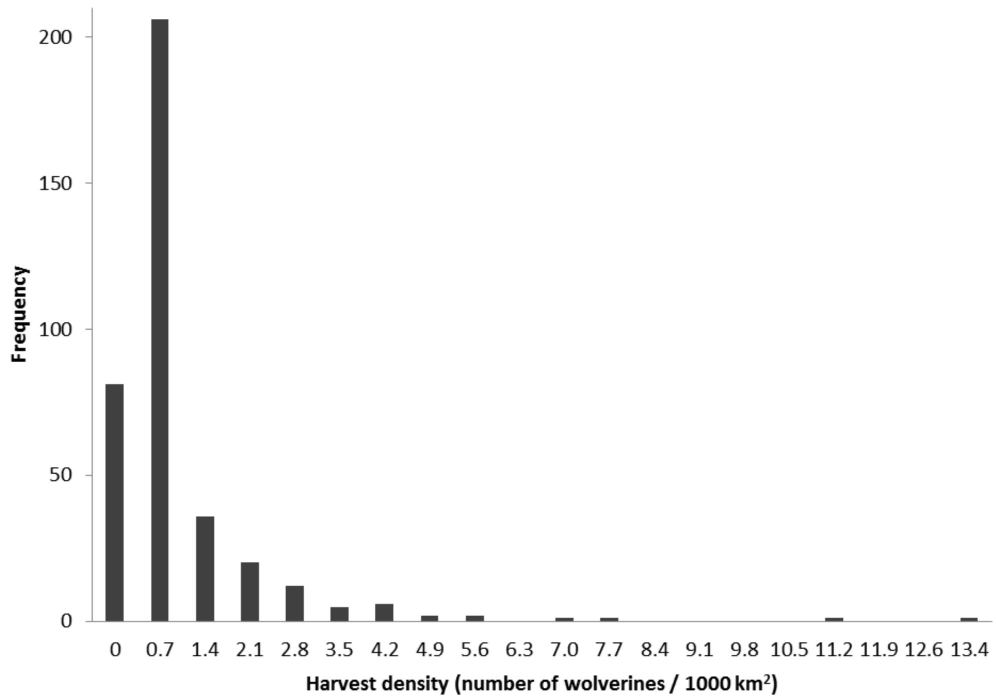

Figure 3. Frequency distribution of mean annual wolverine (*Gulo gulo*) harvest densities (wolverine harvested/1000 km^2) in Registered Trapping Concessions (n = 374) in Yukon during 1988–2015.

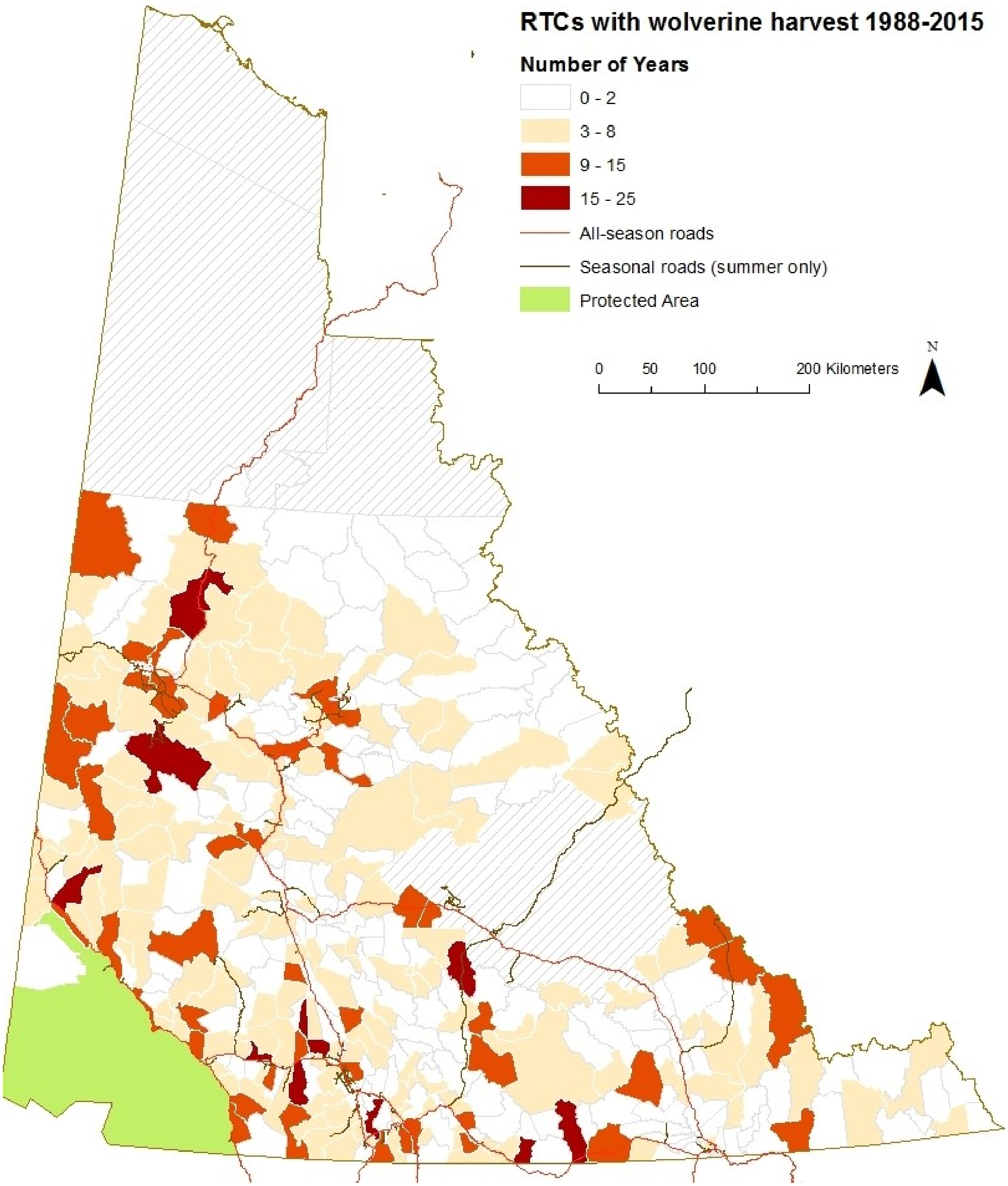

Figure 4. Distribution of Registered Trapping Concessions that reported wolverine (*Gulo gulo*) harvest during 1988–2015 in Yukon, in relation to roadways. Hatched areas indicate large group RTCs, where the specific harvest locations are not known in relation to roadways.

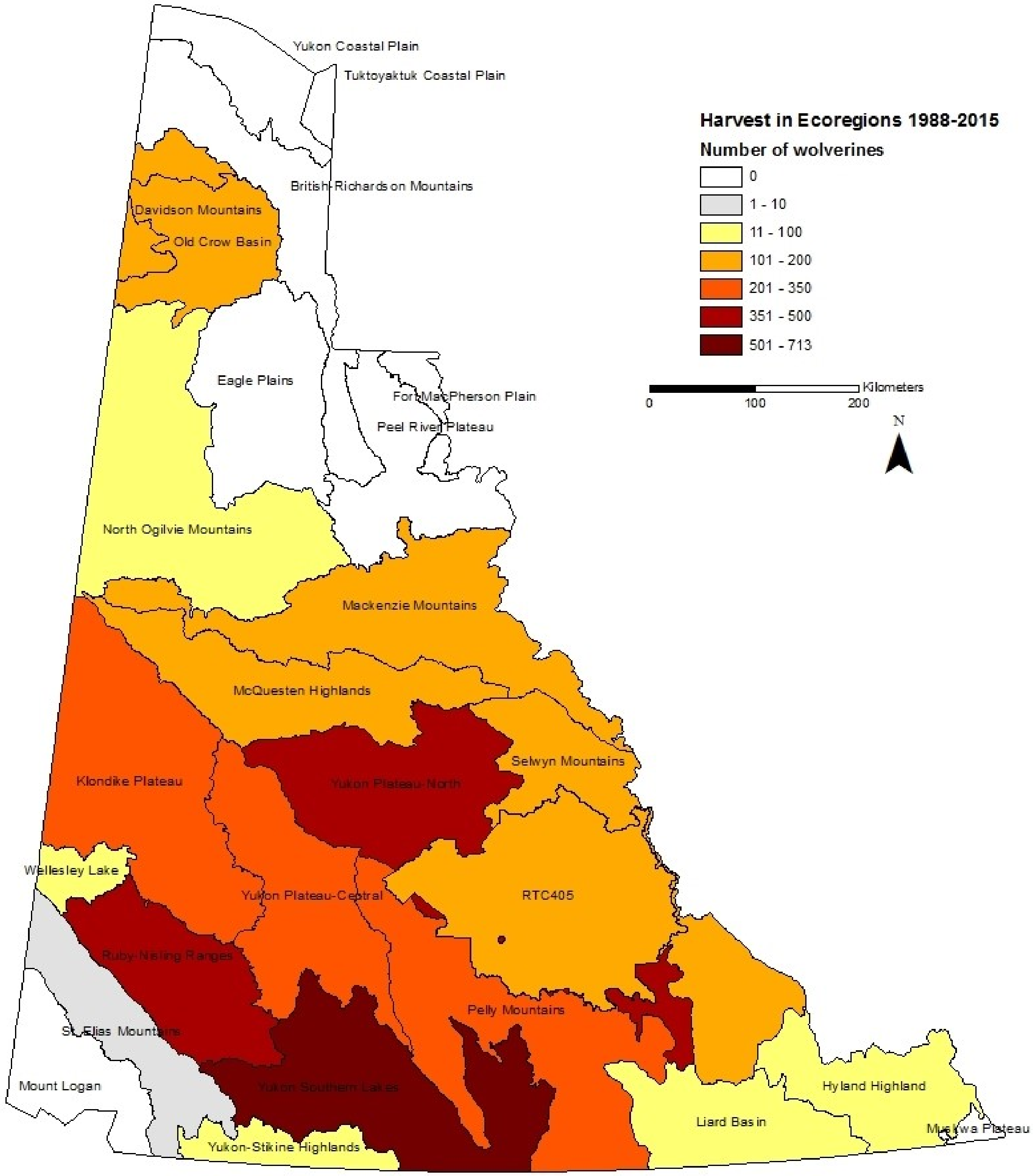

Figure 5. The total number of wolverines (*Gulo gulo*) harvested (n = 3552) in Yukon during 1988–2015 by ecoregion. RTC 405 was treated separately from ecoregions, because the specific wolverine harvest locations within this large RTC are unknown, and thus, not possible to assign to respective ecoregions.

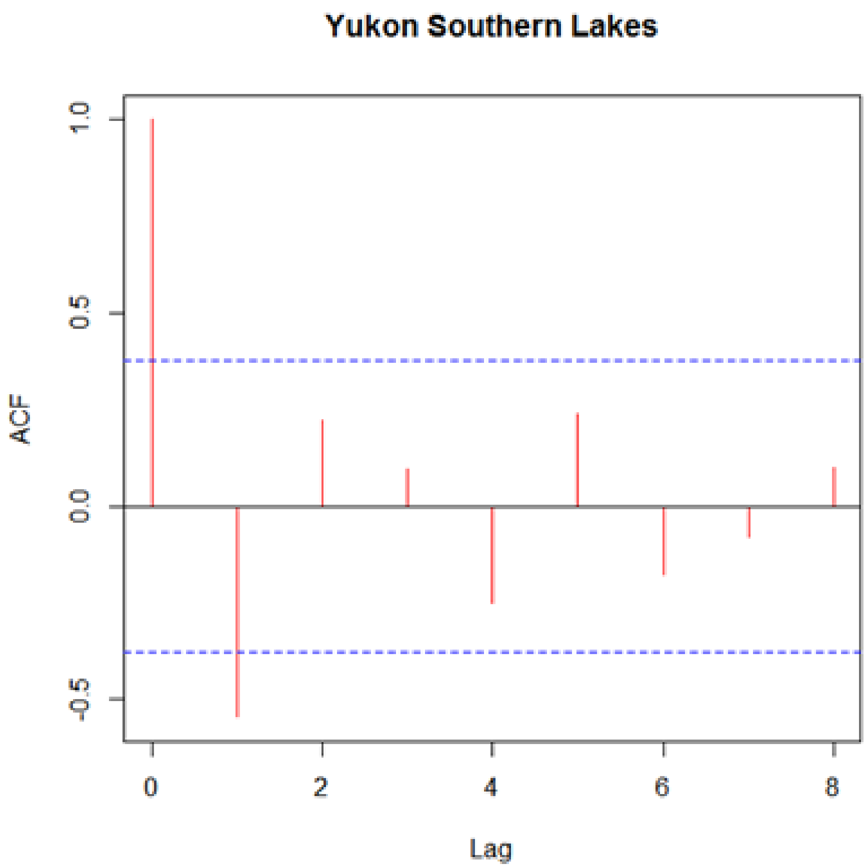

Figure 6. Correlogram of temporal autocorrelation function (ACF) values over 8 time lags for wolverine (*Gulo gulo*) harvest in Yukon Southern Lakes Ecoregion during 1988–2015 (27 years). Blue dotted lines indicate 95% confidence intervals (± 0.385). Significant negative autocorrelation is evident at lag 1.

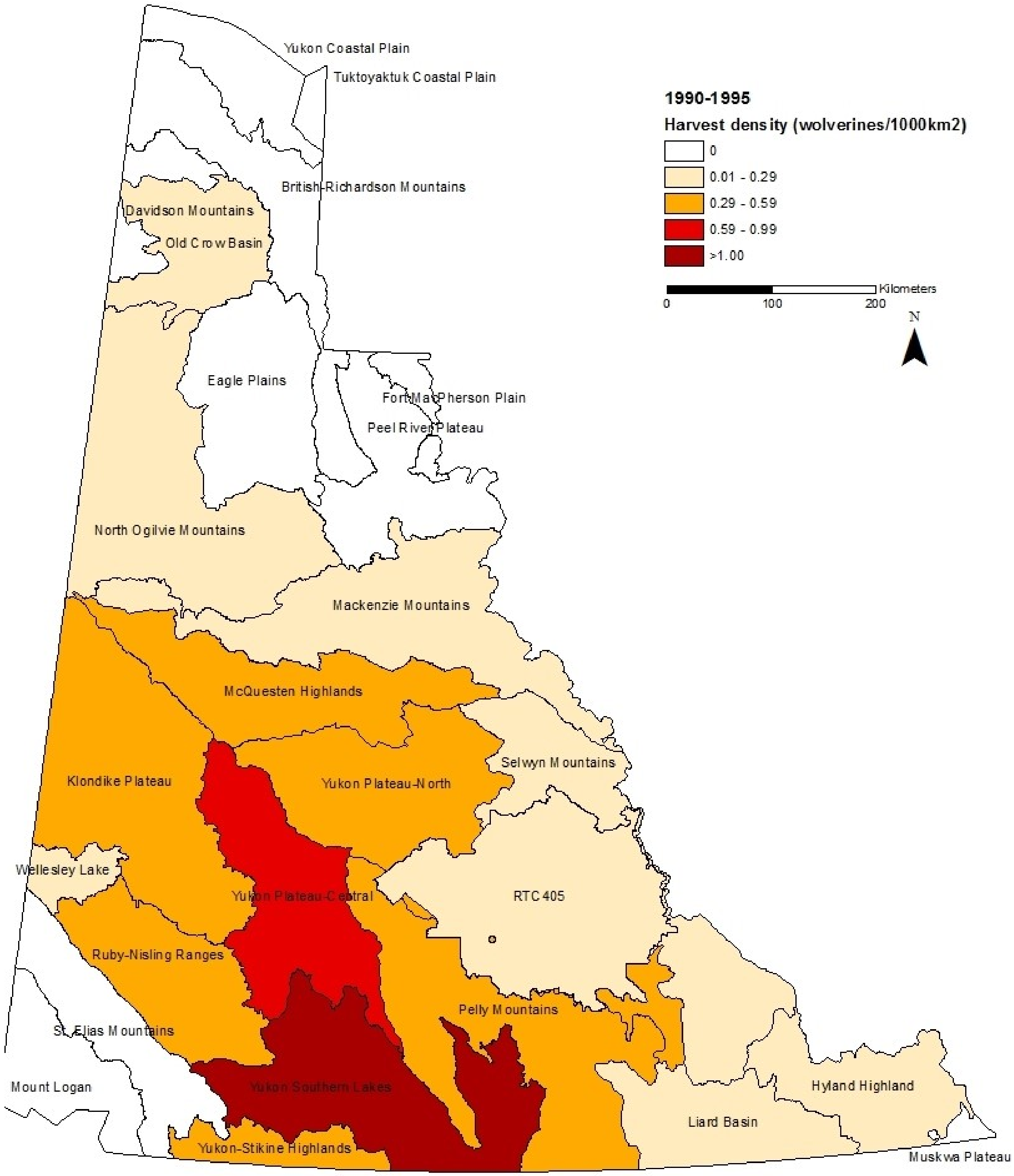

Figure 7. Mean annual wolverine (*Gulo gulo*) harvest density (wolverines harvested/1000 km^2) in ecoregions in Yukon during 1990–1995. RTC 405 was treated separately from ecoregions.

