

Horns and hotspots: detecting change in mountain sheep populations
over large spatiotemporal scales

by

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Abstract

Long-term data is essential for addressing questions about how populations change over time in response to environmental variability, and natural and anthropogenic disturbance. Two species of mountain sheep (*Ovis* spp.) in Canada have been monitored over several decades and provided the data analyzed in this thesis. First, changes in Dall sheep horn size over 16 years in the southern Mackenzie Mountains, NWT were analyzed using a horn size trend modelling approach. We developed general linear models (GLMs) to assess horn size over time, using age at harvest and harvest year (2002 to 2017) as fixed effects, and outfitter area as a random effect. We observed no significant trend in the average horn volume of harvested rams, nor in the mean age at harvest for Dall sheep rams over this period. The current management of Dall sheep in the Mackenzie Mountains may have maintained a population of rams that do not show the decline in horn size associated with selective harvest in other jurisdictions. Second, I used 52 years of annual winter bighorn sheep surveys from the Alberta Rocky Mountains to examine changes in their distribution in the greater part of their northern winter range. Long-term census data over large geographic areas offer an opportunity to track changes in wildlife distribution over time and space, and to detect areas of interest. Using ArcGIS, two methods for analyzing spatial patterns were compared: Kernel density and hotspot analyses. Different clustered distributions and trends across time were observed for ewes and rams. Over time, ewe clusters changed from their northern historic range to new southern ranges, while ram hotspots were consistently located within their historic northern range. Ewes congregated more than rams, but all sheep congregated in larger areas during the recent period compared with earlier periods. In contrast with the hotspot approach, density analyses indicated a larger number of sheep congregations on the landscape, and no change over time. Our study provides the first macroscopic overview of

bighorn sheep distribution in their largest and most intact range in the northern Rocky Mountains. These patterns of bighorn use of space over the last half a century add to our understanding of sheep resiliency to stressors and can inform the priorities for bighorn management in the future.

Dedication

*The red deer loves the chaparral,
The hawk the wind-rocked pine;
The ouzel haunts the rills that race
The cañon's steep incline;
But the wild sheep from the battered rocks,
Sure foot and fleet of limb,
Gets up to see the stars go by
Along the mountain-rim.*

*For him the sky-built battlements,
For him the cliff and scar,
For him the deep-walled chasms
Where the roaring rivers are;
The gentian-flowered meadow-lands,
The tamarack slope and crest,
Above the eagle's screaming brood,
Above the wild wolf's quest.*

*When in the riot of the storms
The snow-flowers blossom fair,
The cattle get them to the plain,
The howlers to the lair.
The shepherd tends his foolish flocks
Along the mountain's hem;
But free and far the wild sheep are,
And God doth shepherd them.*

(Austin 1900:955)

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CHAPTER 1

GENERAL BACKGROUND

Long-term monitoring has been described as the intentional collection of data for a continuous period of longer than ten years (Lindenmayer et al. 2012). Although the specific relevance of a ten-year period may depend on the questions being asked, this definition reinforces the important role of tracking changes in populations and ecosystems over time to learn about the factors that might be affecting them, the magnitude of these effects, and in which ways they are changing or are resilient to change (Magurran et al. 2010, Hughes et al. 2017, Burns et al. 2018). Understanding whether these ecological processes support or weaken the resilience of the system are important considerations in the context of government, industry and community management decisions that influence how these species and environments will persist in the future.

With growing attention being directed towards the impacts of climate change on the entire planet (Holmes et al. 2013, Giron-Nava et al. 2017, Taig-Johnston et al. 2017, Liang et al. 2018), ecologists are also becoming more aware of the influence of longer-term climatic cycles on ecosystems and species. For example, Hik and Carey (2000) found a correlation between Yukon Dall (*Ovis dalli dalli*) ram horn growth variation and the Pacific Decadal Oscillation, a climatic phenomenon that cycles approximately every ten years. It is now widely understood that studies and monitoring efforts whose duration is less than a decade may miss the potentially significant impact of these periodic ecological processes on the system of interest (Lindenmayer et al. 2012, Giron-Nava et al. 2017, Taig-Johnston et al. 2017).

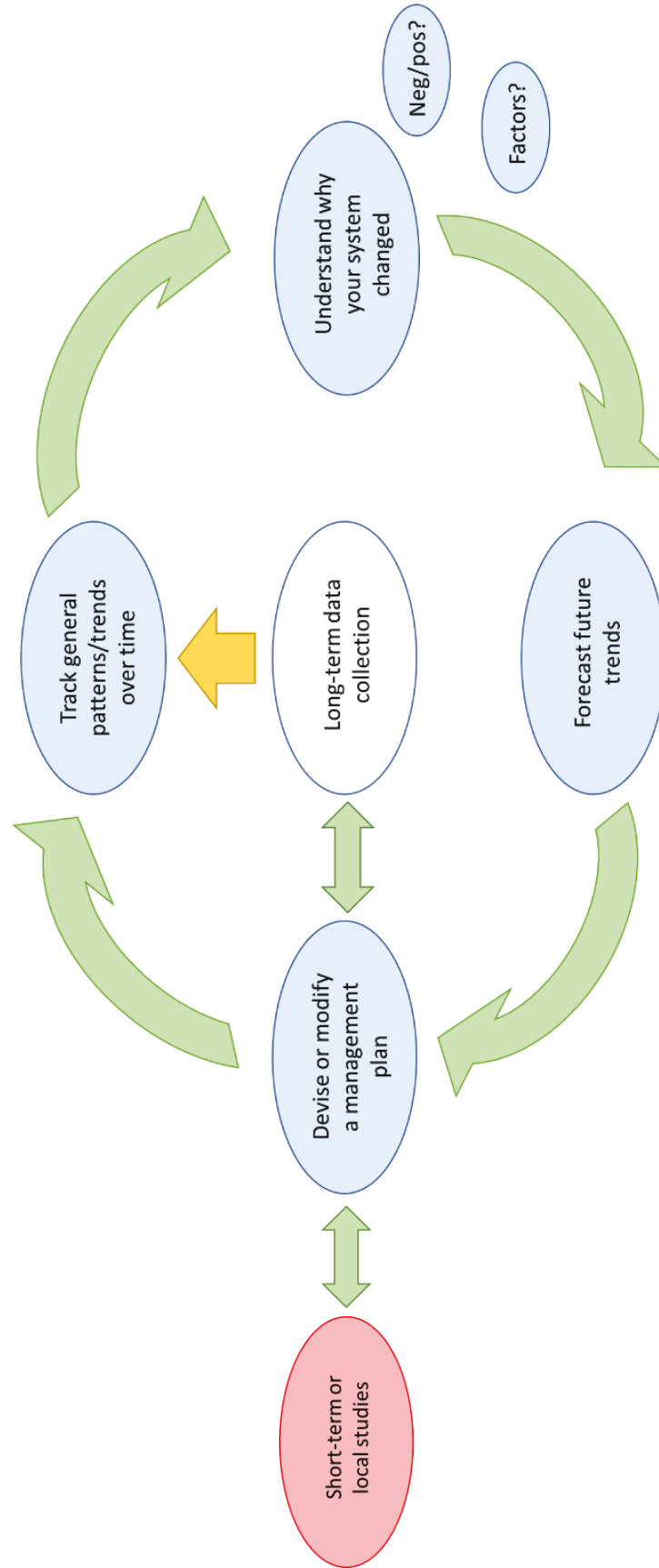


Figure 1.1. The central role of long-term datasets in research and management decisions.

Information from long-term datasets are invaluable (Hughes et al. 2017, Burns et al. 2018); only after such studies are conducted can we predict the effects of longer-term ecological and climatic trends on a system. This does not mean that shorter-term observational or experimental studies are inherently flawed, as these studies may act as primary indicators of change within a population that may encourage more research in the future. It is, however, important to acknowledge their limitations in predictive scope due to their relatively-shorter duration (Festa-Bianchet et al. 2017, Burns et al. 2018).

Good science begins with good questions (Tulloch 2012)

A major criticism of long-term data collection is the large and continuous funding that it requires, often without a clear set of questions (Burns et al. 2018). Monitoring projects without questions or goals may be wasting effort and resources collecting data at biologically uninformative places, times, or scales. On the other hand, well-designed monitoring programs are invaluable. For example, bighorn sheep (*Ovis canadensis*) aerial surveys conducted by the Government of Alberta record annual winter bighorn sheep demographic and location data, for a large portion of their range in the Alberta Rocky Mountains. The inclusion of more detailed observation such as ram horn class or age class from these aerial surveys may not be reliable, and therefore useful, since aerial surveys rely on visibility of sheep, which is often limited by distance and/or weather conditions that ultimately render it difficult to accurately identify sheep age (A. Hubbs, *pers. comm.*). Therefore, monitoring projects, including long-term projects, should begin with a broad understanding of the system, and a list of questions that are useful to address, given the time or resource limitations.

Evolution of North American mountain sheep

North American mountain sheep in the genus *Ovis* evolved during periods of glaciation in and between North America and Siberia (Valdez and Krausman 1999). The Bering land bridge connecting North America and Siberia was the result of a drop in sea levels during the last glacial maximum (Hultén 1937, Hoffecker et al. 2014).

Ancestral mountain sheep are believed to have crossed the Bering land bridge, connecting modern Siberia to Alaska during the Pleistocene. During this slow transition, mountain sheep (known as a subgenra of sheep, *argaliform*) evolved into the sheep we are familiar with today in North America, *pachyceriforms*- whether this evolution event happened strictly in North America (Severtzov's reversed migration hypothesis) or while crossing the Bering land bridge (Cowan's second principle hypothesis) is debated (Valdez and Krausman 1999). A major event separating North American mountain sheep from Siberian mountain sheep followed; melting and receding glaciers flowed back into the oceans, causing a rise in ocean levels and the disappearance of the Bering land bridge (Redmann 1982, Elias et al. 1996, Valdez and Krausman 1999).

In North America, some sheep populations persisted in refugia in Alaska where some areas remained glacier-free, while other populations migrated southward following the melting glaciers, evolving into two species known as thinhorn sheep (in Alaska; *O. dalli*) and bighorn sheep (southwest, USA; *O. canadensis*). Bighorn sheep later moved further north to inhabit the Rocky Mountains in Alberta and British Colombia (Rocky Mountain bighorn sheep; *O. c. canadensis*), leaving several subspecies including desert bighorn sheep (*O. c. nelsoni*, *O. c. mexicana*, *O. c. weemsi*, *O. c. cremnobates*) and California bighorn sheep (*Ovis canadensis sierrae/californiana*) in southwestern United States. Further north, thinhorn sheep spread into the

Mackenzie Mountains (Yukon and Northwest Territories) and northern British Columbia, ultimately evolving into two distinct subspecies, Dall (*O. d. dalli*) and Stone sheep (*O. d. stonei*). Dall sheep typically inhabit the more northern areas of the thinhorn sheep range, such as Alaska and the Mackenzie Mountains, while Stone sheep are predominantly found in northern British Columbia (Valdez and Krausman 1999, Canadian Wildlife Health Cooperative 2016).

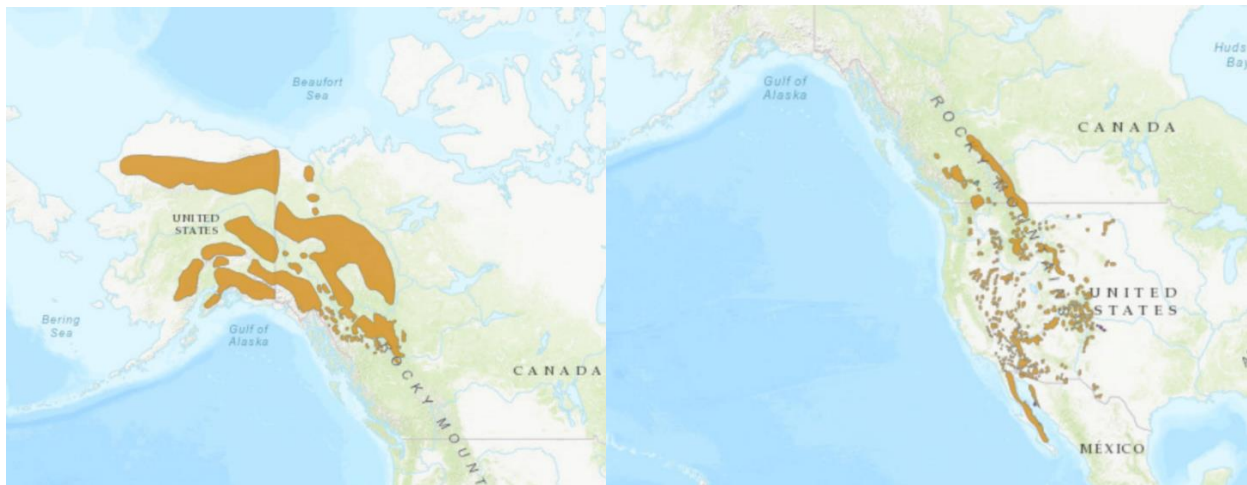


Figure 1.2. Map of North America showing (A) Dall (IUCN 2008a) and (B) Bighorn sheep (IUCN 2008b) species distributions.

Mountain sheep morphology

Bighorn sheep differ from thinhorn sheep mainly in their horn and body size (Valdez and Krausman 1999, Canadian Wildlife Health Cooperative 2016); bighorn rams have thicker horns and larger bodies than thinhorn rams. Generally, bighorns have brown fur and vary minimally amongst subspecies. Most noticeably, Rocky Mountain bighorn sheep have white rumps, while desert bighorn sheep have a dark stripe along their back, ending at the tip of the tail (Nichols and

Bunnell 1999, Demarchi 2004). In comparison, Dall and Stone sheep differ in coat colour, which is white and grey-black, respectively (Canadian Wildlife Health Cooperative 2016).

Depending on sex, age, and season, sheep body mass will vary (Festa-Bianchet et al. 1996). Overall, male bighorn sheep lambs typically weigh 10% more than female lambs, and tend to surpass females in growth by their first year (Festa-Bianchet et al. 1996, Shackleton et al. 1999). Female bighorn sheep will continue to grow until 3-4 years old, when they can weigh 30-90 kg (mean of 51 kg at age 4; Festa-Bianchet et al. 1996), while a male will grow until 6 years old with a mass ranging from 50-130 kg (mean of 77 kg at age 4; Festa-Bianchet et al. 1996, 1997, Shackleton et al. 1999). Though less is known about Dall populations, Dall ewes vary from 30-50 kg, with a mean of 49 kg, and rams from 30-90 kg with a mean of 75 kg in early winter (Nichols and Bunnell 1999). Dall ewes and rams tend to reach maximum body size by 6 years of age.

Sheep weight is sinuous in response to developmental requirements and resource availability in the season (Festa-Bianchet et al. 1996). During the winter, bighorn sheep can lose up to 20 to 23% of their weight, particularly evident in females which typically lose more of their weight during the winter months (Festa-Bianchet et al. 1996, Shackleton et al. 1999). In contrast, Dall sheep may suffer harsher and longer winters with low food quality and availability, and can lose up to 16% body weight (Nichols and Bunnell 1999).



Figure 1.3. Mountain sheep species studied in this thesis. (A) Dall sheep in the Mackenzie Mountains, NWT (Environment and Natural Resources 2020), and (B) Bighorn sheep in the Rocky Mountains, AB (Loewen 2016).

Habitat use, diet and social structure

Mountain sheep live in a variety of mountain habitats (Valdez and Krausman 1999). Mainly occupying high altitude rocky terrain, mountain sheep are adapted to harsh cold climates, and generally live in open landscapes (Alberta Environment and Parks 2015, Canadian Wildlife Health Cooperative 2016). These charismatic mammals tend to prefer wind-swept above-treeline areas with steep slopes, most likely to easily travel and escape predation (known as *escape terrain*; Nichols and Bunnell 1999, Alvarez-Cárdenas et al. 2001). Sheep, especially rams, may also move into forested areas to avoid deep snow, to cool down when hot, and to seek refuge from potential predators (Demarchi 2004). Many factors are known to affect sheep habitat selection, including predation, competition, climate, home range fidelity, proximity of water and ability to travel for food and reproductive purposes (Hik and Carey 2000, Alvarez-Cárdenas et al. 2001, Podrasky et al. 2011, Klein et al. 2019).

In these landscapes, mountain sheep prefer to forage on low vegetation typically found in subalpine tundra or meadow habitats, such as grasses, graminoids, forbs, shrubs, moss, and lichen, depending on availability on terrain (Nichols and Bunnell 1999, Demarchi 2004). Their forage availability varies at different latitudes. Dall sheep, found further north than bighorn sheep, typically rely more heavily on graminoid and lichen species than other categories (Nichols and Bunnell 1999), while bighorn sheep consume more forbs and grasses (Shank 1982, Shackleton et al. 1999). Rams may also consume conifers in small amounts, although more-so in the spring-summer season (Shackleton et al. 1999, Demarchi 2004).

A mountain sheep population separates into two main bands for most of the year; male bands consist only of adult rams (ca. aged 4 and older) and nursery bands consist of adult ewes and their young (Nichols and Bunnell 1999, Demarchi 2004). These two bands group once every year during the rutting season, early to late fall; during this time, adult rams compete for mating opportunities (Alberta Environment and Parks 2015, Canadian Wildlife Health Cooperative 2016).

Excluding the rutting season, the bands vary slightly in locations based on nutrition and protection requirements. Nursery bands may be found at higher more rocky terrain during the winter and spring to shelter their young from predators, which include cougars (*Puma concolor*) and coyotes (*Canis latrans*; Festa-Bianchet et al. 1997, Alvarez-Cárdenas et al. 2001). Mid to late spring, pregnant females give birth in their winter ranges, or a separate lambing range (Demarchi 2004). Meanwhile, male bands may seek higher-nutrition forage from lower elevations throughout the year and may even stray below the treeline.

Mountain sheep can have 2-6 distinct ranges depending on the season, their age, and sex band (Nichols and Bunnell 1999, Demarchi 2004, Lawler 2004). On average females hold 2-3

seasonal ranges, while male bands vary in number of ranges visited. These separate seasonal ranges can be as close-together as different locations on a mountain (Ram Mountain; Coltman et al. 2002, Heffelfinger 2017, Schindler et al. 2017), to as far-apart as completely different mountains.

Alvarez-Cárdenas et al. (2001) found a slight shift of bighorn sheep to lower elevations from winter to summer. However, ewes were historically observed to have moved to much higher elevations with rugged terrain in the spring, potentially for protection from predation during lambing around May-June (Festa-Bianchet 1988, Alvarez-Cárdenas et al. 2001, Roffler et al. 2017). During these warmer months, they tend towards areas with grasses, forbs and sedges (Demarchi 2004).

During the winter, most sheep bands prefer the southern dryer slopes and higher elevations (Nichols and Bunnell 1999, Alvarez-Cárdenas et al. 2001, Demarchi 2004). Females strongly prefer areas near escape terrain (Festa-Bianchet 1988). These areas have thin layers of snow that help preserve vegetation throughout the cold months and are easier to access than areas with dense snowpack (Goodson et al. 1991a, Alberta Environment and Parks 2015, Canadian Wildlife Health Cooperative 2016). In this season, they tend to forage in areas with graminoids as opposed to grasses, forbs or sedges (Nichols and Bunnell 1999, Demarchi 2004).

Mountain sheep tend to have a high rate of return to a particular mountain during a season, showing strong fidelity and rather small home ranges ($\sim 1 \text{ km}^2$; Demarchi 2004, Lawler 2004) during the winter and summer; this is particularly true for females (Demarchi 2004). During the transitional periods of spring and fall, sheep range can grow to up to approximately 60 km^2 (Shackleton et al. 1999, Demarchi 2004, Lawler 2004).

Mountain sheep have distinct routes that take them to and from their seasonal ranges (Demarchi 2004). These ranges and routes intersect with water holes and mineral licks which they consistently return to for vital resources and protection from predation. For example, Podrasky et al. (2011) showed that these movements are consistent across years (*Fig. 1.4*).

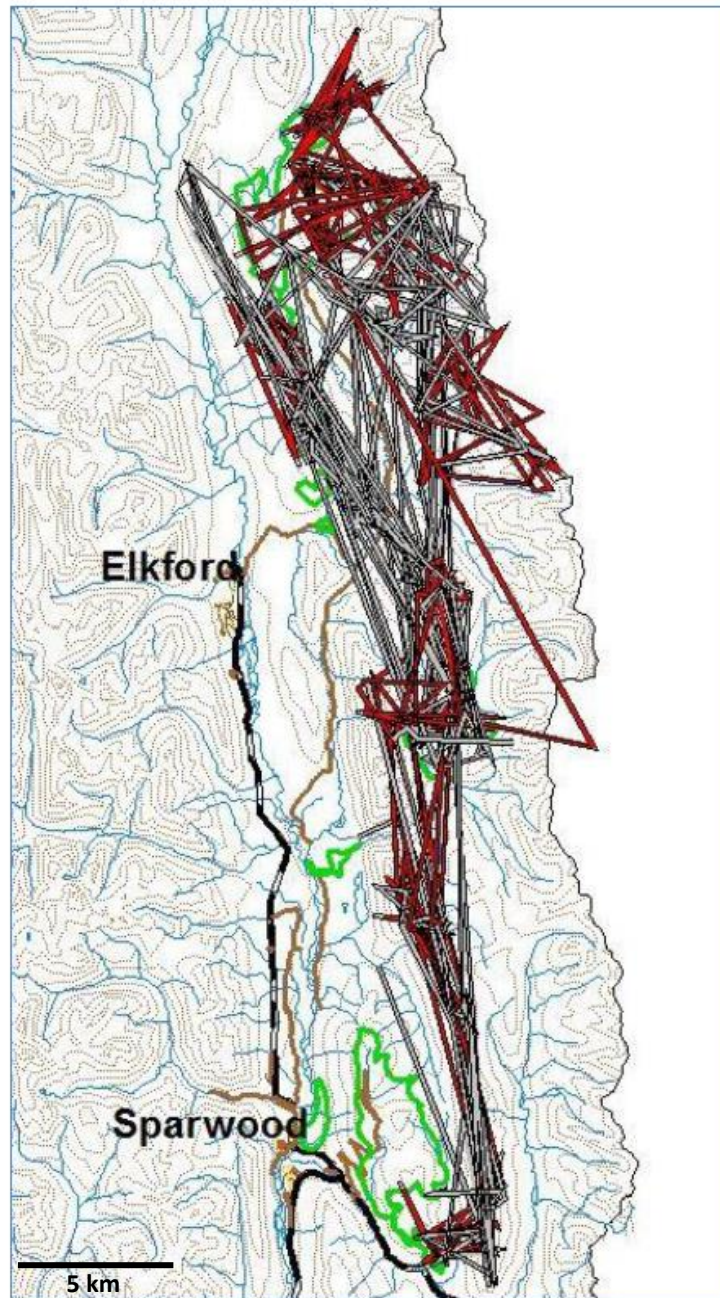


Figure 1.4. Movement patterns of Elk Valley (British Columbia, Canada) bighorn ewes and rams (red and grey lines, respectively) from March 2009 to February 2011 (Podrasky et al. 2011).

Hunting and horns

Biotic factors (e.g., predation, forage availability, and seasonal behaviour) and abiotic factors (e.g., climate and topography) influence where mountain sheep are found on the landscape. One of the most pervasive influences on wildlife is human activity (Pacifici et al. 2018, Tucker et al. 2018, Yurkowski et al. 2018). Humans influence mountain sheep directly through direct contact (e.g., hunting and tourism), or indirectly through landscape alterations or climate change, but trophy and subsistence hunting activities are probably the greatest influences on mountain sheep populations in Canada.

