Elk Harvests and Herd Reconstruction in Alberta for Adaptive Management

by

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ABSTRACT

In wildlife conservation, long-term monitoring is often justified by wildlife agencies as they allow managers to inform stakeholders, avoid conflicts, and to evaluate the results of management interventions. However, many wildlife agencies insufficiently or inadequately use these data in their management decisions. Two of the most common causes of inefficient monitoring are surveillance monitoring (monitor for monitoring sake, without evaluation) or not having the budget to properly monitor management interventions. For example, like most wildlife agencies in North America, Alberta, Canada, has been collecting data on the harvest of its hunted populations, including elk (*Cervus elaphus*), but has not evaluated the regulatory results and trends alongside relevant data such as predator populations abundance. Large predator populations are often believed to cause a decrease in hunter harvest because of direct competition for prey species with the hunter. In Alberta, grizzly bear (*Ursus arctos*), cougar (*Puma concolor*), and wolf (*Canis lupus*) populations have been increasing in recent years. To examine trends in the elk harvest results collected by the Alberta Environment and Parks from 1995 to 2016, we first digitized and attached the annual regulatory history, elk harvest, and hunter success results to each Wildlife Management Unit (WMU) across Alberta and then used linear regression to estimate trend. Over the 22-year period, the average annual harvest increased for both General (3.62%) and Special (9.74%) seasons. Average annual hunter success also increased for both General (0.3%) and Special (0.4%) seasons. Hunter effort showed no significant change ($p > 0.05$). Our results suggest that the increasing large predator populations are not having an impact on the hunter harvest of elk. Furthermore, the data suggests that Alberta's elk populations may even be increasing with Alberta's management interventions.

Alberta has also collected aerial survey data for its elk populations for many years but has done so sparingly due to budget constraints. Although aerial surveys are the most common method of monitoring ungulate populations because of their ability to cover large areas in a short amount of time, they are severely limited by the monetary cost to perform them, forcing places like Alberta to use them infrequently. For example, aerial surveys with moose (*Alces alces*) and elk occur as rarely as once every 10 years per WMU, hindering a wildlife managers ability to detect trends with the data. We demonstrated a method of population estimation using a population reconstruction model as an alternative to aerial surveys to estimate elk population size at a more cost effective and annual basis. To fill the parameters of the model, we conducted postseason (post-harvest) ground classification surveys 2 days per week from 3 February 2018 to 16 March 2018 to find herd composition data on bulls, cows, and juveniles in WMU 302 in southwestern Alberta. Because the reconstruction model requires preseason herd ratios, we then developed a model to convert postseason ratios to preseason ratios using hunter harvest from Alberta's harvest surveys. By updating the reconstruction model with the hunter harvest, our annual elk population estimates were comparable to the most recent aerial survey (a minimum population estimate in the 2015). We believe our method will benefit wildlife managers by giving them the ability to collect population data on an annualized basis, further allowing them to assess population trends and to evaluate the efficacy of their harvest management interventions.

PREFACE

This thesis is an original work by Tyler Steven Trump.

Chapter 2 includes co-author M. Boyce who provided feedback on data analysis and writing. For this manuscript, T. Trump analyzed the data and wrote most of the manuscript. The Alberta Environment and Parks department provided the elk harvest data.

Chapter 3 co-authors include M. Boyce, M. Nagy-Reis, and Jingjing Xu. For this manuscript, T. Trump performed the necessary field data collection, analyzed the data, and wrote most of the manuscript. M. Boyce, M. Nagy-Reis, and Jingjing Xu provided valuable feedback on analysis and writing. The Alberta Environment and Parks department provided the aerial survey and elk harvest data.

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CHAPTER 1 – GENERAL INTRODUCTION

In wildlife conservation, monitoring is often considered to be the heart of adaptive management (Walters 1986). Defined as an iterative process, the idea behind adaptive management in wildlife conservation is that by monitoring, wildlife managers learn from the results of their interventions and then can improve management-based on those interventions and new knowledge (McDonald-Madden et al. 2010; Boyce et al. 2012; Organ et al. 2012a). Although adaptive management has been around for many years and many wildlife agencies strive for it in their management practices, the actual application of adaptive management in wildlife conservation is seldom well implemented (Fontaine 2011; Williams 2011; Organ et al. 2012a). Many wildlife agencies fall short in their pursuit of true adaptive management because they continuously monitor without evaluation of the results, i.e., surveillance monitoring (Nichols and Williams 2006), and sometimes do not have the budgets to properly monitor the management strategy (White 2001).

In Canada and the United States, almost 80% of wildlife agencies monitor the harvest of their hunted populations (Artelle et al. 2018), but the resulting data often are not sufficiently evaluated (Yoccoz et al. 2001). This results in an expenditure of time and money for little to no value gained, emphasizing that monitoring alone is not enough (McDonald-Madden et al. 2010). Harvest estimates can be a useful tool for wildlife managers because these data are typically inexpensive to collect compared to many monitoring techniques and can potentially indicate, or help to indicate, the direction of wildlife population trends (Bender and Spencer 1999; Boyce et al. 2012; Clawson et al. 2015).

In North America, only 52% of wildlife agencies have data on population abundance for wildlife populations (Artelle et al. 2018). Aerial surveys are the most common method of data collection for ungulate population monitoring (Samuel et al. 1987; Bender et al. 2003; Allen et al. 2008; Schuette et al. 2018) because of their ability to cover large areas of land in short amounts of time. Unfortunately, a major limitation to this method of population monitoring is the high monetary cost to perform them (Pettorelli et al. 2007; Boyce et al. 2012; Greene et al. 2017). In Alberta, Canada for example, aerial surveys for moose (*Alces alces*; Boyce et al. 2012) populations can occur as rarely as once every 10 years per Wildlife Management Unit. This gap between monitoring efforts prohibits a wildlife manager's ability to detect trends and again represents an inefficient use of time and funding.

The province of Alberta has been collecting both harvest and aerial survey data on elk (*Cervus elaphus*) populations for many years. In Chapter 2, we used hunter harvest data to evaluate the success of current management interventions and to assess whether increasing large predator populations are influencing the overall hunter harvest. To do this, we examined trends in harvest, hunter success, and hunter effort between the years of 1995 and 2016. This chapter will be submitted for publication in the *Wildlife Society Bulletin*. In Chapter 3, we addressed the aerial survey data by looking at the limitations of the current monitoring method and suggested population reconstruction as an alternative that could increase both the quality and quantity of data gained. This chapter is prepared as a manuscript for publication in the *Journal of Wildlife Management*.

CHAPTER 2 – SUSTAINABLE ELK HARVESTS IN ALBERTA WITH INCREASING PREDATOR POPULATIONS

INTRODUCTION

During the past century, wildlife management in North America has been remarkably successful at restoring many wildlife populations, including elk (*Cervus elaphus*; Thomas & Toweill 1982). The reasons for the recovery of many wildlife populations have been captured by the North American Model of Wildlife Conservation (Organ et al. 2012b). One of the foundations for the North American model has been science-based management, yet, in practice, data frequently are insufficient or inadequately used for making management decisions (Artelle et al. 2018; Artelle 2019).

An approach for injecting science into wildlife management decision-making is the use of adaptive management whereby management manipulations, e.g., harvests, are modelled; the harvest is then manipulated, and population response is documented by monitoring. After comparing results of manipulation by population monitoring, the original model can be revisited and adjusted according to data. This process is iterated, gradually increasing the precision and accuracy of harvest-model predictions (Walters 1986).

In Alberta and several other jurisdictions in western North America, elk population monitoring has been done predominately by aerial surveys (Allen et al. 2008). However, the cost is high and, as a consequence, aerial ungulate surveys are conducted infrequently, typically only once every 10 years (Boyce et al. 2012). Nearly 80% of wildlife agencies across Canada and the United States collect data on harvest (Artelle et al. 2018; Artelle 2019), however, oftentimes these data are not sufficiently evaluated, with the connection between intervention and outcome going unexplored (Yoccoz et al. 2001).

Objectives for elk management are usually to ensure sustainable harvests. With few data available for setting regulations and quotas, management typically maintains consistent levels unless something appears to have gone wrong, e.g., a sharp decline in harvests or anecdotal field reports by biologists and hunters. Also, trends in harvests are supported by occasional aerial surveys. Elk harvests in Alberta are mostly regulated by harvests under General or Special licenses. General harvests, also known as Open Entry Harvests, do not limit the number of hunters who can hold this license type, but they are controlled with antler-point-restrictions (APRs) that target specific age and sex classes (Wallingford et al. 2017). In Alberta there are only 3-point (elk having an antler that has two tines that are 3 inches or greater projecting from a main beam) and 6-point minimum (elk having an antler that has at least five tines that are 3 inches or greater projecting from a main beam) APRs. General harvests with APR's may limit survival of bulls in older age classes (Bender and Miller 1999; Bender 2002), but they offer maximum hunter yields and protect the reproductively significant cows and breeding-capable subadult males (Prothero et al. 1979). Special harvests, also known as Limited Entry Harvests, restrict the number of hunters who can participate by limiting the number of licenses to achieve a quota of antlerless elk. By limiting licenses sold, Special harvests can limit hunter yields, but by allowing removal of females these licenses offer wildlife managers better control over the elk harvested than with General harvests of branch-antlered males.