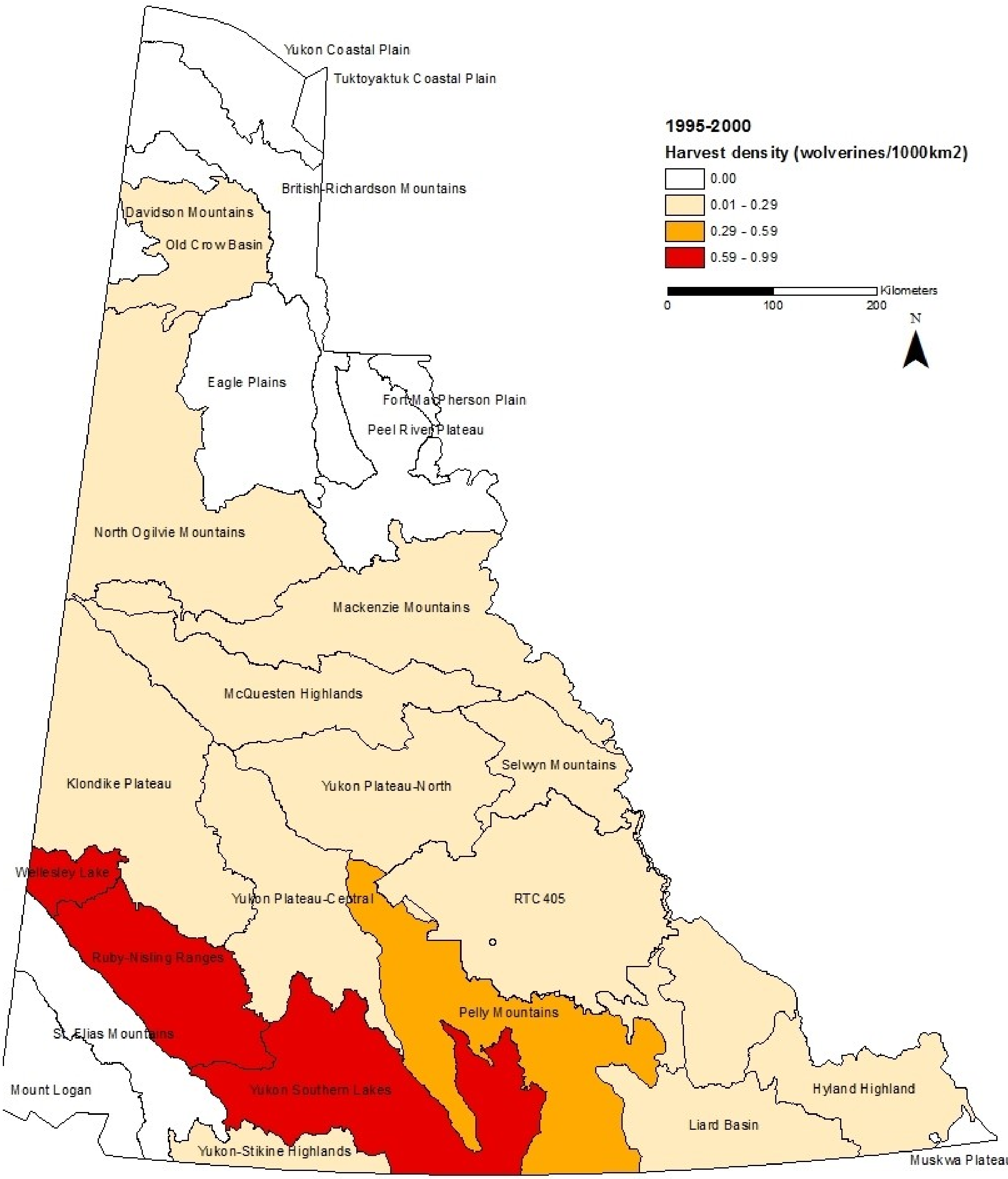

Figure 8. Mean annual wolverine (*Gulo gulo*) harvest density (wolverines harvested/1000 km^2) in ecoregions in Yukon during 1995–2000. RTC 405 was treated separately from ecoregions.

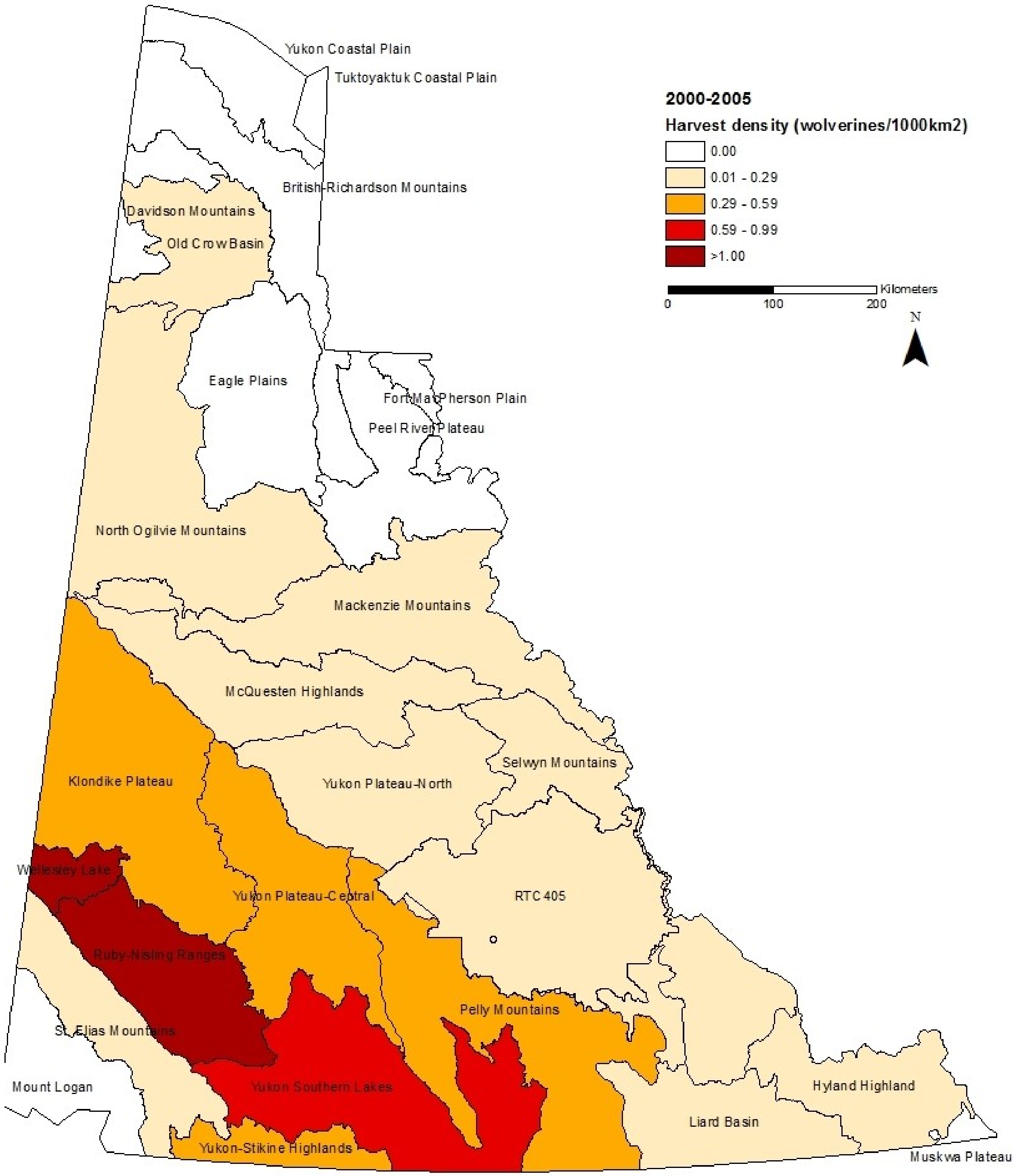

Figure 9. Mean annual wolverine (*Gulo gulo*) harvest density (wolverines harvested/1000 km^2) in ecoregions in Yukon during 2000–2005. RTC 405 was treated separately from ecoregions.

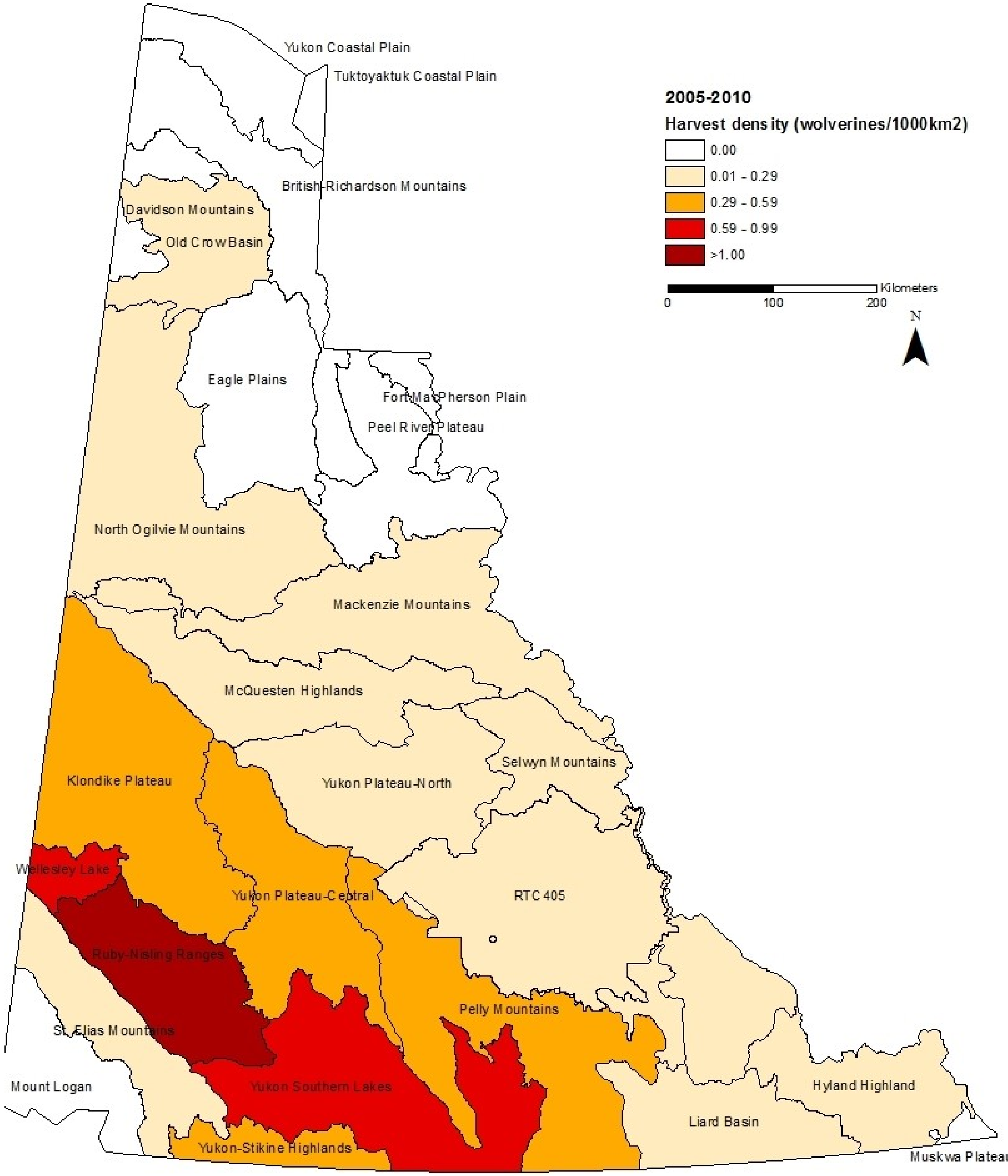

Figure 10. Mean annual wolverine (*Gulo gulo*) harvest density (wolverines harvested/1000 km^2) in ecoregions in Yukon during 2005–2010. RTC 405 was treated separately from ecoregions.