Mountain sheep rams compete with other males for opportunities to mate (Coltman et al. 2002). This drive to compete for mates has led to the sexually-selective evolution of weaponry to aid in competitions amongst other males (Coltman et al. 2002, Pigeon et al. 2016). Horns are not shed each year (as with antlers), and instead grow in segments called *annuli* stacked one on top of the other (Eamer 2014, Carvalho et al. 2017). Annuli are demarcated by a deep crease, which marks the winter season when sustenance is scarce. Horns are built from keratin and grow from the horn core out, growing wider and longer each year in a helical direction (a full curl ram possesses a set of horns whose tip of each horn returns to the level of the skull; Monteith et al. 2017). The tip of a ram horn is typically referred to as the lamb sheath, since it is the horn core exposed that grows during the first year. Ram horn size varies due to many factors including mother pre-natal condition, environmental and human stresses, resource availability and quality, individual body condition, and genetics (Hoefs and Nowlan 1997, Monteith et al. 2017). Horn size heritability from parents to son may range from 32%-43%, suggesting a considerable contribution from parent genes as well (Alberta Environment and Parks 2015, Douhard et al. 2017).

Similar to all sheep, males grow horns faster than females, and continue growing horns past year One (Festa-Bianchet et al. 1996, Shackleton et al. 1999). Male bighorn ram horns are bigger than Dall ram horns, and could accumulate length of about 88.3 cm at mean harvest age of 7.6 years (1996-2014, WMU400 AB; Alberta Environment and Parks 2015) and 88.97 cm at mean harvest age of 10.3 years (1996-2014, Mackenzie Mountains; Larter and Allaire 2017), respectively. Hoefs and Nowlan (1997) compared Dall sheep in the wild and in captivity, and showed that captive horn length surpassed those of wild by minimum 5 cm, by 8 years of age. Another study by Hik and Carey (2000) revealed the effect of various climatic factors and phenomena on horn size change over time. These studies demonstrate the importance of resource limitations and environmental factors on ram horn size.

Recent studies draw a connection between areas with high hunting pressure and ungulate horn size decline with time (Coltman et al. 2003, Allendorf and Hard 2009, Festa-Bianchet et al. 2014). Hunters typically prefer males with larger antlers or horns. When under high hunting pressure, this selection brings forth the possibility that males with faster growing antlers or horns will have less mating opportunities, and therefore fewer “fast-growing” genes passed to the next generation (Coltman et al. 2003, Allendorf and Hard 2009, Douhard et al. 2016). For example, Crosmarty et al. (2013) observed a significant decline in horn size in impalas (*Aepyceros melampus*) and sable antelopes (*Hippotragus niger*), two species under notable hunting pressure in Zimbabwe, Africa. Another study by Douhard et al. (2016) identified a significant decline in Stone sheep horn size over 37 years in an area with high hunting pressure, and no decline in an area with low hunting pressure, in northern BC.

Horns are also highly regarded in many cultures. In western society, mountain sheep often are used to symbolize areas of rugged wilderness (Valdez and Krausman 1999). In

addition, local indigenous communities have relied on horns to shape weapons, ornaments, and utensils. Amongst sheep, large horns represent dominance within the population; size is often a good indicator of superior fitness, and of victory in competition with other rams during the rut (Coltman et al. 2002, 2003, Alberta Environment and Parks 2015, Douhard et al. 2016, 2017, Monteith et al. 2017).

Mountain sheep are particularly at risk of high hunting pressure, as they fall victim to both trophy hunting (Fish and Wildlife Division 2012, Festa-Bianchet et al. 2014, Larter and Allaire 2017) and subsistence harvests (Veitch et al. 1998, Alberta Environment and Parks 2015, Larter and Allaire 2017). Horns are a precious commodity worldwide and, as such, attract both trophy hunters and tourists to Canadian mountain sheep habitat (Coltman et al. 2003, Douhard et al. 2016). The trophy hunting and tourism industries in many parts of Canada are major contributors to the local economy and conservation efforts (Veitch et al. 1998, Fish and Wildlife Division 2012, Alberta Environment and Parks 2015, Canadian Wildlife Health Cooperative 2016).

To harvest a sheep, a hunter needs to possess a seasonal sheep license and tag (Fish and Wildlife Division 2012, Larter and Allaire 2017). Each year, wildlife licenses are sold to the public as either a General (unlimited licenses are sold) or Special license (a draw is used to distribute and sell limited licenses). A hunter may be classified as Resident (lives within the province or territory), Non-Resident (lives outside the province or territory), or Non-Resident Alien (lives outside the country). Today, any Alberta Resident can purchase a license to hunt one legal ram with at least one horn (Festa-Bianchet et al. 2014). However, both Non-Resident and Non-Resident Alien big game hunters must hunt using a licensed outfitter's guide services in Alberta and NWT (Fish and Wildlife Division 2012, Larter and Allaire 2017).

Currently, the only jurisdiction in North America that does not have a cap on ram trophy hunting licenses is the province of Alberta (Alberta Environment and Parks 2015). Furthermore, two southern regions in Alberta that currently enforce a Special hunting license for ram trophy hunting still hold a minimum legal ram horn curl of $\frac{4}{5}$, as compared to its western and southern counterparts that hold a full curl regulation (A. Hubbs, *pers. comm.*). Thus, bighorn sheep harvest was about 40% higher in Alberta than in other areas, and has been increasing since 2005 (Fish and Wildlife Division 2012). Sheep harvest in 2020 is prohibited in mine sites or in provincial parks. According to an Alberta government harvest report in 2012 (Fish and Wildlife Division 2012), mean Resident and Non-Resident/Non-Resident Alien harvest from 1992 to 2011 was 138 and 41 sheep, respectively.

Thesis structure and objectives

In Chapter 2, I investigate the changes of Dall ram horn size over 16 years (2002-2017) in the southern Mackenzie Mountains, using Northwest Territories' (NWT) government harvest data. I examine if, and how, horn volume changes over time, and the possible relationship to hunting management and intensity. This chapter summarizes the changing condition of Dall rams over the past decade, but also assesses the development of management approaches with respect to potential hunting pressures. The NWT Dall sheep populations are some of the most intact mountain sheep populations worldwide due to the remoteness of NWT's mountains. Consequently, no survey or inventory data has been collected in this area, leaving harvest data as our only glimpse into Dall sheep population condition. This research was conducted in collaboration with NWT Regional Biologists in Fort Simpson to better inform management decisions for Dall sheep in the NWT.

In Chapter 3, I use 52 years of bighorn sheep winter range inventory data (1967-2018), from Alberta's Rocky Mountain range, to examine bighorn sheep distribution trends over the landscape and with time, to identify areas of importance to sheep and guide future conservation activities for bighorn sheep in their most intact range in the world. This winter range inventory dataset was collected aerially and is one of the largest available datasets for large mountain vertebrates. Its initial purpose was to track bighorn sheep population structure over the years, and as a result includes information on sex and age classes within the population per year. Due to the remote nature of mountain habitat, it is important to acknowledge and make use of long-term monitoring datasets when available to gain a clearer understanding of mountainous terrain and habitat change over time in response to a changing climate. Moreover, Alberta Rocky Mountains are home to one of the last big and relatively undisturbed mountain sheep ranges. These mountains are also the focus for many studies on horn size and population status because Alberta is a major trophy hunting destination. The project is a collaboration with the Alberta Biodiversity Monitoring Institute (ABMI), the Government of Alberta, and the Alberta Environment and Parks.



Figure 1.5. Photograph depicting a band of bighorn sheep along a sloped gradient, observed during winter aerial surveys in the northern Rocky Mountains (Photo: J. Kneteman).

CHAPTER 2

DALL SHEEP HORN SIZE AND HARVEST MANAGEMENT IN THE MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES

Introduction

Social dominance and reproductive success of mountain sheep (*Ovis* spp.) rams are linked to both horn size and age (Geist 1971, Valdez and Krausman 1999). Furthermore, horn annuli have provided a useful indicator of habitat quality, seasonal environmental conditions, and effects of selective harvest (Hik and Carey 2000, Hedrick 2011, Festa-Bianchet et al. 2014, Douhard et al. 2017, Monteith et al. 2017). Across most of their native North American ranges, mountain sheep ram horns are getting smaller due to hunting pressure (Coltman et al. 2003, Loehr et al. 2010, Hedrick 2011, Festa-Bianchet et al. 2014, Pigeon et al. 2016) - a consequence of both trophy hunting (Fish and Wildlife Division 2012, Festa-Bianchet et al. 2014, Larter and Allaire 2017) and subsistence harvest (Veitch et al. 1998, Alberta Environment and Parks 2015, Larter and Allaire 2017). Studies on declining horn size of bighorn sheep (*O. canadensis*) in Alberta, Canada, drew attention to horn size trends worldwide (Coltman et al. 2003, Hedrick 2011, Festa-Bianchet et al. 2014, Pigeon et al. 2016). Harvest leads to artificial selection against genotypes with faster-growing horns, causing a human-induced decline in ram horn size. The harvest of Stone sheep (*O. dalli stonei*) in northern British Columbia has led to a similar decline in ram horn size, in that horn growth was slower with high hunting pressure compared to low hunting pressure (Douhard et al. 2016).

In the Northwest Territories (NWT), Canada, regional officers and outfitters typically assume that hunting pressure on mountain sheep is less intensive than in the southern provinces

(British Columbia, Alberta) or Yukon (Alberta Environment and Parks 2015, Larter and Allaire 2017). Hunting pressure itself, however, is difficult to assess unless population data are available to calculate the ratio of sheep hunted to the population size. Thus, in the NWT, the influence of hunting pressure on Dall ram horn size is overlooked, and presence of changes in horn size is unknown (Heimer 2006, Heffelfinger 2018).

Dall sheep (*O. d. dalli* Nelson, 1884) are northern mountain specialists, adapted to living in cold, and quickly changing conditions (Loehr et al. 2010, Canadian Wildlife Health Cooperative 2016). They are the most abundant subspecies of thinhorn sheep in the Mackenzie Mountains (Canadian Wildlife Health Cooperative 2016), but detailed information about their population dynamics and distribution is limited by the remoteness of their habitat (Simmons 1982, Veitch et al. 1998, Hik and Carey 2000). Increasing harvest pressure, resource development, and concerns about climate change have resulted in more extensive monitoring and management efforts in recent years (Larter and Allaire 2017). Currently, legally-hunted rams must have a minimum $\frac{3}{4}$ horn curl in the NWT. Ram horns are highly sought worldwide; Dall sheep are one of the most important trophy species in Canada (Coltman et al. 2003) and one of the most hunted trophy species in the Mackenzie Mountains, with approximately 65% of all non-resident hunters purchasing Dall sheep tags in 2016 (ca. 76% of all tags were successful hunts; Larter and Allaire 2017).

The objective of this study was to examine the changes of Dall ram horn size over time in the southern Mackenzie Mountains. We used annual harvest data over 16 years to assess temporal trends in horn volume of harvested rams, and to discuss potential effects of hunting pressure on Dall ram populations in the southern Mackenzie Mountains (Douhard et al. 2017). In

some models, we accounted for the influence of harvest region (i.e., outfitter area), reflecting the significance of local management and harvest on the sheep horn size trend.

Study area

Harvest data were collected in the southern Mackenzie Mountains range, NWT, Canada (Fig. 2.1, Table SM2.1). The Mackenzie Mountains (ca. 140 000 km²) is a globally-recognized trophy hunting destination, with Dall sheep as one of its major attractions (Veitch et al. 1998, Larter and Allaire 2017). This mountain chain attracts hunters due to its undisturbed landscape, and is a tourist destination for a variety of outdoor activities, for example tourism in the Nahanni National Park and Reserve and the Canol Heritage Trail (Veitch et al. 1998). The area is in the Taiga Cordillera ecozone (Ecological Framework of Canada 2020), home to various ecotypes including the tail end of the Rocky Mountains and beginning of the Mackenzie Mountains. These high elevation communities typically consist of alpine and sub-alpine shrubs, forbs, grasses and lichens, upon which large mammals such as mountain goats (*Oreamnos americanus*) and Dall sheep can forage (Canadian Councils of Resource Ministers 2010, Condon 2013). Carnivores such as wolverines (*Gulo gulo*) and grizzly bears (*Ursus arctos horribilis*) are found in northern mountain ranges.

The Mackenzie Mountains are divided into harvest management zones. Currently, eight outfitters are licensed to provide big game hunting services under the NWT Wildlife Act. Each licensed outfitter has exclusive guiding rights within their zone, which enhances the outfitter's ability to practice sustainable harvest through annual allocation of harvest effort (Larter and Allaire 2017). Thus, different outfitter areas may account for accessibility of hunters to Dall rams differently (either through guides or landscape). To include the effect of outfitter area in the horn

size model, we followed the division of the four southern NWT outfitters: South Nahanni, Nahanni Butte, Redstone, and NWT. Outfitter area is included in our model analyses as a random effect (*Fig. 2.1*).

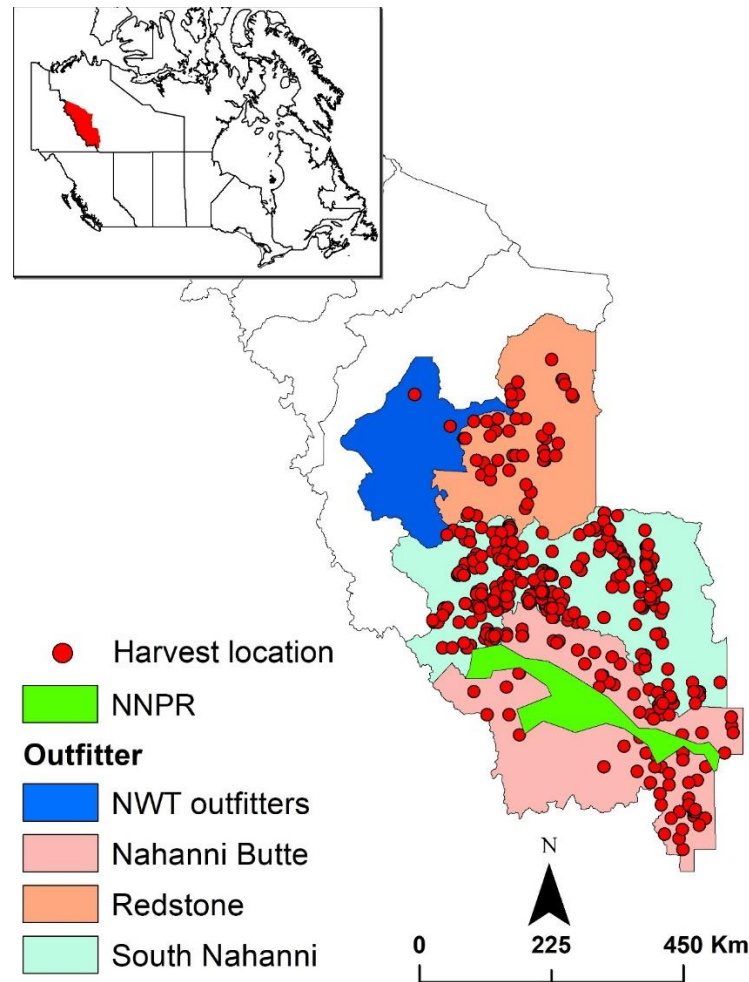


Figure 2.1. Dall sheep ram harvest ($n=755$) between 2002 and 2017 in the Mackenzie Mountains, Northwest Territories, Canada. Each segmented area represents an independent outfitter area, identified as *OA* in our model. NNPR = Nahanni National Park Reserve. NNPR polygon shown is the area prior to recent park expansion (implemented starting in 2016).

Methods

Hunting Pressure

Sheep population size data is lacking in our study area, so we attempted to assess hunting pressure using a ratio of the number of licenses purchased annually to the sheep population range (km²; *Table SM2.2*), which was then compared to other areas where mountain sheep were hunted in Canada. We adopted the same protocol that was used to compare the effect of “high” and “low” hunting pressure on Stone sheep horn size (Douhard et al. 2016; *Table SM2.2*).

Horn Growth Measurements

Reporting Dall sheep harvest date and outfitter area is mandatory, and a uniquely numbered plug is inserted in the horn by GNWT Renewable Resources officers. We sampled Dall rams reported at the Fort Simpson and Fort Liard offices in 2002-2017 and measured basal circumference, total horn length, distance between right and left horn tips, and each annulus' circumference and length. Most of the measurements (>90%) were conducted by two local wildlife biologists. Measurements were made on right horns following a standardized protocol (Canadian Wildlife Health Cooperative 2016). On the rare occasion that the right horn was damaged or severely broomed, measurements were made on the left horn instead.

We calculated the volume of each annulus using the equation of a cylinder, $V = \frac{\pi h}{3}(R^2 + Rr + r^2)$, with the exception of the horn tip (Annulus 1) whose volume was estimated using the equation of a cone, $V = \frac{\pi hr^2}{3}$ (Total volume = sum (annulus volumes); Hik and Carey 2000). Age was determined by counting the number of annuli on a horn. We removed ram measurements for

categories of age at harvest, harvest year, and outfitter area that had fewer than three rams. This resulted in the removal of rams harvested at ages 5 and 15 ($n < 3$, 2 rams removed; *Table SM2.1*).

Models

We developed general linear models (GLMs) to assess changes in horn size over time. Total horn volume was included as the response variable, and harvest year (*Year*; 2002 to 2017) was included as a fixed effect. Age at harvest (*Age*; 6 to 14) was also included as a covariate fixed effect, as it is expected to affect horn volume in a predictable manner (generally, the older the ram, the larger the horns will be). Outfitter area (*OA*; South Nahanni, Nahanni Butte, Redstone, and NWT) was included as a random effect to account for potential differences in local management and harvest on the ram horn size trend across the southern Mackenzie Mountains.

Table 2.1. Model set used to assess ram horn size change over time (years). *Age* refers to the age of the ram at harvest. *Year* refers to the year at which the ram was harvested. *OA* identifies the outfitter area where the ram was hunted. * indicates the assessment of interaction of two effects (e.g., *Age*Year* assesses the interaction between *Age* and *Year* effects). *Horn Volume = null* represents the model that includes no fixed or random effects (i.e., a horizontal line across years), and indicates no horn change over time.

Model set
Horn Volume = <i>Age</i>
Horn Volume = <i>Year</i>
Horn Volume = <i>Age</i> + <i>OA</i>
Horn Volume = <i>Year</i> + <i>OA</i>
Horn Volume = <i>Age*Year</i>
Horn Volume = <i>Age*Year</i> + <i>OA</i>
Horn Volume = null

Using Akaike's Information Criterion (AIC), we compared the models' fits to the horn volume dataset to determine which factors need to be included to best explain the horn size variation. All statistical analyses were performed in R 2.14.0 (R Development Core Team 2017).

Results

A total of 755 rams were measured and analyzed during the 16 years, ranging from 6 to 14 years old (*Table SM2.1*). Over the 16-year period, we observed no significant trend in the mean horn volume of harvested rams (*Fig. 2.2B*), nor in the mean age at harvest for rams over this period (*Fig. 2.3*). Our best model for horn volume that included *Year* (Horn Volume =

$Year*Age + OA$) illustrated that mean horn volume increased slightly from approximately 1900 to 1950 cm^3 (Fig. 2.2B). Over the study period, the mean age at harvest was consistently around 10 years (Fig. 2.3).

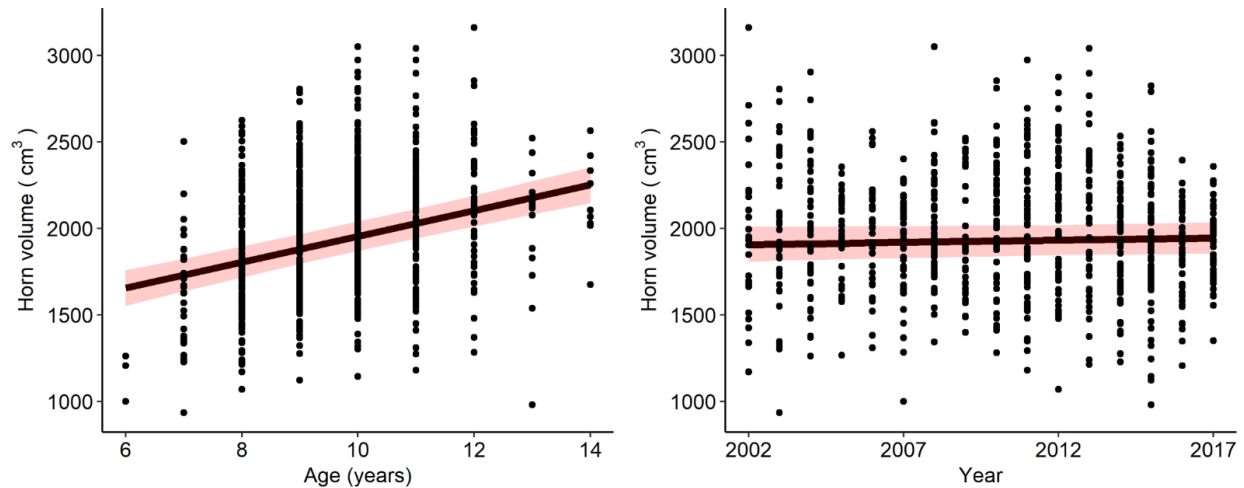
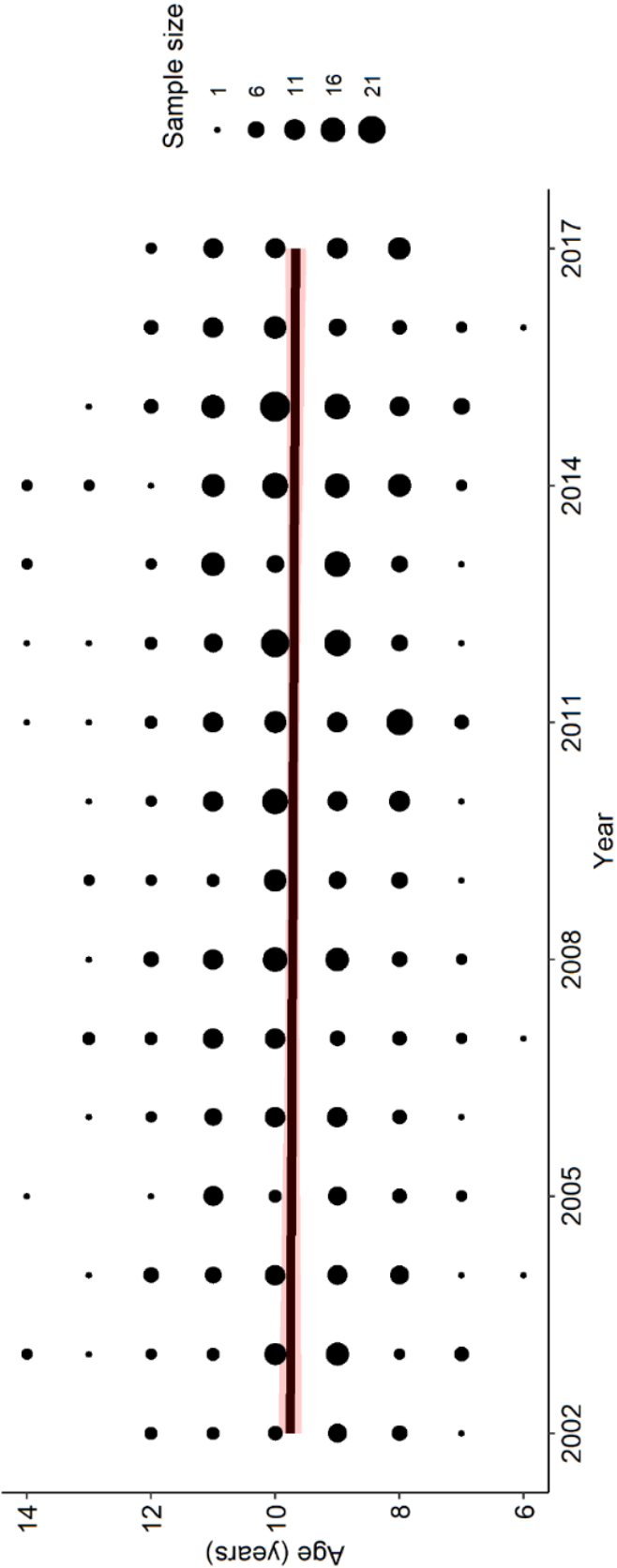


Figure 2.2. Representations of two models of best fit, Horn Volume = $Age + OA$ (A) and Horn Volume = $Age*Year + OA$ (B). A) Mean horn volume for each age of harvest. B) Mean horn volume for each year harvested. All panels include a shaded area representing the 95% confidence intervals.