Due to recent conservation efforts, large carnivore populations have been increasing in many western states and provinces in North America. For example, in Alberta grizzly bear (*Ursus arctos*; Morehouse and Boyce 2016), cougar (*Puma concolor*; Knopff et al. 2014) and wolf (*Canis lupus*; Robichaud and Boyce 2010) populations have been increasing, as have damage claims on livestock depredation (Morehouse et al. 2018). A common belief about increasing large predator populations is that they compete with hunters by decreasing ungulate populations through additive mortality (National Research Council 1997; Meadow et al. 2005; Jacques and Van Deelen 2010; Clark et al. 2014), thereby resulting in decreased hunter harvest and hunter success.

Societal goals in the form of hunter satisfaction often accompany the biological goals of a wildlife agency (Decker et al. 1980). Aggregate hunter satisfaction can be difficult to measure because what one hunter views as a satisfactory hunt might not be for a different hunter. For example, hunter age and lifetime hunting experience (Hazel et al. 1990), hunter to hunter interaction and viewing harvestable wildlife (Gigliotti 2000), trophy characteristics (Decker et al. 1980; Montieth et al. 2018), and species of the hunted animal (Hazel et al. 1990) can influence perception of a satisfactory hunt. Quantifiable measures of satisfaction commonly collected by wildlife agencies include hunter success and hunter effort (Heberlein and Kuentzel 2002; Skalski et al. 2007), with success being defined as the successful harvest of the target species and hunter effort defined as the number of days spent hunting.

Like many agencies in the study by Artelle et al. (2018), Alberta has collected hunter harvest and success data for elk but has not evaluated the province's regulatory results and trends with the growing predator populations in mind. Therefore, our objective was to assess the results of Alberta's hunter harvest, hunter success, and hunter effort in relation to the rising predator populations within the province. We envisage 2 questions that can be answered from an analysis of these hunter-harvest data: (1) has harvest management been sustainable? And (2) have elk harvests declined as a consequence of increasing large predator populations in Alberta? To evaluate the trend in hunter harvest and hunter success, we examined harvest data from 1995 to 2016 collected by the Alberta Environment and Parks (2018) (AEP), and compared trends in these data with occasional aerial survey data. Because of increases in all three of Alberta's large predator populations, we expected a negative trend in total hunter harvest and success.

STUDY AREA

For purposes of wildlife management, the province of Alberta is divided into Wildlife Management Units (WMU), legislatively recognized areas of land (Figure 1) for which harvest regulations are designated. There are currently 189 WMUs in Alberta and 148 of those have regulated elk harvests. WMUs throughout the province have gone through many border adjustments over time, resulting in more WMUs currently than in the past. However, during the time frame of our study (1995-2016) WMU's have remained mostly constant. WMU's can be grouped into larger Zones that coarsely mimic the natural ecological regions and sub-regions of Alberta (Natural Regions Committee 2006). These 5 zones include the Prairie (Zone 1), Parkland (Zone 2), Foothills (Zone 3), Mountain (Zone 4), and Northern Boreal WMU's (Zone 5) (Table 1). Hunting is prohibited in Jasper, Banff, Waterton Lakes, and Wood Buffalo national parks as well as many provincial parks and recreation areas. Areas with no licensed hunter harvests have been excluded from this study.

METHODS

Harvest Estimates

We obtained data on estimated elk harvests from 1995-2016 from AEP (Alberta Environment and Parks 2018). All estimates were based on hunter responses to harvest surveys that were delivered post-harvest to people who bought a license, although survey method varied over the years. From 1995 to the early 2000s, surveys were delivered to hunters by post or by telephone. In the mid to late 2000s, the AEP shifted to a combination of email and mail-in surveys that have persisted. No harvest estimates are available prior to 1995. Presently, hunters are encouraged, but not required, to complete post-harvest surveys; this has resulted in a degree of non-response. The AEP has accounted for this non-response by using the results of the hunters who did respond and extrapolating to the remaining hunter population. This assumes that the proportion of harvest success among hunters who responded is the same as those who did not respond and that the surveys are representative of Alberta's actual hunter harvest and success. Harvest surveys record if a hunter was or was not able to hunt and if they hunted, the total number of days that they spent hunting. The surveys also ask whether the hunt was successful or not; if the hunt was successful, information about what class of animal was harvested (e.g. bull, cow, or juvenile) and in which WMU is collected. Hunter success within individual WMUs is then used in a 5-year average to help determine the number of Special licenses to be issued for the next harvest.

Trend Estimates

We digitized the annual regulatory history for each WMU, as well as beginning and end dates of each harvest season into a spreadsheet using regulation guides from 1970 to 2016. We included estimated elk harvest and hunter success for each WMU from the harvest surveys between 1995-2016 (Alberta Environment and Parks 2018) to link elk harvested to their respective General and Special regulations. Lastly, we applied the respective Zone designation (1-5) to each WMU.

We used linear regression to estimate trends and Spearman rank to assess correlation between hunter harvest and success across time for both General and Special harvests.

RESULTS

Regulations

Before 1973, regulations in Alberta allowed harvest of both antlered and antlerless elk during General seasons (Alberta Government 1970-2016). Between 1973 and 1987 the first antler point-based system, a 5-point antler minimum General season, was introduced and was replaced in

1988 with either a 6-point or a 3-point resident/6-point nonresident General season. Over the next few years, all WMUs independently lost the resident and nonresident General harvest designations and became solely 6-point or 3-point General seasons. To limit the cow harvest, in 1975, the antlerless General season became either an Archery-Only General season or a quota-harvest Special season and has remained that way since.

Harvest: Temporal and Spatial

During our study period, in total, 100,290 elk were harvested in Alberta during General and Special seasons (Table 2). While both harvest types resulted in approximately 50,000 elk each, the composition of harvest under each regulation type was different, with General harvests being primarily bulls and Special harvests being primarily cows and calves.

The number of elk harvested provincially, for both General and Special harvests, has trended upwards indicating that harvests were sustainable (Figure 2). The average harvest in General seasons increased by 3.62% annually, with a ranked correlation between harvest and year, $r_s = 0.61$. The harvest in Special seasons increased by 9.74% annually, with a high ranked correlation between harvest and year, $r_s = 0.96$.

Across all years of analysis, of the five natural regions, Zones 3 and 5 contained most of the total elk harvests with 30,665 (65.0%) and 6,824 (14.5%) elk respectively for General seasons and 29,558 (55.5%) and 10,758 (20.2%) elk, respectively for Special seasons (Table 1). Hereafter the zones differed in their descending order by harvest type. Zones 2, 4, and 1 accounted for 5,570 (11.8%); 3,915 (8.3%); and 221 (0.5%) elk, respectively in the total General elk harvest, while Zones 1, 2, and 4 accounted for 5,584(10.5%); 4,465 (8.4%); and 2,860 (5.4%) elk respectively, in the total Special season harvest.

Hunter Success and Effort: Temporal and Spatial

The mean annual hunter success rate was 8.8% and 33.1% for the General and Special seasons, respectively, each trending upwards over time (Figure 3). General season hunter success increased by 0.003 annually, with a significant correlation between hunter success and year, r_s = 0.67. For Special seasons, hunter success increased by 0.004 annually, reflected by a ranked correlation between hunter success and year, r_s = 0.52. These trends in hunter success were not attributable to changes in hunter effort because we found no significant correlation between hunter effort and year (r_s= 0.29, $P > 0.05$; Figure 4).

For the five natural regions, Zone 1 had the highest mean hunter success for both General (12.7%) and Special (51.0%) seasons (Table 1). Hereafter the zones differed in their declining order by harvest type. For General seasons, mean hunter success declined in order of Zone 5 (10.9%), 2 (9.9%), 3 (7.7%), and 4 (4.3%). For Special seasons, mean hunter success declined in order of Zone 3 (34.2%), 2 (33.6%), 5 (29.4%), and 4 (22.6%).

DISCUSSION

Although the AEP has not evaluated how elk hunter harvest and hunter success has changed in recent years, evidence indicates that their harvest policies have been sustainable, and have resulted in positive trends over time. Also, continued increases in hunter harvest have been sustained despite increasing large predator populations. Although we found some limitations of the data, e.g., missing harvest records for 2008 when post-season survey methods changed, we nevertheless found consistent trends throughout the data. The annual number of elk hunters also has increased since 1995 for both General and Special harvests (Alberta Environment and Parks 2018). With a rise in the number of hunters from 17,045 in 1995 to 31,641 in 2016 for General-season harvests and 2,003 in 1995 to 12,959 in 2016 for Special-season harvests (Alberta

Environment and Parks 2018), an increase in both elk harvested and hunter success, and no significant change in elk hunter effort, data suggests that Alberta's elk populations are increasing. This is also consistent with the few aerial surveys that have been conducted across the province.