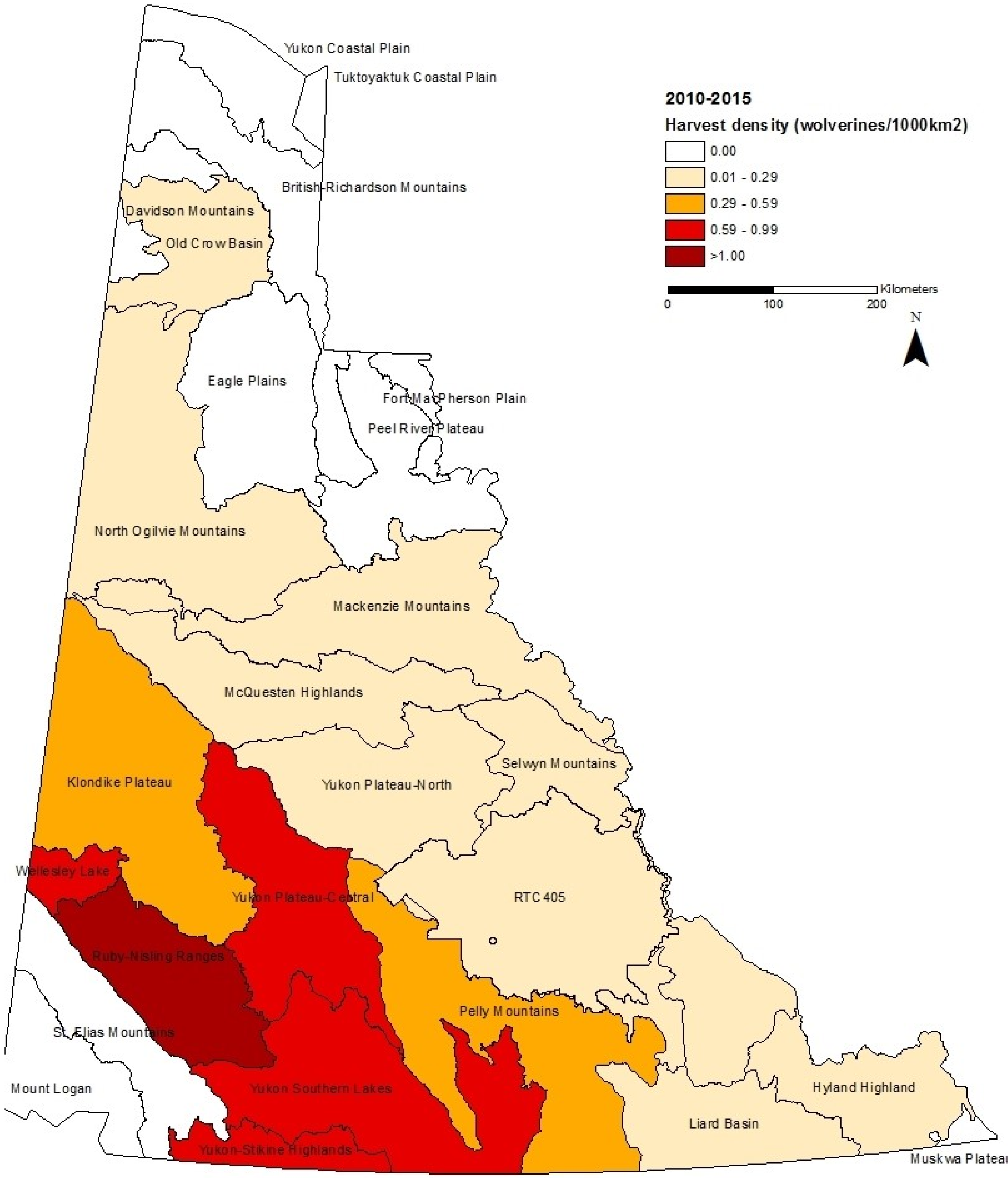

Figure 11. Mean annual wolverine (*Gulo gulo*) harvest density (wolverines harvested/1000 km^2) in ecoregions in Yukon during 2010–2015. RTC 405 was treated separately from ecoregions.

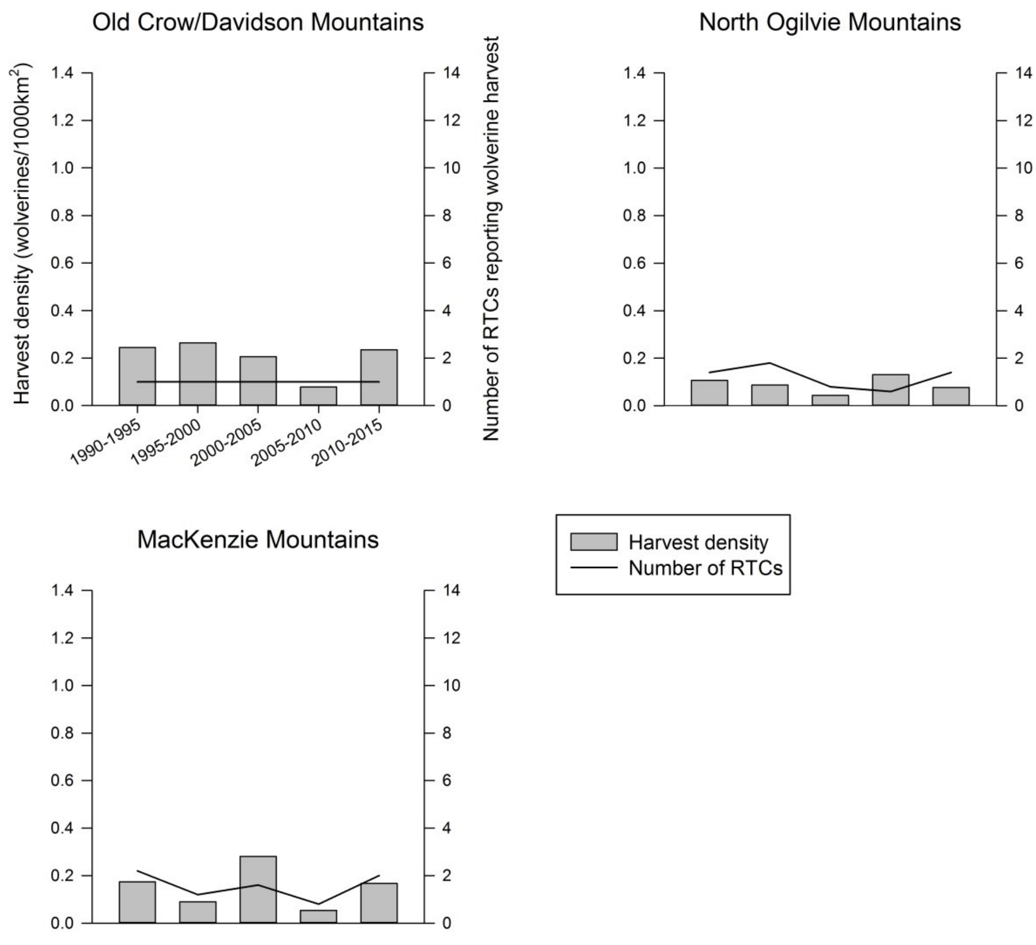

Figure 12. The mean annual wolverine (*Gulo gulo*) harvest densities and the number of Registered Trapping Concessions (RTCs) reporting wolverine harvest in ecoregions in northern Yukon, averaged over 5-year time periods during 1990–2015. There was no significant trend in harvest density over time in any of the northern ecoregions.

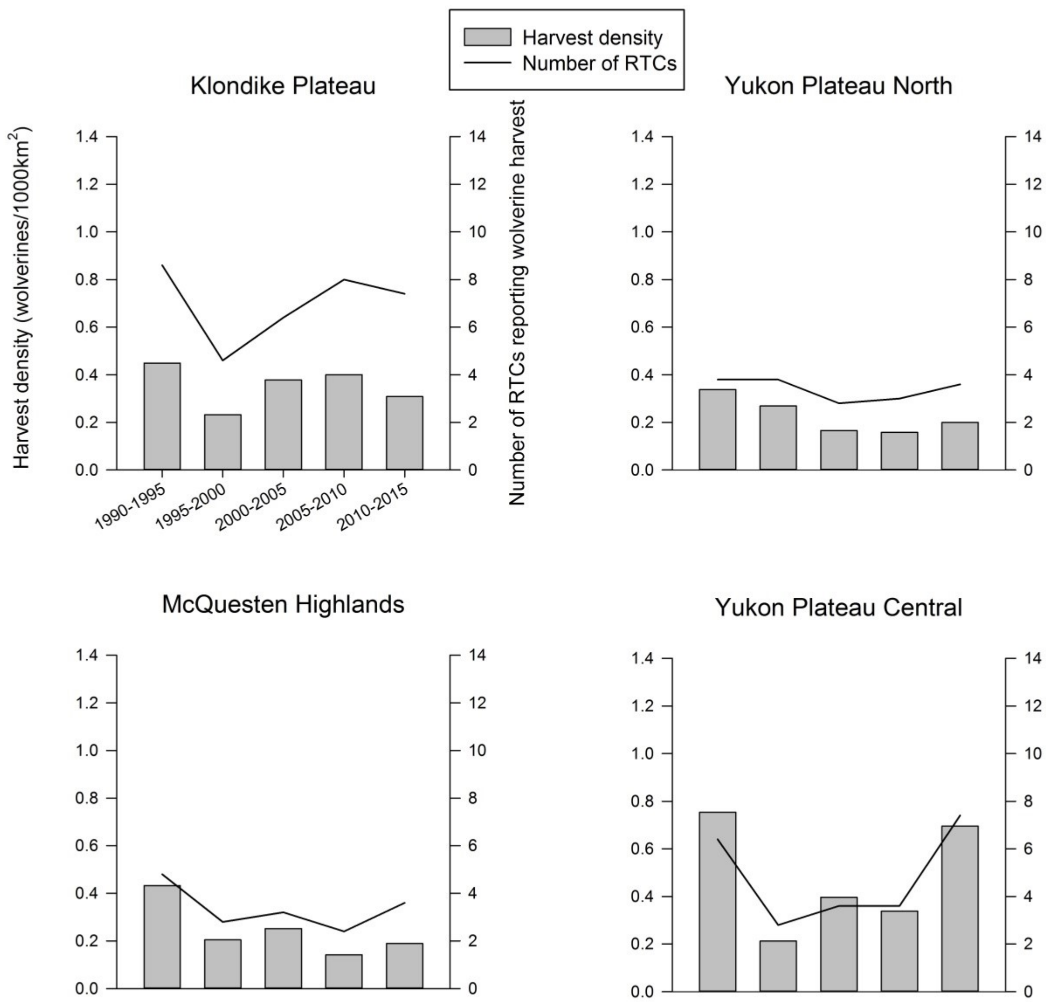

Figure 13. The mean annual wolverine (*Gulo gulo*) harvest densities and the number of Registered Trapping Concessions (RTCs) reporting wolverine harvest in ecoregions in central Yukon, averaged over 5-year time periods during 1990–2015. Decreasing harvest density trends were observed in McQuesten Highlands and Yukon Plateau North.

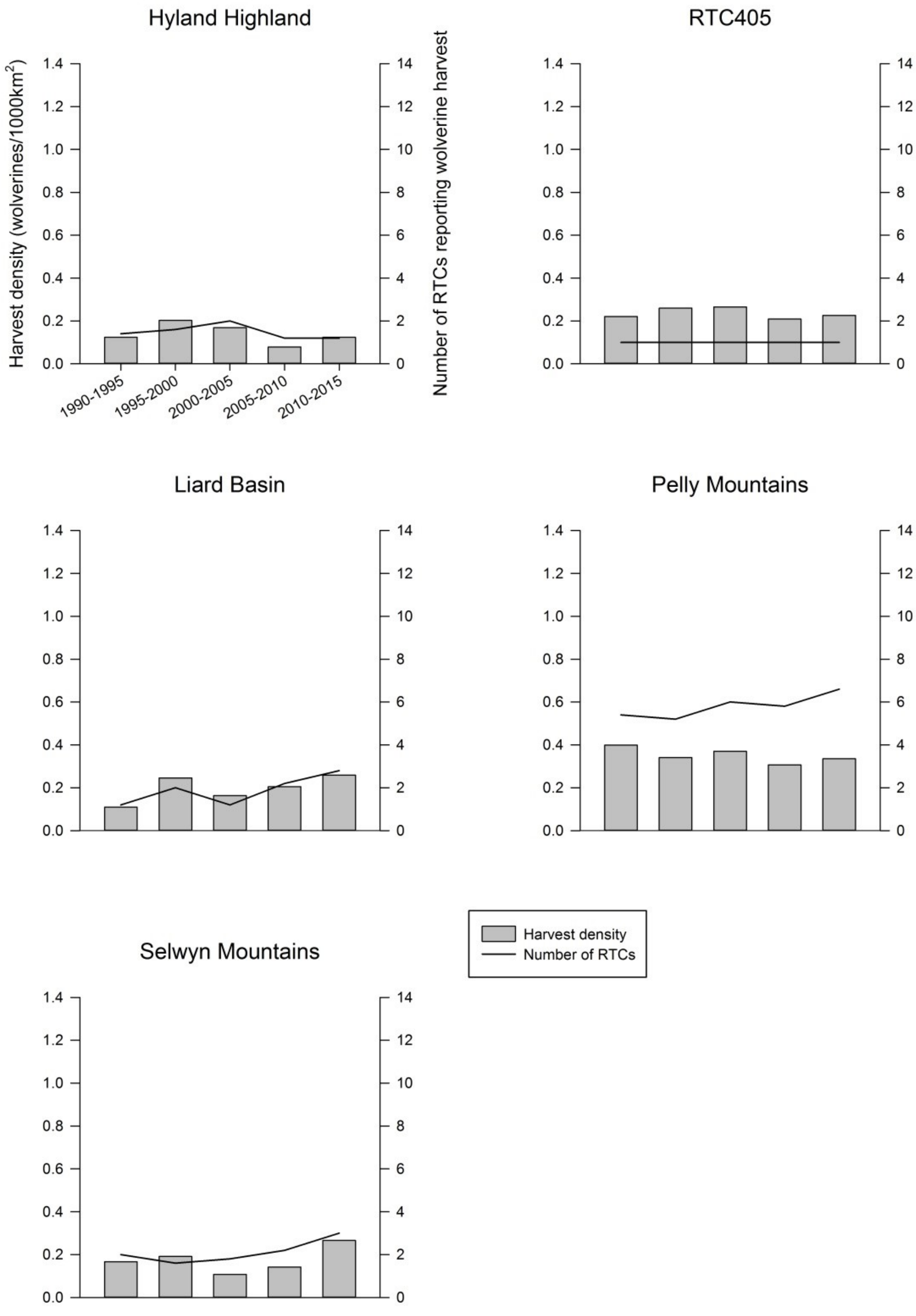

Figure 14. The mean annual wolverine (*Gulo gulo*) harvest densities and the number of Registered Trapping Concessions (RTCs) reporting wolverine harvest in ecoregions in eastern Yukon, averaged over 5-year time periods during 1990–2015. There was no significant trend in harvest density over time in any of the eastern ecoregions.

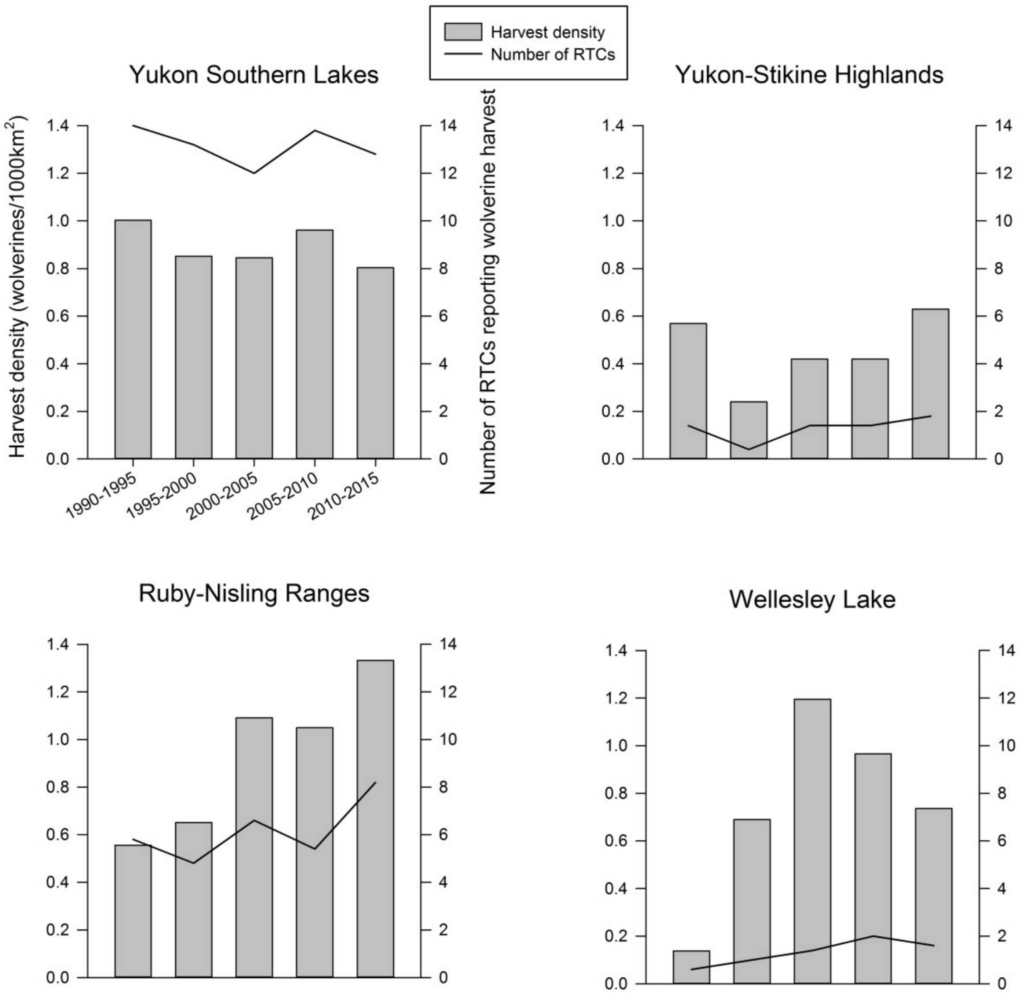

Figure 15. The mean annual wolverine (*Gulo gulo*) harvest densities and the number of Registered Trapping Concessions (RTCs) reporting wolverine harvest in ecoregions in southwestern Yukon, averaged over 5-year time during 1990–2015. An increasing harvest density trend was observed in Wellesley Lake and Ruby-Nisling Ranges.