All models showed no significant horn volume trend over time (*Table 2.2*). Models including outfitter area as a random effect (except for Horn Volume = $Year + OA$) had the lowest AIC values, and therefore highest AIC rankings (10868 and 10871, lowest to highest AIC; *Table 2.2*). All models including age at harvest as a fixed effect had the highest AIC rankings (10868, 10871, 10919, and 10921, lowest to highest AIC; *Table 2.2*). Models including harvest year as a fixed effect (except for Horn Volume = $Age * Year + OA$) had the lowest AIC rankings and fit the harvest data poorly (10871, 10921, 10942, and 10983, lowest to highest AIC; *Table 2.2*), two of which had AIC rankings that were poorer than the null model (Horn Volume = $Year + OA$, and Horn Volume = $Year$). The effect of age at harvest on horn volume was significantly positive (confidence intervals for β estimates did not include zero) for all models (*Table 2.2*, *Fig. 2.2A*). Horn volume did not significantly change over the years, as confidence intervals for β estimates for the effect of harvest year included zero for all models (*Table 2.2*, *Fig. 2.2B*). The best model included a random effect of outfitter area on the intercept in the linear regression (*Table SM2.3*).

Table 2.2. Generalized linear models for Dall ram horn volume from 2002 to 2017 in the Mackenzie Mountains, NWT, Canada. AIC = Akaike Information Criterion. Δ AIC = Difference in AIC from the best fitting model (in bold). Estimates = β estimates, calculated for *Age* and *Year* effects in the model, separately. * = Estimates in which the confidence interval does not include zero (i.e., significant). Ages 5 and 15 were excluded from the following models due to low sample size ($n < 3$).

Model	AIC	Δ AIC	Estimates (\pm Confidence Interval)	
			<i>Age</i>	<i>Year</i>
Horn Volume = <i>Age</i> + (1 OA)	10868	0	74.40 (± 16.5228)*	-
Horn Volume = <i>Age</i> * <i>Year</i> + (1 OA)	10871	3	-	-
Horn Volume = <i>Age</i>	10919	51	72.75 (± 17.2298)*	-
Horn Volume = <i>Age</i> * <i>Year</i>	10921	53	-	-
Horn Volume = 1	10940	72	-	-
Horn Volume = <i>Year</i> + (1 OA)	10942	74	-	1.76 (± 6.0797)
Horn Volume = <i>Year</i>	10983	115	-	-4.47 (± 5.8906)

Discussion

We expected that the models that included the random effect of outfitter area would support the data the most, suggesting that accessibility to rams would affect horn size of rams over time. Moreover, we expected that horn volume would remain constant over time, based on the observation that Dall ram hunting pressure appears to be lower in the Northwest Territories (Alberta Environment and Parks 2015, Larter and Allaire 2017) compared to other monitored populations of Dall, Stone, and bighorn sheep (*Table SM2.2*). Both expectations were supported

by the harvest data, with the models that best supported the data including the outfitter area as a random effect.

Within the limits of our study area, we assumed that every sheep that was hunted was reported, although some sheep may have been illegally hunted and not reported, in which case hunting intensity may have been stronger than calculated. Moreover, most studies that observed a trend had analyzed harvest data over 30 or more years (Coltman et al. 2003, Loehr et al. 2010, Crosmarby et al. 2013, Festa-Bianchet et al. 2014, Douhard et al. 2016). Since we only had 16 years of NWT Dall ram harvest data available, we had to assume that this period would be long enough to observe a horn size trend, if present.

Our results showing no trend in horn size over time of rams exposed to hunting was similar to a study on alpine ibex (*Capra ibex*; Büntgen et al. 2018) but contrasts with research on other sheep populations in Canada (Coltman et al. 2003, Loehr et al. 2010, Festa-Bianchet et al. 2014, Douhard et al. 2016). The absence of a significant trend might have occurred because the majority of the rams in our study were older at harvest (around 10 years old, peak Dall ram reproductive contribution age of approximately 5-7 years; Nichols and Bunnell 1999), likely giving rams enough time to contribute reproductively to the population, and ultimately affecting next-generation lamb numbers and genetic diversity. In comparison, bighorn rams were mainly hunted by 4 or 5 years, leaving arguably little time to contribute reproductively (peak bighorn ram reproductive contribution age of approximately 6-7 years; Festa-Bianchet et al. 2014, Kardos et al. 2018).

We found that the average ram age at harvest did not significantly change over time. Festa-Bianchet et al. (2014) suggested that an increase in mean age at harvest of bighorn rams

over time was related to a decline in horn size growth rates. If ram horn growth is slowed, trophy hunters should target older rams to meet the legal or larger desired horn size.

Dall sheep rams play a major role in the northern hunting industry and the measure of a high-quality ram is dependent on horn size. Coltman et al. (2003) first demonstrated the concerns of a shift towards smaller horns for the hunting industry. A concern to their population stability is that rams are harvested before they have an opportunity to reproduce successfully, which can affect the number of lambs produced and genetic diversity within a population (Coltman et al. 2003, Douhard et al. 2016). With bighorn sheep, large horns effectively improve reproductive success by around age 7 (Coltman et al. 2002). It is possible that the Dall ram horn size model showed no declining trend over time because the majority of rams were >7 years old when harvested (mean age of 10), and therefore likely to have already contributed to the next generation's lamb production and gene pool. It is still not well understood how much of this trend in other populations of sheep is due to hunting pressure and how much is owed to other factors (e.g., population density, land management, or climatic factors), resulting in either a genetic or phenotypic response in ram horns (Loehr et al. 2010, Boyce and Krausman 2018, Kardos et al. 2018).

Crosmarty et al. (2013) concluded that the effect of hunting pressure on ungulates may vary among species. For example, although hunting pressure for impalas and kudus (*Tragelaphus strepsiceros*) were similar relative to sable antelopes, the effects on horn growth were different. Over time, horn growth decreased for impalas but increased for kudus in response to increased hunting pressure. Though these grassland species use their horns for different reasons from mountain sheep, his finding suggests that variation among species may reflect their ability to obtain resources, and their dependence on and access to resources. However, why some

species of ungulate “tolerate” or respond to hunting pressure better than others is not understood as of yet.

To study the effect of hunting pressure intensity on horn size decline, a study on a subspecies of thinhorn sheep, Stone sheep, in northern B.C. reported a decline in Stone ram horn size over four decades (Douhard et al. 2016). This trend was more pronounced in the area with high hunting pressure than in the area with low hunting pressure and, as a result, they concluded that hunting pressure intensity played a role in the ram horn size trend.

Though similar trends have been reported in many ungulate studies, some exceptions occur. Büntgen et al. (2018) observed no evolutionary change in horn size over 35 years for alpine ibex, despite the presence of hunting. No trend was identified for Iberian ibex (*Capra pyrenaica*) either, suggesting that horn size change over time may be dependent on species-specific life history and local conditions related to human disturbance or climate (Carvalho et al. 2017).

Due to the lack of detailed sheep population records, our study is accompanied by certain limitations. Dall sheep are relatively philopatric to one area (ca. 60 km²; Lawler 2004), but sheep cohorts found near outfitter edges may still stray from their outfitter of birth. Their horns may then have been affected by a different hunting intensity than that associated with the outfitter area the ram was harvested in. Additionally, horn size may fluctuate with the quality of habitat available to sheep in the future (Crosmery et al. 2013, Carvalho et al. 2017, Douhard et al. 2017). For example, increasing temperature in high altitude areas may increase productivity in their habitat, increasing forage availability to lambs and mothers, and potentially resulting in faster growing horns (i.e., younger legal rams). Alternatively, lower food availability might ultimately

affect the number of large-horned rams available to reproduce in the population, resulting in a horn size decline over time.

To address this effect of climate and landscape on horn size, it would be useful to investigate the influence of intra- and inter- annual climatic and landscape effects on horn growth over time by incorporating historical climate (e.g., temperature) estimates for each outfitter. Recorded body mass, size, and condition for documented rams can identify the body-to-horn size ratio and how climate exposure during its life may influence it (Festa-Bianchet et al. 1997, Hik and Carey 2000). Particularly with a more variable and warming climate, understanding how horns may be affected by these external conditions may help us better understand how horn size and hunting will change in the future.

CHAPTER 3

HALF A CENTURY OF BIGHORN SHEEP DISTRIBUTIONS ACROSS THEIR ALBERTA ROCKY MOUNTAIN WINTER RANGE

Introduction

Wildlife monitoring provides records of changes in population numbers or distribution that are essential for agencies responsible for wildlife management (Vos et al. 2000, Singh and Milner-Gulland 2011, Burns et al. 2018, Fortin et al. 2018). Sustained and consistent monitoring is necessary for understanding how species and ecosystems are changing over time, particularly in relation to nearby disturbances and human influence (Alberta Environment and Parks 2015, Burns et al. 2018). The resulting inventories can be used to devise hypotheses and test causative relationships to protect species and their habitats (Singh and Milner-Gulland 2011).

However, wildlife monitoring is often expensive, and many monitoring efforts are of short-term durations. As a result, they can be poorly suited to forecast future conditions (Giron-Nava et al. 2017, Burns et al. 2018). Small-scale studies can support research focused on local population dynamics, but often do not reveal how these populations or communities interact with their surroundings at landscape or ecosystem levels (Festa-Bianchet et al. 2017, Fish and Wildlife Division 2019). Spatially-extensive and long-term studies are essential for assessing population trends associated with climatic or ecosystem changes, including periodic events such as the Pacific Decadal Oscillation (Hik and Carey 2000, Burns et al. 2018).

Long-term census data over large geographic areas provide an opportunity to track changes in wildlife populations over time and space (Vos et al. 2000, Parviainen et al. 2013, Festa-Bianchet et al. 2017, Giron-Nava et al. 2017). Tracking changes is crucial to identify

unusual population demographic trends, to test causative relationships, and to more effectively invest in and execute management actions that maintain population health, resilience, and resistance to disturbance.

A prerequisite for determining the effects of habitat or landscape change on a population is an understanding of historic spatio-temporal trends within their distribution. Two commonly-used methods to analyze distribution patterns of a population from census data are (i) kernel density and (ii) hotspot spatial analyses (Anselin et al. 2000, Gross et al. 2000, Ehlers et al. 2016, Lin et al. 2017). Kernel density analysis assesses the proximity of individuals by using a kernel density estimate function (KDE), to rank the distances of a point to other points within a neighbourhood (Silverman 1998, ArcGISPro 2020a, 2020b). This function, overlayed onto the historic points on a map, can then estimate the probability of individuals being present in a given area, based on the rankings of the points known. Some diverse applications of kernel density analysis include description of standing and downed dead trees (Carpenter 2005, Harmon 2011), assessment of a species' concentration on the landscape in relation to the presence of other factors (Gotelli and Ellison 2002, Simao et al. 2018), and the use of animal distribution to study their relationship with parasite abundance (Stanko et al. 2002).

In contrast, spatial autocorrelation analyses or “hotspots” are used to determine where individuals tend to concentrate, or where they prefer to be, by assessing the proximity of significantly-clustered individuals to other significantly-clustered individuals (Poudyal et al. 2016, Yurkowski et al. 2018). Hotspot analyses are commonly utilized in tourism research to recognize clusters of visitation, and in epidemiology to study concentrations of disease outbreak (Nyandwi et al. 2017, Khan 2018, Tewara et al. 2018, Luenam and Puttanapong 2019, Stopka et al. 2019). This approach may also be used to identify contaminated sites (Liu et al. 2013, Hojati

2019) or the concentration of natural disasters and anthropogenic disturbances on the landscape over multiple timesteps (Hsu and Su 2012, Lin et al. 2017, Soltani and Askari 2017, Lim et al. 2019). In wildlife research, spatial autocorrelation methods were used to assess seagrass macrobenthic patchiness, concentrations of fish assemblages, and hotspots of diversity for arctic marine predators in North America (Yurkowski et al. 2018, Barnes and Hamylton 2019, Catchpole et al. 2019). The use of Geographic Information Systems (GIS) to study population-level hotspots at landscape or homerange scales is a recent application (Long and Nelson 2013).

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis* Shaw, 1804), an ungulate endemic to high elevation habitat, has been a subject of monitoring for decades in Canada (Demarchi 2004, Olson et al. 2008, Alberta Environment and Parks 2015, Canadian Wildlife Health Cooperative 2016), yet their spatial distribution across their northern range is largely unknown. Mountain landscapes are characterized by extremely variable temperatures and weather, rocky and uneven terrain, and low productivity with limited nutritional value (Festa-Bianchet 1988, Loehr et al. 2010, Canadian Wildlife Health Cooperative 2016). Large herbivores in mountain environments are uniquely adapted and particularly sensitive to changes in climate, availability of escape terrain and food, as well as land use changes due to development and other human activities (Márquez et al. 2011, Imperio et al. 2013, Pepin et al. 2015, Klein et al. 2019). Especially true in the north, high-elevation mountain habitat has experienced little direct human disturbance as compared to low elevations and valleys due to its exclusivity and rough or inaccessible terrain (Imperio et al. 2013, Nature Conservancy Canada 2013, Laberee et al. 2014, Larter and Allaire 2017). Therefore, incremental changes in human exposure may drastically affect population and community stability in high-elevation ecosystems.

Alberta's population of bighorn sheep is the largest and most intact in the world (Cutlac and Weber 2014, Alberta Environment and Parks 2015, Malaney et al. 2015). Ram horns are a special trophy hunting interest and also have a substantial value to the economy of Alberta (ca. 2400 resident ram licenses and special licenses sold in 2012; Coltman et al. 2003, Hedrick 2011, Fish and Wildlife Division 2012, Festa-Bianchet et al. 2014). The effects of habitat degradation and anthropogenic stresses, such as hunting, have motivated the Alberta government to survey bighorn sheep populations in the Rocky Mountains annually for more than 50 years. Currently, sheep populations in the Rocky Mountains are monitored and studied at the scale of individual ranges; little is known about populations of sheep in the Rockies as a whole (Kneteman 2016). Albertan bighorn sheep management protocols are in the process of revision and modification, providing a unique and timely opportunity to assess bighorn distribution patterns on the landscape.

Using 52 years of annual winter bighorn sheep surveys spanning the entire Alberta Rocky Mountains (outside of the National Parks), and the two methods of spatial distribution analysis, we attempt to describe bighorn distribution in the greater part of their northern winter range. We determine (1) where bighorn sheep are distributed across the winter landscape; (2) how their distribution changes across three periods between 1967 and 2018; and (3) whether these distributions vary between ewes and rams.

Methods

Study area

The study area encompasses the Canadian Rocky Mountains east of the British Columbia-Alberta border (49° to 55° N latitude; ~40 000 km²; Shackleton et al. 1999). This area,

along with central and eastern BC, is part of the sixth largest Canadian ecozone, the Montane Cordillera Ecozone (490 000 km²; Scudder and Smith 2011). It is characterized as mountainous with steep cliff peaks and expansive valleys, with the highest elevation of 3 747 m above sea level on top of Alberta's Mount Columbia (Canadian Geographic Society 2002, Demarchi 2004).

Four major rivers originate in Alberta's Rocky Mountains: the Smoky River, Athabasca River, North Saskatchewan River and Bow River (*Fig. 3.1A*). These large drainages were used to divide our study area into five population zones, which roughly corresponded to genetic subdivisions within this sheep population (Deakin et al. 2020).

The northern boundary of our study area is also the northern limit of bighorn sheep ranges in North America. The western boundary is marked by the eastern limits of the national parks, as well as the Alberta-British Columbia border where the parks end. Given that Rocky Mountain bighorn sheep are endemic to mountainous terrain, bighorn sheep do not extend past our eastern study area border (the eastern limits of the Rocky Mountains; Demarchi 2004, Olson et al. 2008, Alberta Environment and Parks 2015). Our southern boundary was identified by the USA-Canada border (*Fig. 3.1A*).

Alberta's Rocky Mountains are home to more than 15% of bighorn sheep in the world (Alberta Environment and Parks 2015). They typically utilize the arid vegetation of drier south-facing slopes because they move and feed more easily uninhibited by deep snow cover (Podrasky et al. n.d., Goodson et al. 1991, Festa-Bianchet et al. 1997). Moreover, above treeline grasslands with steep and rocky terrain are preferred to easily spot and protect themselves from ambush predators, such as cougars (Festa-Bianchet 1988, Rominger et al. 2004). Steep rocky areas, for sheep, may act as escape terrain when at risk of predation, since few predators can outclimb sheep (Nichols and Bunnell 1999, Alvarez-Cárdenas et al. 2001). Sheep prefer to forage on low

vegetation typically found in subalpine tundra or meadow habitats, such as grasses, graminoids, forbs, moss, and lichen (Demarchi 2004). They may also consume conifers in small amounts (Shackleton et al. 1999, Demarchi 2004).

Anthropogenic disturbance in the Rocky Mountains is an important factor shaping the landscape for bighorn sheep (Keller and Bender 2007, Bleich et al. 2009, Brown et al. 2010, Alberta Environment and Parks 2015, Douhard et al. 2017). These disturbances include linear features like roads, railways, electrical transmission lines and pipelines, and localized activity such as forest fires and mines. Further south, sheep are exposed to human encroachment through roads, recreational sites and livestock, fire suppression, as well as diseases from encounters between domestic and wild sheep from the USA (Krausman et al. n.d., Rubin et al. 2002, Keller and Bender 2007, Malaney et al. 2015, Garrison et al. 2016).

The Cadomin surface coal mines are a localized anthropogenic landscape feature in Alberta's northern Rocky Mountains, east of Jasper National Park (44.5 km², WMU438; Williamson et al. n.d., Alberta Ministry of Environment and Sustainable Resource Development 2013, Alberta Environment and Parks 2015). These mines contain both Luscar mine (Teck Coal Ltd.; 1969-2000's) and Gregg River mine (Gregg River Resources Ltd.; 1982-1998). The Cadomin mines are currently undergoing land reclamation (Teck Coal Limited 2019). Another smaller coal mine project north of Grande Cache, the Smoky River Coal lease, was abandoned and underwent less reclamation than the Cadomin mines (Alberta Environment and Parks 2015). In addition to mine presence, prescribed burns are practiced to maintain habitat for bighorn sheep by inhibiting overstory and woody growth (Webb 2015, Clapp and Beck 2016). No surveying was conducted at the site of a runaway burn in Jasper National Park from 1987 to 2011 (Talbot

Lake, 2003, ca. 25 km from the Cadomin mines; Alberta Environment and Parks 2015, Kneteman 2016).

Due to the lack of consistent data in the National Parks (Jasper, Banff, and Waterton), no national park survey data was included in this study. However, Willmore Wilderness Provincial Park (north of Jasper National Park) survey data were included in the analyses.

Winter census survey data

Winter sheep surveys were conducted between November and March from 1967 to 2018 (52 years). For wildlife survey and management purposes, Alberta is divided into *Wildlife Management Units* (WMUs; *Fig. 3.1B, 3.2*). Every year, select WMUs were surveyed based on weather condition, terrain, number of hours available for helicopter charter (budget), and number of years since the previous survey (the target is to sample any given WMU every two years). The frequency of WMU surveys varied from 1 to 24 (2% to 50%; *Fig. 3.1, 3.2*). Consequently, the survey resulted in a large dataset that also had several gaps.

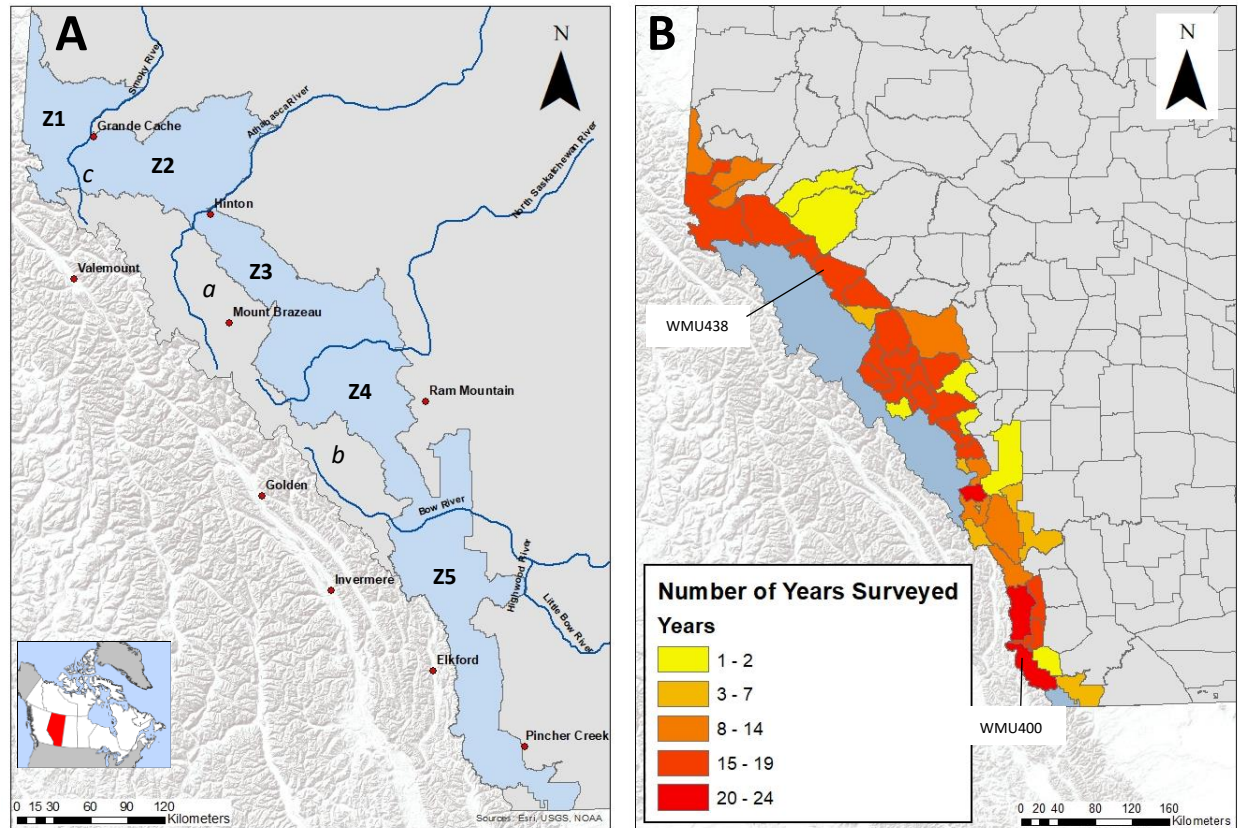


Figure 3.1. (A) Zones and landscape features within the study area (Alberta, Canada; map of 2020). Z1 to Z5 indicate the different zones of the study, separated by major rivers. *a* and *b* identify Jasper and Banff National parks, respectively, and *c* shows the Willmore Wilderness Provincial Park. (B) Survey intensity over the 52-year period within each of Alberta's Wildlife Management Units (WMUs). WMUs are the fundamental units for census and management of wildlife in Alberta. Coloured WMU's indicate the number of annual bighorn sheep surveys performed between 1967 and 2018. The area east of the coloured WMUs signifies the national and provincial parks, whose data is not included in the study due to insufficient data collection.