From 1995 to 2016, the General harvest also contained most of the bull harvest, while the Special harvest was mostly antlerless elk. In ungulate herds, the bull demographic tends to have relatively little consequence for overall recruitment of the herd (Bender et al. 2002; Mysterud et al. 2002; Bishop et al. 2005). For example, in elk, sex ratios can be as skewed as 1 bull for every 25 cows, before reproductive performance is negatively influenced (Haigh and Hudson 1993; White et al. 2001). This allows Alberta to manage its bull elk with minimum point General harvest strategies that are implemented to protect cows and juveniles while still maintaining hunter opportunity (Biederbeck et al. 2001). We also found that Special harvests are primarily being used by wildlife managers to target reproductive females and juveniles (Bender et al. 2002; Mysterud et al. 2002; Bishop et al. 2005). These limited-quota licenses are allotted to hunters in limited numbers to keep removals moderate. However, in areas having conflicts with agriculture, antlerless removals can be used to reduce herd size (Giles and Findlay 2004; Hegel et al. 2009; Wallingford et al. 2017).

Although both total elk harvested and predator populations are increasing provincially within Alberta, a single exception can be found in Zone 4, the Mountain WMUs. Here the total elk harvest declined -4.07% annually from 1995-2016. When compared to Zone 3 where harvests have increased by 4.78%, the adjacent Zone to the east, there was a significant difference in average trend of harvest ($P < 0.05$). We suspect this is because Zone 4 is where most of Alberta's grizzly bears are located (Stenhouse et al. 2015, Alberta Environment and

Parks 2016, Morehouse and Boyce 2016, Boulanger et al. 2018), which have been shown to be associated with high mortality rates in juvenile elk in the Rocky Mountains (Barber-Meyer et al. 2008, Griffin et al. 2011). Knowing that the grizzly bear population has been increasing (Stenhouse et al. 2015, Alberta Environment and Parks 2016, Morehouse and Boyce 2016) thereby reducing recruitment (DeCesare et al. 2012), combined with hunter harvests focused predominately on the most reproductive elk within the herd (Wright et al. 2006), a decline in elk populations and total harvest in mountain WMUs is not unexpected.

The ruggedness of terrain and thickness of vegetation reduces hunter access by increasing effort required by the hunter and decreasing the visibility of the prey animal (McCorquodale et al. 2003; Lebel et al. 2012), whereas road access can increase densities of hunters (Gratson and Whitman 2000). Separating WMU's by natural region allowed us to examine the relationships between landscape and habitat and hunter harvest and success. The landscapes and vegetation among the 5 natural regions vary from mountains to plains and trees to grasslands. As an example of how topography and habitat might affect hunter success and harvest, the open, grassy-plains habitats of the Prairie Zone (Zone 1) had the greatest annual mean hunter success rate yet having the lowest total harvest for both General and Special seasons. High hunter success can be explained by the high visibility for hunters, which limits the ability of elk to escape (Lebel et al. 2012). While most of the elk harvest in this Zone comes from its Limited Entry Harvest, low numbers also can be explained by the limited vegetation cover and flat terrain, which provide little habitat security leaving few elk left for harvest (McCorquodale et al. 2003). The Foothills (Zone 3) is characterized by rolling hills and mixed forests where more elk were harvested than all the other Zones combined. This area provides optimal habitat for elk with a balance of habitat security and forage in the form of tree patches and grasslands, and it encompasses many known areas of migration for some of Alberta's major elk herds (Benz et al. 2016; Eggeman et al. 2016; Paton et al. 2017; Prokopenko et al. 2017).

Long-term monitoring programs by wildlife agencies are often justified for informing stakeholders (Campbell and Mackay 2009), avoiding conflicts (Artelle et al. 2018), and for evaluating the results of management interventions to improve techniques (Nichols and Williams 2006; McDonald-Madden et al. 2010). This study highlights the importance of evaluating the results of monitoring data such as harvest surveys, despite a paucity of data about population size. Greater detail about trends in abundance could be obtained by increasing the frequency of aerial surveys (Allen et al. 2008) or by conducting surveys of hunter observations (Ericsson and Wallin 1999; Solberg and Saether 1999; Boyce and Corrigan 2017). Although aerial surveys of elk in Alberta have been too infrequent to provide adequate monitoring, when combined with trends in harvests distributed among WMUs, clearly Alberta's harvest management is sustainable. Despite increasing numbers of elk hunters and large carnivores in Alberta, both the number of elk harvested and hunter success has been increasing throughout the province except in mountain WMUs (zone 4).

MANAGEMENT IMPLICATIONS

Increasing harvests and abundance of elk (Chapter 3) indicates that the AEP is managing elk herds sustainably throughout the province. Further, we found that increasing large predator populations, does not necessarily mean a loss to prey populations. If habitats are sufficient to support a larger prey population, then the prey population may be able to support a larger population of predators (Errington 1967; Morehouse et al. 2018). For example, Walters et al. (1981) found that as prey populations increased, wolf territory size decreased, leaving more room for additional wolf packs. Nevertheless, a growing elk population might be cause for concern for management of other ungulates. In recent years, Alberta's elk, moose, and deer populations have increased because of early successional habitats created by industrial development, but woodland caribou (*Rangifer tarandus caribou)* populations have been in decline (Hervieux et al. 2014; Knopff et al. 2014). These changes have been linked to increasing predator populations, such as wolves and cougars, for which population trends have been subsequently linked to Alberta's increasing populations of alternative prey. Known as apparent competition (Holt and Lawton 1994), a possible additive effect on the decline of the woodland caribou could be that some ungulate populations are growing substantially enough that they are indirectly causing a decline of woodland caribou. This has led some to speculate that closer management of these increasing ungulate populations may need to be considered when trying to manage predators that are negatively affecting at-risk ungulate populations (Latham et al. 2011). However, despite inadequate data and flaws in the Alberta data-archiving system, elk are thriving, and harvest management has been adequate to ensure viable and sustainable herds of elk throughout the province.