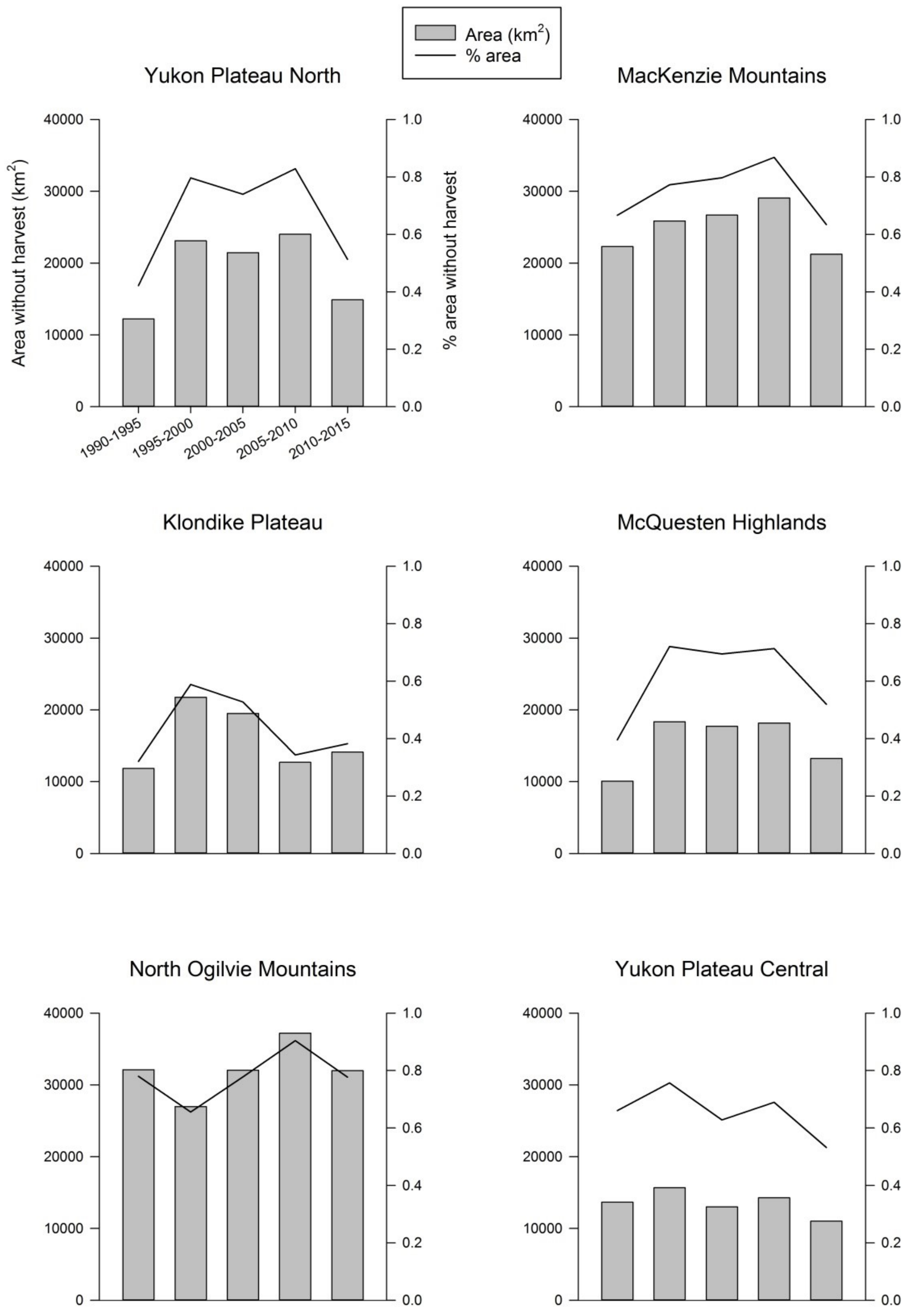

Figure 16. Mean annual amount (km^2) and percent (%) of area without wolverine (*Gulo gulo*) harvest in ecoregions in northern and central Yukon, averaged over 5-year time periods during 1990–2015.

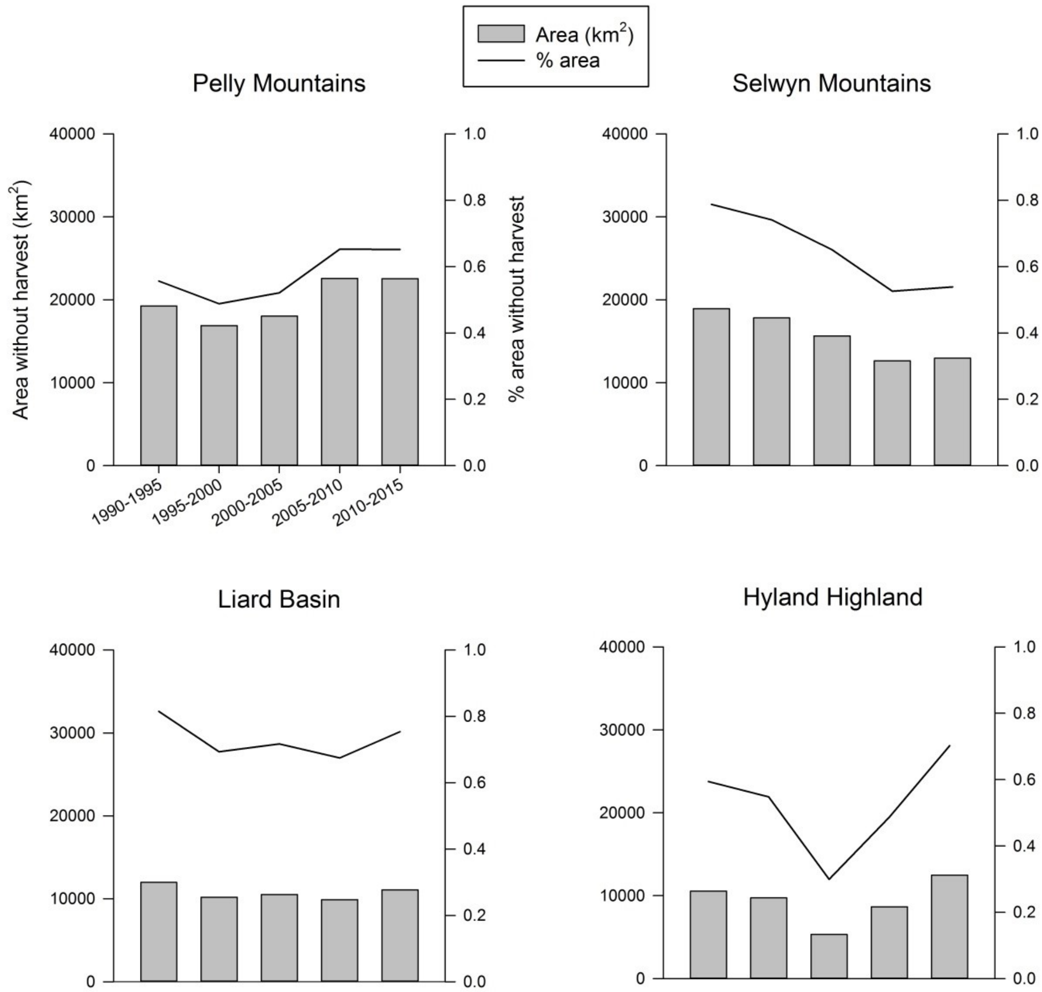

Figure 17. Mean annual amount (km^2) and percent (%) of area without wolverine (*Gulo gulo*) harvest in ecoregions in eastern Yukon, averaged over 5-year time periods during 1990–2015.

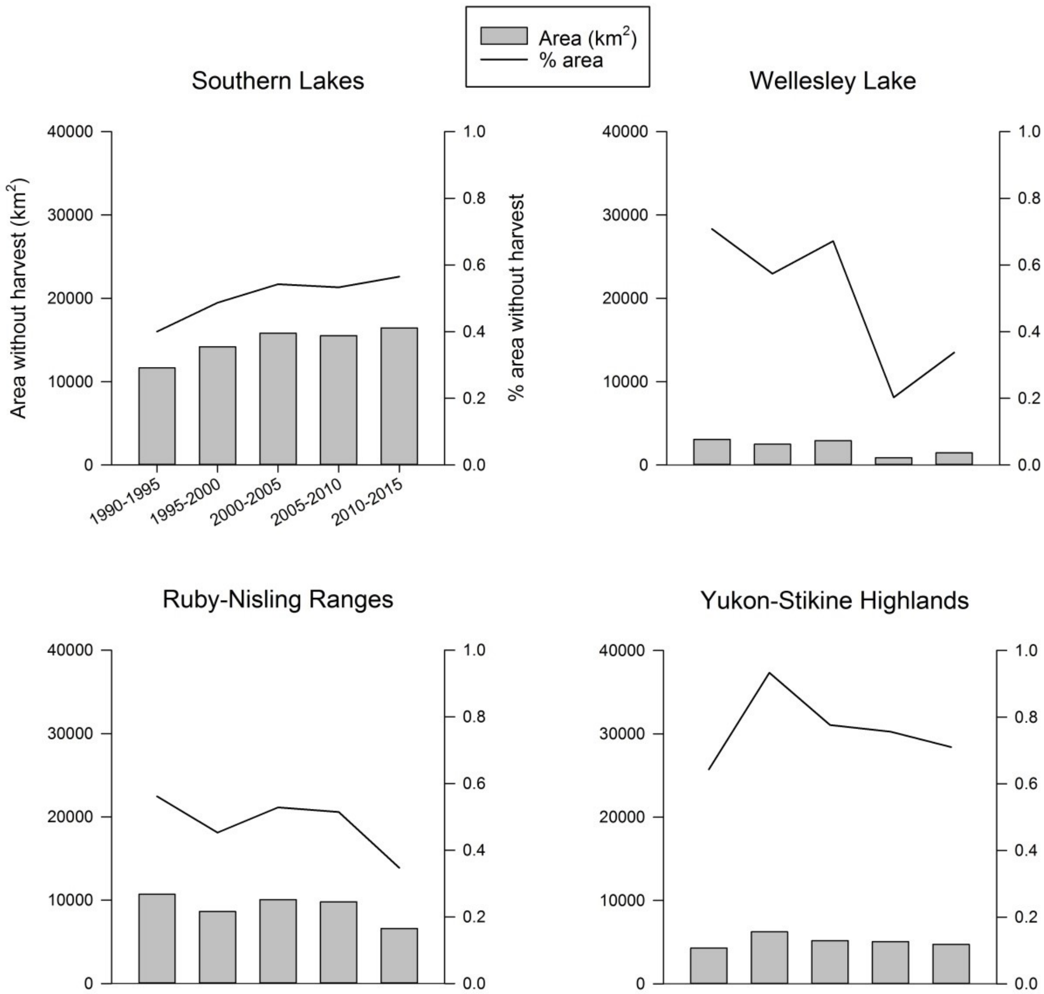

Figure 18. Mean annual amount (km^2) and percent (%) of area without wolverine (*Gulo gulo*) harvest in ecoregions in southwestern Yukon, averaged over 5-year time periods during 1990–2015.

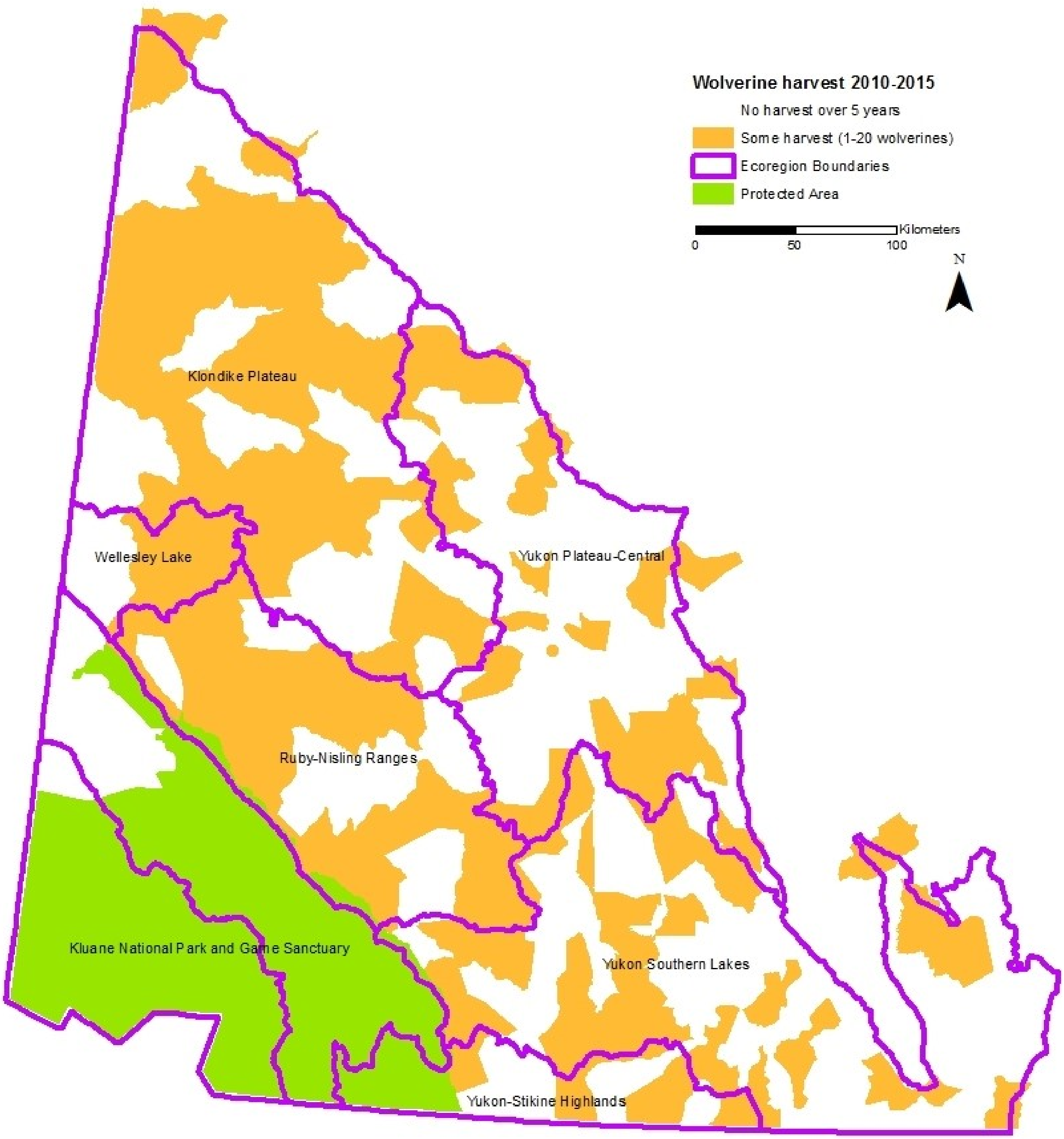

Figure 19. Distribution of area without wolverine (*Gulo gulo*) harvest in ecoregions in southwestern Yukon during 2010–2015. Green area indicates permanently protected areas, and white areas are temporal *de facto* refugia (no harvest of wolverines over 5 years).