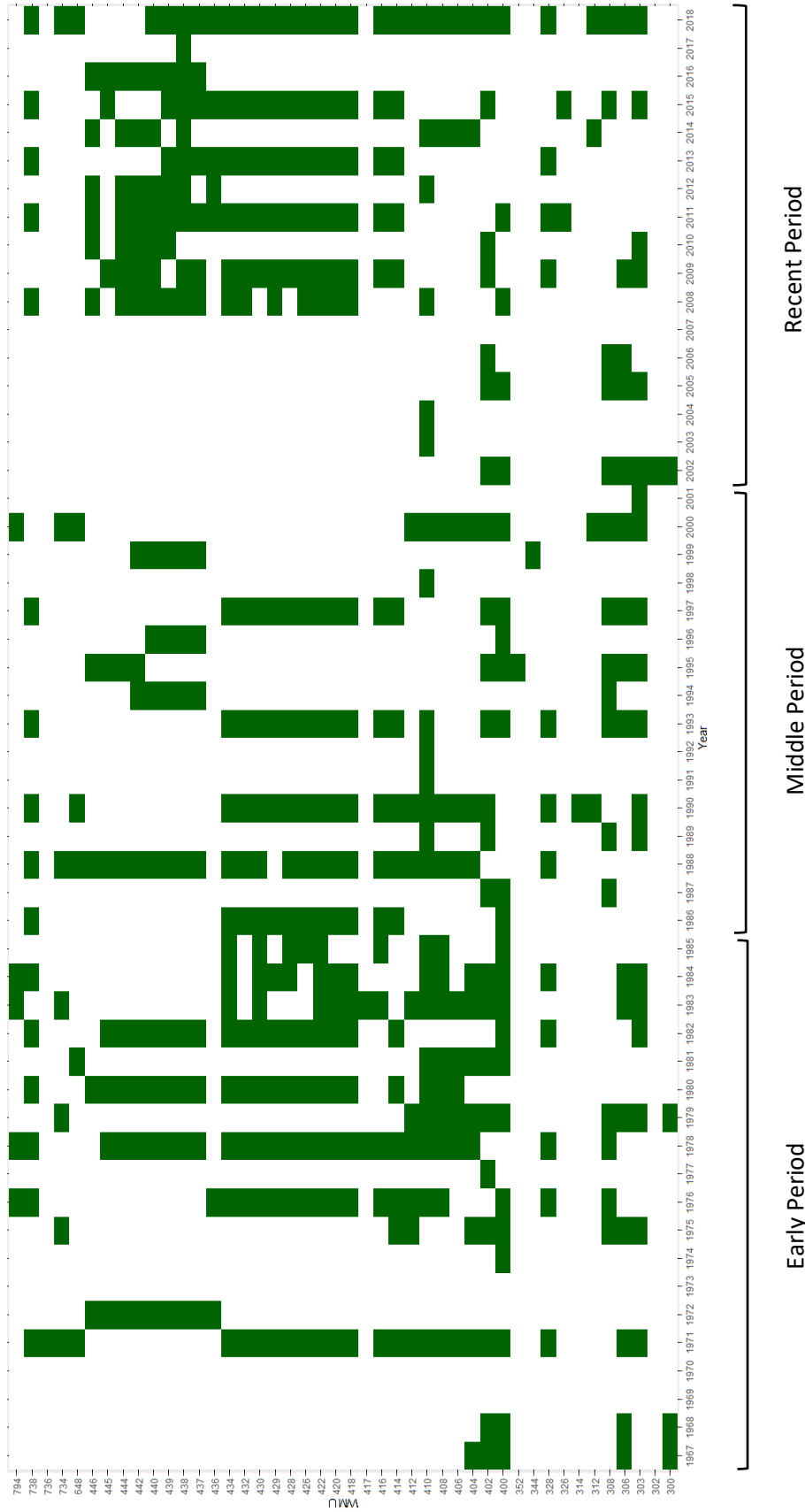


Figure 3.2. Years for which each WMU was surveyed between 1967 and 2018. Green blocks at the intersection of a WMU (y-axis; e.g., WMU300) and year (x-axis; e.g., 1967) indicates that the selected WMU was surveyed during that current year's winter. Years 1969, 1970, 1973 and 2007 are not illustrated because no sheep aerial surveys were conducted during these years. Early, Middle and Recent periods are displayed as 1967 to 1985, 1986 to 2001, and 2002 to 2018.

Note that an area surveyed that saw no sheep was not included in the dataset, and therefore was treated as if no survey was conducted at that WMU, in that year (i.e., 0 sheep at WMU = N/A). Therefore, more WMUs may have been surveyed throughout the time period, however, are not recognized as having been surveyed.

All census data was standardized and combined into one database with the following information: geographic coordinates (latlong; Projected Coordinate System, datum type: NAD_1983_CSRS_10TM_AEP_Forest), year of survey, total number of sheep, age (adults, juveniles, young (i.e., lambs), unknown age), and sex (male, female, unknown sex). Ram curl classes were also recorded as $\frac{4}{5}$ or larger curl (i.e., full curl), $\frac{3}{4}$ curl, $\frac{1}{2}$ curl and $\frac{1}{4}$ curl.

Assumptions and sampling bias

Sampling bias, based on efforts of acquiring data, is a well-known issue when analyzing large-scale and/or long-term monitoring datasets (Lindenmayer et al. 2012, Festa-Bianchet et al. 2017, Burns et al. 2018). This problem is typically either neglected or simply acknowledged as an inherent problem of large assimilated datasets, however such inconsistencies in the dataset can result in a higher likeliness of observing hotspots in areas that are more accessible, and therefore more surveyed, than areas that are not. Consequently, this uncertainty can make it difficult to interpret results for effective management action.

To account for potential survey sampling bias, we divided our census data into three periods: Early (1967-1985), Middle (1986-2001), and Recent (2002-2018; *Fig. 3.2*). Grouping the years into three 16-year periods (recall that four of the 52 years were not surveyed), rather than assessing every year separately for example, helped account for the absence of data in

certain WMUs because a period of years is more likely to see a complete sampling of all WMUs at least once than a yearly analysis.

Temporal bias was also accounted for by using a representative weighted dataset, calculated as follows:

$$\text{Weighted dataset} = \frac{S}{t} \times T$$

Where, S = number of sheep at a location

t = number of years that a WMU was surveyed in a given time period

T = number of years in that time period (*all years = 48, three periods = 16*)

This weighted dataset effectively extrapolated the number of sheep observed in each WMU based on their historic sampling frequency, to represent the number of sheep that would be observed if all areas were surveyed equally.

Spatial trend analyses

A hotspot analysis is a spatio-statistical assessment of how clustered an organism is on a landscape, and asks where these clusters are (Poudyal et al. 2016, Yurkowski et al. 2018). The hotspot analysis calculates the probability that the sheep survey locations are randomly distributed (H_0). Quantitatively, a hotspot analysis uses vectors to calculate distances between points and clusters (ArcGIS 2018a). A minimum distance between individual points is first calculated (or given); if the points are closer than this minimum distance, they are converged to

form one point (i.e., a *cluster*) and given a score based on proximity. Then these converged points are ranked by their proximity to each other (calculated as a z-score; ArcGIS 2018b).

A hotspot is identified when a highly ranked converged point is close to other highly ranked converged points, or its *neighbours* (ArcGIS 2018c). Statistically, this event means that the points are not randomly distributed, and identified clusters are significantly close to one another on the landscape (these points are given a positive z-score). A coldspot is identified when the highly ranked converged point is far away from its neighbours. Statistically, this implies that the points are still not randomly distributed, but these clusters are not close to one another in that area (these points are given a negative z-score). If randomly distributed, the individual points in that area are given a z-score of 0.

Mapping software can be used to determine where clusters are geographically located on the landscape. ArcGIS provides two hotspot analysis options: (1) generic *Hot Spot Analysis (Getis-Ord Gi*)* and (2) *Optimized Hot Spot Analysis* tools. Both options use Getis-Ord Gi* as their statistical analysis approach to clustering assessment (Manepalli et al. 2011, Jana and Sar 2016, ArcGIS 2018a, 2018c). With the generic hotspot tool, one can directly input the neighbourhood size surrounding each point. Increasing the neighbourhood size would likely increase the value given at that point and therefore potentially increase the presence of hotspots (and vice versa). ArcGIS optimized hotspot analyses are most commonly used to assess clustering of points on a landscape. The optimized hotspot analysis automatically calculates a neighbourhood size for each individual point to optimize the chances of observing a true hotspot, as compared to the distribution throughout the study area. It is important to note that the optimized hotspot analysis tool compares locations to other locations, and does not consider how many points are recorded at each location. Therefore, to study the distribution of recorded sheep

on the landscape, we expanded the final dataset to list each row as a separate sheep point, rather than a separate location (*Fig. SM3.1, SM3.2*).

Studying spatial distribution over the landscape, over time, compares the distances between each point's location; thus, it relies on the existence of multiple other locations, where more locations recorded with fewer points at each increases the likelihood of seeing a real hotspot compared to few locations with more points at each. The hotspot analysis may classify an area as a hotspot if there are few locations with multiple sheep identified at each site, yet may claim a random distribution if there are many locations with few sheep at each site. In sum, the more detail in survey point locations, the more effective the hotspot analysis will be at detecting true clusters.

To assess the distribution across the entire time period (1967-2018), we conducted kernel density and optimized hotspot analyses of sheep census numbers for the entire study area using ArcGIS *Kernel density* and *Optimized hotspots analysis* (Getis-Ord G_i^*) tools. We tested the kernel density search radius prior to the main analyses to determine whether general density patterns were altered by the choice of search radius size (*Fig. 3.3, SM3.3*).

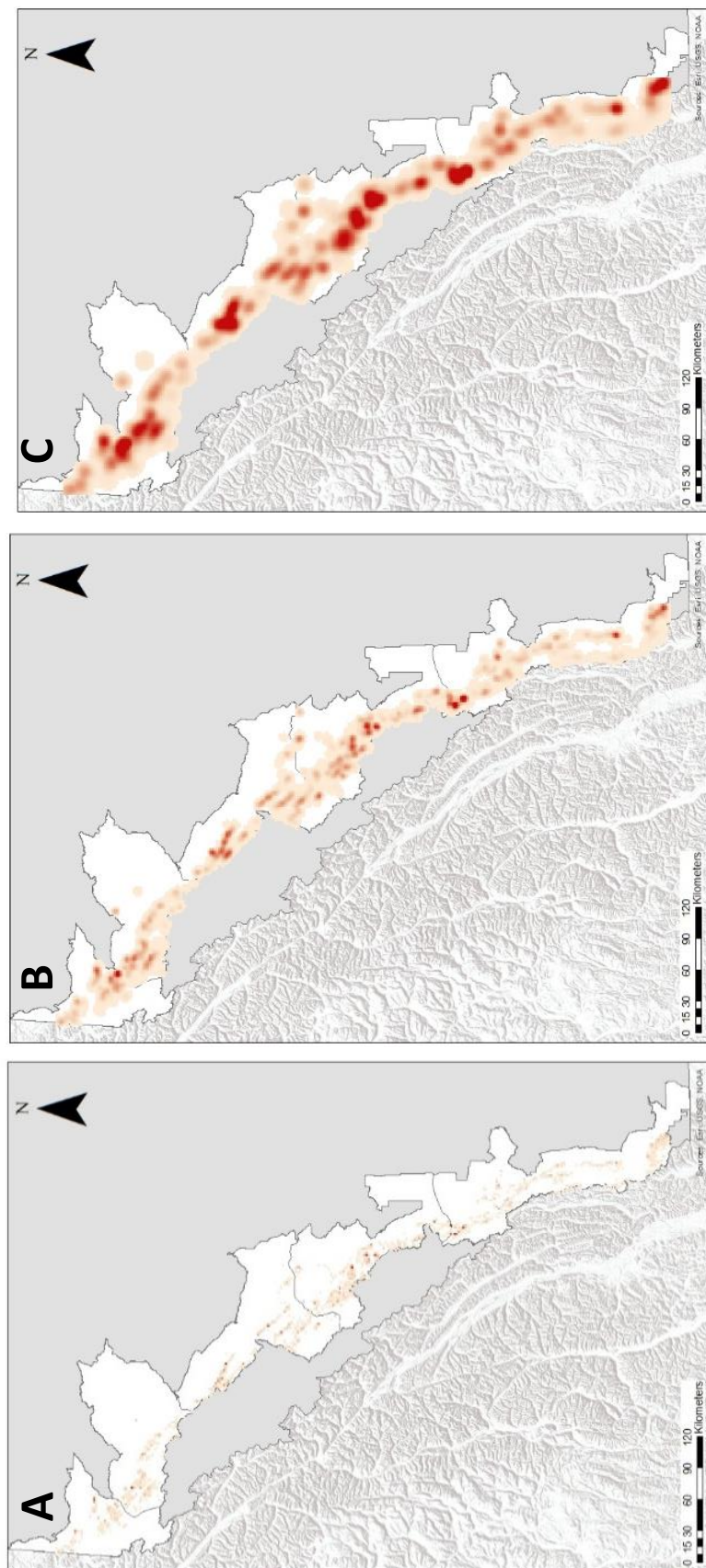


Figure 3.3. Effect of various search radius sizes (i.e., neighbourhood size) on sheep kernel density analysis heatmap. The sheep heatmap illustrates (A) a 1 km search radius, (B) a 5 km search radius, and (C) a 10 km search radius. Cell size = 2000 m.

To assess the distribution of each time period separately, kernel density (cell size = 2000m, radius = 10 000 m) and optimized hotspot analyses were conducted again for each period, across the whole study area.

To assess density distribution changes between the three periods, correlation analyses were conducted using the *Band Collection Statistic* tool in ArcGIS. This tool separated the individual sheep from the hotspot area (i.e., neighbourhood), within which the hotspot was assessed. This approach compared each neighbourhood's ranking across periods. To assess the intensity of hotspot changes between periods, we developed a binary assessment that determined if a cell remained a hotspot at a 95% confidence level, or changed its status, between the two time periods.

All analyses were repeated for adult ewes and rams, separately.

Results

Changes in distribution

We observed three similarly-sized hotspots in the Early period (1967-1985) along the Smoky River (Zones 1-2; 8 hotspot cells (HC), $\geq 95\%$ conf.), south of the Athabasca River (Zone 3; 9, 1 HC, $\geq 95\%$ conf.), and south of Bow River (Zone 5; 7 HC, $\geq 95\%$ conf.). In the Middle period (1986-2001), the northern hotspot disappeared, while the hotspot south of Athabasca River was noticeably smaller (Zone 3; 2 HC, $\geq 95\%$ conf.), and the southernmost hotspot changed in appearance but not in size. A third hotspot appeared in the middle of Zone 4 (2 HC, $\geq 95\%$ conf.). Hotspots in the Recent period (2002-2018) grew in size. We found an enlarged hotspot south of the Athabasca River (Zone 3; 10 HC, $\geq 95\%$ conf.), and a larger

hotspot in Zone 4 (16 HC, $\geq 95\%$ conf.). Around Bow River, we continued to see a hotspot (Zone 4-5; 6 HC, $\geq 95\%$ conf.; *Fig. 3.4*).

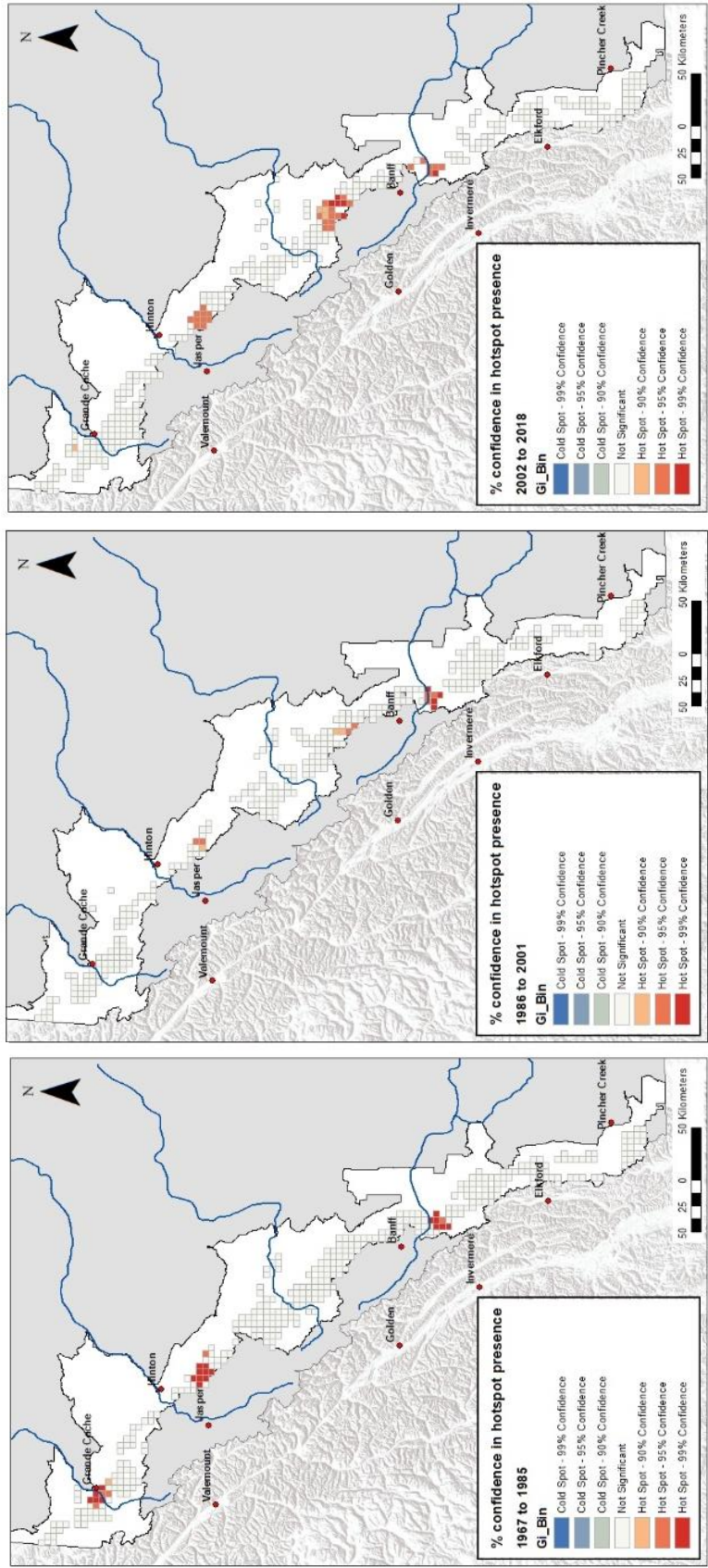


Figure 3.4. Areas of bighorn sheep clustering based on the number of surveyed sheep pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains sheep that are randomly distributed on the landscape.

The binary assessment of hotspot change between periods at a 95% confidence level revealed that 16.5% of the hotspots remained hotspots between Early and Middle periods, 21% of the hotspots remained hotspots between Early and Recent periods, and 21% of the hotspots remained hotspots between Middle and Recent periods (*Table 3.1*).

Table 3.1. Change (number of cells and percent) in hotspots for all sheep, ewes and rams between periods. Cells represent hotspot neighbourhoods of a program-generated size, within which the proximity of significantly-clustered clusters are assessed at a 95% confidence level (*Fig. SM3.6, SM3.7, SM3.8, Spatial trend analyses*). Total number of hotspot cells (changed and unchanged; right column) between periods are also recorded.

All Sheep	# cells that changed		# cells that remained hotspots		Total
Early to Middle	228	(83.5%)	45	(16.5%)	273
Early to Recent	325	(78.7%)	88	(21.3%)	413
Middle to Recent	249	(79.0%)	66	(21.0%)	315
Ewes					
Early to Middle	307	(100%)	0	(0%)	307
Early to Recent	385	(100%)	0	(0%)	385
Middle to Recent	246	(88.2%)	33	(11.8%)	279
Ram					
Early to Middle	117	(69.6%)	51	(30.4%)	168
Early to Recent	166	(76.1%)	52	(23.9%)	218
Middle to Recent	123	(73.2%)	45	(26.8%)	168

Across the three periods, densities of sheep (or probability of sheep presence) remained widely distributed, with highest probability of observing sheep around the Smoky River (Zones 1-2), south of the Athabasca River (Zone 3), just south of the Saskatchewan River (Zone 4), and around the Bow River (Zones 4-5; *Fig. 3.5*).

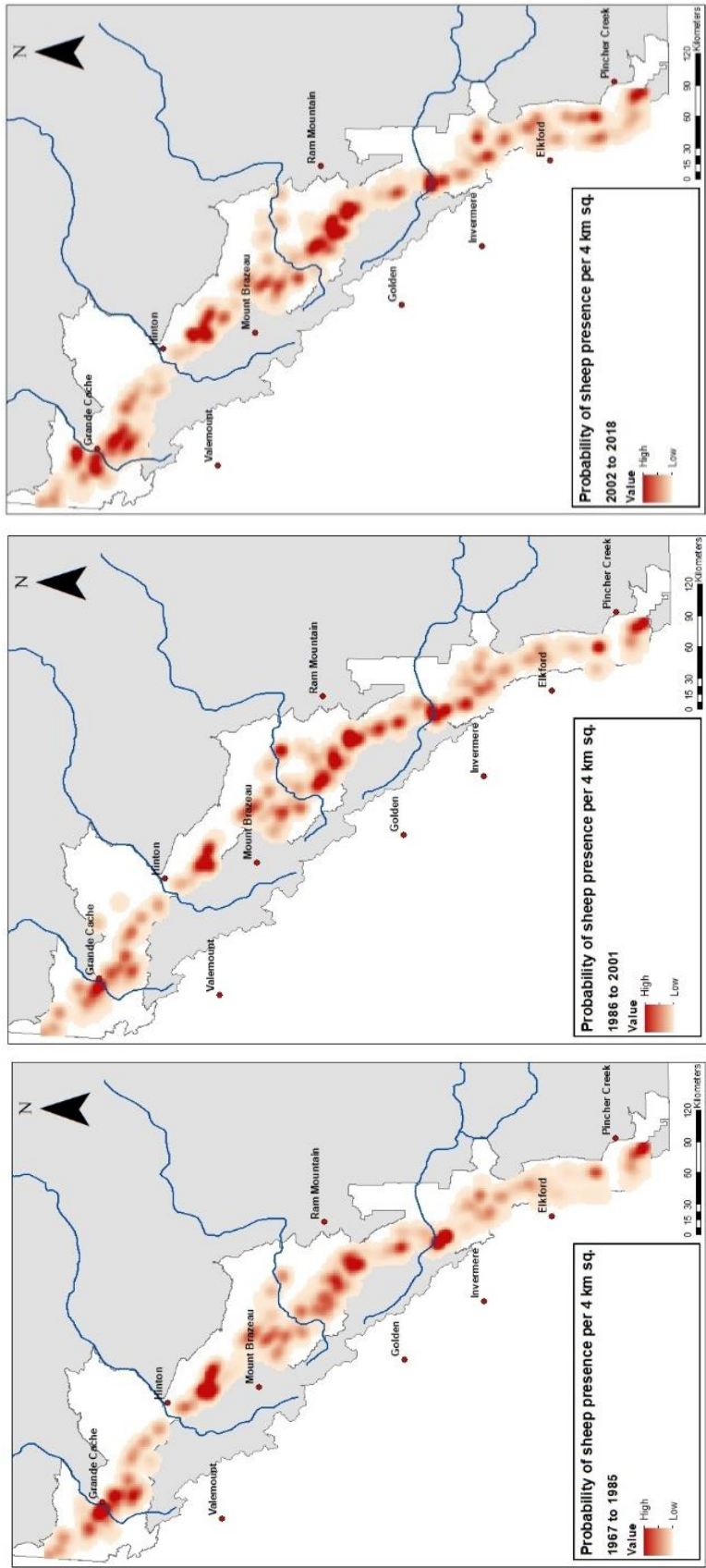


Figure 3.5. Probability of bighorn sheep presence within a 4 km² area in Alberta's Rocky Mountains, pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). Shading indicates the estimated cumulative number of sheep over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* sheep, and the kernel density analysis; this estimate is not an actual number of sheep in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.