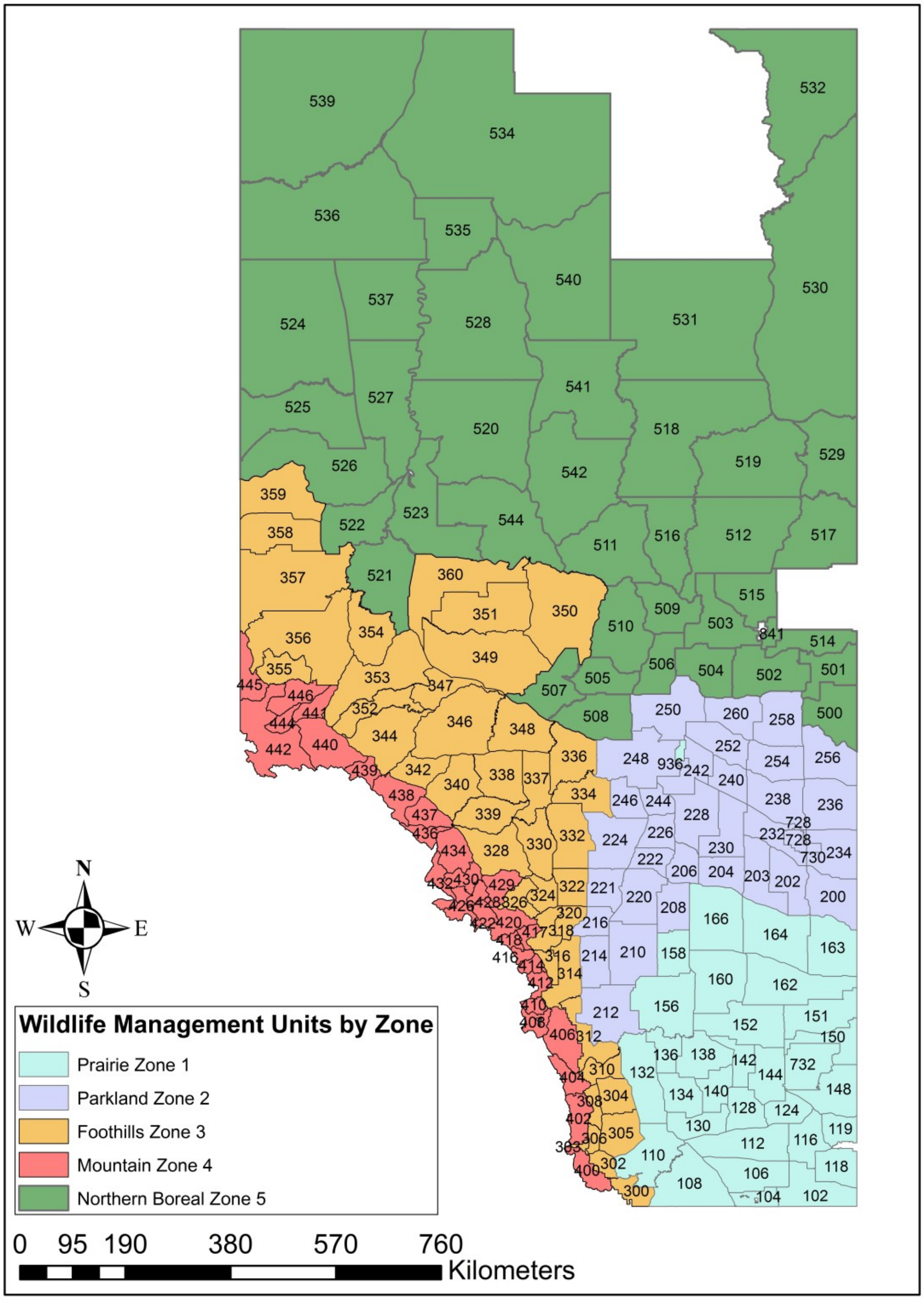

Figure 1. Wildlife Management Units of Alberta, Canada by Wildlife Management Area/Zone. Jasper, Banff, Waterton Lakes, and Wood Buffalo National Parks and provincial parks and recreation areas are not included as part of the WMU system.

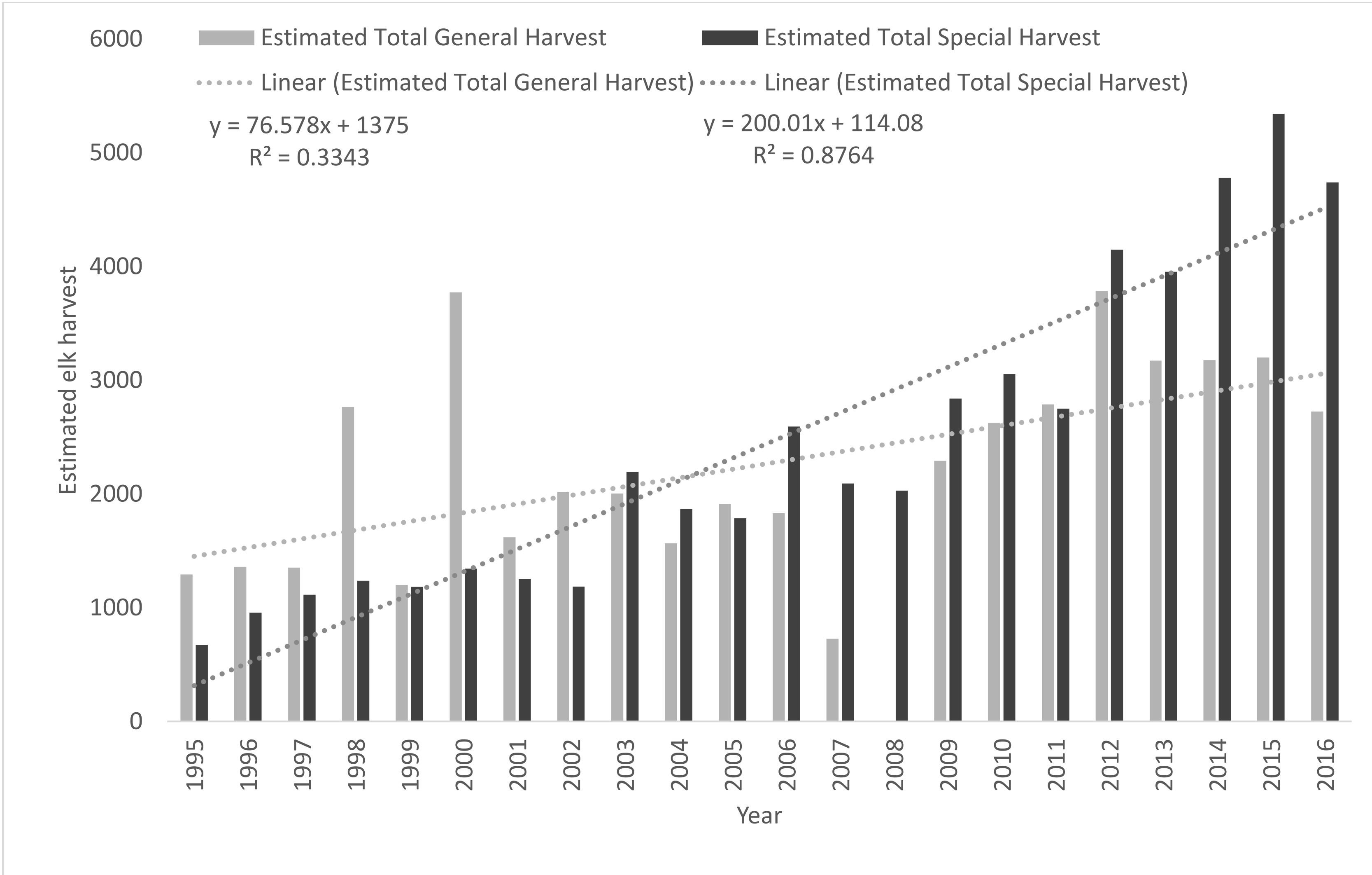

Figure 2. The total estimated elk harvest in Alberta by year for General and Special harvests from 1995 to 2016 across all wildlife management units.

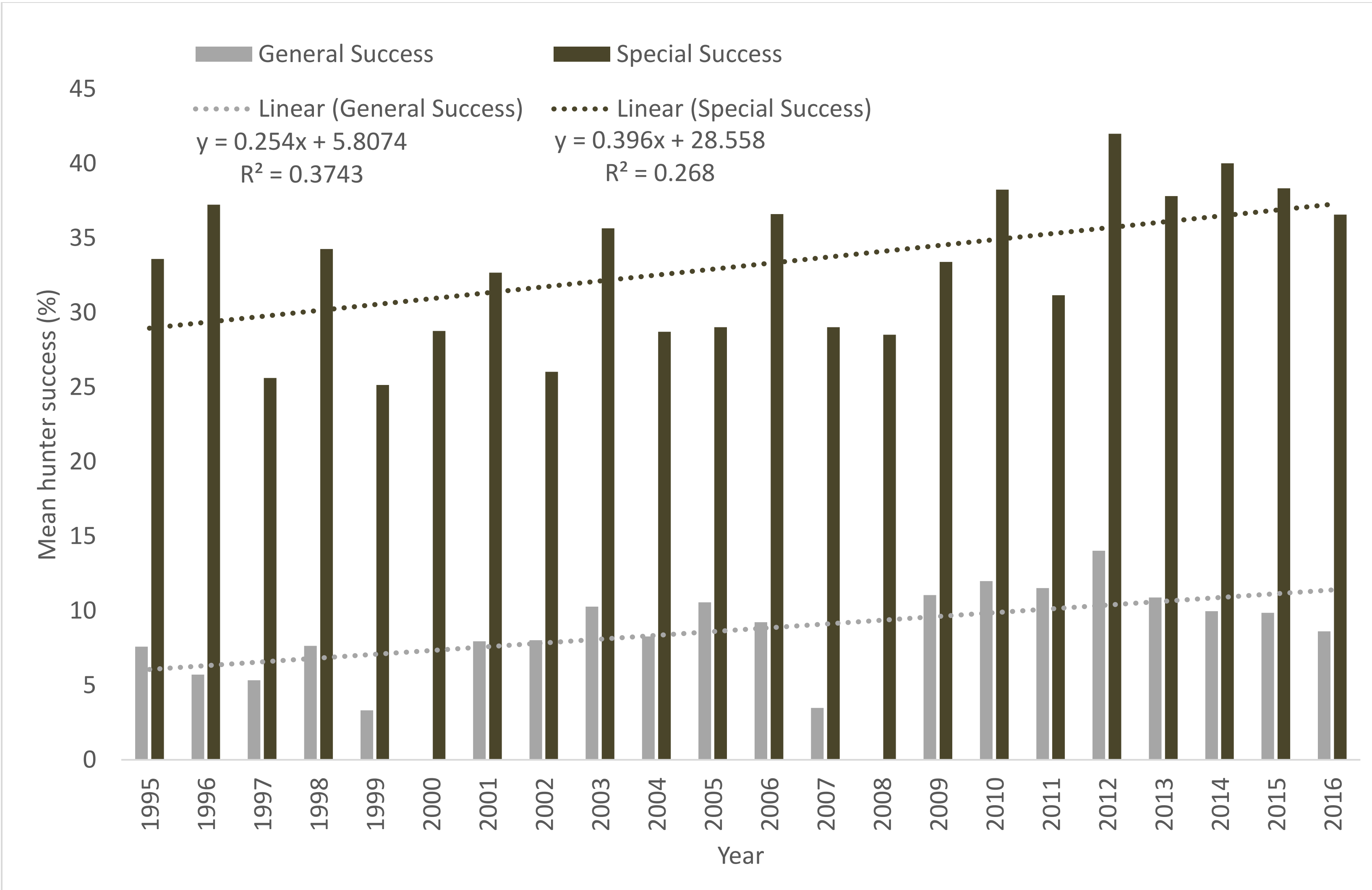

Figure 3. Mean annual hunter success (%) for General and Special elk harvests in Alberta from 1995 to 2016 across all wildlife management units.