CHAPTER III: Population Characteristics of Harvested Wolverine (*Gulo gulo*) in Yukon, Canada

Introduction

Harvest records are commonly used to inform furbearer management, because field data on wildlife populations that span large spatial and temporal scales are rarely available. Harvest rates have been used to monitor population trends and to assess the effects of harvest regulations (e.g. Linnell *et al.* 2010), but these may not reflect actual population change, as capture probabilities and harvest effort may fluctuate due to factors unrelated to population abundance (e.g. Smith *et al.* 1984; McKelvey *et al.* 2010; DeVink *et al.* 2011). However, when combined with demographic data, such as sex and age structure, and reproductive characteristics of the harvested population, harvest rate information can inform furbearer management and be used to assess harvest sustainability, as well as detect change in the structure of the harvested population in response to environmental covariates or management interventions (Rolley 1985; Chilelli *et al.* 1996; Fryxell *et al.* 2001; Anderson and Lindzey 2005).

The demographic structure of harvested furbearer populations typically does not reflect the true population structure; rather, the sex and age composition of the harvested segment of the population is a function of trapping pressure (e.g. Whitman 2003; Fortin and Cantin 2005) and sex- and age-dependent vulnerability to harvest (Buskirk and Lindstedt 1989; Anderson and Lindzey 2005). Mustelid harvest, in general, tends to be biased toward adult males and young animals (King 1975; Banci and Proulx 1999; Fryxell *et al.* 2001). Males generally have larger home ranges and they may disperse earlier and farther than females (Banci and Harestad 1990; Vangen *et al.* 2001; Dawson *et al.* 2010; Persson *et al.* 2010); thus, they are more likely to encounter traps. Male-biased harvest is desirable from a management perspective, because an increasing prominence of females in the harvest may limit recruitment. A harvest approaching or exceeding 50% females may compromise harvest sustainability (Fortin and Cantin 2005; Dalerum *et al.* 2008).

In northwestern Canada and Alaska, wolverine (*Gulo gulo*) are a valuable species for fur trappers, and data on wolverine populations are often limited to harvest records. While wolverine populations in much of northern Canada are considered stable based on harvest statistics and local knowledge, population estimates are limited and trends and harvest sustainability are unknown (Slough 2007; COSEWIC 2014). Harvest data are often the only data available to guide the management of elusive furbearers, such as wolverine, because they occur at naturally low densities in remote areas and are difficult and costly to monitor at the spatiotemporal scales meaningful for management. Wolverine populations are likely susceptible to over-harvest (Weaver *et al.* 1996; Banci and Proulx 1999) due to their naturally low density and low population growth rates, and harvested populations likely act as sink populations that rely on dispersing animals from unharvested source populations (i.e. refugia; Krebs *et al.* 2004; Dalerum *et al.* 2008).

Female wolverine exhibit delayed implantation (Wright and Rausch 1955), which is a bet-hedging reproductive strategy that allows flexibility to produce litters or forgo successful reproduction when they are in poor physical condition. While the pregnancy rate of adult females is typically high (Rausch and Pearson 1972; Banci 1987), indicating that most mature females mate successfully, it does not indicate actual productivity (Magoun 1985; Banci and Harestad

1988), and their annual reproductive output has been reported to be very low (e.g. 0.7 kits/female in Alaska and Sweden [Magoun 1987; Persson *et al.* 2006]). Added to their low density and productivity, wolverines are considered sensitive to habitat fragmentation, human disturbance (May *et al.* 2006; Krebs *et al.* 2007) and potentially climate change (Copeland *et al.* 2010; McKelvey *et al.* 2011), particularly in the southern portion of their range. Due to the combination of these factors, wolverines were assessed as a species at risk in Canada (COSEWIC 2003).

In 2005, we initiated a wolverine carcass collection program in Yukon, Canada, in part to assess the demographic structure of the harvested population, which provides important information for evaluating the sustainability of the harvest. Yukon provides an opportunity to undertake this assessment without the confounding effects of habitat fragmentation or other anthropogenic disturbance found in the southern and more developed regions of the wolverine range. Because vulnerability to capture likely varies among different sex- and age-classes, we expected to see a higher proportion of the most vulnerable cohorts (adult males and juveniles) in the harvest, and fewer individuals from the least vulnerable cohort (adult females), especially during the late harvest season (February and March), which coincides with the onset of the denning period. Finally, we were interested in assessing the harvest of reproductive females and examined the harvest of females in relation to the predicted timing of parturition.

Materials and methods

Study area

Wolverines were obtained from across Yukon, Canada. Yukon is approximately 482,000 km^2 and the human population is approximately 36,700 people (Yukon Bureau of Statistics 2014), with the majority of people (~76%) located in the City of Whitehorse. Much of the territory is void of human infrastructure or access, and remains largely unfragmented by anthropogenic disturbance. Yukon has a rugged and complex topography, characterized by mountain ranges, plateaus, valleys and lowlands. The climate is subarctic continental, which is relatively dry. The annual precipitation ranges from 250 to 600 mm, which mostly falls as snow from October to May. The temperature varies seasonally, ranging from -15 to -30 °C in January and from 10 to 15°C in July. Much of Yukon is characterized by boreal forest in valley bottoms, and shrub communities and alpine tundra at and above the treeline, respectively (Smith *et al.* 2004).

The wolverine population in Yukon is estimated at 3500–4000 resident animals, based on habitat suitability density estimates and expert opinion (Banci 1987; COSEWIC 2014). Harvest management was subsequently informed by harvest records and trapper questionnaires, which suggested a stable harvest (Slough 2007). The mean annual harvest during 1988–2014 was 131 ± 31 (SD) animals (Yukon Department of Environment, unpublished data).

Fur harvest in Yukon is managed by spatial and temporal regulation. There is no bag limit. Trappers can harvest furbearers only in trapping areas assigned to individual, licensed trappers, and the harvest season occurs in winter (from 1 November to 10 March), when the pelts are considered prime. During this time of the year, juvenile wolverines become independent and most males and some females disperse. Pregnant females start denning during late winter, and they typically give birth in February or March (Rauch and Pearson 1972; Banci and Harestad 1988; Inman *et al.* 2012b).

In addition to wolverine, large carnivores, such as wolf (*Canis lupus*), brown bear (*Ursus arctos*), black bear (*Ursus americanus*) and lynx (*Lynx canadensis*) range throughout Yukon. Common prey species include moose (*Alces americanus*), caribou (*Rangifer tarandus*), beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*) and arctic ground squirrel (*Urocitellus parryii*).

Wolverine carcasses

We solicited voluntary submission of skinned wolverine carcasses by licensed fur trappers between 2005 and 2014. Trappers provided the location and harvest date of each wolverine carcass submitted. Trappers are legally required to check traps once a week at minimum; consequently, the actual kill date may be up to 6 days earlier than the reported harvest date. Carcasses were kept frozen at -20°C for 6–10 months prior to necropsy. There was no incentive for fur trappers to submit or withhold information on particular sex or age-class of wolverine they harvested.

We determined sex and reproductive status or each carcass examined, and collected a tooth for aging. Sex was determined by the presence or absence of a baculum or a reproductive tract. Age was determined in a commercial laboratory (Matson's Laboratory LLC, Milltown, Montana) via counting cementum annuli of a premolar, or in rare cases (2%), a canine tooth. Wolverines with no cementum annuli were classified as juveniles; those with one cementum annuli were classified as sub-adults, and those with ≥2 cementum annuli were considered adults. Because the accuracy of age estimation for wolverines from cementum annuli is largely unknown, due to a lack of studies comparing known-age wolverines and cementum age, error in age determination is possible.

Reproductive status and litter size were determined from excising the reproductive tract and macroscopically looking for the presence of fetuses. We also dissected the ovaries to determine the presence and count of corpora lutea (Banci and Harestad 1988). We measured the mass of fetuses using an electronic scale (±0.1 g). A female was considered reproductive based on the presence of corpora lutea or fetuses. Reproductive females were deemed to be close to parturition when their fetuses appeared fully developed. Wolverine kits are fully furred at birth and typically weigh >90 g (Blomqvist 1995, 2012). Thus, reproductive females with well-developed and furred fetuses, whose weights were nearing 90 g, were considered to be near parturition.

Analyses

We assessed temporal autocorrelation by examining autocorrelation function (ACF) plots for each age- and sex-class, over 6 time lags, using SYSTAT (version 13). Substantial autocorrelation was noted if the correlation function exceeded the upper or lower 95% confidence interval. ACF or PACF plots did not reveal any substantial autocorrelation in our data, as all correlation functions were well within the 95% confidence intervals.

We tested for differences in the sex and age composition of the harvested population, and their interaction, using a two-way analysis of variance (ANOVA), where sex and age class were the main treatments. We used the likelihood ratio chi-square (*G*-test) for testing for differences in the sex and age structure, and reproductive status, among years. We used *G*-tests and paired *t*-tests for investigating differences in the sex and age structure between early (1 November to 31 January) and late (1 February to 10 March) in the harvest season. We based the division of the early and late season on the approximate onset of wolverine denning (Inman *et al.* 2012b). We used R (version 3.1.1) for all statistical tests, and $P \leq 0.05$ to denote statistical significance.

Results

Wolverine submissions

Trappers submitted 655 wolverine carcasses during 8 trapping seasons from 2005–2006 to 2013–2014. We were unable to administer the carcass collection program in winter 2012–2013. On average, 82 ± 11 (SD; range = 68–101) wolverine carcasses were submitted each season, which represented 67 ± 8% of the annual total harvest (range = 56–79%; Table 5). Cementum age was determined for 640 (98%) of wolverines. Carcasses originated across Yukon and they were submitted throughout the trapping season, and our sample closely represents the spatial and temporal distribution of the total harvest. We are thus confident that our sample was random and accurately reflected the entire harvest.

Wolverines were harvested throughout the trapping season from the beginning of November to the end of the open season on March 10. The harvest increased as the season progressed (Table

5); few wolverines were harvested in November (6%), followed by December (21%), January (29%), February (32%) and the first ten days of March (12%). The proportion of harvest between the early season (November through January) and the late season (February through early March) ranged from 40–70% and 30–60% among years, respectively, but the difference was not significant ($G_7 = 11.1$, $P = 0.13$). However, the mean harvest rate (adjusted for the different length of the early and late season) was significantly higher in the late season than the early season (0.8 ± 0.2 and 0.5 ± 0.1 wolverines/day (SD); $t_7 = -5.20$, $p < 0.01$).

Sex and age structure

The wolverine harvest was dominated by males ($F_{1,48} = 42.290$, $P < 0.001$) and young animals ($F_{2,48} = 4.173$, $P = 0.022$). The mean annual harvest consisted of 41% young males (juveniles and sub-adults), 25% adult males, 20% young females and 15% adult females. The age structure by sex for males ($n = 417$) was 30% juveniles, 33% subadults and 37% adults; and 28% juveniles, 29% sub-adults and 43% adults for females ($n = 223$). However, the interaction term for sex by age class was not significant ($F_{2,48} = 0.028$, $P = 0.973$), suggesting that the overall age structure of harvest was similar for both sexes. The mean and median cementum ages of harvested animals were 1.9 ± 2.2 (SD) and 1, respectively. The mean ages of females (2.0 ± 2.4) and males (1.8 ± 2.2) in our sample population of harvested wolverine were not significantly different ($t_{422} = 1.12$, $P = 0.27$). The oldest male and female in our sample were estimated to be 11 and 12 years old, respectively.

The sex ratio ranged from 1.3–2.9 males per female (Fig. 20.), but the difference was not significant among years ($G_7 = 8.62$, $P = 0.28$). However, the overall age structure differed significantly among years ($G_{14} = 34.28$, $P = 0.002$), and was most pronounced for juveniles. The proportion of juveniles in the harvest ranged from 12% (2007–2008; $n = 11$) to 41% (2011–2012; $n = 33$). The difference in age structure among years was more pronounced for females ($G_{14} = 33.81$, $P = 0.002$) than males ($G_{14} = 25.05$, $P = 0.034$; Fig. 21.), with the proportion of adults in the harvested female cohort ranging from 25% to 67%. The adult proportion in the female cohort was particularly high over two consecutive harvest seasons (67% in 2007–2008, $n = 27$; and 65% in 2008–2009, $n = 20$), but decreased in the following years.

The mean sex ratio (years pooled) was 2.1 ± 0.7 (males per female) for the early season and 1.9 ± 0.8 for the late season, indicating a slightly higher female proportion of harvest during the onset of the denning season, but this difference was not significant ($t_7 = 0.89$, $P = 0.40$). However, the age structure of harvest differed significantly between the early and late season ($G_2 = 16.8$, $P < 0.001$). The juvenile proportion of harvest dropped from 37% ($n = 121$) in the early season to 22% ($n = 55$) in the late season, and the proportion of sub-adults and adults increased from 27% ($n = 87$) and 36% ($n = 117$) in the early season to 35% ($n = 89$) and 43% ($n = 110$) in the late season, respectively (Fig. 22.).

Reproduction

At the time of their harvest, 44% of females were reproductive. The proportion of reproductive females by cementum age class was 81%, 38%, and 1%, for adults, sub-adults, and juveniles, respectively. Among adults, 64% of two year old females were reproductive, increasing to >90% for females 3–5 years old, then dropping to 76% for females ≥ six years old. The proportion of reproductive adult females ranged from 71% to 100% among years, but the difference was not significant ($G_7 = 7.12$, $P = 0.42$).

Active gestation was observed in 48 females harvested after mid-January, the majority of which were adults (85%), with the mean cementum age of 4 ± 2.1 (SD) years old (range = 1–9). Those harvested in mid to late January ($n = 8$) were mostly in the early stages of gestation; only two females had discernible fetuses. In February, most females had discernible fetuses (83%; $n = 29$), whereas in March ($n = 9$), females had well-developed fetuses or were post-partum ($n = 2$). We were able to determine the harvest date and the mean mass of fetuses per litter for 23 female wolverines (Fig. 23.). The mass of fetuses varied widely over the harvest dates, indicating individual variation in the timing of gestation, and consequently, parturition, although females near parturition ($n = 5$) were observed after mid-February. The average litter size was 2.8 ± 0.9, based on macroscopic observation of fetuses, with a similar average number of corpora lutea (2.7 ± 1.0). The sample size for litter size was too small in some years to allow comparison among years.