Between all pairs of periods, correlation values were positive and greater than 0.65. Figure 5 shows high correlations of sheep distribution between all periods, with correlation values of 0.70 between the Early and Middle periods; 0.78 between Early and Recent periods; 0.68 between Middle and Recent periods (*Table 3.2*). A high correlation suggests little change in densities between periods, therefore sheep density analyses reveal little change in distribution over time.

Table 3.2. Correlation of sheep, ewe and ram distributions between periods. *P1*, *P2*, and *P3* refer to Early, Middle, and Recent time periods, respectively (*Spatial Trend Analyses*).

	P1 - P2	P1 - P3	P2 - P3
Kernel density of all sheep	0.696	0.779	0.678
Kernel density of ewes	0.691	0.688	0.791
Kernel density of rams	0.783	0.802	0.756

Distribution of bighorn sheep across the landscape

Over the entire 52 years, sheep hotspots were present north of Smoky River (Zone 1; 4 HC, $\geq 95\%$ conf.), south of Athabasca River (Zone 3; 14 HC, $\geq 95\%$ conf.), south of Saskatchewan River (Zone 4; 1 and 9 HC, $\geq 95\%$ conf.), and around Bow River (Zones 4-5; 13 HC, $\geq 95\%$ conf.; *Fig. 3.6A*). Bighorn density analyses tended to remain widely distributed across the landscape, with the highest probability of detecting sheep around Smoky River (Zones 1-2), south of the Athabasca River (Zone 3), south of Saskatchewan River (Zone 4), around Bow River (Zones 4-5), and above the southern border of our study area (Zone 5; *Fig. 3.6B*).

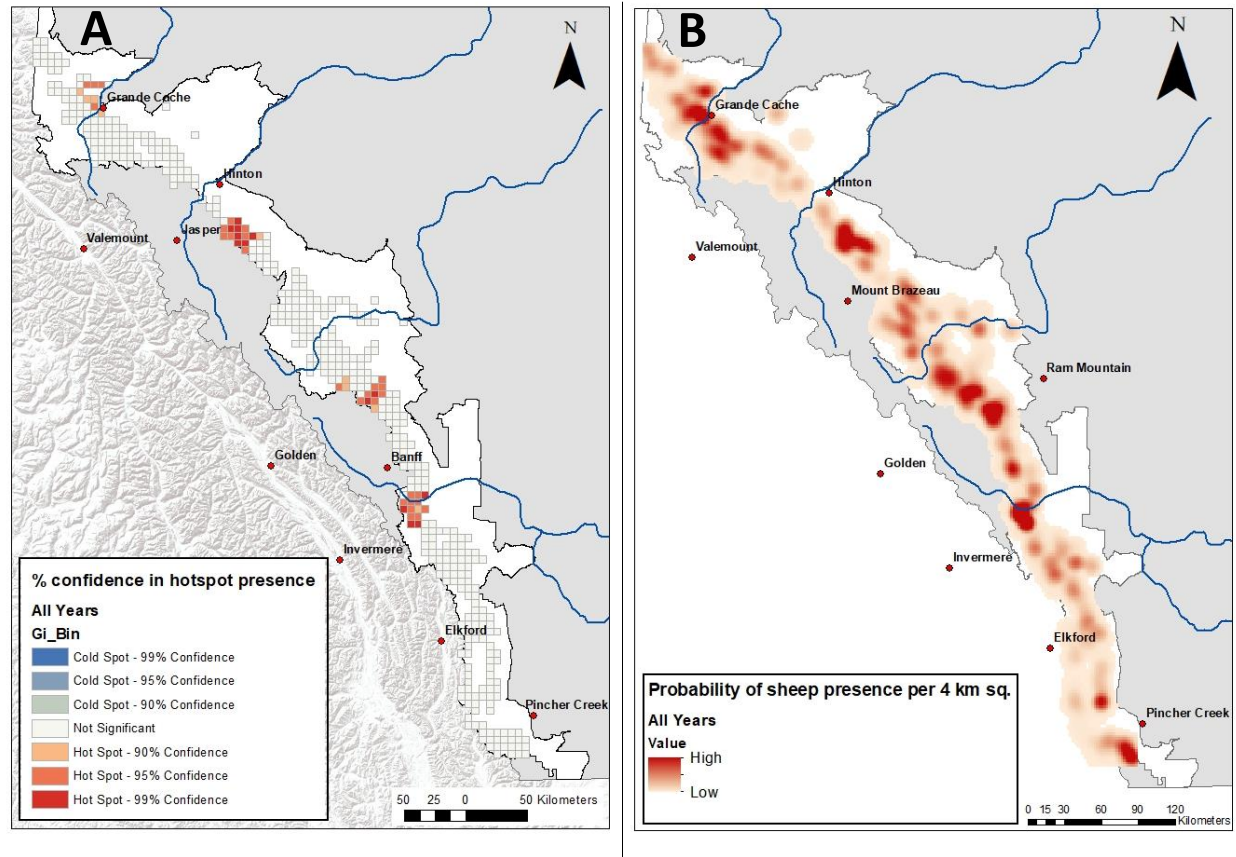


Figure 3.6. Map (A) illustrates the areas of sheep clustering, based on the number of surveyed sheep pooled over the entire study period (1967-2018). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains sheep that are randomly distributed on the landscape. Map (B) shows the probability of bighorn sheep presence within a 4 km² area in Alberta's Rocky Mountains, pooled over the entire study period (1967-2018). Legend demonstrates estimated cumulative number of sheep over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* sheep, and the kernel density analysis; this estimate is not an actual number of sheep in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.

Differences between ewes and rams

Hotspot locations varied significantly for ewes and rams. In the Early period, ewes were clustered in two northern areas, around Smoky River (Zones 1-2; 14 HC, $\geq 95\%$ conf.) and south of Athabasca River (Zone 3; 11 HC, $\geq 95\%$ conf.). Ewes became less concentrated in the north and instead, hotspots were found south of Saskatchewan River (Zone 4) and around Bow River (Zones 4-5), in the Middle (7, 1, 6 HC, $\geq 95\%$ conf.) and Recent (20, 2 HC, $\geq 95\%$ conf.) periods (*Fig. 3.7*). Rams maintained a hotspot south of Athabasca River (Zone 3) in Early (9 HC, $\geq 95\%$ conf.), Middle (7 HC, $\geq 95\%$ conf.), and Recent (14 HC, $\geq 95\%$ conf.) periods of the study. A second hotspot was present around Bow River (Zones 4-5) in the Early (7 HC, $\geq 95\%$ conf.) and Recent (1 HC, $\geq 95\%$ conf.) periods, and a third hotspot appeared south of Saskatchewan River (Zone 4) only during the Middle period (2 HC, $\geq 95\%$ conf.; *Fig. 3.8*).

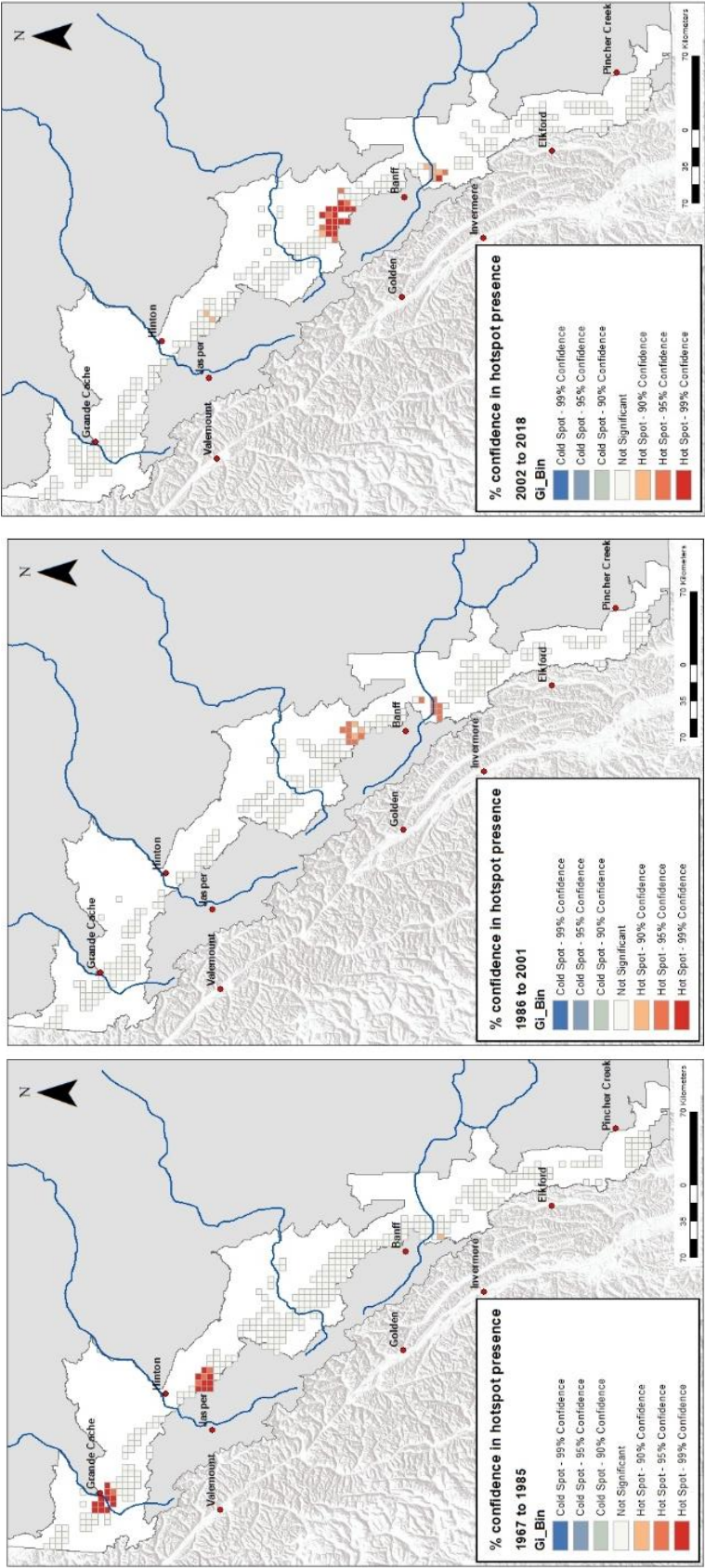


Figure 3.7. Areas of ewe clustering based on the number of surveyed ewes pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains ewes that are randomly distributed on the landscape.

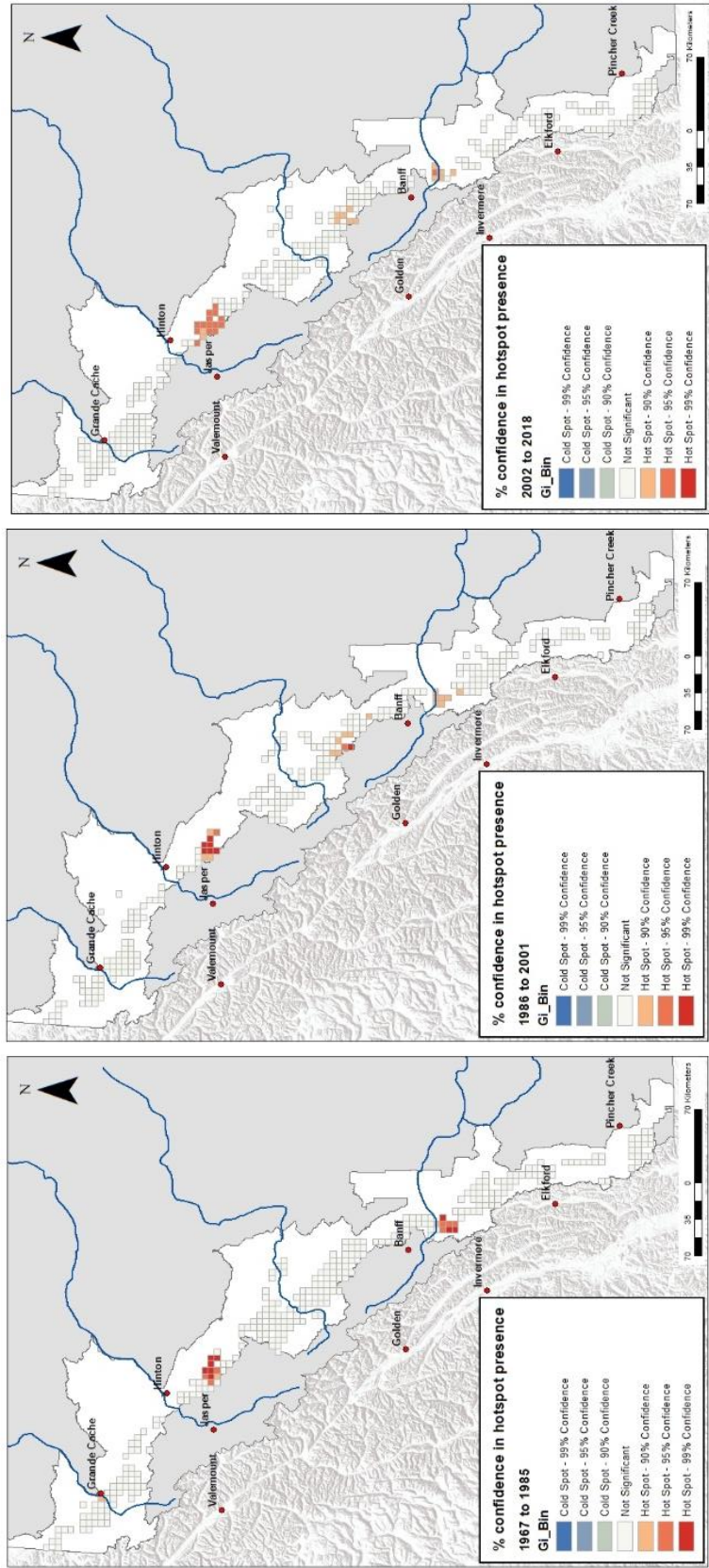


Figure 3.8. Areas of ram clustering based on the number of surveyed rams pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains rams that are randomly distributed on the landscape.

No single ewe hotspot cell (0%) remained the same from Early to the two more recent periods, and 12% of ewe hotspot cells remained hotspots between the two more recent periods. Ram hotspots did not change as severely between any of the periods; 30% of hotspots stayed hotspots between Early and Middle periods, 24% remained hotspots between Early and Recent periods, and 27% remained hotspots between Middle and Recent periods (*Table 3.1*).

Lastly, ewes had more hotspot cells than rams in all periods (total ewe HC: 23, 24, 22; total ram HC: 16, 9, 15; *Table 3.1*). One might also recognize that the Recent period held the largest hotspots for ewes, rams and total sheep, as compared to the two earlier periods (20 HC, 14 HC and 16 HC, respectively; $\geq 95\%$ conf.).

Density analyses showed similar distributions and trends as the hotspot analyses for both ewes and rams, with some exceptions. Ewes were also densely distributed in an area south of Bow River (Zone 5) in the Early period and became densely distributed south of the Athabasca River (Zone 3) in the Recent period (*Fig. SM3.4*). Additionally, ram distribution revealed a dense area north of Smoky River (Zone 1) through all three periods, and a high density developed in the middle of Zone 4, in Middle (congruent with the hotspot analysis above) and Recent periods (*Fig. SM3.5*).

We observed little to no change in densities between periods; both ewes and rams densities had high positive correlation values of 0.69 and 0.78 (Early to Middle periods), 0.68 and 0.80 (Early to Recent periods) and 0.79 and 0.76 (Middle to Recent periods), respectively (*Table 3.2, Fig. SM3.4, SM3.5*). Ram densities were more correlated across periods than both ewes and total sheep, except when comparing between distributions in the Middle and Recent periods where ewes were most correlated.

Over the entire 52 years, ewe hotspots were present south of Athabasca River (Zone 3; 3 HC, $\geq 95\%$ conf.), south of Saskatchewan River (Zone 4; 2 and 2 HC, $\geq 95\%$ conf.), and around Bow River (Zones 4-5; 7 HC, $\geq 95\%$ conf.; *Fig. SM3.9A*), whereas only one large ram hotspot was present south of Athabasca River (Zone 3; 23 HC, $\geq 95\%$ conf.; *Fig. SM3.10A*). Similar to total sheep density, ewe density analyses remained widely distributed across the landscape, with the highest probability of detecting ewes around Smoky River (Zones 1-2), south of the Athabasca River (Zone 3), south of Saskatchewan River (Zone 4), around Bow River (Zones 4-5), and above the southern border of our study area (Zone 5; *Fig. SM3.9B*). In comparison, the highest probability of detecting rams was south of the Athabasca River (Zone 3) and south of Bow River (Zones 4-5; *Fig. SM3.10B*).

Discussion

Main trends

The results showed that, (i) from the Early period to the two most recent periods, ewe clusters disappeared completely from their northern historic range and appeared in new southern ranges; (ii) the occurrence of ram clusters remained at their historic northern range during the time studied; (iii) ewes seemed to congregate more than rams; (iv) all sheep seemed to congregate in larger areas in the Recent period compared to earlier periods.

Potential explanations for observed trends

Historically, Rocky Mountain bighorn sheep appear to have been distributed unevenly across space and time. Attempts to understand causes of change in other systems have led researchers to believe that a multitude of factors, both environmental and anthropogenic, may

influence a system's behaviour and condition (Krausman et al. n.d., Rubin et al. 2002, Allen et al. 2016, Mazor et al. 2018, Klein et al. 2019). Environmental or climatic changes may include changes in temperature, precipitation, extreme or sudden climatic events and disturbances (e.g., wildfires), vegetation community, and ecosystem function. These changes may be indirectly linked to anthropogenic effects. Human influence may take form of biotic introductions or invasions, agriculture and livestock diseases, construction of features (e.g., road networks, pipelines, trains, buildings, and machinery), resource extraction, pollution, human-induced fires, and direct anthropogenic stresses (e.g., hunting and poaching). The behaviour of any system is likely a result of many of these factors, and their interactions. I did not explore these causations, but focused on the observable trends of bighorn sheep distribution. Consequently, we can only make suggestions of what factors may be most influencing these distributions over space and time, based on previous research.

The most recent period saw larger hotspots than earlier periods for all sheep, including ewe and ram analyses separately. This event requires more understanding of the trends and processes within the Recent period (2002 to 2018), however, a potential explanation may include the effects of climatic changes across sheep habitat. High elevation environments are particularly sensitive to changes in climate and landscape (Márquez et al. 2011, Imperio et al. 2013, Pepin et al. 2015, Klein et al. 2019). Climate fluctuations can ultimately affect vegetation structure and productivity, as well as winter snow cover depths, affecting food availability for herbivores and species composition at higher trophic levels (Goodson et al. 1991a, Imperio et al. 2013, Boulangeat et al. 2014, Mason et al. 2014). Mountain sheep are sensitive to changes in snow cover depth, since increased depth can decrease their abilities to access forage underneath and escape predation, while little to no snow reduces abundance of preserved and available forage

throughout the winter. In response to climate warming, alpine biotic communities are expected to shift to higher elevations (Schneider 2013, Boulangéat et al. 2014). Furthermore, increased vulnerability and occurrence of wildfires due to increased aridity in bighorn sheep habitat over time may leave fewer ideal sheep habitats in the winter months (*Fig. 3.9*; ALCES; A. Hubbs, *pers. comm.*). Variability in both biotic and abiotic factors, such as snow depth, may restrict sheep to the more and more limited areas that can support these populations during the winter, ultimately reducing sheep resiliency to anthropogenic and other disturbances (Williamson et al. n.d., Bleich et al. 2009, Kneteman 2016). Modelling climatic factors that may affect sheep habitat selection will be important in understanding the effects of a changing climate on sheep distribution.

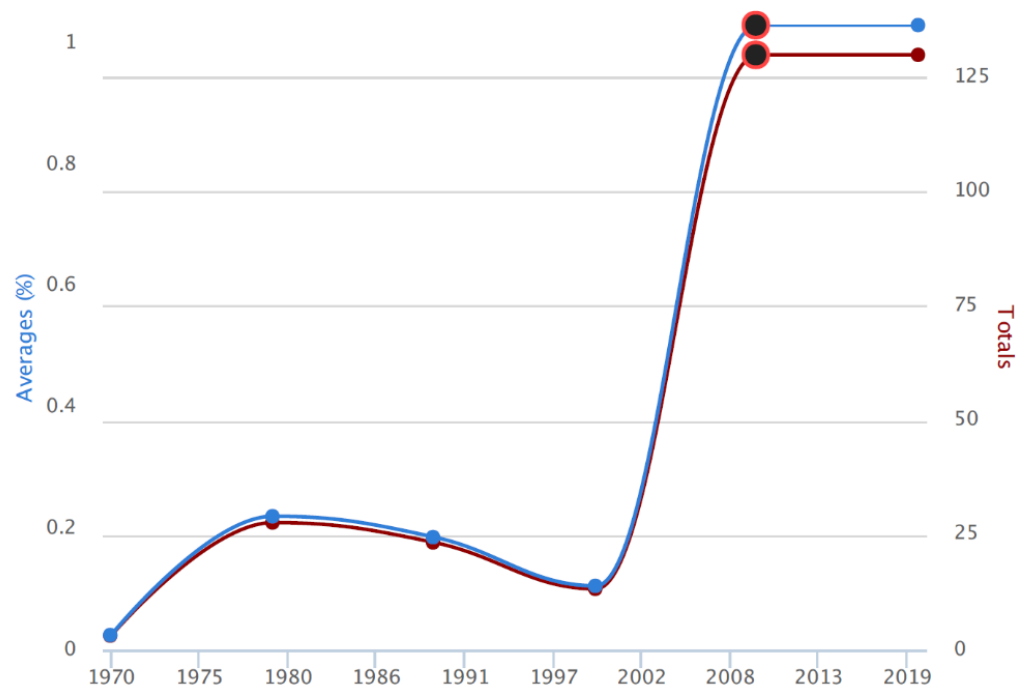


Figure 3.9. Number of wildfires (red) and average percent of land area burned (blue) for each decade from 1970 to 2019 (ALCES; A. Hubbs, *pers. comm.*). Wildfire occurrence and size data were obtained from the Alberta government webpage (wildfire.alberta.ca), for the entire sheep winter range (Mountain Goat and Sheep sensitivity (LAT) layer; study area = 12 457.76 km², cell size = 2000 m).

Due to climate warming, treelines and woody vegetation are growing at higher elevations (Schneider 2013, Boulangeat et al. 2014). To counteract this effect of climate warming and maintain low-ground vegetation at higher elevations, prescribed burns are used periodically (Alberta Environment and Parks 2015). Ideally, prescribed burns will restrict growth of woody vegetation at higher elevations frequented by sheep and maintain ideal sheep habitat (Didkowsky 2013, Webb 2015). Literature on the effect of fire on sheep habitat use, however, is conflicting;

Bleich et al. (2009) observed that bighorn sheep use of fire-affected habitat was 26% less than an unburned habitat near a mine. They argued that this effect occurred because the habitat was burned too frequently, resulting in habitat that does not reach conditions that are ideal for sheep. Another study by Clapp and Beck (2016) recognized that bighorn sheep did not use habitat recently burned by prescribed fires. Because we could not include national park survey data, it is unclear at the scale of our study whether the Talbot Lake fire (in the Recent period) attracted rams to the area or diverted ewes and/or rams to the Cadomin mines as opposed to around Talbot Lake. Demographic survey records of sheep in the burned area identified approximately 200 sheep pre-fire, and less than 100 sheep post-fire, with significantly more rams identified in 2013 (Alberta Environment and Parks 2015, Kneteman 2016). To better assess the large-scale effect of fire on local sheep, assessing hotspot trends within the Recent period at the Talbot Lake area may help identify if sheep congregated in or around the burned area, if the congregations moved towards or away from the burned area over time, and if the movement occurred immediately after or years after the burn. The immediate effect of the burn may have deterred sheep from the area, congruent with the above studies, but may have attracted sheep over time due to the re-established vegetal community. These studies highlight a gap in knowledge of the impact of prescribed burns on bighorn habitat use, and a necessity to better understand this impact and adjust bighorn habitat management accordingly.