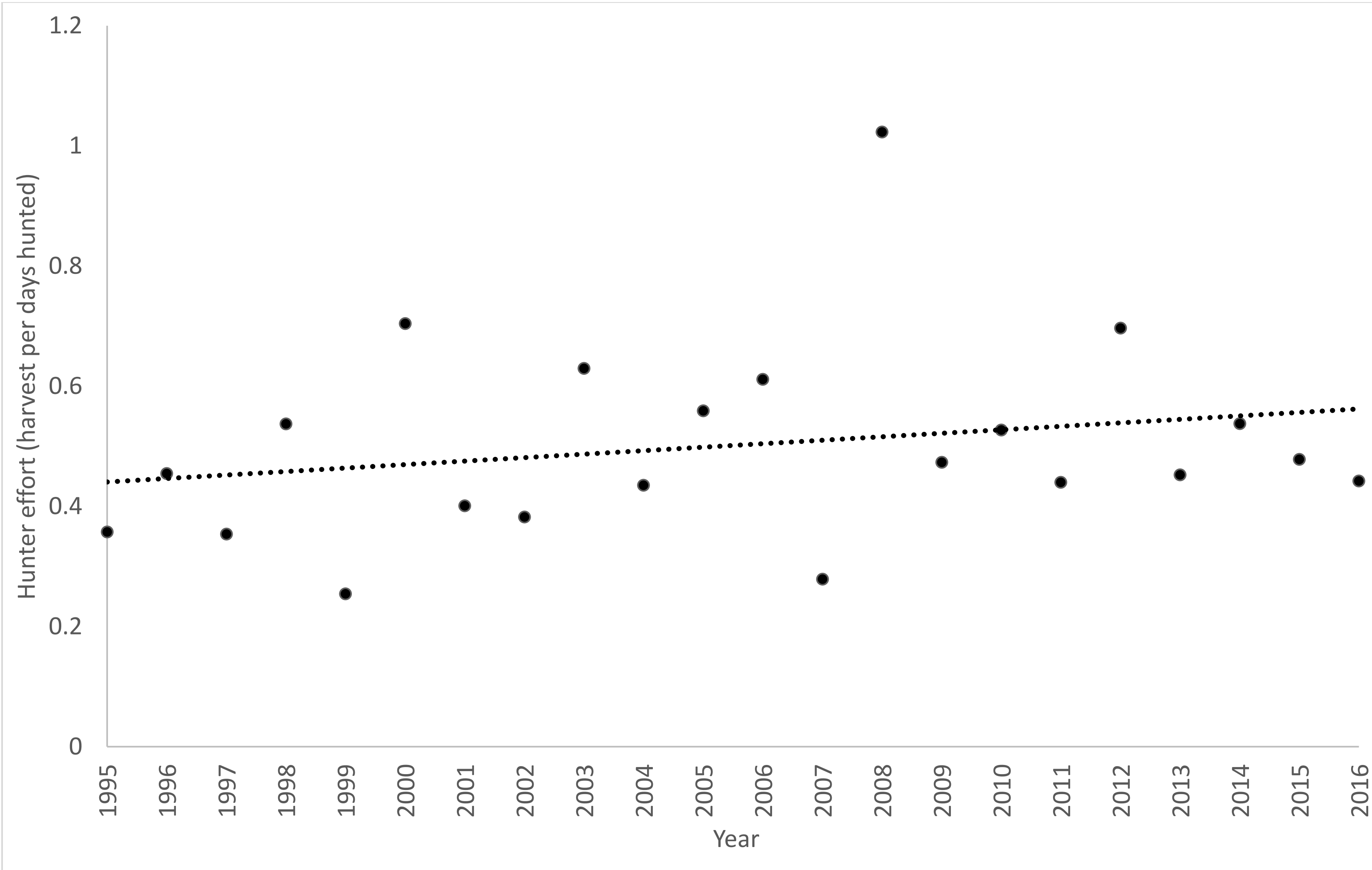

Figure 4. Annual hunter effort (total harvest per number of days hunted) for Alberta's licensed elk hunters from 1995 to 2016. We found no significant temporal trend in hunter effort ($P > 0.05$).

Table 1: Alberta's 5 Zones separated by Natural Region, defining characteristics, and total elk harvest and hunter success. For a more detailed description of each Zone, use the Natural Regions and Subregions of Alberta (Natural Regions Committee 2006).

Zone and WMU's	Natural Region/km^2	Defining Characteristics	Total Harvest (H) and Annual Hunter Success (S) by Season	
			General	Special
Zone 1: Prairie WMU's - **100 series** - **732**	Grassland Natural Region - 95,565 km^2	- Level plains and rolling hills - Mixed grasses - Few rivers and lakes	- H: 221 - S: 12.7%	- H: 5,584 - S: 51%
Zone 2: Parkland WMU's - **200 series** - **728,730, & 936**	Parkland Natural Region - 60,747 km^2	- Rolling hills - Grasslands and aspen stands - Mostly cultivated	- H: 5,570 - S: 9.9%	- H: 4,465 - S: 33.6%
Zone 3: Foothills WMU's - **300 series**	Foothills Natural Region - 66,436 km^2	- Rolling hills to mountainous - Mixed forests	- H: 30,665 - S: 7.7%	- H: 29,558 - S: 34.2%
Zone 4: Mountain WMU's - **400 series**	Rocky Mountain Natural Region - 49,070 km^2	- Mountainous, deep valleys, elevated meadows - Mixed forests, open grasslands, barren mountain tops	- H: 3,915 - S: 4.3%	- H: 2,860 - S: 22.6%
Zone 5: Northern Boreal WMU's - **500 series** - **841**	Boreal Forest Natural Region - 381,046 km^2 Canadian Shield Natural Regions - 9,719 km^2	Boreal Forest - Flat plains and rolling hills - Mixed forests - Numerous wetlands Canadian Shield - Rolling hills of exposed bedrock - Forests where possible - Lichens, mosses, and ferns	- H: 6,824 - S: 10.9%	- H: 10,758 - S: 29.4%

Table 2: Total number of elk harvested by regulation type in Alberta, Canada from 1995-2016.

Regulation	Bulls	Cows	Juveniles	Total Elk / Regulation
General (including General Archery)	43,043 (91%)	3,605 (8%)	529 (1%)	47,177 (100%)
Special (including Special Archery)	4,939 (9%)	41,997 (79%)	6,177 (12%)	53,113 (100%)
Total Elk / Class	47,982	45,602	6,706	100,290

CHAPTER 3 – ESTIMATING ELK POPULATION PARAMETERS USING POSTSEASON HERD CLASSIFICATIONS AND RECONSTRUCTION

INTRODUCTION

Ungulates are often priority targets of monitoring programs because of their high economic value to society and their importance within ecological systems (Ripple et al. 2015; Schuette et al. 2018). One of the most common methods of data collection for ungulate population monitoring is aerial surveying (Samuel et al. 1987; Bender et al. 2003; Allen et al. 2008; Schuette et al. 2018). Highly regarded for covering large areas in relatively short amounts of time, aerial surveys provide managers a way to collect demographic and population status data on ungulate herds (Boyce et al. 2012; Greene et al. 2017). However, this method has several limitations, such as the need for optimal flight conditions, biases associated with sightability (Caughley 1974; Samuel et al. 1987; Eberhardt et al. 1998; McCorquodale 2001; Gilbert and Moeller 2008), and the high monetary cost (Pettorelli et al. 2007; Boyce et al. 2012; Greene et al. 2017).

Due to the costs of flights, time between consecutive aerial surveys usually extends beyond 10 years for both moose (*Alces alces*; Boyce et al. 2012) and elk (*Cervus elaphus*; present study) in Alberta, Canada. Large gaps in time between surveys diminishes the value of monitoring because they constrain a manager's ability to evaluate outcomes of interventions, which is a fundamental step in adaptive management (Organ et al. 2012a). Adaptive management is an iterative process in which wildlife managers learn from the results of their interventions through monitoring and then improve upon those interventions with that gained knowledge (Walters 1986; McDonald-Madden et al. 2010; Organ et al. 2012a). Lack of funding is in fact a common source of failure for intensive monitoring programs (Singh and Milner-Gulland 2011) and inhibits true adaptive management because wildlife agencies often only have the budget to implement the management strategy, but not the monitoring to evaluate the strategy (White 2001). Or after monitoring is completed, agencies often fail to perform a follow-up rigorous evaluation resulting in "surveillance monitoring" (i.e., monitoring for the sake of monitoring; Nichols and Williams 2006).