Discussion

We assessed variability in harvest sex and age structure of wolverine across broad spatial and temporal scales, in order to provide data that may be useful in ensuring the sustainability of the harvest. We were particularly interested in the variability of adult females in the annual harvest, given that they are likely the most demographically important segment of the population (Dalerum *et al.* 2008). Our main findings were that the harvest was dominated by juveniles in most years, the percentage of adult females in the harvest varied among years, adults constituted a higher proportion of the harvest later in the harvest season than earlier, and that toward the end of the harvest season some adult females were harvested when they were in late gestation or post-partum.

Wolverine harvest in Yukon was skewed toward males and young animals, similar to that reported by Banci (1987), 30 years earlier, and from other studies in western Canada (Lee 1995; Lofroth and Ott 2007; Webb *et al.* 2013). A high harvest of juveniles may indicate either a healthy population with high reproductive output, or conversely, an exploited local population (Bodkin et al. 1996), where adult residents have been harvested and trapped individuals are dispersing animals from surrounding areas (i.e., a population sink). Source-sink population dynamics may characterize the wolverine population in areas of Yukon with consistent harvest pressure. The reproductive output of wolverines is naturally low, so the prominence of young animals in the harvest could reflect the influx of transient animals from untrapped areas, rather than high local reproductive output.

Juvenile and sub-adult males comprised 41% of the mean annual wolverine harvest in Yukon. High proportions of young males are expected in harvested wolverine populations, because vacant areas created by the removal of resident animals may be filled by dispersing animals, which are typically young males (Magoun 1985). Dispersing animals are more vulnerable to being trapped, compared to residents, because they may travel widely in search of available territory, thus increasing their likelihood of encountering traps. Wolverines generally disperse prior to reaching sexual maturity. The average age at dispersal was 13 months in Norway, with more variation in the age at dispersal for females (7–26 months) than males (7–18 months; Vangen *et al.* 2001). Because males typically hold larger home ranges than females (Persson *et al.* 2010), and consequently, fewer home ranges are available to males, dispersing individuals may have to search widely for available territory. This may cause males to remain in the transient population for extended periods of time, even years (Magoun 1985; Inman *et al.* 2012a), and thus remain vulnerable to harvest longer than females. In regularly harvested areas, home range behavior may be disrupted altogether due to insufficient time for individual territory establishment (Hornocker and Hash 1981; Banci 1987).

While the sex ratio of harvest did not fluctuate significantly among years during our study, the age structure did. This may be due to annual variation in either juvenile abundance or their trap vulnerability. The abundance of juveniles in the winter population may vary depending on the reproductive success of females in the previous year, as well as their survival during their first summer. It is also possible that the vulnerability to trapping is not constant among years. During food scarcity, wolverines are likely to travel more in search of food. Because juveniles may be inexperienced in securing food, they may be more attracted to novel food sources, and, hence, more vulnerable to traps than adults during food scarcity. Further research is needed to elucidate the reasons for the predominance of juveniles harvested in exploited furbearer populations, which will vary spatially and temporally, and depend on local conditions at the time.

Several studies suggest that harvested wolverine populations should be regarded as sink populations that rely on immigration, and that wolverine harvest is very unlikely to be viable on a local scale without augmentation by immigrants (Krebs *et al.* 2004; Golden *et al.* 2007a; Dalerum *et al.* 2008). Given that much of Yukon's land area is remote and unfragmented, and trapping activity has declined or remained steady over the last decades (Yukon Department of Environment, unpublished data), it is possible that naturally occurring refugia have sustained the harvest of wolverine over broad spatial scales. However, identification and monitoring of potential refugia is warranted, particularly for areas where adjacent harvest pressure and human encroachment could limit the future function of these areas (Golden *et al.* 2007a). The allocation of trapping concessions to individual trappers may alleviate local harvest pressure by spreading the effort over large geographic areas, but this strategy should be evaluated to improve the likelihood of the sustainability of wolverine harvest.

Survival of adults has the greatest impact on wolverine population viability, and as with other species occuring at low density, such as polar bear (*Ursus maritimus*), the survival of adult females is vital for the sustainability of harvest (Taylor *et al.* 1987; Dalerum *et al.* 2008). Adult females constituted 15% of the mean annual harvest in Yukon, indicating either lower availability or vulnerability to harvest, relative to other harvested cohorts. The proportion of adult females was higher in two consecutive trapping seasons (2007–2008 and 2008–2009) than the other years for which data were available; however, the harvest of female wolverines overall was below average during those years (< 30% versus a mean of 34%), and the proportion of young animals harvested was high in the following years, providing no evidence of decreased recruitment. Unfortunately, with available data, it is not possible to determine whether abundance or harvest vulnerability is responsible for the relatively annual variability in the percentage of adult females in the harvest.

The increased harvest in late winter could result from either increased trapping effort or greater vulnerability of wolverines to trapping, or a combination. We were not able to evaluate trapper effort, although we expected some increase in late winter due to better snow and ice conditions for accessing trapping areas, and longer daylight hours, compared to earlier in the harvest season. Wolverines may be more vulnerable to trapping in late winter due to low food availability, which may result in extended movements. The proportion of adult wolverines in the harvest increased in late winter, largely due to greater harvest of adults rather than reduced harvest of juveniles. Adult males may extend their movements for breeding opportunities, and high energetic demands of reproduction may influence adult female habitat selection in late winter (Magoun 1985; Magoun and Copeland 1998; Krebs *et al.* 2007; May *et al.* 2012). Additionally, trap vulnerability of adults may consequently change throughout the season, due to factors such as food availability or snow depth.

Our findings confirm that female wolverines do not typically reach sexual maturity until two years old (Banci and Harestad 1988), as 81% of harvested adult females, but only 38% of sub-adults, were reproductive. Other studies suggest the prime age for successful reproduction for female wolverines is 4–7 years old, but that successful reproduction in wolverine further depends on the combination of age-related reproductive costs and winter food availability (Persson 2005; Rauset *et al.* 2015). In our study, over 90% of 3–6 year old females were reproductive, and the mean age of actively gestating females was four years old. However, food availability is largely unpredictable, because wolverines may rely largely on scavenging opportunities. Nevertheless, while wolverines may generally be opportunistic feeders (van Dijk *et al.* 2008b), the diet of reproductive females may differ from males and non-reproductive females (Lofroth *et al.* 2007; van Dijk *et al.* 2008a; Koskela *et al.* 2013b), suggesting they may make behavioural adaptations to optimize litter production.

Our study confirms large individual variability in the timing of reproductive chronology, as reported elsewhere (Banci 1987; Inman *et al.* 2012b). Active gestation was not evident in our sample prior to mid-January. Based on a 45-day gestation period (Inman et al. 2012b), parturition would then occur in late February. We also detected early stages of gestation in animals harvested after mid-February, predicting parturition for late March or early April. Because the harvest season extends to 10 March in Yukon, denning females with dependent kits may legally be trapped, as confirmed by the incidence of two post-partum females trapped in early March in our sample. The harvest of denning female wolverines is a potential concern regarding harvest ethics, because of the inevitable mortality of dependent kits in their natal den (*sensu* Parker and Rosell 2001). Establishing a harvest season to ensure protection of denning female wolverines is difficult, given variability in the timing of denning. However, our data demonstrate that most reproductive wolverines are in advanced stages of gestation after mid-February, a time when they remain susceptible to legal harvest.

Our data demonstrate that harvest managers should expect annual variation in the proportions of the sex- and age cohorts harvested, and the value of long-term longitudinal data from carcass collection programs for monitoring for change and trends for species that are otherwise difficult monitor at broad spatiotemporal scales. Our study also points to management interventions that can be applied to further promote the sustainability of the harvest of wolverine in Yukon. Specifically, the late winter harvest likely has a larger impact on the population than the early winter harvest, because of the increased proportion of adults in the harvest and the possibility of trapping reproductively active females that are near-term or post-partum at the onset of the denning season. Adjustment to the length of the harvest season in late winter would likely reduce this impact. However, any changes in the regulatory regime for wolverine harvest should be done within an adaptive framework to ensure that such changes have the desired outcome (e.g. Fryxell *et al.* 2001).

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Table 6. Wolverine (*Gulo gulo*) carcass submissions from licensed fur trappers in Yukon from winter 2005–2006 to 2013–2014. Harvest month was unknown for some carcasses. Absolute numbers (*n*) are indicated in parentheses.

Harvest season	**Percent of harvest submitted (*n*)**	**Percent of harvests per month (*n*)**				
		November	**December**	**January**	**February**	**March**
2005-2006	70.8 (68)	1.7 (1)	19.0 (11)	31.0 (18)	31.0 (18)	17.2 (10)
2006-2007	78.8 (78)	7.0 (5)	11.3 (8)	38.0 (27)	33.8 (24)	9.9 (7)
2007-2008	66.9 (93)	3.4 (3)	23.0 (20)	32.2 (28)	26.4 (23)	14.9 (13)
2008-2009	57.3 (75)	12.1 (8)	16.7 (11)	30.3 (20)	22.7 (15)	18.2 (12)
2009-2010	75.4 (101)	6.1 (6)	35.7 (35)	13.3 (13)	35.7 (35)	9.2 (9)
2010-2011	56.2 (73)	4.8 (3)	12.7 (8)	28.1 (24)	38.1 (24)	6.3 (4)
2011-2012	61.4 (81)	5.6 (4)	9.7 (7)	26.4 (19)	44.4 (32)	13.9 (10)
2012-2013	-	-	-	-	-	-
2013-2014	67.2 (86)	3.9 (3)	33.8 (26)	29.9 (23)	22.1 (17)	10.4 (8)
Mean	**66.7 (655)**	**5.6 (33)**	**21.3 (126)**	**29.1 (172)**	**31.8 (188)**	**12.3 (73)**

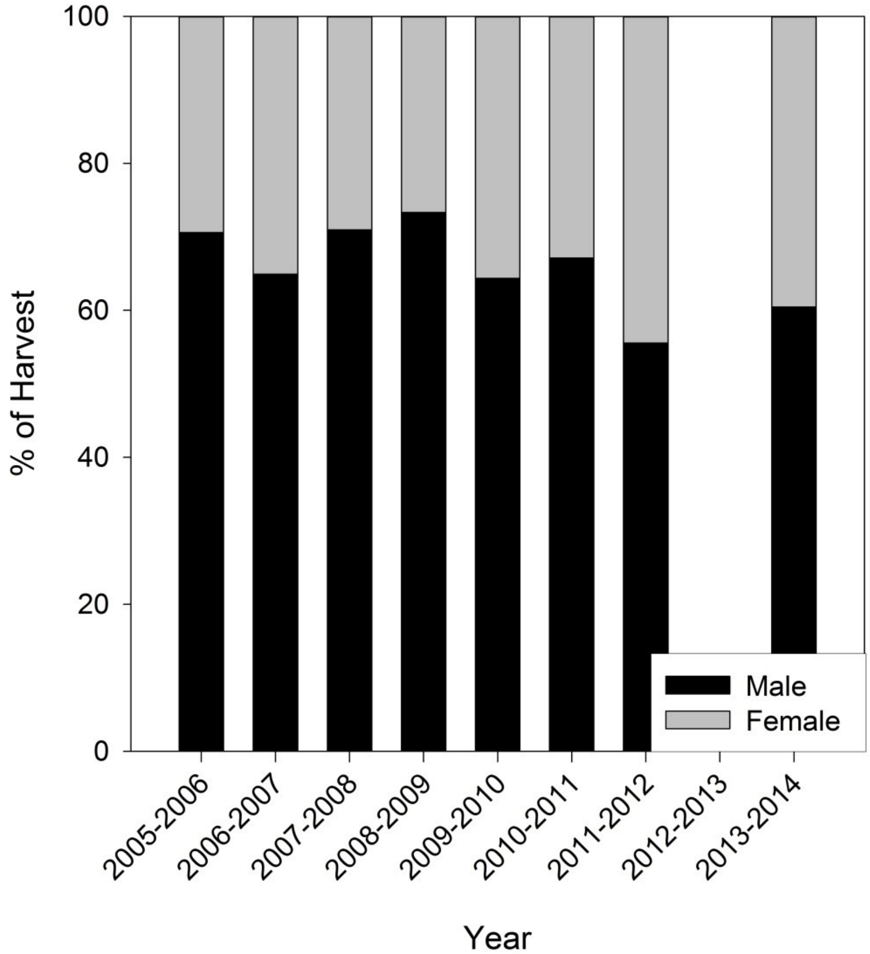

Figure 20. The proportion of male and female wolverine (*Gulo gulo*) harvested in Yukon from winter 2005–2006 to 2013–2014 (data were not available for the 2012–2013 trapping season). The sex ratio did not differ significantly among years ($G_7 = 8.62$, $P = 0.28$).

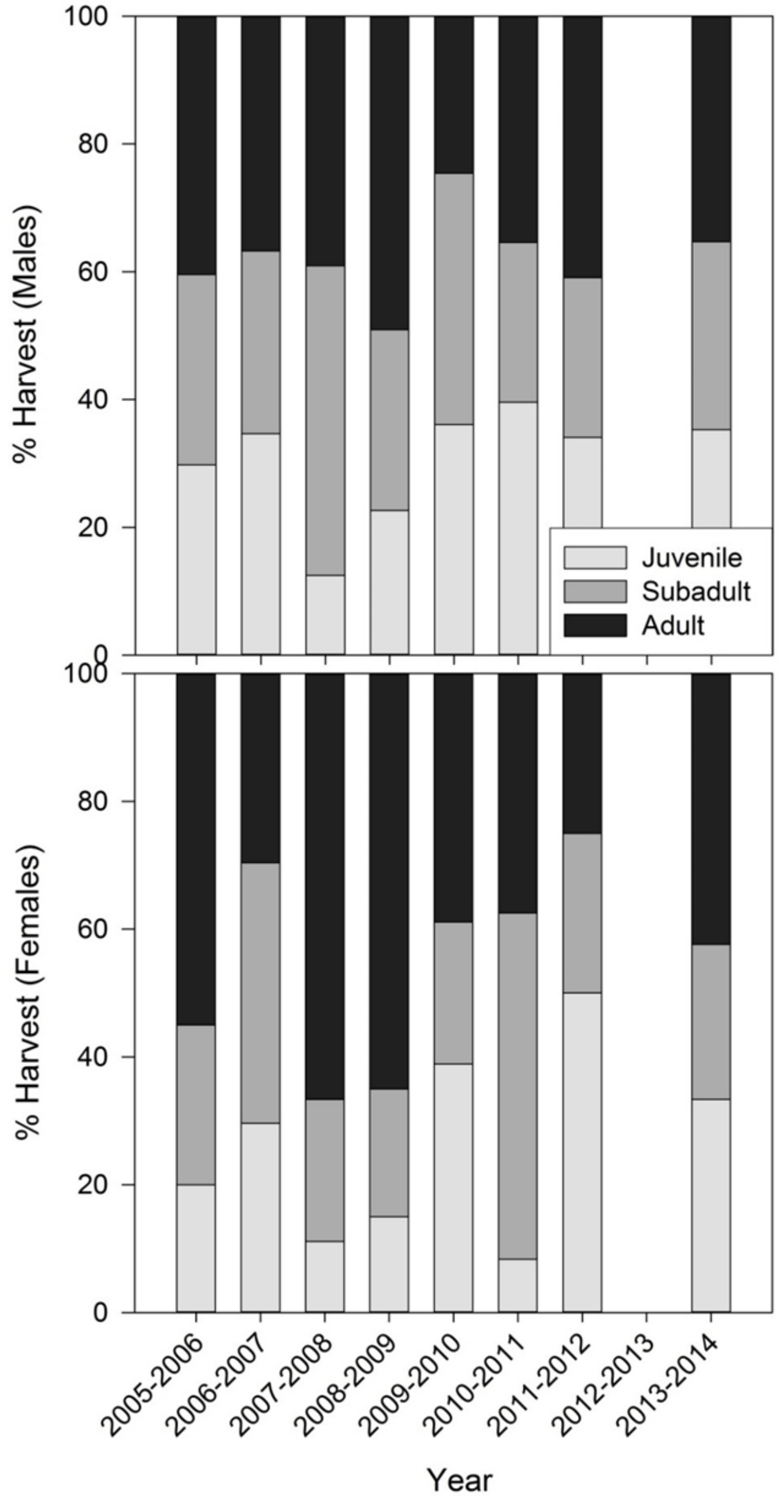

Figure 21. The distribution of age classes of wolverine (*Gulo gulo*) harvested in Yukon from winter 2005–2006 to 2013–2014 (data were not available for the 2012–2013 trapping season). The overall and sex-specific age class structure differed significantly among years ($G_{14} = 34.28$, $P = 0.002$).