Rocky Mountain bighorn sheep habitats in Alberta are generally well connected, enabling ease of movement between seasonal ranges (Alberta Environment and Parks 2015, Kneteman 2016). Connectivity is particularly important for sheep because sheep size, movement and unique landscape requirements leave sheep distribution fragmented into ranges, which suit different needs seasonally (Bleich et al. 1990, 2009, Allen et al. 2016). This connectivity is, however,

continuously threatened by industrial incentive, resource extraction and urban spread, particularly in the southern mountains of the Rocky Mountain range (Yellowstone to Yukon 2020). For example, research has stressed the importance of land connectivity and effects of road development on connectivity (Keller and Bender 2007, Allen et al. 2016). Additionally, many studies have revealed the ramifications of interaction between mountain and domestic sheep on bighorn populations (Brown et al. 2010, Hedrick 2011, Cassirer et al. 2017, Boyce and Krausman 2018).

Though wild sheep typically show high fidelity to their seasonal ranges (Valdez and Krausman 1999), work by Kneteman (2016) revealed that Alberta bighorn sheep locally shifted their use of habitat from native to novel ranges, possibly in response to human disturbances. Supporting this finding, recent aerial surveys show evidence of an increased ewe population on reclaimed northern mine sites during the winter and, especially, the fall (Alberta Environment and Parks 2015). A noticeably substantial increase in ewes on mines in 2005 and 2008 surveys is suspected to have been a result of deterrence from the runaway Talbot Lake fire in 2003 (J. Kneteman, *pers. comm.*). In 2015, the Alberta government reported that more than 10% of Albertan bighorn sheep were near the Cadomin mines (Alberta Environment and Parks 2015). Recent studies have also shown that sheep select for mine sites, which may be due to the abundance of low ground vegetation with high nutrition and an extended growing season (Williamson et al. n.d., Jansen et al. 2006, Bleich et al. 2009, Kneteman 2016).

The stark changes in ewe distribution pattern between the Early and two most recent periods is particularly surprising. Despite the presence of few anthropogenic stressors in their northern Rocky Mountain range, as compared to its southern counterparts, recent evidence suggests that one major anthropogenic feature may have contributed to ewe distribution changes

over time. Historically, large productive concentrations of bighorn sheep have occupied native ranges in WMU 438, along with the adjoining Rocky, Athabasca and Brazeau River drainages in Jasper National Park (Alberta Environment and Parks 2015). During the Middle and Recent periods of our study, ewes appeared to be dispersed from their northern historic ranges, potentially into a new range further south. During these two periods, surface mining of the Luscar and Gregg River Mine areas converted historically forested land in WMU 438 to simplified agronomic plant communities, which remain succulent late into the fall after native alpine vegetation cures (Teck Coal Limited 2019). Reclamation of landscape disturbances typically consists of planting non-native, low maintenance plants that remain succulent later into the fall than native alpine vegetation (Alberta Environment and Parks 2015). Surface mining choice of agronomics and sheep predator-avoidance land feature preferences (e.g., steep walls and open spaces) might have encouraged this rapid decluttering of ewes from adjacent native ranges into ranges near the Luscar and Gregg River mine reclamation sites since the late 1980's (Williamson et al. n.d., Bleich et al. 2009, Kneteman 2016).

Although sheep are likely attracted to mines for their high walls and agronomic vegetation (Jansen et al. 2006, 2007, Bleich et al. 2009), the demographics of sheep on Luscar and Gregg River mines document the lowest reproductive and long-term recruitment potentials in all of Canada, which are inadequate to sustain a population, and require immigration from adjacent native ranges to sustain presence (Kneteman 2016). As such, sheep congregations near the Luscar and Gregg River mines may act as an “ecological trap” for bighorn sheep (Fessler 2003, Jansen et al. 2007, Bleich et al. 2009, Kneteman 2016). First, vegetation grown in reclaimed mine sites are exposed to high levels of metals from mine activity, which can have sublethal to toxic effects on nearby sheep (Fessler 2003, Alberta Environment and Parks 2015,

Kneteman 2016). Second, since the planted vegetation are introduced to the habitat, local flora may outcompete these temporary high-nutrition options over time, and the nutritional gain associated with these sites would diminish. For sheep, this may mean a lower quality or quantity of forage in preparation for the fall rut and winter, ultimately reducing their performance and survival throughout the winter (Shank 1982, Wagner and Peek 2006, Meldrum and Ruckstuhl 2009, Creech et al. 2016, Monteith et al. 2017). Lastly, reclaimed surface mine sites may attract a variety of other herbivores, bringing with them competition and predation. Increased herbivores in the area may then increase resource competition for vegetation. The elevated number of herbivores in the area may also result in an increase in local predators, leaving these sheep atypically vulnerable (Beale and Boyce 2018). Starvation, lack of nutrition and predation may result in a sheep population decline in the future and a decrease in their next-generation survival. Oversimplification of ecological responses to mining disturbance from coal mining industries may in part be responsible for sheep congregations and decline (Kneteman 2016), and needs to more closely align with current literature on sheep response to mining activity- starting with an attempt to deter sheep from these disturbed areas using native vegetation implementation and barriers as a reclamation strategy.

Ram concentrations within their winter historic ranges did not change as much as the ewes over time. Our research focused on winter distribution, and little is known about large-scale sheep distribution in the other seasons, especially in the northern parts of their range. Ewes and rams converge at least once a year during the rutting season to compete for mating opportunity and to mate. It is possible that in the fall (i.e., rutting season), rams moved with ewes to these reclamation zones in the two most recent periods, due to the establishment of the nutritive and abundant agronomic vegetation. The abundance of rams was particularly evident from 2002-

2012 (Alberta Environment and Parks 2015), likely as a result of the non-native vegetation growth. However, we cannot come to this conclusion from our results alone. Studying annual ewe-ram change in distribution in and around the mine site during the last two periods would be essential to understand how hotspot intensity and location change on a more local scale.

These examples of environmental and Anthropogenic disturbances may not single-handedly be responsible for Rocky Mountain bighorn sheep, and ewe and ram distribution, however they may at least in part be responsible for these changes. Currently, Canadian Rocky Mountain bighorn sheep are the most intact, connected and resilient populations of bighorn sheep in the world, however changes in the influence of these factor may compromise their resilience in the future. The accumulation and interaction of such factors may weaken sheep resilience and affect condition of sheep populations in the wake of other challenges. Understanding the roles of each of these factors on bighorn distribution over their entire range is critical for maintaining sheep resilience and persistence in the future years.

Statistical differences between two spatial analyses

The human mind is so good at finding patterns that it can find patterns where patterns do not biologically or statistically exist (Silverman 1998). We used spatial autocorrelations to assess the likeliness of a pattern (in this case, a cluster) being present on the landscape, and we used correlation matrices and comparison of hotspot presence (at a 95% confidence) between periods to identify how similar the layout of two periods are to one another. In the context of spatial analysis approaches, we set out to explore (A) how the outcomes of two different spatial distribution analyses differ, and (B) how we can compare spatial distributions over time.

The two spatial analysis approaches we used, kernel density and optimized hotspot analysis, may have yielded different outcomes because of the assumptions inherent within each. Density and hotspot analyses over the three periods revealed different sheep distribution changes. Unlike the hotspot analyses, density analyses identified more sheep congregations on the landscape, and little changes over time. This may have occurred because density analyses do not account for outliers to the clusters (ArcGIS 2018a, 2018b, ArcGISPro 2020b), which may more-so reflect local disturbances (such as the helicopter flying overhead), rather than an actual regional preference by the sheep populations. Each point is independent of the others in this type of spatial analysis, and clustering is identified based solely on proximity of individual points in a neighbourhood. Therefore, as we observed in our study, as the scale grows these distributions may become more cluttered with high density areas (compared to the hotspot analysis approach). Density is a simpler analysis approach to study general trends in space and are used mainly to study sessile population distribution (e.g., tree stands), or populations of wildlife over small scales and/or short time periods (Gross et al. 2000, Lomolino 2001, Gotelli and Ellison 2002, Carpenter 2005, Ehlers et al. 2016, Simao et al. 2018).

A hotspot analysis is an approach which removes the noise of population movement in order to examine relevant or biologically significant cluster trends at a larger scale. This approach assesses the proximity of significantly-clustered clusters to other significantly-clustered clusters (ArcGIS 2018b, 2018a). Hotspots therefore account for outlier points better than densities. For example, a cell with an individual point that is distant from other points may be assigned a low-density value, however it may be considered not significant (i.e., randomly distributed) in a hotspot analysis. This relative weighting may mean that hotspots are more conservative in their assessment of spatial clustering than density analyses. We observed this

distinction throughout our hotspot analyses for bighorn sheep, where we found fewer distinct and more-localized hotspots.

On a related note, no coldspots were seen in our analyses of sheep distributions over the entire Rocky Mountain study area. This is likely to have occurred for two reasons; areas of clustering or avoidance were only identified at confidence levels of 90% or higher, and therefore areas of sheep avoidance may have been present (i.e., $z\text{-score} < 0$) but were not illustrated because they were not present enough on the landscape given the scale. Furthermore, this sheep dataset only reported areas where sheep were present, and consequently did not record where sheep were not found. Thus, identifying where sheep clusters were absent (i.e., coldspots) may not be accurate or informative using this dataset. Coldspots may be seen at closer and more local scales, where clustering can be seen in more detail and areas of avoidance are more prominent given the scale. Studying sheep distributions at a sheep zone- or WMU-scale will allow us to identify areas where sheep were attracted and deterred from, which can then be more applicable in a sheep management context.

Ewe redistribution away from native ranges raises a concern about the usefulness of the Luscar-Gregg River mine's sheep survey method to understanding large-scale sheep distribution trends. Attaching the total number of sheep observed on-site to one coordinate makes it impossible for a cluster of sheep to be identified on-site using the hotspot analysis method. Hotspots are defined by a *cluster* of significantly-clustered individuals. The mine identified one cluster of many individuals, and consequently this cluster cannot be near any other clusters. This method of data collection highlights an issue with cluster detection by hotspot analyses which is that number of locations are a critical element of hotspot analyses. As further evidence, the kernel density analysis identified a highly dense area of ewes near the mine site in the Recent

period (*Fig. SM3.4*). Because the hotspot analysis revealed that points near the mine were distributed randomly and the density analysis identified a high-density area around or near the mine, this may be due to lack of location data in the area.

Limitations of aerial surveys and spatio-statistical analyses

Ewes were clustered into more and geographically larger hotspots than rams across each of the periods. Not surprisingly, this trend is likely due to the fact that survey efforts consistently found more ewes than rams yearly, in most WMUs. A typical composition of sheep in historic ranges are 65% ewes and 35% rams (Kneteman 2016). A higher number of ewes recorded increases the chances of seeing ewe hotspots, relative to rams. This effect may also be partly a relic of survey effort; during winter months, rams are typically found at lower elevations than ewes, and may even be below the treeline to be sheltered from harsh winds and snowfall, and gain access to more nutritious vegetation (Valdez and Krausman 1999, Demarchi 2004). As such, rams may also be less detectable by helicopter than ewes, since helicopter flights typically focus near the tops of mountain ranges, adding to the issue of “sightability” and sampling effort.

Sheep are difficult to classify from aerial surveying alone due to sheer distance between the surveyor and the sheep. Therefore, it is possible that sheep were poorly classified during sampling; this is a particular concern for counting adult ewes. Adult rams are distinguished with their large bodies and large, curled horns. Adult rams also form a separate band after the rut, making a band of rams identifiable. Alternatively, nursery bands consist of adult ewes, as well as male and female lambs and juveniles. Distinguishing between a yearling male and adult ewe is particularly difficult since they both possess short horns with no annuli and are of similar body size. This discrepancy may have positively skewed the number of ewes identified compared to

the adult rams. Conducting hotspot analyses with all nursery band members may be useful to identify nursery band distribution patterns compared to ram bands. Note that an area surveyed that saw no sheep was not included in the dataset, and therefore was treated as if no survey was conducted at that WMU, in that year (i.e., 0 sheep = N/A). Therefore, more WMUs may have been surveyed throughout the time period, however, are not recognized as having been surveyed.

Another element not addressed by the spatial analysis techniques was the effect of topography on sheep distribution. In this study, optimized hotspot analyses outputted cells larger than 4 km², and as such may have included steep elevational gradients within each cell. Since each cell is given one score to rate proximity of individuals, it is possible that ewe and ram hotspots differed widely across elevation (Festa-Bianchet 1988), however this discrepancy was not acknowledged by the analyses performed. Modelling the effect of elevation on sheep distribution is the next step to distinguish between the preferred clustering areas for both ewes and rams. Marking and tracking movement of ewes and rams separately during the winter months using collars or remote cameras will be important to understand what areas are important to ewes and rams separately, and where to enforce sex-specific management expectations, such as with trophy hunting.

A weakness inherent to spatial statistical approaches is that, since it is strictly an analysis of trend, it cannot investigate causation. Therefore, we do not know the extent to which the spatial trends reveal real patterns on the landscape, or simply reflect sampling effort bias (Lin et al. 2017, Hojati 2019, Lim et al. 2019). Such biases may surface when conducting hotspots on a landscape that is not equally surveyed or not surveyed by the same surveyor, or when comparing hotspots from different times which may not be surveyed with equal effort. Uneven survey effort was most evident across the study area from ca. 1998 to 2008 (late Middle and early Recent

periods), where fewer than 32% of the WMUs were sampled per year. The Talbot Lake area itself was not surveyed for about 16 years prior to, and 8 years after, the fire. Lack of surveys in this area rendered it difficult to confidently identify the large-scale effect of burned habitat on sheep distribution over time. This information is the biggest loss to the study, since current knowledge on fire-sheep interaction is poor, and burn practices are a common resolution for sheep habitat degradation (caused by climate warming). Research has shown that sheep response to burns is dependent on the type of burn practice (Clapp and Beck 2016) and time after burn (Michalsky 1987), and presently, research is being conducted to assess intensity of fire effect on sheep population numbers through radio collar data (A. Hubbs, *pers. comm.*).

These spatial analyses reveal patterns that can then be further investigated to determine what local factors may be affecting sheep distribution and habitat selection, or even to determine where future projects can be situated to study sheep movement or behaviour at a local level while maximizing sheep sample size. Sheep management may also choose to select for areas with higher winter sheep activity to protect from anthropogenic disturbances during the months of low resource availability (Alberta Environment and Parks 2015). This research is a stepping-stone, that opens doors to many questions relevant to understanding sheep distribution and future resilience of the biggest bighorn population in the world.

The whole is not necessarily the sum of its parts.

Large-scale datasets are important to detect larger changes in wildlife populations or landscapes, which might not necessarily be detected at smaller spatial scales (Giron-Nava et al. 2017, Burns et al. 2018). For example, barren-ground caribou (*Rangifer tarandus groenlandicus*) populations in northern Canada vary greatly in population size and trajectory, where most

studied herds are stable but many less accessible herds are declining rapidly (Virgl et al. 2017). Studying barren-ground caribou at a larger scale would identify overall trends which may be missed if not observed as a whole. Similar to these caribou, sheep inventory has been studied more locally in the past. Our study is part of a first step to a larger scale understanding of what factors affect habitat selection by bighorn sheep.

Long-term monitoring datasets are also useful for documenting the occurrence of sudden and/or large-scale events (e.g., landslides), which can then be used to study the impact of such events on monitored populations (Bleich et al. 2009, Lin et al. 2017, Nyandwi et al. 2017, Lim et al. 2019). The concept of species resiliency to disturbance is gaining attention due to these growing anthropogenic impacts and spread across wildlife habitat (Kneteman 2016). Resiliency of a population is affected by a multitude of factors, including: population size, genetic pool, endemism, forage quality, habitat connectivity, and home range size (Halford et al. 2004, Morecroft et al. 2012, Kneteman 2016, Cassirer et al. 2017). Records of these events and their analysis are crucial for understanding and forecasting the effects of anthropogenic or natural disasters on populations and the ecological systems they're a part of, and can help us better prepare for rehabilitation measures that improve the speed and overall recovery of these ecosystems.

CHAPTER 4

MANAGEMENT IMPLICATIONS

I present new research on two of the last large and mostly intact mountain sheep populations in the world. I used existing NWT harvest data of Dall (*Ovis dalli dalli*) rams and Alberta winter inventory data of bighorn sheep (*Ovis canadensis*) to better understand historic patterns of change in mountain sheep populations, and to cover a major gap in current literature to support the next generation of mountain sheep management plans and inventory programs in Canada. Despite interest in mountain sheep persistence by governments (e.g., as a tourist attraction, or as an umbrella species for conservation in high elevation systems) or from industry (e.g., hunting), these two datasets have not yet been assimilated and utilized to understand population trends over a large part of their range, over a long period of time. This information could be used to influence monitoring and management of mountain sheep in Canada, ultimately tending to government and industry interests.

Dall rams and trophy hunting in the NWT

Each outfitter in the NWT is responsible for management of hunting activity in their area, and to ensure that localized overharvest does not occur, within the framework of the rules and regulations established by the government of the NWT (Veitch et al. 1998, Larter and Allaire 2017). This co-management strategy enhances the outfitter's ability to practice sustainable harvest and manage the allocation of harvest effort and areas within their zone.

The remoteness and isolation of the Mackenzie Mountains and distance from NWT communities result in a low level of subsistence harvest and harvest by resident hunters (Larter

and Allaire 2017). Consequently, sheep harvest within each zone is almost exclusively by the outfitters' clients. The current management of Dall sheep in the Mackenzie Mountains appears to have maintained a population of rams that do not show the decline in horn size associated with selective harvest in other jurisdictions, such as Alberta. The resilience of this approach, however, may be challenged by other environmental changes associated with rapid warming.

Within our study area in NWT, little to no data is available for a Dall sheep population census. As highlighted in previous chapters, global warming risks changes in function of northern and higher elevation habitat, and may drastically affect sheep population structure and function within its ecosystem in the future (Festa-Bianchet et al. 1997, Hik and Carey 2000, Márquez et al. 2011, Imperio et al. 2013, Pepin et al. 2015, Larter and Allaire 2016). Not only do mountain sheep act as ‘canaries’ to changes in climate at northern high elevations, but the widespread foraging of these large herbivores may significantly modify the vegetation communities (Shank 1982, Festa-Bianchet 1988, Goodson et al. 1991a, 1991b), potentially fast-tracking changes in high-elevation community structure and amplifying the effect of climate warming. As a result, understanding northern populations of mountain sheep has never been more important, and implementation of sheep census data collection by government or outfitters is recommended for the future.

Climate fluctuations can ultimately affect vegetation structure and productivity, as well as winter snow cover depths, affecting food availability for herbivores and species composition at higher trophic levels (Goodson et al. 1991a, Imperio et al. 2013, Boulangeat et al. 2014, Mason et al. 2014). Mountain sheep are sensitive to changes in snow cover depth, since increased depth can decrease their abilities to access forage underneath and escape predation, while little to no snow reduces abundance of preserved and available forage throughout the winter. In response to

climate warming, alpine biotic communities are expected to shift to higher elevations (Schneider 2013, Boulangeat et al. 2014).

Bighorn sheep congregations in Alberta's Rocky Mountains

Management needs to reflect where sheep congregate. Local land management likely has an impact on sheep attraction to, or deterrence from, certain areas, and ultimately their distribution geographically. Mapping where sheep are found can help assess what areas are critical to sheep and should be managed more carefully. Currently in Alberta, the long-term goals of mine sites and government land management are very different. Mining industries plant nutrient-rich forage to rapidly increase visits of wildlife to the mine sites as a measure of landscape rehabilitation (Alberta Environment and Parks 2015). Government wildlife initiatives, in contrast, typically focus on reducing the overall role of mined areas on wildlife movement and community function, aiming to minimize the potential local and deleterious effects of mine sites on sheep populations discussed above, such as sublethal metal effects and competition. Stronger government regulation may change this current disparity, aligning mine site goals to better reflect the needs of the wildlife communities influenced by the site presence for optimal long-term landscape rehabilitation. Restricting sheep access to mine sites using fencing or low-quality forage, for example, may help deter sheep from mine sites during the initial years of land reclamation.

Hotspot maps can also influence hunting restrictions, where hunting tags may be limited in WMUs that host large sheep congregations. Currently, different WMUs hold different curl regulations for hunting; most WMUs use a $\frac{4}{5}$ curl minimum for legal ram hunting (two WMUs in southern Alberta use a full curl minimum; A. Hubbs, *pers. comm.*), one of the most liberal ram

hunting regulations in the world (Fish and Wildlife Division 2012, Alberta Environment and Parks 2015). In fact, even WMUs that hold special licenses (i.e., a draw system to limit hunting in an area of high demand) rather than general licenses hold a $\frac{4}{5}$ curl minimum for legal ram hunting. Though Alberta holds the largest intact population of bighorn sheep in the world, Alberta-based studies have already revealed a significant decline of bighorn ram horn size due to selective hunting pressures against rams with fast-growing horns within the population (Coltman et al. 2003, Festa-Bianchet et al. 2014, Poisson et al. 2020). Therefore, this minimum curl is particularly controversial because WMUs that distribute special licenses do so to reduce hunting pressure on rams, yet hunters are still permitted a younger trophy ram kill than most other jurisdictions (A. Hubbs, *pers. comm.*). This decline in ram horn size across generations may affect mating success within a population, ultimately potentially affecting future generations (Coltman et al. 2003, Allendorf and Hard 2009). In line with our research, we suggest elevating minimum curl regulations in WMUs that hold ram hotspots: south of Athabasca River (Zone 3) and north of Bow River (Zone 4).

Moreover, high hunting pressure in a sheep hotspot area may lead to a sudden reduction in resiliency of sheep to other direct human disturbances such as mining or wildfires, and potential decline in population size and survivability in the long term. Hunting limitations that better reflect the distribution of sheep on the landscape will potentially reduce the negative impacts on sheep populations as a whole. For example, our research suggests that there may be some advantages for adopting a draw system for ewes and rams in hotspot areas such as south of Athabasca (Zone 3), Saskatchewan (Zone 4) and Bow rivers (Zone 5).

Large datasets are difficult to work with in research mainly due to the unavoidable problem of sampling effort bias. Although more data is typically better to examine population

trends, ultimately, less-frequent and equal-interval data collection is preferable to frequent but discontinuous data collection (Lindenmayer et al. 2012). Equal interval data collection allows for greater analytical power when examining distribution patterns over continuous time. Similarly, surveying the same WMUs per survey year, or circulating through a set of WMUs per survey will allow us to make conclusions about the change in distribution in each region of sheep home range equally. Varying survey efforts per WMU can cause drastically skewed numbers of sheep observed per region, which then alters the spatial patterns seen on the landscape. One way to remedy the dilemma where some WMUs are less accessible by helicopter is to use alternatives to helicopter surveying, such as drone technology. These would likely sample as many sheep as could be seen in a helicopter and minimize the presence of holes in the dataset due to poor winter weather or inaccessibility (*Fig. 3.2*). Though data surveying techniques have room to improve, long-term and large-scale datasets nevertheless have an important place in ecological research to help us better understand whole-range and long-term trends, and ultimately better predict future outcomes for populations and communities in response to growing anthropogenic disturbances, land modifications and climate change.