An alternative method for monitoring ungulate populations are ground surveys. This method is typically less costly than aerial surveys (Singh and Milner-Gulland 2011; Schuette et al. 2018), which allows them to be done on a more consistent basis. In addition, managers can survey areas too dangerous for flights and more easily assess animal classification (Singh and Milner-Gulland 2011; Greene et al. 2017). However, because ground surveys are often unable to evaluate large areas in a timely manner, this method tends to focus on assessing herd sex and age demographics.

Surveys of sex and age ratios are much more attainable than total population counts and have long been used to evaluate population parameters in wildlife populations (Kelker 1940; Allen 1942; Hanson 1963). Ratios can be used to estimate population demographics such as recruitment and growth (Bonenfant et al. 2005; Harris et al. 2008; DeCesare et al. 2012), or can be implemented, alongside other variables, into models that estimate abundance (Millspaugh et al. 2009; Skalski et al. 2012b). Population reconstruction models typically require herd ratios that are representative of the population, along with harvest data and mortality rates, to estimate animal abundance (Allen 1942). Most wildlife agencies in North America collect these data using hunter harvest surveys and aerial/ground composition counts. Such models have been applied to several species including moose (Fryxell et al. 1988), elk (Gove et al. 2002), greater sage-grouse (*Centrocercus urophasianus*; Broms et al. 2010), sika deer (*Cervus nippon*; Ueno et al. 2010), black-tailed deer (*Odocoileus hemionus*; Skalski et al. 2012a), and wild turkey (*Meleagris gallupavo*; Clawson et al. 2015).

The population reconstruction model that we use has been developed for elk to estimate herd size and herd demographics (bulls, cows, and juveniles) using demographic ratios (cow/bull, juvenile/cow) obtained before harvest (i.e. preseason), and harvest data (Bender and Spencer 1999). However, despite the utility of the model, preseason herd ratios often cannot be estimated reliably; though postseason ratios can be obtained when elk are found on winter ranges (i.e., postseason; Smith and McDonald 2002; DeCesare et al. 2012). Therefore, our objective is to propose a method to find preseason herd ratios using postseason counts, and facilitate the reconstruction and estimation of elk population size using data that most present-day agencies collect (Artelle et al. 2018). To demonstrate the method, we have combined our models and those developed by Bender and Spencer (1999) to estimate elk population size for a Wildlife Management Unit (WMU) in southwestern Alberta over the last 4 years.

STUDY AREA

Our elk study focused on Wildlife Management Unit (WMU) 302 (708.53 km^2), in the Foothills region of southwest Alberta, Canada (Figure 5). A WMU is a legislatively recognized area of land with specific harvest regulations. For WMU 302, regulations for elk harvest include a 3-point/Antlerless General Archery season, a 3-point General season, and an Antlerless Special season. With the fiscal year beginning with the harvest season in the fall, a year designation hereafter indicates the fiscal year (not a calendar year) unless stated otherwise. There is also Indigenous harvest, however, this is usually unknown and not a recorded part of the harvest estimate. Land ownership within WMU 302 is a combination of public and privately-owned land, but most is private (82%). Climate is characterized by cold, dry winters and warm, dry summers, with the average annual temperature and precipitation being around 1.7 °C and 600 mm, respectively (Natural Regions Committee 2006). Topography is variable but is generally composed of rolling hills and some mostly flat meadows on the easternmost side that gradually get rougher further west. WMU 302, it is bordered by mountain WMUs to the west, prairie WMUs to the east, and the continuation of foothill WMUs to the north and south. Vegetation is characterized as a combination of large wooded patches of either mixed-wood or deciduous trees and grasslands. Other large wild herbivores in the area include mule deer (*Odocoileus hemionus*), white-tail deer (*O. virginianus*), pronghorn (*Antilocapra americana*), moose, and bighorn sheep (*Ovis canadensis*). Natural predators of elk in the area include American black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), wolves (*Canus lupus*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*). The livestock in this region are predominately cattle and horses.

METHODS

Ground Classification

In WMU 302, we conducted postseason ground classification surveys 2 days per week, weather permitting, sunrise to noon (4-5 hours), from 3 February 2018 to 16 March 2018. Using a route established around documented winter ranges, we surveyed for approximately 32 total hours, excluding days when winter weather halted our efforts. Winter counts were used because snow at higher elevations cause a winter migration of the elk out of the mountains and into more accessible winter ranges (Killeen et al. 2014). We classified juveniles and cows according to morphological characteristics (following Smith and McDonald 2002). By surveying during February and early March, we were able to classify bulls before they lost their antlers. These counts followed the last hunter harvest, which allowed us to estimate the minimum annual population (Daniels 2006). To choose the best sampling day, we selected the day with the lowest sampling error which was measured using the binomial component of sampling variance

$$Var(P_i) = P_i(1 - P_i)/n_i$$

where P_i is the proportion of class i (e.g. bulls, cows, or juveniles) and n_i is the sample size of class i (Kelker 1940). All observations were done with binoculars and spotting scopes; elk were classified as bulls, cows, and juveniles. Cows (females >1 year of age) and juveniles (elk <1 year of age) were distinguished by criteria set forth by Smith and McDonald (2002). Bulls were further subcategorized by antler points (e.g. spike, 3-point, 5-point, and 6-point) (Bender and Miller 1999). We also recorded date, time, temperature, wind direction and speed, cloud cover, visibility (e.g. low clouds, fog, snow), snow cover, location (UTMs), slope and terrain characteristics, herd activity, and observers.

Reconstruction

The most-recent aerial survey for WMU 302 was conducted by the Alberta Environment and Parks (AEP) on February 21st, 2015. Transects were flown to record females, juveniles, and bulls, categorizing bulls by antler points when possible and classified antler size as small, medium, and large when it was not possible. If the category of animal was unclear, they were listed as unknown. The local biologists consider the aerial survey results to be minimum population estimates due to the knowledge of elk winter-range locations (Allen et al. 2008). We therefore used this count as a proxy for abundance. Because 82% of the 1,128 elk found in this aerial survey were listed as unknown, we assumed that the composition of the elk herds found during the aerial surveys were of a similar composition as the herds that we classified during winter 2018 (e.g. male, female, and juvenile ratios; Alberta Environment and Parks 2018a). We justify this assumption because elk harvest regulations within WMU 302 have been constant since 1990 and because of the relatively short amount of time between 2015 and 2018.

Before reconstruction, preseason cows/bull ratios were estimated using the postseason ratios from our ground surveys by

$$R_{C/B} = r_{C/B}(1 - M_H) + M_H \left(\frac{H_C}{H_B}\right)$$

where $R_{C/B}$ and $r_{C/B}$ are the preseason and postseason ratio of cows/bull, respectively. M_H, H_B, and H_C are the bull harvesting rate and the number of harvested bulls and harvested cows, respectively. Preseason ratios of juveniles/cow were estimated using the postseason ratios from our ground surveys by

$$R_{J/C} = r_{J/C}\left(1 - \frac{H_C}{N_C}\right) + \frac{H_J}{N_C}$$

or

$$R_{J/C} = r_{J/C}(1 - M_C) + \frac{H_J}{N_C}$$

where $R_{J/C}$ and $r_{J/C}$ are the preseason and postseason ratio of juveniles/cow, respectively. H_J, N_C, and M_C are the number of harvested juveniles, the total number of cows; and the cow harvesting rate, respectively. Calculations for obtaining preseason ratios from postseason ratios are presented in Appendix 1.

We then estimated the preseason elk population size for 2014-2017 using the reconstruction model developed and validated by Bender and Spencer (1999):

$$N_1 = (H_B/M_H) * (1 + R_{C/B} + R_{C/B} * R_{J/C})$$

$$N_B = H_B/M_H$$

$$N_C = N_B * R_{C/B}$$

$$N_J = N_C * R_{J/C}$$

where N_1, N_B, and N_J are the total preseason elk and the number of bulls and juveniles respectively. Like Bender and Spencer (1999), we assumed that all bull mortality only came from hunter harvest, disregarding predation on bulls.

To find the number of bulls harvested (H_B) in WMU 302 for 2014-2017, we used bull harvest estimates by the AEP. These estimates were found using responses to harvest surveys that hunters completed either by mail or telephone after the elk harvest season is over (Chapter 2). Hunters are not required to fill out the surveys, therefore, once the responses are returned, the results provided by the hunters who did respond are then extrapolated to the remaining hunters who did not respond, giving an estimation of total harvest. This assumes that responding hunters carry the same proportion of harvest to non-harvest success as those who did not respond.