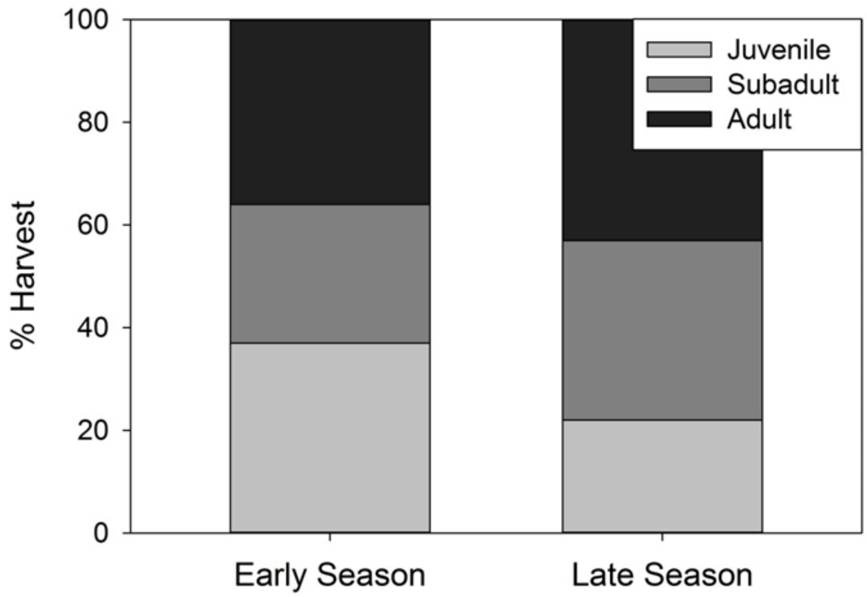

Figure 22. The distribution of age classes of harvested wolverine (*Gulo gulo*) in early (November through January) and late (February through early March) harvest season in winters 2005–2006 to 2013–2014 (data were not available for the 2012–2013 trapping season). The age structure of harvest differed significantly between the early and late season ($G_2 = 16.8$, $P < 0.001$).

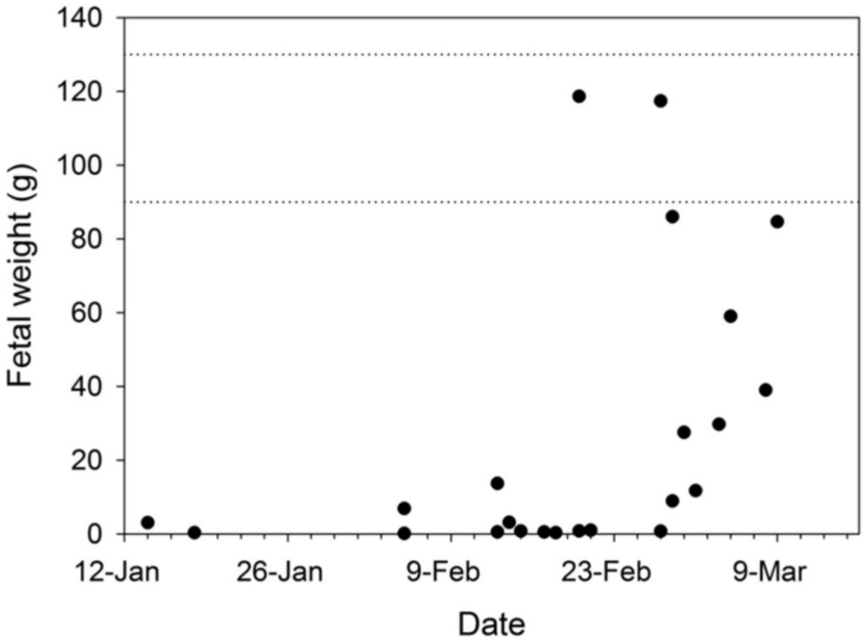

Figure 23. The mean fetus weight of pregnant wolverine (*Gulo gulo*) harvested in Yukon from winter 2005–2006 to 2013–2014 (*n* = 23; years pooled). The dashed lines represent the range of birth weights of wolverine kits in captivity in Europe. The birth weight data is from *G. g. gulo*, which may be larger overall than *G. g. luscus* (L. Blomqvist, personal communication; Blomqvist 1995; 2012; Shilo and Tamarovskaya 1981).

CHAPTER IV: Synthesis and Management Recommendations

Synthesis

In this thesis, I addressed two aspects of wolverine (*Gulo gulo*) harvest that contribute to the assessment of sustainable harvest of this sensitive furbearer species in Yukon, including the spatiotemporal patterns of harvest and the population characteristics of the harvested population.

First, I examined the spatiotemporal distribution and trends of wolverine harvest. Wolverine harvest from 1988 to 2015 has been relatively stable. Annual fluctuations in harvest closely followed the number of traplines that report wolverine harvest each year, indicating that the harvest fluctuates based on trapline utilization, whereas the mean number of wolverines harvested on individual traplines has remained stable. Wolverine harvest is likely affected by overall fur trapping and trapline utilization trends, particularly in relation to key economic species, such as lynx (*Lynx canadensis*).

Wolverine harvest was concentrated in southwestern Yukon, whereas harvest densities in eastern and northern Yukon have been consistently low over time. The estimated harvest rates in northern and eastern Yukon were generally low (< 6%); thus, likely sustainable at local scales (Krebs *et al.* 2004). Limited road access likely contributes to the low harvest in these areas. In addition, large concession sizes and large *de facto* refugia likely sustain viable wolverine source populations. The wolverine harvest in ecoregions in southwestern Yukon, on the other hand, may rely on dispersing animals to reoccupy harvested areas (*i.e.* source-sink dynamics), because harvest rates were comparatively high (> 10%) over time (Banci and Proulx 1999; Dalerum *et al.*

2008). Source populations may be present within the ecoregions in *de facto* harvest refugia; however, their extent may be limited compared to the northern and eastern regions in Yukon. Moreover, extensive protected areas in southwestern Yukon, such as Kluane National Park and Game Sanctuary, and adjacent protected areas in northwestern British Columbia and southeastern Alaska, likely support important wolverine source populations. Estimated harvest rates were consistently high (10–24%) in regions adjacent to these protected areas, indicating that wolverines are likely dispersing between these areas.

Most wolverine trappers harvested wolverines infrequently and in low numbers, indicating conservative or opportunistic wolverine trapping practices. However, wolverine appeared to be a primary target species for some trappers. My data show that relatively few wolverine trappers harvested most of the wolverines; thus, the influence of few trappers on harvest patterns may be disproportionally high. Wolverine pelts have a consistently high value; thus, targeting wolverines can be economically attractive. Harvest densities of up to 7–23 wolverines/1000 km^2 over one trapping season indicate that wolverine populations may be locally high, albeit likely augmented by dispersers from adjacent unharvested areas.

Second, I examined the population characteristics of harvested wolverines in Yukon. Wolverine harvest followed a population structure typical for harvested mustelid populations (King 1975; Banci and Proulx 1999; Fryxell *et al.* 2001), with the harvest dominated by young males, which are typically the dispersers in wolverine populations (Magoun 1985; Inman *et al.* 2012a). More adults were harvested in late winter than early winter. Because adult animals, particularly females, are more valuable to population productivity (Dalerum *et al.* 2008), harvest in the late winter may have a greater impact on wolverine populations than in the early winter.

Active gestation was evident in harvested pregnant females in late winter. The timing of gestation and parturition varied widely for individual wolverines, similar to other regions (Inman *et al.* 2012b). Harvested pregnant females were projected to give birth after mid-February up until late March. Consequently, some females are in late stages of pregnancy, or may already have kits in a den, when they are still subject to harvest during the latter part of the harvest season.

Management Recommendations

Several recommendations for harvest management emerged from this study. These recommendations are broken down by the two main interest groups: harvest managers and wolverine trappers. Recommendations for harvest managers include suggestions for harvest monitoring and harvest regulation. Recommendations for trappers include harvest practices that can be adopted by individual trappers within the current regulatory framework, and which could be promoted in the Yukon Trapper Education Program and outreach activities.

Harvest managers

Results from this study offer insight into the status of wolverine harvest in Yukon, and potential management recommendations for improved harvest data collection and for ensuring sustainable and ethical harvest.

Fur sealing records for wolverine, and the carcass collection program, provide important data for monitoring wolverine harvest. In the absence of wolverine population data, these harvest data are important for the management of wolverine harvest. Currently, wolverine harvest data do not include harvest effort. Without data on harvest effort, inferences about wolverine populations, such as abundance, may not be reliable based on harvest data (*e.g.* Smith *et al.* 1984; McKelvey *et al.* 2010; DeVink *et al.* 2011). Potential population declines would be difficult to confirm without knowledge of trends in harvest effort. Thus, collecting wolverine trapping effort data in Yukon would be useful. Currently, Environment Yukon sends a trapper questionnaire to all licensed fur trappers in order to gain local knowledge on perceived population levels and trends for game and furbearer species. Trapper questionnaires have been in use since 1977, and this data collection venue may be the most efficient tool for collecting harvest effort data on wolverine, because it is already well-established and it would reach all trappers, including those that attempted to harvest wolverines unsuccessfully.

I identified two potential concerns related to sustainable and ethical harvest of wolverines. First, harvest densities were consistently high in southwestern Yukon, particularly in Southern Lakes and Ruby-Nisling ecoregions. The harvest rates in these areas may not be sustainable without immigration from harvest refugia. Harvest refugia are considered possibly the single most important land use planning mechanism for the conservation of wolverine populations, and a system of spatial controls of trapped and large untrapped areas may ensure long-term persistence of wolverine (Krebs *et al.* 2004). Currently, under-utilized RTCs likely provide spatial controls for harvest; however, the availability of these *de facto* harvest refugia is not monitored, nor guaranteed to continue. Monitoring potential harvest refugia for wolverine would be desirable across their range (Golden *et al.* 2007a); however, in Yukon the priority would be in the southwest. Controlling temporal *de facto* harvest refugia, where warranted, may be an effective harvest management tool for wolverine harvest (*e.g.* through rotating temporary closures; Squires *et al.* 2007), in order to allow new occupation and successful breeding in previously harvested areas. Wolverine harvest in Yukon appears to align along road corridors. Access is likely an important factor limiting RTC utilization, particularly in remote regions. Consequently, an increase in access (*e.g.,* for resource development), into previously untrapped areas would likely increase harvest pressure on wolverine. Careful impact assessment and road planning should be considered in these cases.

Second, I found that adult wolverines are harvested more late in the harvest season (February to early March) than earlier (November to January). From the perspective of wolverine population persistence, harvest in the early winter is preferable to late winter in order to protect the breeding segment of the population. Closing the harvest season earlier would likely protect adults, particularly breeding females, which often are in advanced stages of pregnancy, or already denning, in late February. The harvest of denning females inevitably leads to mortality of dependent kits in a den. The harvest of pregnant or denning females should be avoided for population sustainability and ethical reasons. Closing the harvest season by 15 February would protect most females that are in late stages of gestation or denning. In comparison, the wolverine harvest season in northern British Columbia (Skeena Region) closes on 28 February, and in northern Alberta on 31 January. In Northwest Territories and Alaska, the season closes variably among regions between 28 February and 15 April. In Yukon, different regional closure dates could also be considered.

Trappers

Trapline ownership brings with it the ethical, ecological and traditional responsibility to harvest only what is needed without jeopardizing local wildlife populations or ecosystem functions. Trappers may choose to protect local wolverine harvest sustainability by limiting their trapping effort to the early winter to protect adult wolverines, particularly females. Wolverine pelts are also in their peak prime in early winter. Many adult females are in late stages of pregnancy, or already denning, by late February. Late season wolverine harvest may not only result in the mortality of pregnant females, but also her dependent kits in a den. Trappers should consider not harvesting wolverines after mid-February.

High levels of harvest are likely not sustainable on any trapline without immigration of wolverines from other areas. Protecting wolverine source populations is critical for sustaining wolverine harvest for future years. RTCs that are not used for wolverine harvest may be critical wolverine sources. Because harvest in one RTC may depend on adjacent RTCs for repopulating the area, communication between neighboring trappers may be useful for safeguarding the local wolverine population, particularly in southwestern Yukon, where RTCs are relatively small and wolverines may range through several traplines.

Currently, trappers are the main data source for wolverines in Yukon. Without harvest records and carcass submissions, our knowledge of wolverine populations and trends would be limited, because it is too costly to monitor elusive species such as wolverine in the long term. An important contribution that trappers can make to wolverine monitoring efforts is to maintain a trapline journal that notes their trapping effort (*e.g.,* the number of traps/kilometers/days spent on trapping wolverines), and also wolverine observations, abundance and behavior. Information, such as wolverine den sites, hunting/scavenging observations, natural mortality events, or other observations related to wolverine ecology are valuable to wildlife management. By sharing such notes and records with wildlife managers, trappers can further enhance their contribution to improving wolverine management in Yukon.