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Supplemental Material

Chapter 2

Table SM2.1. Global sample size table of Dall sheep rams harvested between 2002 and 2017, in the Mackenzie Mountains, NWT, Canada (n=755). Sample sizes are organized by age, year, and outfitter area. NB = Nahanni Butte, SN = South Nahanni. Totals for the sum of a category combination are in bold.

		2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	
		755	24	40	41	28	35	39	54	34	52	60	61	52	69	81	41	44
Total	NB	369	20	26	30	20	22	24	24	9	30	30	40	30	27	30	5	2
	NWT	27	0	0	0	0	0	0	0	0	0	0	0	0	1	7	0	19
	Redstone	52	0	0	1	1	3	0	0	0	1	7	4	2	9	12	12	0
	SN	307	4	14	10	7	10	15	30	25	21	23	17	20	32	32	24	23
	Total	2	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
5	NB		0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Redstone		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SN		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	3	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
6	NB		0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Redstone		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SN		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	31	1	4	1	2	1	2	2	1	4	1	1	2	6	2	0	
Age	NB		1	3	1	1	1	2	1	1	2	1	0	1	3	1	0	
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
	Redstone		0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	
	SN		0	1	0	1	0	0	0	0	1	0	1	1	1	1	0	
	Total	120	5	2	8	4	4	4	5	6	11	19	6	6	14	9	4	13
	NB		3	0	5	3	2	0	2	2	8	9	6	5	5	3	1	1
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	
	Redstone		0	0	0	0	1	0	0	0	1	0	0	3	0	1	0	
	SN		2	2	3	1	1	4	3	4	3	9	0	1	6	5	2	9
	Total	184	8	14	9	8	10	5	15	7	9	10	19	18	16	18	7	11

	NB		8	8	6	4	3	3	5	3	6	5	15	10	4	6	0	1
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	9
	Redstone		0	0	0	0	2	0	0	0	0	1	1	2	4	2	3	0
	SN		0	6	3	4	5	2	10	4	3	4	3	6	8	9	4	1
	Total	204	4	12	10	3	10	10	16	13	18	12	22	7	18	27	13	9
10	NB		4	10	7	3	8	8	10	2	6	7	11	4	10	10	0	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2
	Redstone		0	0	1	0	0	0	0	0	1	1	1	0	2	3	6	0
	SN		0	2	2	0	2	2	6	11	11	4	10	3	6	11	7	7
	Total	142	3	3	6	9	7	10	10	3	10	10	8	15	14	15	10	9
11	NB		3	3	6	7	5	6	4	0	7	5	5	8	5	3	1	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	4
	Redstone		0	0	0	1	0	0	0	0	0	1	0	0	0	6	2	0
	SN		0	0	0	1	2	4	6	3	3	4	3	7	8	5	7	5
	Total	44	3	2	5	1	2	3	5	2	2	3	3	2	1	4	4	2
12	NB		1	1	4	1	2	1	1	1	1	2	1	1	0	4	1	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Redstone		0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
	SN		2	1	1	0	0	2	4	1	1	0	1	1	1	0	3	1
	Total	15	0	1	1	0	1	3	1	2	1	1	1	0	2	1	0	0
13	NB		0	0	1	0	1	2	0	0	1	0	1	0	0	0	0	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Redstone		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SN		0	1	0	0	0	1	1	2	0	1	0	0	2	1	0	0
	Total	9	0	2	0	1	0	0	0	0	0	1	1	2	2	0	0	0
14	NB		0	1	0	1	0	0	0	0	0	0	0	1	2	0	0	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Redstone		0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
	SN		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Total	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
15	NB		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	NWT		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Redstone		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	SN		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table SM2.2. Number of licenses bought and hunting pressure on sheep populations in the Alberta Rocky mountain range (AB bighorn), northern British Columbia (BC Stone) and Yukon Mackenzie Mountains range (YT Dall), in comparison to the Northwest Territories Mackenzie Mountains range (NWT Dall). Hunting pressure was calculated using Douhard et al. (2016) protocol.

	AB bighorn	BC Stone		YT Dall	NWT Dall	AB bighorn	BC Stone		YT Dall	NWT Dall
Monitored area (km ²)	52481	23360	19194	140000	140000		Low (Skeena)	High (Peace)		
Year	# licenses					Hunting pressure (# licenses/area)				
1971	1150					0.0219				
1972	1000					0.0191				
1973	1307					0.0249				
1974	936					0.0178				
1975	1470					0.0280				
1976	1827	233.6	364.7			0.0348	0.01	0.019		
1977	2266	257.0	441.5			0.0432	0.011	0.023		
1978	2526	327.0	422.3			0.0481	0.014	0.022		
1979	2877	210.2	364.7			0.0548	0.009	0.019		
1980	2587	257.0	403.1	4300		0.0493	0.011	0.021	0.0307	
1981	2839	257.0	460.7	4500		0.0541	0.011	0.024	0.0321	
1982	2892	186.9	364.7	4800		0.0551	0.008	0.019	0.0343	
1983	3099	186.9	326.3	4400		0.0590	0.008	0.017	0.0314	
1984	3397	140.2	287.9	4300		0.0647	0.006	0.015	0.0307	
1985	3333	163.5	307.1	4100		0.0635	0.007	0.016	0.0293	
1986	3332	163.5	499.0	3800		0.0635	0.007	0.026	0.0271	
1987	2535	233.6	479.9	4000		0.0483	0.01	0.025	0.0286	
1988	2543	163.5	556.6	4000		0.0485	0.007	0.029	0.0286	
1989	2494	257.0	671.8	3800		0.0475	0.011	0.035	0.0271	
1990	2337	280.3	652.6	3800		0.0445	0.012	0.034	0.0271	
1991	2089	280.3	614.2	3700	365	0.0398	0.012	0.032	0.0264	0.0026
1992	2037	257.0	729.4	3700	370	0.0388	0.011	0.038	0.0264	0.0026
1993	2030	280.3	691.0	3750	380	0.0387	0.012	0.036	0.0268	0.0027
1994	1990	257.0	614.2	3650	358	0.0379	0.011	0.032	0.0261	0.0026

1995	1936	327.0	671.8	3700	350	0.0369	0.014	0.035	0.0264	0.0025
1996	1786	233.6	614.2	3700	385	0.0340	0.01	0.032	0.0264	0.0028
1997	1786	233.6	633.4	3750	353	0.0340	0.01	0.033	0.0268	0.0025
1998	1886	233.6	844.5	3800	350	0.0359	0.01	0.044	0.0271	0.0025
1999	1883	233.6	787.0	3600	325	0.0359	0.01	0.041	0.0257	0.0023
2000	1886	186.9	633.4	3500	335	0.0359	0.008	0.033	0.025	0.0024
2001	1885	257.0	595.0	3400	335	0.0359	0.011	0.031	0.0243	0.0024
2002	1885	186.9	633.4	3600	340	0.0359	0.008	0.033	0.0257	0.0024
2003	1835	210.2	556.6	3500	350	0.0350	0.009	0.029	0.025	0.0025
2004	1836	140.2	345.5	3400	348	0.0350	0.006	0.018	0.0243	0.0025
2005	1833	233.6	518.2	3600	395	0.0349	0.01	0.027	0.0257	0.0028
2006	2084	210.2	575.9	3600	410	0.0397	0.009	0.03	0.0257	0.0029
2007	2185	257.0	633.4	3550	405	0.0416	0.011	0.033	0.0254	0.0029
2008	2279	280.3	652.6	3750	400	0.0434	0.012	0.034	0.0268	0.0029
2009	2371	327.0	671.8	4000	340	0.0452	0.014	0.035	0.0286	0.0024
2010	2322	280.3	652.6	3750	380	0.0442	0.012	0.034	0.0268	0.0027
2011	2265	303.7	691.0	3750	400	0.0432	0.013	0.036	0.0268	0.0029
2012	2466			4100	403	0.0470			0.0293	0.0029
2013	2412			4200	400	0.0460			0.03	0.0029
2014	2420			4350	400	0.0461			0.0311	0.0029
2015					447					0.0032
2016					380					0.0027
AVERAGE						0.0416	0.0101	0.0289	0.0276	0.0027

□

Table SM2.3. Generalized linear models for Dall ram horn volume from 2002 to 2017 in the Mackenzie Mountains, NWT, Canada. *Age* = Dall sheep age at harvest. *Year* = Dall sheep year of harvest. *OA* = Outfitter area where Dall sheep was harvested. AIC = Akaike Information Criterion. Δ AIC = Difference in AIC from the best fitting model (in bold). * = Estimates in which the confidence interval does not include zero (i.e., significant). Ages 5 and 15 were excluded from the following models due to low sample size ($n < 3$).

Random Effect	Model	AIC	Δ AIC	Estimates (\pm Confidence Interval)	
				<i>Age</i>	<i>Year</i>
Intercept	Horn Volume = <i>Age</i> + <i>Year</i> + (1 <i>OA</i>)	10850	0	74.57 (± 16.5424)*	2.53 (± 5.8212)
Slope†	Horn Volume = <i>Age</i> + <i>Year</i> + (0+ <i>Age</i> + <i>Year</i> <i>OA</i>)	10852	2	70.10 (± 19.698)*	2.65 (± 5.8212)
Slope and Intercept†	Horn Volume = <i>Age</i> + <i>Year</i> + (1+ <i>Age</i> + <i>Year</i> <i>OA</i>)	10859	9	68.69 (± 27.0676)*	2.66 (± 5.8212)
None	Horn Volume = <i>Age</i> + <i>Year</i>	10919	69	72.54 (± 17.2284)*	-4.06 (± 5.6448)
Null	Horn Volume = 1	10931	81	-	-

† indicates that the model failed to converge.

Chapter 3

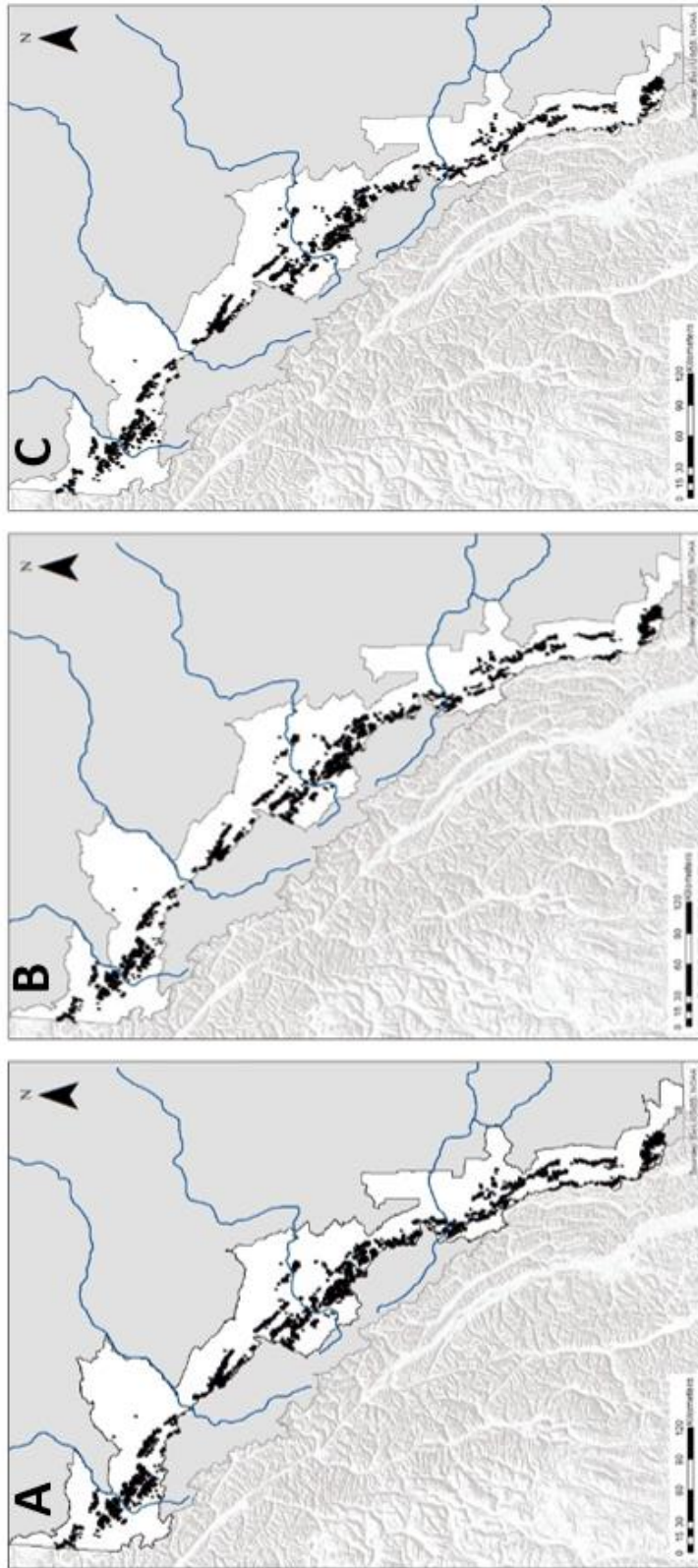


Figure SM3.1. (A) Sheep, (B) Ewe, and (C) Ram locations in the Rocky Mountain study area, across the 52 years.

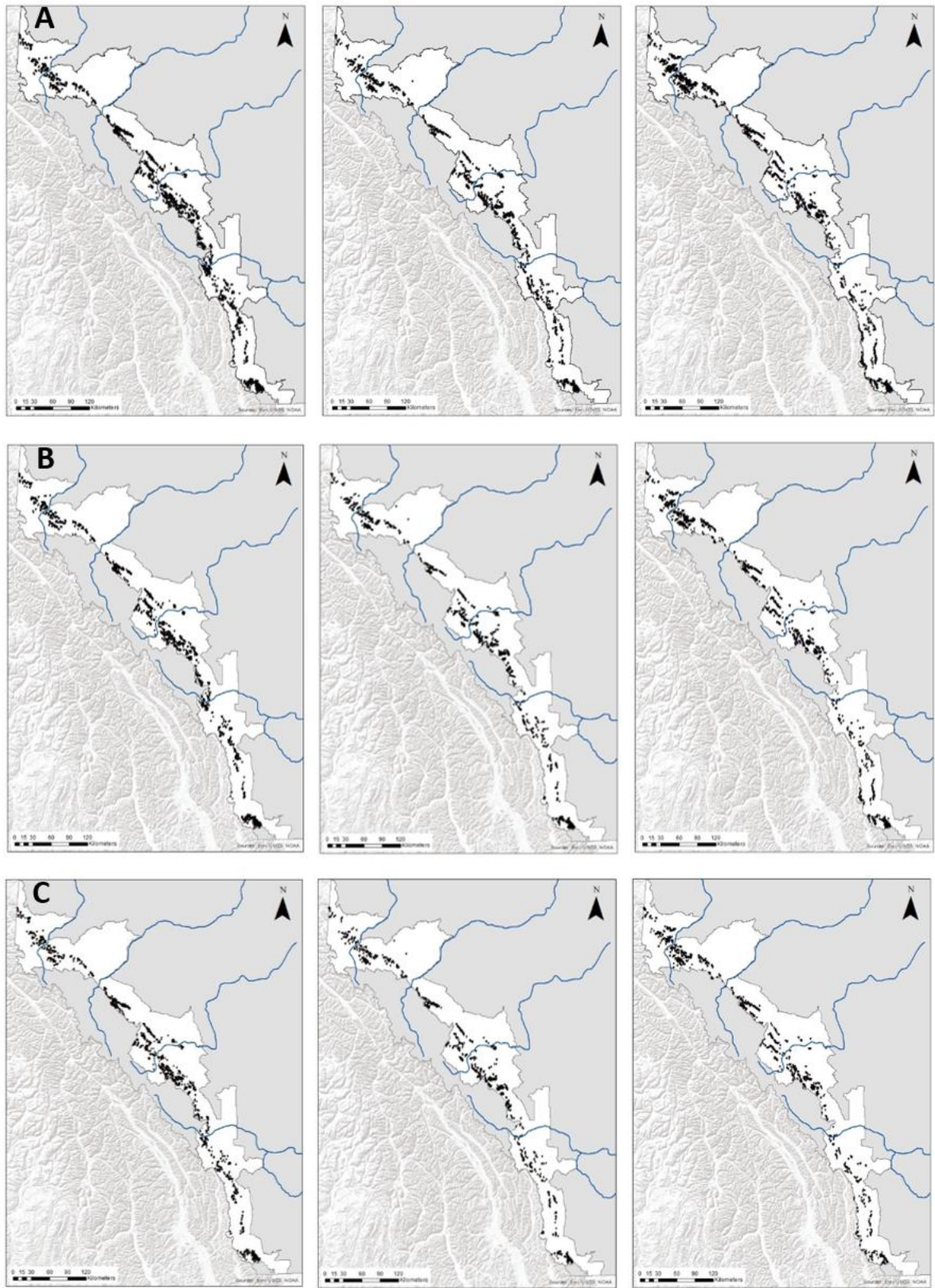


Figure SM3.2. (A) Sheep, (B) Ewe, and (C) Ram locations in the Rocky Mountain study area, across Early, Middle and Recent periods (left to right).

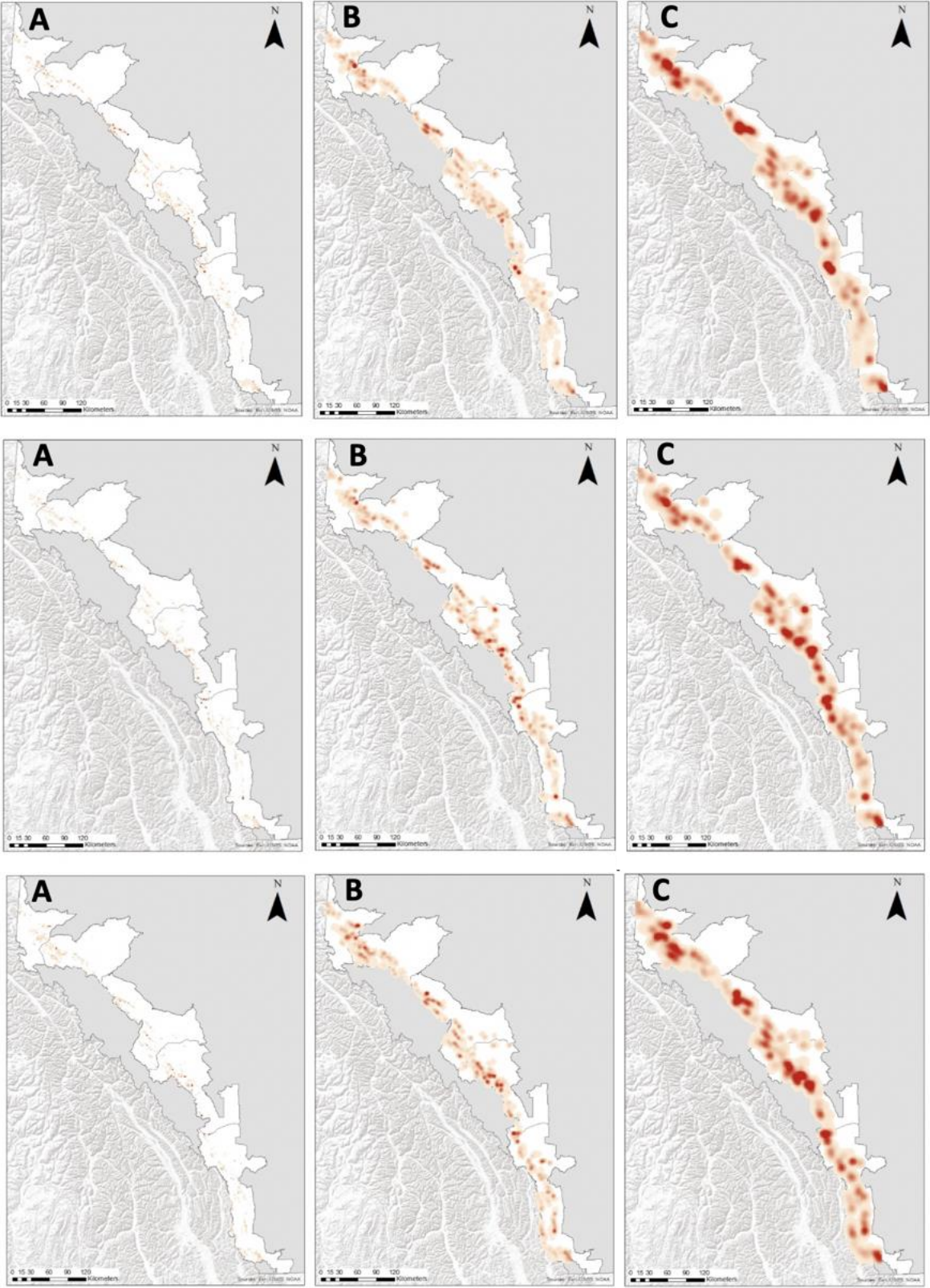


Figure SM3.3. Effect of various search radius sizes (i.e., neighbourhood size) on sheep kernel density analysis heatmap for the Early period (top row), Middle period (middle row), and Recent period (bottom row). The sheep heatmap illustrates (A) a 1 km search radius, (B) a 5 km search radius, and (C) a 10 km search radius. Cell size = 2000 m.

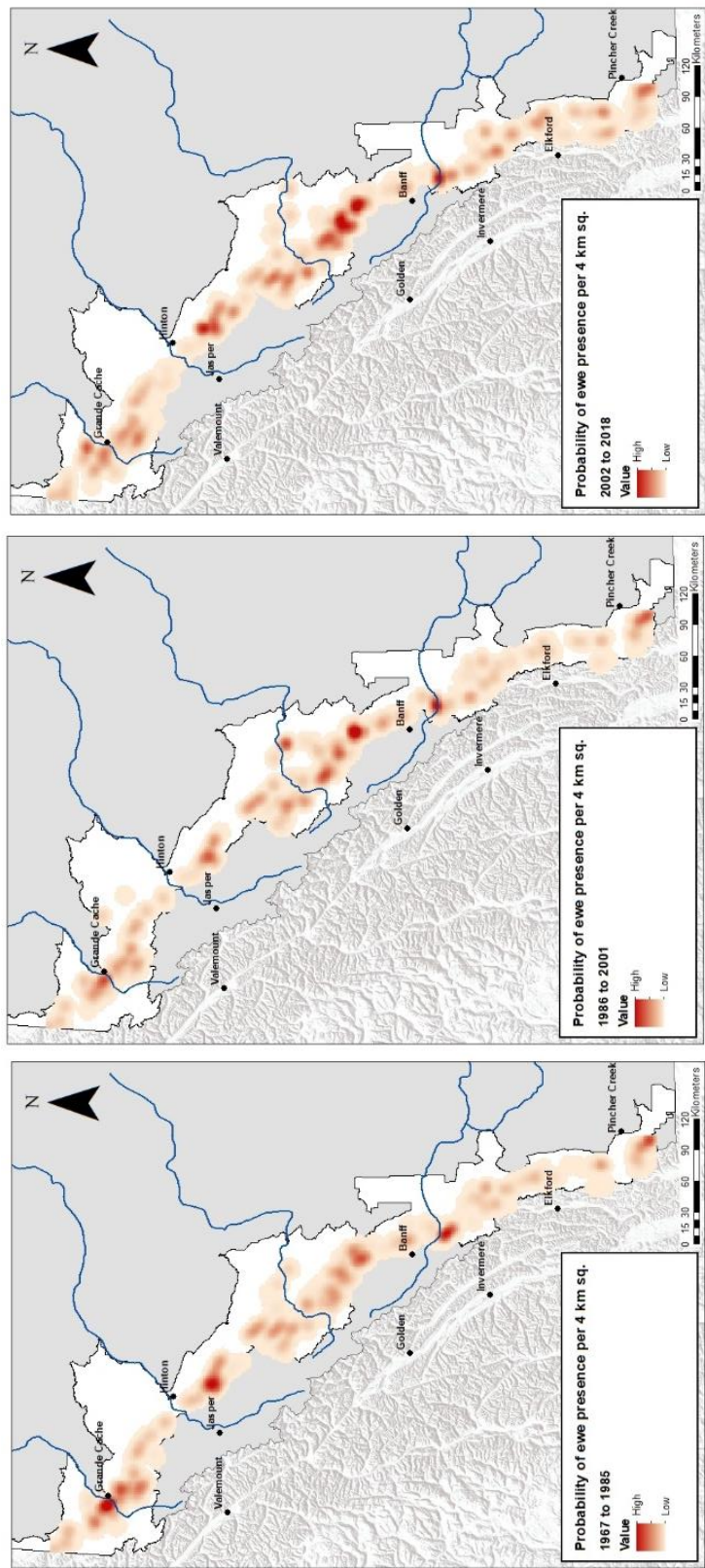


Figure SM3.4. Probability of bighorn ewe presence within a 4 km² area in Alberta's Rocky Mountains, pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). Legend demonstrates estimated cumulative number of ewes over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* ewes, and the kernel density analysis; this estimate is not an actual number of ewes in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.