To estimate the bull harvest rate (M_H) of WMU 302, we estimated the total preseason bull population by summing the bull harvest (bulls taken during the harvest) and the estimated total bull demographic from the aerial survey results for the 2014 fiscal year (bulls remaining after the harvest). We then divided the estimated bull harvest (H_B) of 2014 by the preseason bull population. With 2014 being the only year for which we had a postseason population count, we assumed that bull harvest rate was constant through 2017.

To find sampling variance and standard deviation for the total preseason elk population (N_1), we used the expressions

$$V(N_1) = \left(R_{B/N1} - r_{B/N2}\right)^{-2}\left(N_1{}^2 * V\left(R_{B/N1}\right) + N_2{}^2 * V\left(r_{B/N2}\right)\right)$$

$$\sigma(N_1) = \sqrt{V(N_1)}$$

where $R_{B/N1}$ and $r_{B/N2}$ are the preseason and postseason proportion of bulls within the herd, respectively, and N_2 is the total postseason elk population (Seber 1973).

RESULTS

Based on our field composition counts, the date with the least sampling error was March 4th, 2018 (Table 3). Here we found 55 bulls, 261 cows, and 83 juveniles, resulting in postseason ratios of 0.32 juveniles/cow ($r_{J/C}$), and 4.75 cows/bull ($r_{C/B}$). Herd composition was 21% juveniles, 65% cows, and 14% bulls. Applying these composition data to the aerial survey from February 2015, we estimated that for the 1,128 postseason elk, there were 155 bulls, 738 cows, and 235 juveniles. During the 2014 hunt an estimated 101 bulls were harvested (Alberta Government 2018) and combined with the 155 bulls from the minimum population estimate aerial survey, this yields a preseason estimate of 256 bulls and a bull harvest rate (M_H) of 39% for the 2014 harvest season.

By annually updating our calculated preseason ratios of cows/bull ($R_{C/B}$) and juveniles/cow ($R_{J/C}$) and the number of bulls harvested (Alberta Government 2018), the population reconstruction for 2014 to 2017 estimated preseason herds to be 1,229; 993; 775; and 796 elk, respectively (Table 4).

DISCUSSION

Because wildlife agencies seldom have access to true population counts (Norton et al. 2013), having a method to estimate population size on a recurrent basis would greatly increase the quality and utility of monitoring efforts. Many wildlife agencies cannot afford annual aerial surveys to monitor their wildlife populations (Singh et al. 2011; Boyce et al. 2012). In our study area, for example, the most recent population monitoring efforts were aerial surveys done in the winters of 2006 and 2015. With 9 years between surveys, these efforts hold no real value in informing management about the effectiveness of the harvest, which is the key purpose of monitoring in adaptive management (Organ et al. 2012a). By using data from postseason ground classification and harvest, and applying our ratio modeling approach, we were able to estimate elk herd populations annually.

We used postseason surveys, conducting composition counts during the preseason or postseason are constrained by both feasibility and risks of sampling biases, which are associated to behavioral activities of the elk within the two seasons. In the past, the peak of the rut (preseason) has been considered the best time to perform elk surveys, based on the assumption that males would be more detectable with cow herds (Langvatn 1977). However, not only can peak rutting behavior differ between year and location (Ciucci et al. 2009) but can also vary between mature bulls and yearlings, with sexual activity occurring up to a month apart between age classes (Prothero et al. 1979). Because of this, Ciucci et al. (2009) and Jarnemo et al. (2017) warned that unless timing of the survey occurs at the actual peak of the rut, when bulls are most active and more likely to be counted, preseason results could be biased. Ciucci et al. (2009) further suggest that preseason ratios should not be used because of this bias. Additionally, preseason estimates are often not feasible for many wildlife agencies, because during this period elk herds are typically found in areas of restricted access and little visibility.

Although most wildlife agencies collect postseason ratios rather than preseason ratios (Clutton-Brock and Albon 1989; Smith and McDonald 2002; DeCesare et al. 2012), there are still risks associated with postseason counts. First, once the harvest season has begun, elk sometimes select for areas of poor access in an effort to avoid hunters (Ranglack et al. 2017). This avoidance behavior can limit an observer’s ability to assess composition immediately following the harvest. However, after the harvest is complete and elk are given time to acclimate to the absence of hunters, wintering aggregations can make it much easier to get respectable counts of adequate sample size (Czaplewski et al. 1983). Second, Bender and Spencer (1999) also cautioned against using true postseason ratios in their model because bulls are typically harvested at a higher rate than cows, and social behaviors often lead to a separation of bull and cow herds post-rut (Bender and Miller 1999; Bender et al. 2003). Not only does our postseason to preseason model take harvested elk into account, but our methodology surveys elk when they have aggregated on their winter ranges (Smith and McDonald 2002; DeCesare et al. 2012). Additionally, in our study area, elk wintering ranges were well documented (Killeen et al. 2014) and we found that both cow and isolated bull herds congregated prior to winter storms and remained together 3-4 days immediately after, before separating again (Pers. Obs.). Third, although sexual dimorphism facilitates identifying adult bull elk, juveniles and cows may be particularly difficult to classify. During the postseason, juveniles are almost one year old and nearly full grown, so proper training is necessary prior to collecting data (see Smith and McDonald 2002 for guidelines). Finally, winter severity may limit observations during some years. Snow depth can increase the movement of bulls to wintering ranges (i.e. if winter snow accumulation is not severe enough, bulls may not travel to wintering ranges), potentially causing a gender bias in favor of females in postseason ground classifications in years of low snow accumulation (Boyce 1989; Clutton-Brock and Albon 1989). However, because this method allows for annual counts rather than decadal counts, the impact of years with less than optimal snow accumulation could be decreased through an annual average.

We developed a model to convert postseason to preseason ratios to make use of an established reconstruction model, to take advantage of the concentrations of elk found on winter ranges, and to handle issues caused by rutting behaviors during the preseason (Ciucci et al. 2009;

Jarnemo et al. 2017). Our estimates were comparable to the most recent minimum population estimate based on the 2015 aerial survey and the population trend matches that found for hunter harvest (Chapter 2). Therefore, reconstruction can be a cost-effective population estimator, especially considering that most wildlife agencies already collect the necessary data (e.g. hunter harvest). Like Bender and Spencer (1999), we assumed that all bull mortality prior to classification is due to harvest, that mortality has remained constant, and that herd composition ratios have remained unchanged over the 4 years that we reconstructed. Although elk harvest regulations have remained constant since 1990 in our study area and we believe these assumptions to be acceptable, managers adopting these methods would be able to complete ratio assessments annually and increase the precision of the reconstruction. We also assumed in our models that harvest estimates by harvest surveys are representative of the actual harvest. This was done because currently harvest surveys are the only means to assess harvest in Alberta, however, in order to reduce sampling error, harvest estimates must be exact. Studies have shown that nonresponse to harvest surveys can impact their validity (Rosenberry et al. 2004; Lukacs et al. 2011) and Alberta is currently exploring mandatory harvest reporting to eliminate non-response as a factor (Anne Hubbs, AEP, pers. comm.).

Because most North American wildlife agencies have access to hunter-harvest data (Artelle et al. 2018), we believe that by using a combination of ground survey classification and our postseason to preseason ratio conversion model to obtain the necessary herd demographics for reconstruction would be widely applicable. Managers can then decrease their dependence on expensive aerial monitoring efforts, while allowing for population estimation on a more consistent basis. Alternatively, citizen science methods can be used to obtain observations of animals by hunters (Singh et al. 2014; Boyce and Corrigan 2017). These methods will benefit wildlife managers by allowing them to assess population trends, to evaluate the efficacy of harvest management, and ultimately to better implement true adaptive management (Organ et al. 2012a).