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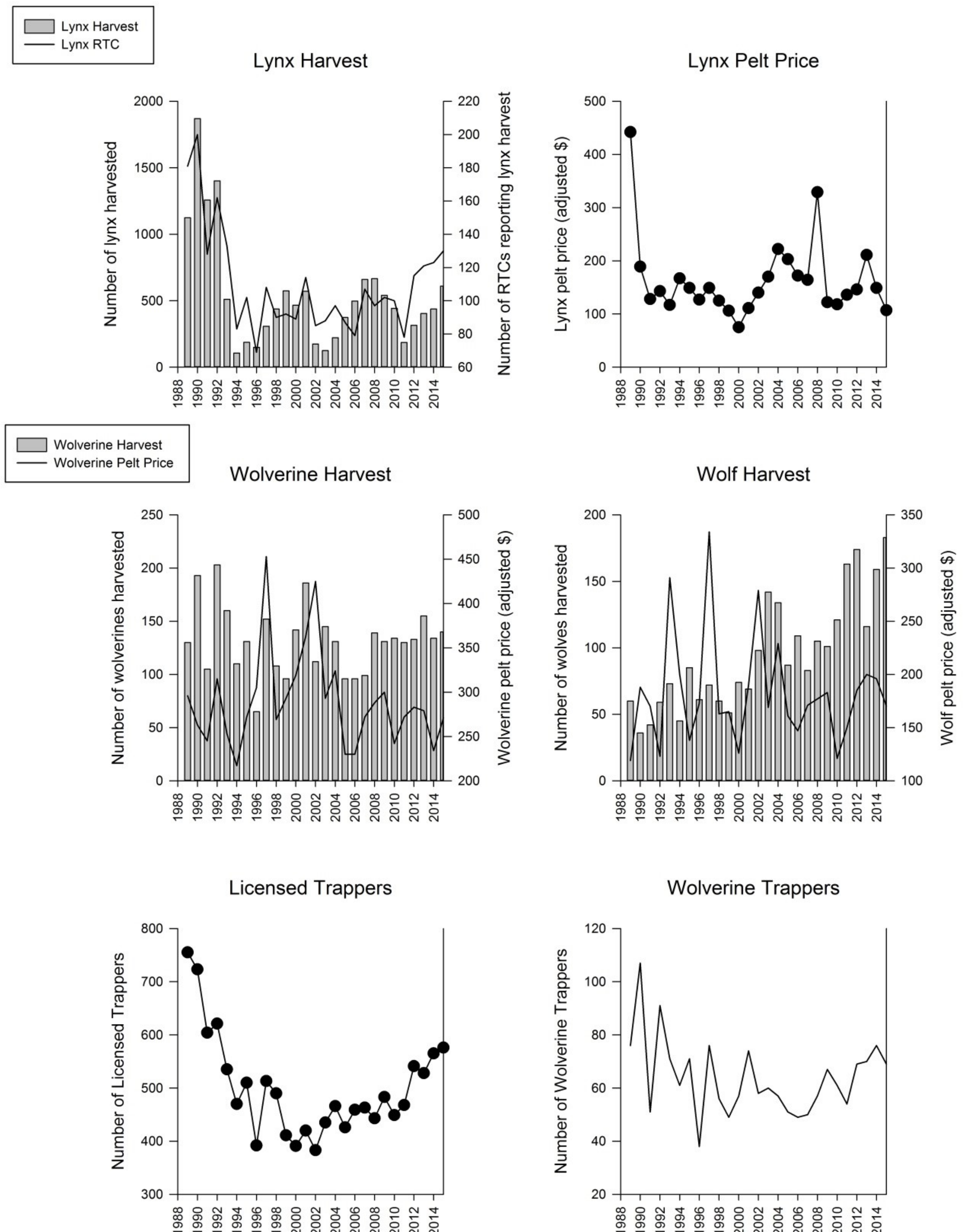
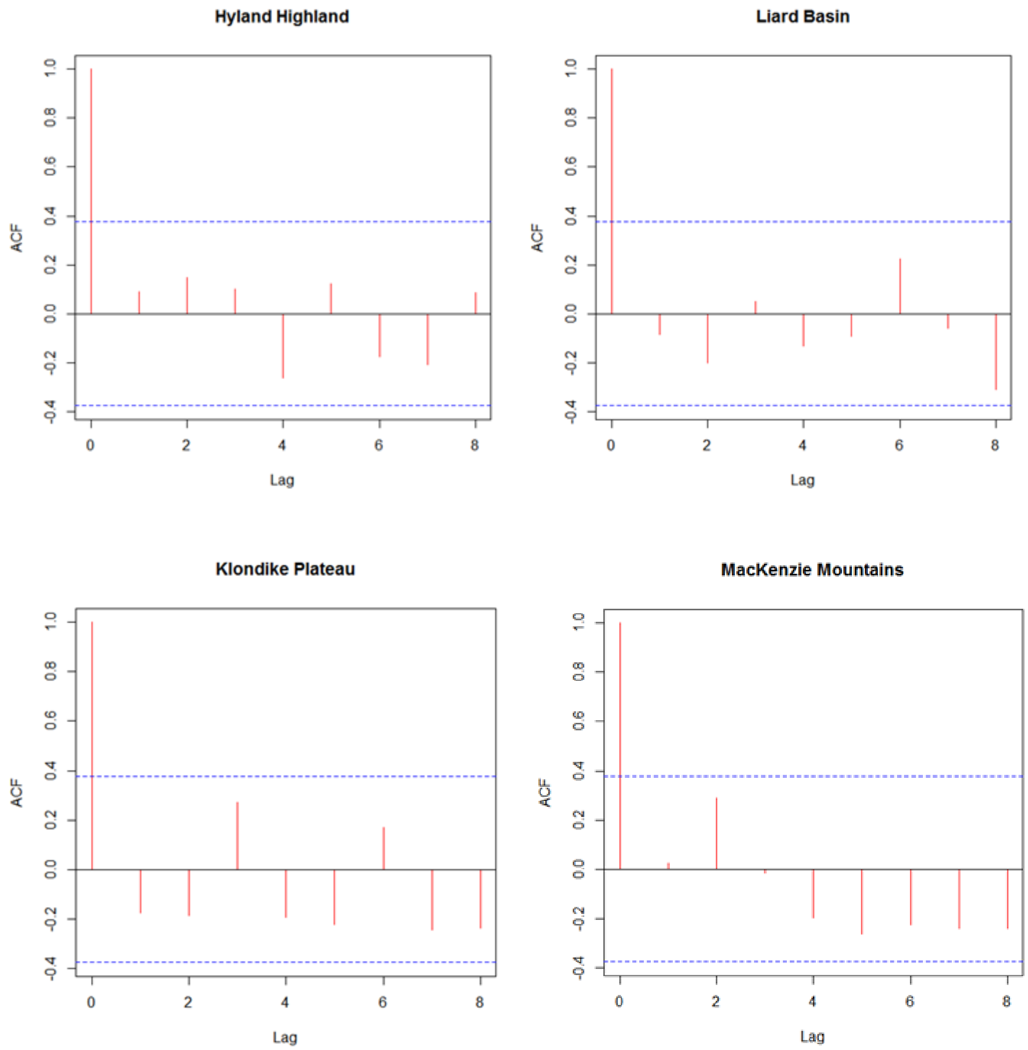
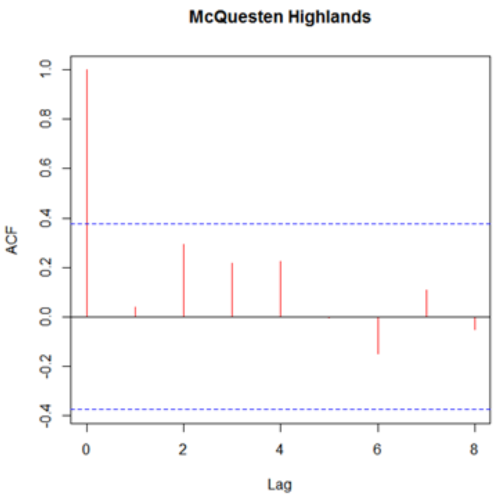
Appendix

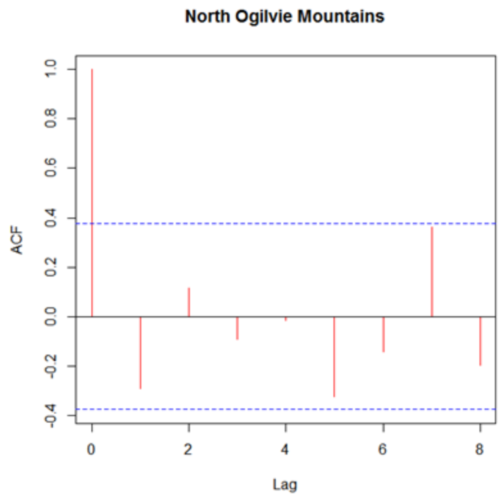
Appendix 1. Annual fur harvest metrics for lynx (*Lynx canadensis*) harvest, lynx pelt price, wolverine (*Gulo gulo*) harvest, wolverine pelt price, wolf (*Canis lupus*) harvest, wolf pelt price, the number of licensed trappers, and the number of wolverine trappers during 1988–2015 in Yukon.

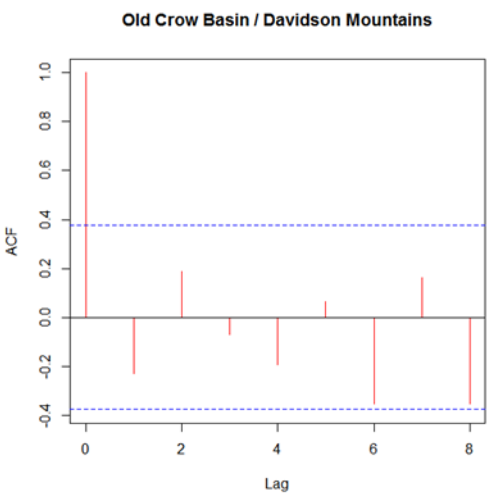


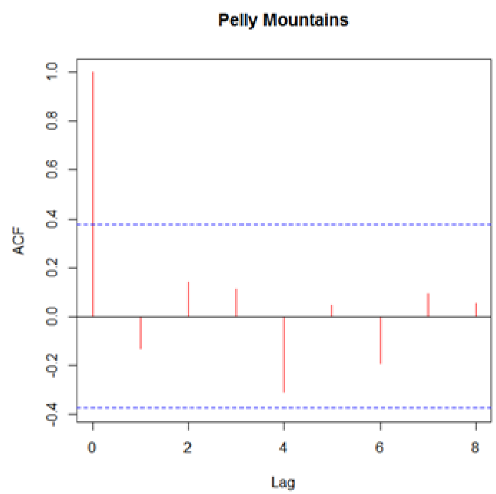
Appendix 2. Correlograms for temporal autocorrelation function (ACF) values over 8 time lags for wolverine (*Gulo gulo*) harvest in ecoregions during1988–2015 in Yukon. The blue dotted lines indicate 95% confidence intervals (± 0.385).

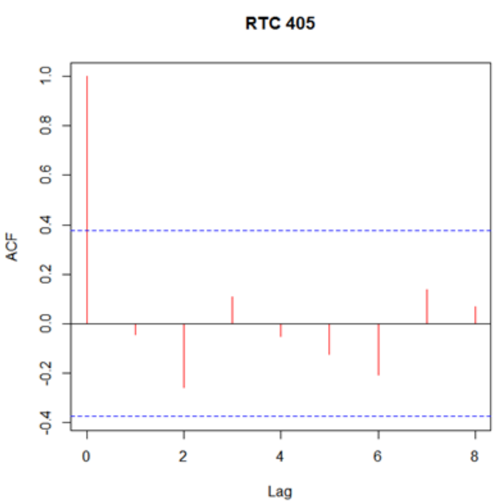


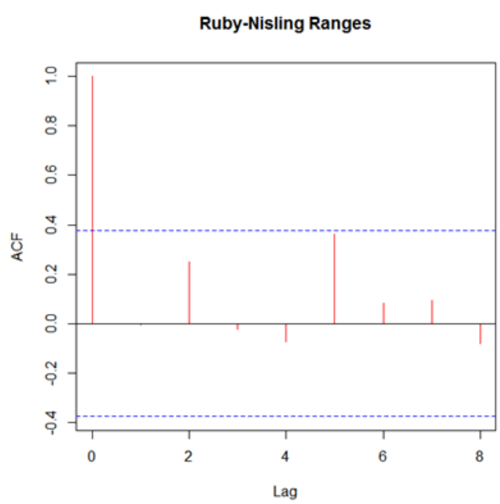

McQuesten Highlands
ACF
Lag

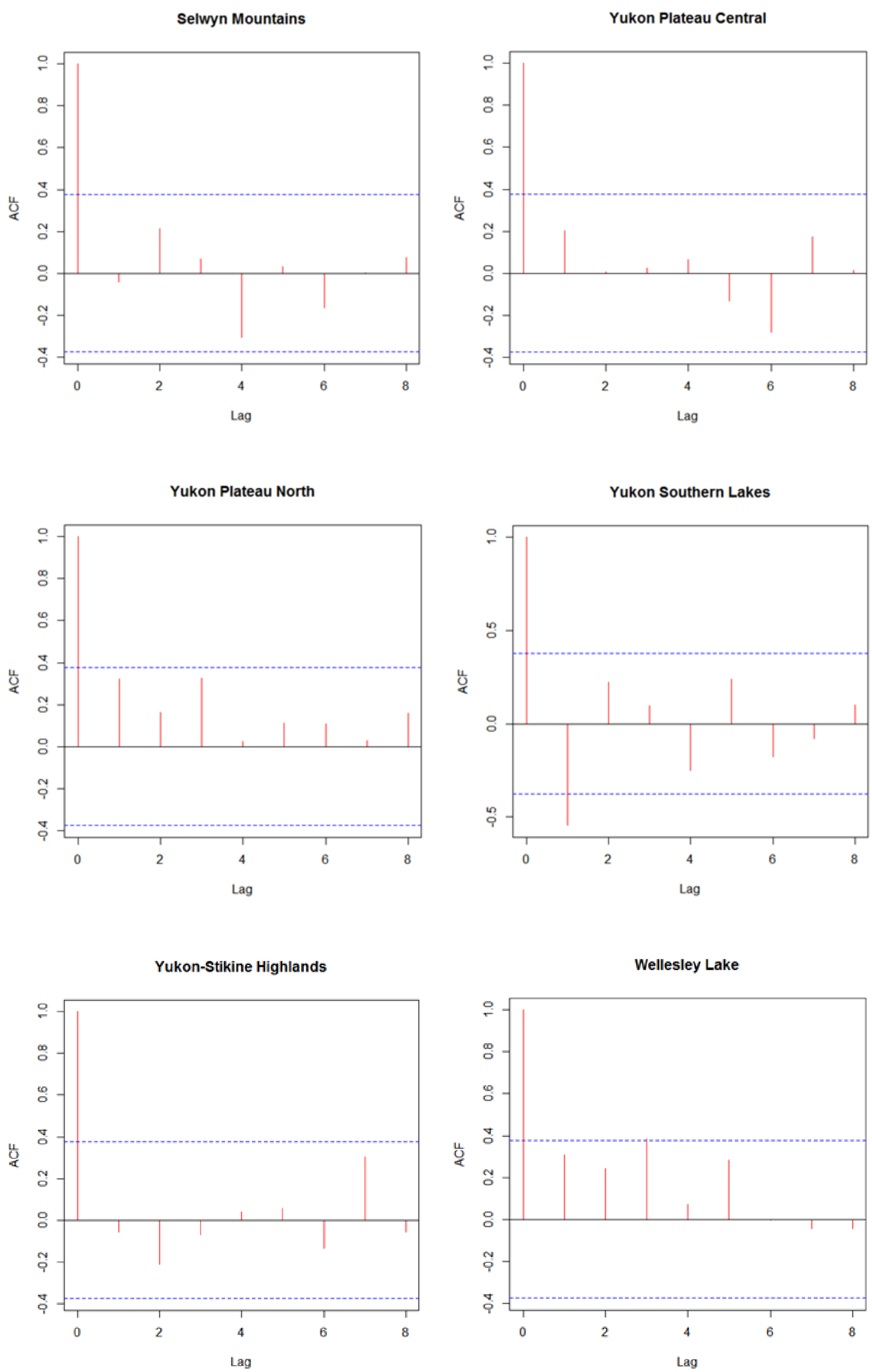

North Ogilvie Mountains
ACF
Lag


Old Crow Basin / Davidson Mountains
ACF
Lag


Pelly Mountains
ACF
Lag


RTC 405
ACF
Lag


Ruby-Nisling Ranges
ACF
Lag


Selwyn Mountains
Yukon Plateau Central
Yukon Plateau North
Yukon Southern Lakes
Yukon-Stikine Highlands
Wellesley Lake
ACF
Lag