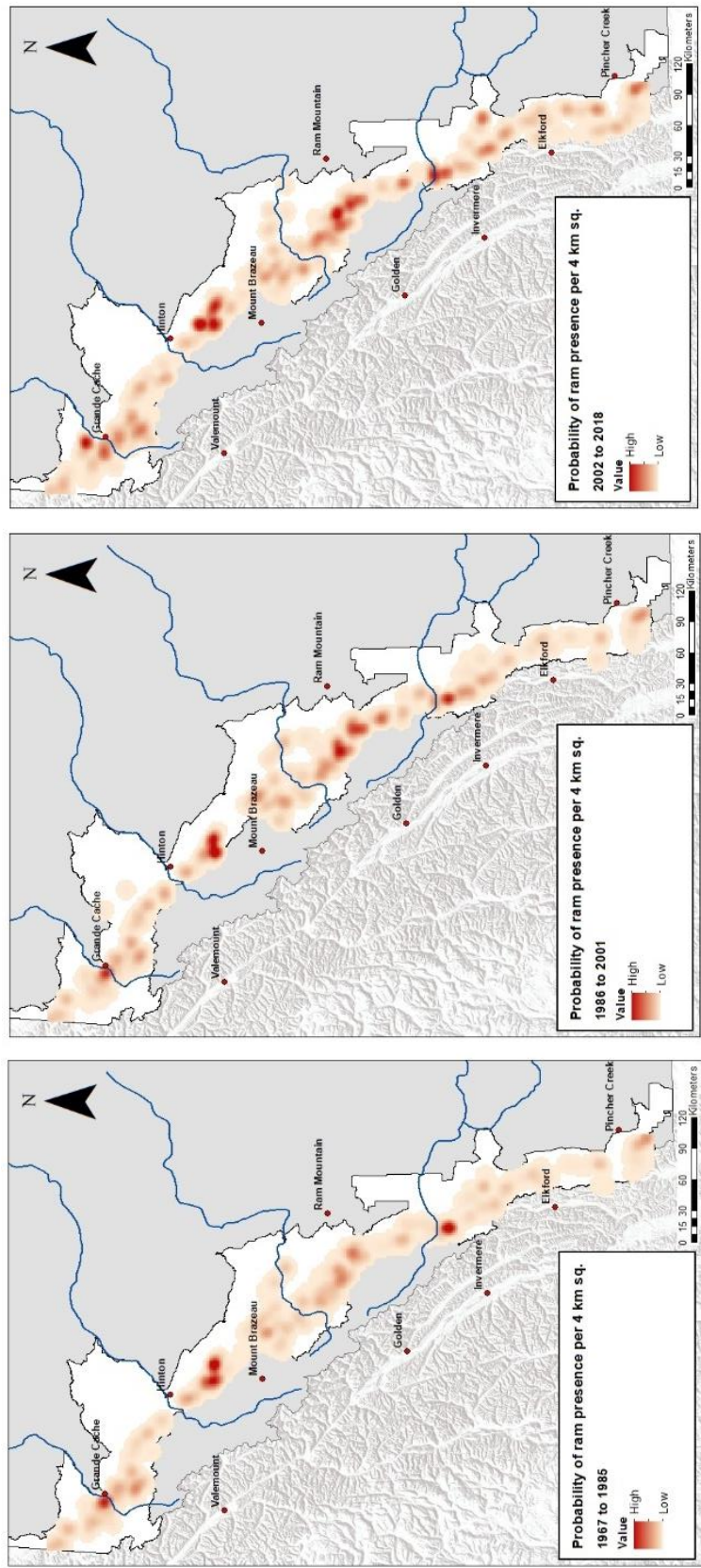


Figure SM3.5. Probability of bighorn ram presence within a 4 km² area in Alberta's Rocky Mountains, pooled over each 16-year period (1967-1985, 1986-2001, 2002-2018, respectively). Legend demonstrates estimated cumulative number of rams over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* rams, and the kernel density analysis; this estimate is not an actual number of rams in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.

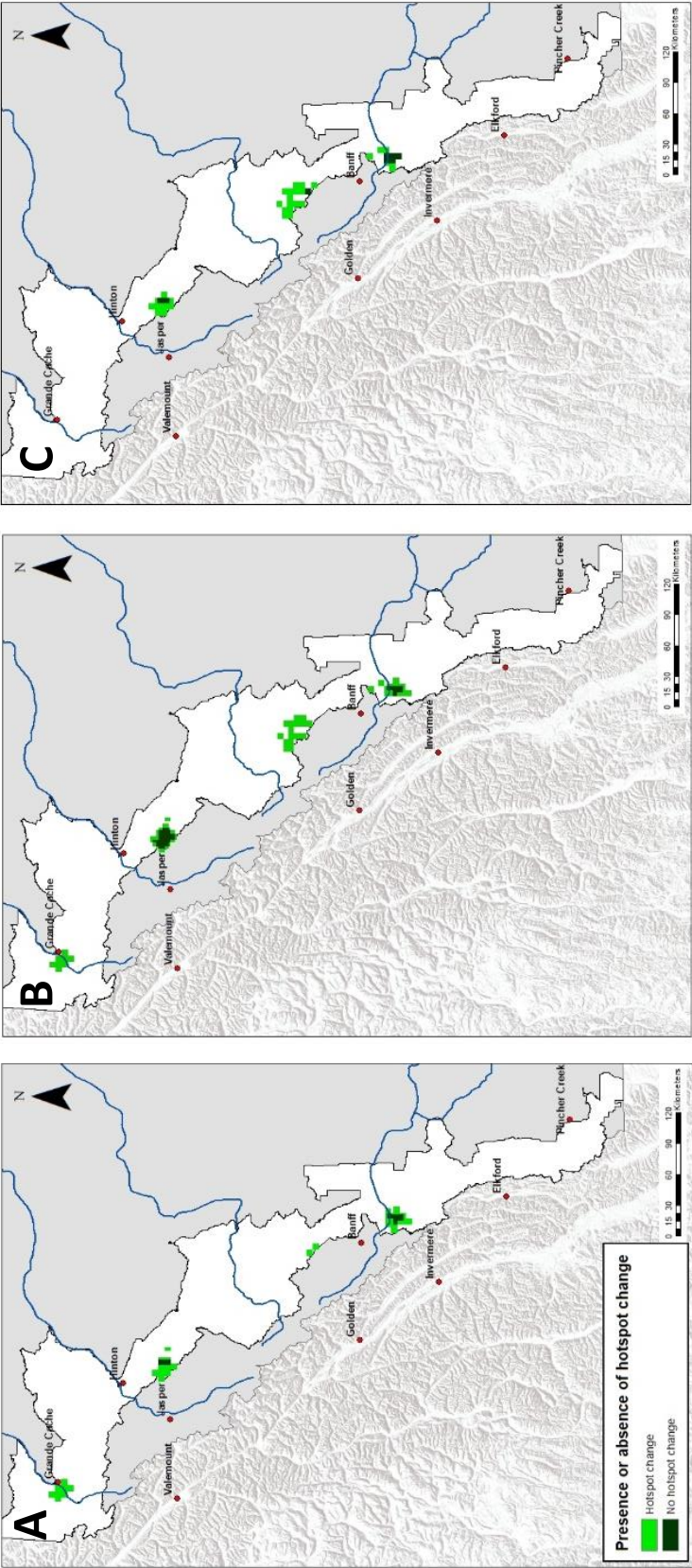


Figure SM3.6. Change in presence of bighorn sheep between (A) Early and Middle periods, (B) Early and Recent periods, and (C) Middle and Recent periods, at a 95% confidence. Raster cell size = 2 000 m.

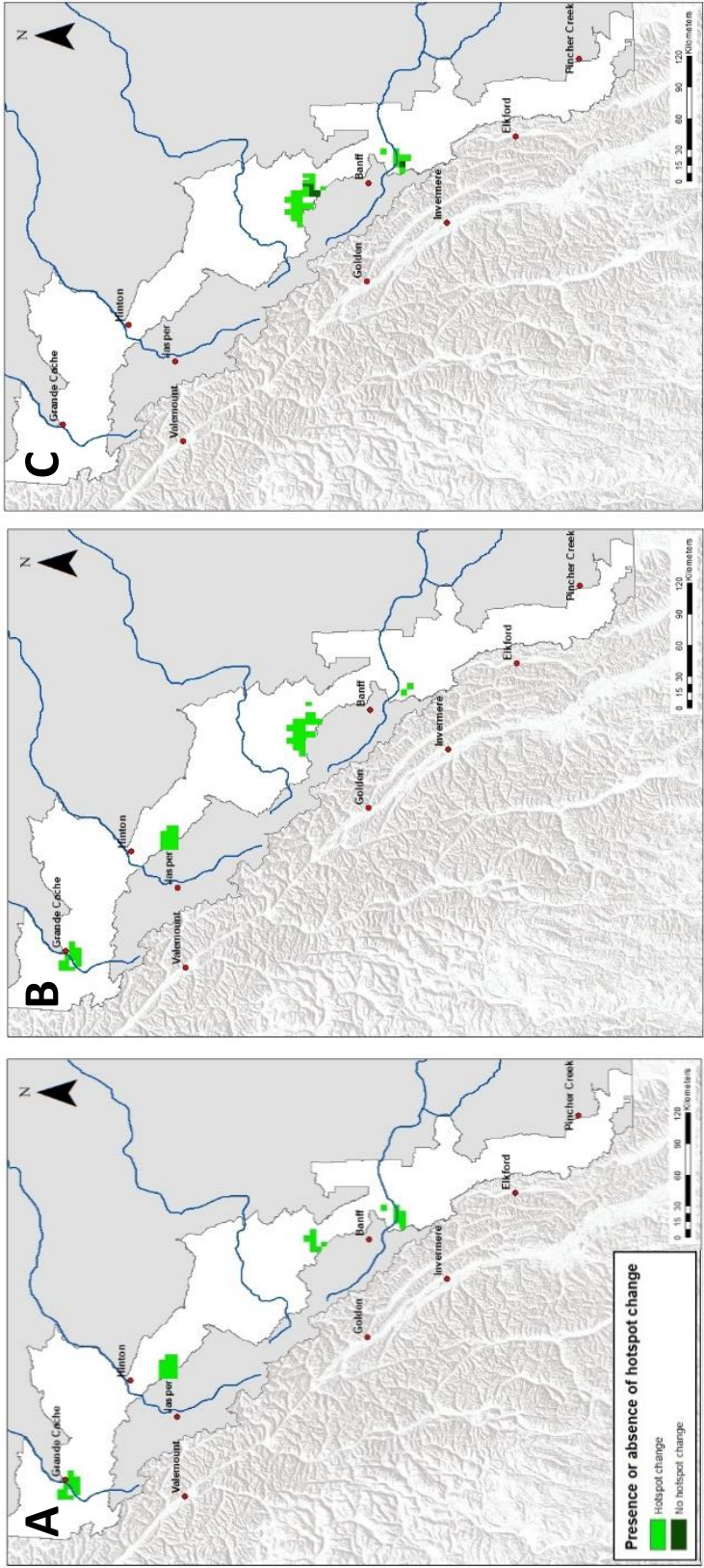


Figure SM3.7. Change in presence of bighorn ewe between (A) Early and Middle periods, (B) Early and Recent periods, and (C) Middle and Recent periods, at a 95% confidence. Raster cell size = 2 000 m.

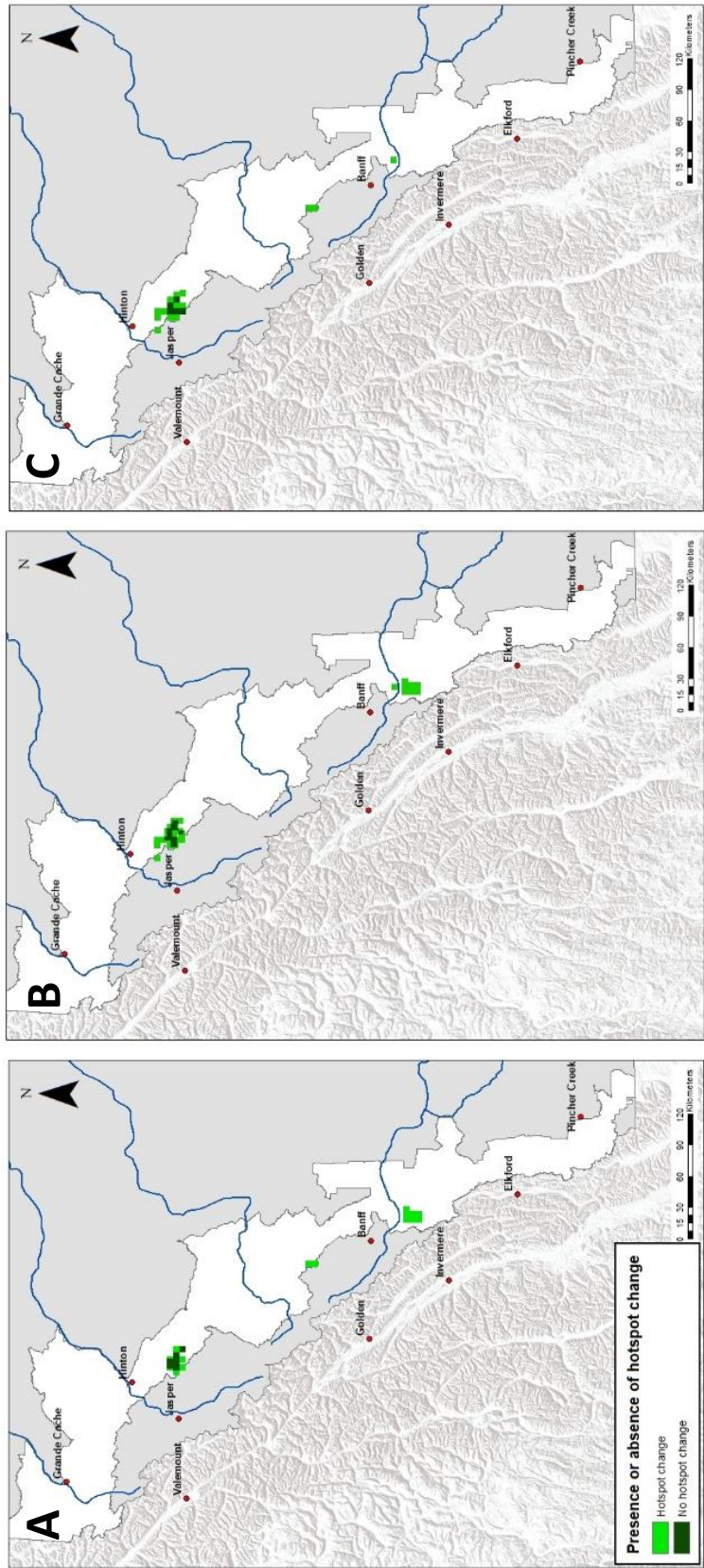


Figure SM3.8. Change in presence of bighorn ram between (A) Early and Middle periods, (B) Early and Recent periods, and (C) Middle and Recent periods, at a 95% confidence. Raster cell size = 2 000 m.

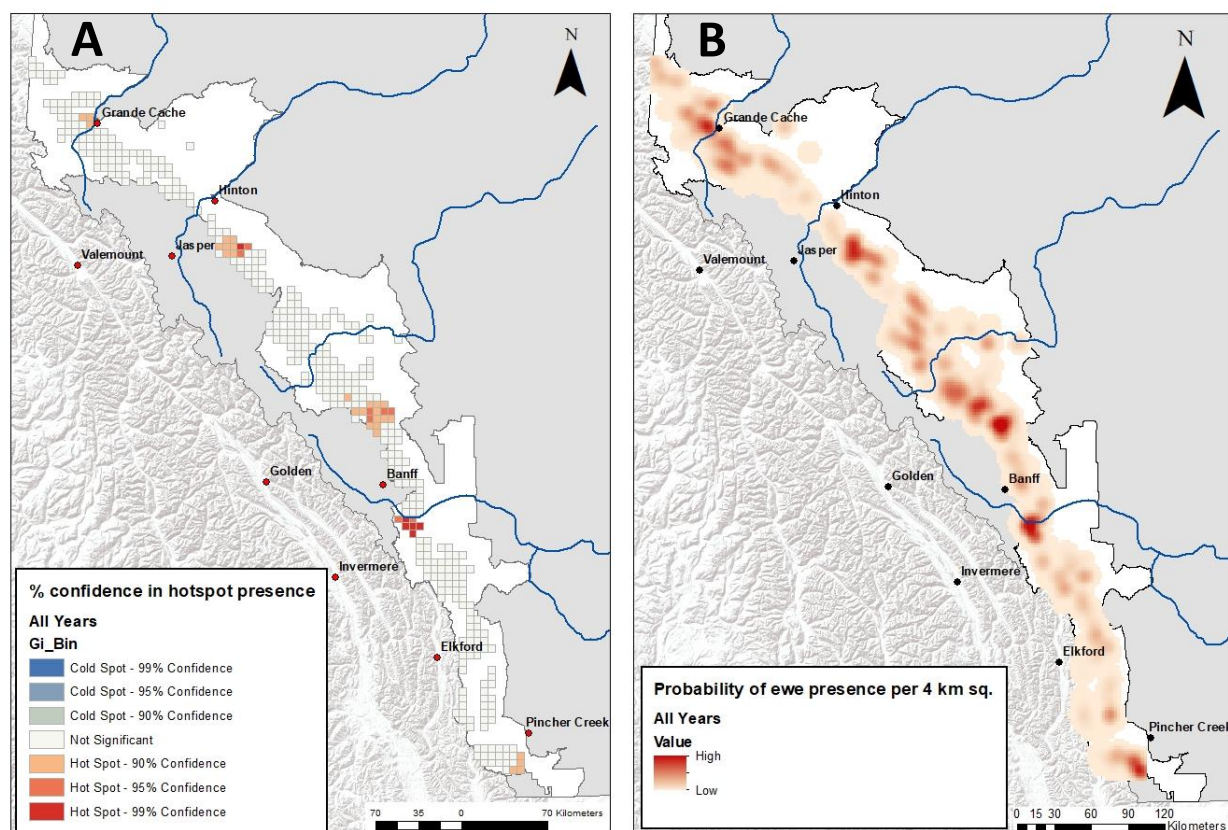


Figure SM3.9. Map (A) illustrates the areas of ewe clustering, based on the number of surveyed ewes pooled over the entire study period (1967-2018). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains ewes that are randomly distributed on the landscape. Map (B) shows the probability of bighorn ewe presence within a 4 km² area in Alberta's Rocky Mountains, pooled over the entire study period (1967-2018). Legend demonstrates estimated cumulative number of ewes over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* ewes, and the kernel density analysis; this estimate is not an actual number of ewes in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.

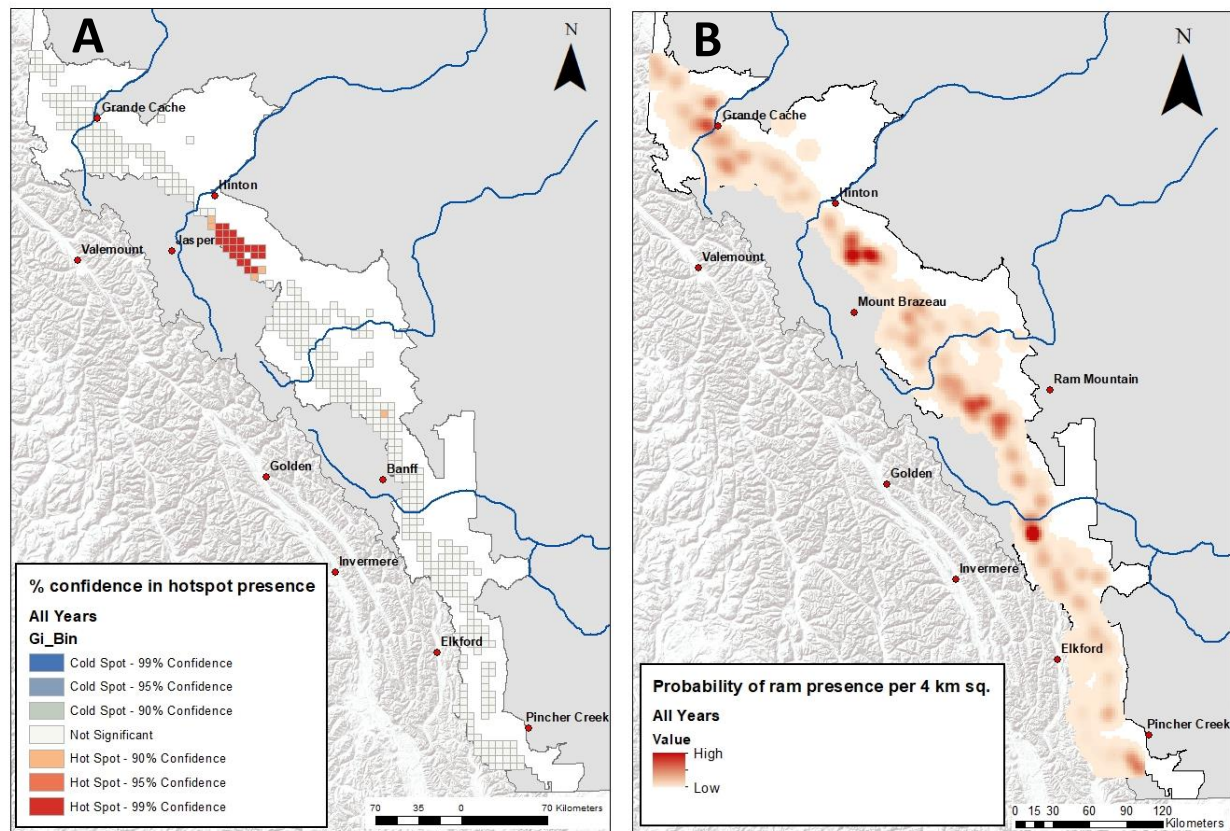


Figure SM3.10. Map (A) illustrates the areas of ram clustering, based on the number of surveyed rams pooled over the entire study period (1967-2018). A red *Hot Spot* cell represents an area with significant clustering, at 90, 95 or 99% confidence. A blue *Cold Spot* represents an area with significant avoidance, at 90, 95 or 99% confidence. A white *Not Significant* cell represents an area that contains rams that are randomly distributed on the landscape. Map (B) shows the probability of bighorn ram presence within a 4 km² area in Alberta's Rocky Mountains, pooled over the entire study period (1967-2018). Legend demonstrates estimated cumulative number of rams over all years within that period. This estimate is derived from the dataset indicating the number of *surveyed* rams, and the kernel density analysis; this estimate is not an actual number of rams in a given area. Raster cell size = 2 000 m; density search radius = 10 000 m.