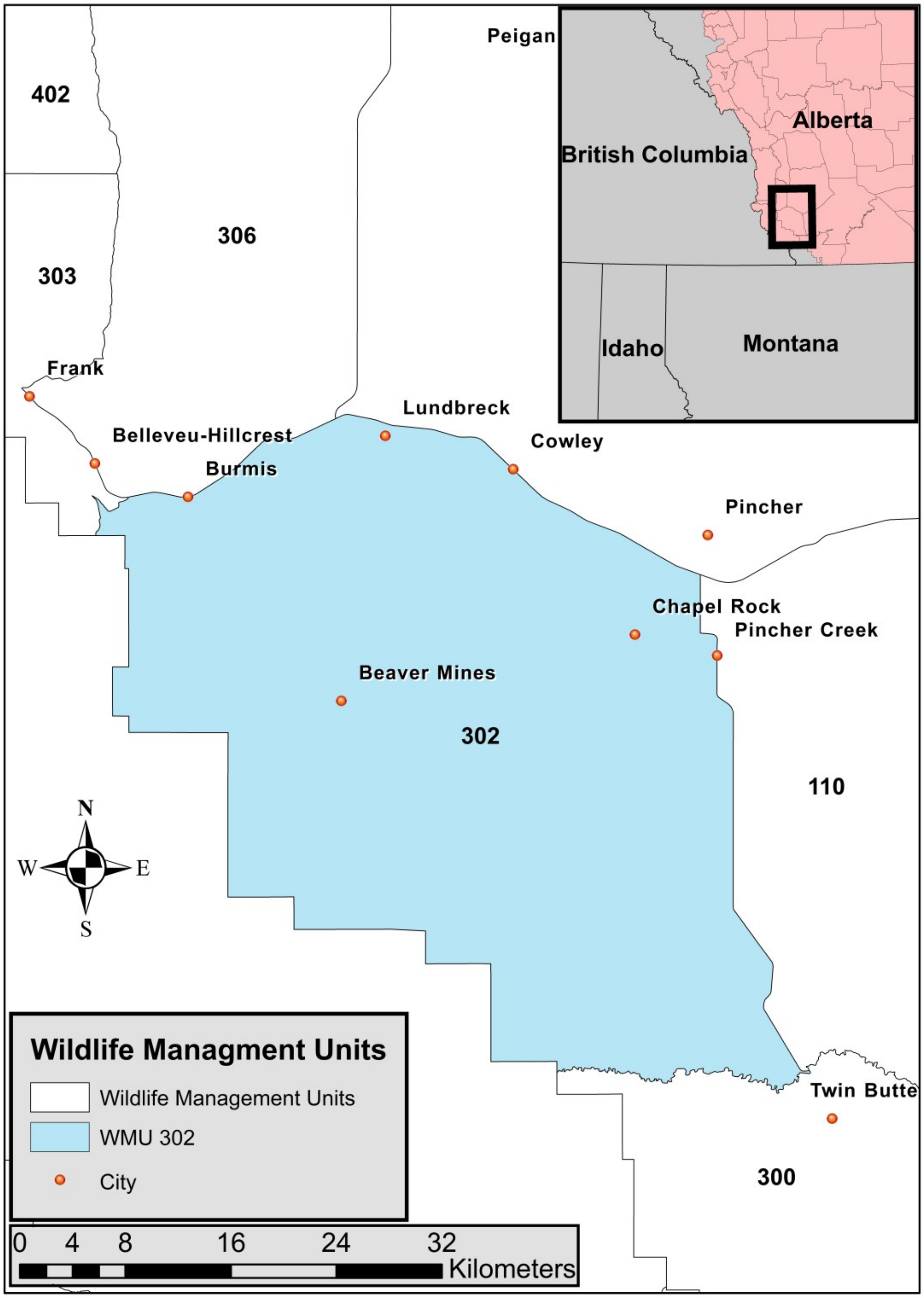

Figure 5. Location of Wildlife Management Unit 302 in southwest Alberta, Canada where ground classification of elk took place from February to March 2018.

Table 3. Sampling error by date per stage-class used to determine which date was most representative of the actual elk population in WMU 302 in southwestern Alberta, Canada, winter 2018. Data were from ground classifications, using the binomial component of sampling variance.

Sampling Date	**Sampling Error**		
	Juveniles	Cows	Bulls
February 9th	0.022644	0.009496	0.021914
February 16th	0.014167	0.003611	0.015556
March 4th	0.001985	0.000867	0.002161
March 9th	0.00221	0.000873	0.002381

Table 4. Preseason cow/bull and juvenile/cow ratios, population reconstruction estimates, and sampling variance for WMU 302 in southwestern Alberta, Canada. Ratio data were found using our postseason to preseason model and our ground survey results. Population estimates were found using the preseason ratios and Bender and Spencer's (1999) reconstruction model.

Year	$R_{C/B}$	$R_{J/C}$	Population Estimate	Sampling Variance (σ)
2014	2.88	0.32	1,229 (256 bulls, 738 cows, 235 juveniles)	259.21
2015	2.95	0.31	993 (204 bulls, 602 cows, 187 juveniles)	241.66
2016	2.88	0.33	775 (161 bulls, 463 cows, 151 juveniles)	208.01
2017	3.42	0.29	796 (147 bulls, 504 cows, 145 juveniles)	297.24

CHAPTER 4 – CONCLUSION

The common theme for both Chapters 2 and 3 is the importance of evaluating long-term monitoring efforts, while also making sure those efforts are of a quality that ensures that evaluation is possible. Long-term monitoring commitments in wildlife conservation are often justified by wildlife agencies because they allow managers to inform stakeholders (Campbell and Mackay 2009), avoid conflicts (Artelle et al. 2018), and for evaluating the results of management interventions to improve techniques (Nichols and Williams 2006; McDonald-Madden et al. 2010). The province of Alberta has been collecting hunter harvest and aerial survey data for many years but has fallen into the pitfalls of both surveillance monitoring (Nichols and Williams 2006) and not having the budget to implement an effective monitoring strategy (White 2001). These issues severely limit the value of each dataset within an adaptive management setting and constitute an assessment of the data.

In Chapter 2, by examining trends within the hunter harvest data that the Alberta Environment and Parks (AEP) collects annually, we found that increasing populations of grizzly bears (Morehouse and Boyce 2016), cougars (Knopff et al. 2014), and wolves (Robichaud and Boyce 2010) in Alberta are not causing a decline in the hunter-harvest of elk. In fact, we believe that because elk harvest, hunter success, and number of hunters have been steadily increasing over the past 22 years, along with no significant change in hunter effort, provincial elk populations may be increasing along with these predators. We hypothesize that elk populations may be increasing due to conservative harvests that mostly target the less reproductively significant bulls, however, future research would have to be done to definitively address that question. Additionally, we suggest an examination of the impact that increasing populations of elk have on at-risk species such as the woodland caribou. For example, increasing ungulate populations have been associated with increasing predator populations (Hervieux et al. 2014; Knopff et al. 2014), which in turn have been linked to a decline in woodland caribou populations (Latham et al. 2011).

In Chapter 3, we found that like many agencies, aerial survey data collected by the AEP, which is used to estimate elk populations, was severely limited by the cost to perform the flights. Using a specific Wildlife Management Unit as an example, we estimated the elk population using a combination of Chapter 2's hunter harvest data, ground surveys, and a reconstruction model developed by Bender and Spencer (1999). This method of population estimation allowed us to collect elk population estimates with significantly less cost than aerial surveys, while also accruing estimations on an annual basis.

In this thesis, I indicated the importance of thoroughly evaluating the results of long-term monitoring efforts using Alberta's elk harvest as a primary example. I also acknowledged the limited ability that decadal aerial population surveys have in informing wildlife managers of population trends. Therefore, I looked at an alternative method of estimating elk populations using a reputable reconstruction model that was previously inhibited by the type of data that wildlife agencies typically collect. I believe that wildlife agencies that may be struggling with similar situations, whether it be surveillance monitoring or budgetary restrictions, may be able to use these examples to their benefit and increase the quality of their long-term monitoring commitments.

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APPENDICES

APPENDIX 1. CONVERTING PRESEASON RATIOS TO POSTSEASON RATIOS

To find preseason cow to bull ratios from postseason cow to bull ratios, we used the expressions from Bender and Spencer (1999) for N_C and N_B:

$$r_{C/B} = \frac{N_C - H_C}{N_B - H_B}$$

$$r_{C/B} = \frac{\left(\frac{H_B}{M_H} * R_{C/B}\right) - H_C}{\frac{H_B}{M_H} - H_B}$$

$$R_{C/B} = r_{C/B}(1 - M_H) + M_H\left(\frac{H_C}{H_B}\right)$$

Where N_B, and N_C are preseason numbers of bulls and cows, respectively; H_B and H_C are the number of harvested bulls and cows, respectively; M_H is the bull harvesting rate; and $R_{C/B}$ and $r_{C/B}$ are the preseason ratio of cows to bulls and the postseason ratio of cows to bulls, respectively.

To find preseason juvenile to cow ratios from postseason juvenile to cow ratios, we used the expressions from Bender and Spencer (1999) for N_J and N_C:

$$r_{J/C} = \frac{N_J - H_J}{N_C - H_C}$$

$$r_{J/C} = \frac{\left(N_C * R_{J/C}\right) - H_J}{N_C - H_C}$$

$$R_{J/C} = r_{J/C}\left(1 - \frac{H_C}{N_C}\right) + \frac{H_J}{N_C}$$

or

$$R_{J/C} = r_{J/C}(1 - M_C) + \frac{H_J}{N_C}$$

Where H_J is the number of harvested juveniles; M_C is the cow harvesting rate; and $R_{J/C}$ and $r_{J/C}$ are the preseason ratio of juveniles to cows and the postseason ratio of juveniles to cows, respectively.