Grizzly bear population ecology and large carnivore conflicts in southwestern Alberta

by

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Abstract

Human-wildlife conflicts are a global conservation challenge. Reserves and protected areas usually do not adequately provide for the space needs of large carnivores, resulting in overlap between carnivore home ranges and private lands. Private lands often can provide valuable habitats, but wherever large carnivores and people share the landscape there is potential for conflict. I reviewed 16 years of records of complaints about grizzly bears, wolves, black bears, and cougars in southwestern Alberta and evaluated temporal and distribution patterns of these complaints. Conflicts were most frequently associated with bears reflecting a diversity of conflict types attributable to their omnivorous diets. In contrast, wolf and cougar incidents were almost exclusively related to killing or injury of livestock. Complaints for both bear species have increased over the past 16 years while cougar and wolf complaints have remained relatively constant. Increasing grizzly bear conflicts could be due to an increasing grizzly bear population. I used non-invasive genetic sampling and spatially explicit capture-recapture methods to estimate grizzly bear density and abundance in southwestern Alberta – a small part of a much larger international population of grizzly bears. I established 899 bear rub objects for bear hair sample collection across the study area by surveying trail networks, using GIS layers, and working with over 70 landowners to identify priority sampling areas. Though yearly variation occurred, I estimated an abundance of approximately 67.4 (95% CI 50.0 – 91.1) resident grizzly bears. However, the number of grizzly bears using the study area was much higher [2013: females = 68.9 (95% CI 58.4 – 97.2), males = 102.6 (95% CI 81.2 – 154.2); 2014: females = 63.0 (95% CI 48.9 – 102.6), males = 108.6 (95% CI 80.8 – 177.0)]. In contrast with my resident bear estimate, these numbers represent the number of bears that southwestern Alberta residents could have encountered, i.e., the total population of bears that had potential to have been involved in conflict. Access to supplemental food sources might have contributed to the population increase. The provincial government fed grizzly bears road-killed ungulates each spring during 1998-2013 attempting to reduce spring predation of livestock by grizzly bears. I evaluated the efficacy of this intercept-feeding program by monitoring 12 feeding locations, and using DNA, I identified 22 grizzly bears (19 males, 3 females) at the intercept-feeding sites – a small portion of the number of bears using the study area. Despite intercept feeding, conflicts between grizzly bears and agriculture have increased at a rate that exceeds the estimated rate of increase in the grizzly bear population. The propensity for a grizzly bear to be develop conflict behaviour might be a result of social learning between mothers and cubs, genetic inheritance, or both learning and inheritance. In addition to hair samples collected from rub objects, I targeted private agricultural lands for additional hair samples at grizzly bear incident sites. I completed a parentage analysis to evaluate evidence for social learning versus genetic inheritance of conflict behavior. My results support the social-learning hypothesis but not the genetic-inheritance hypothesis. Offspring from non-problem mothers are not likely to be involved in incidents or human-bear conflicts themselves, whereas offspring are more likely to show conflict behaviour when their mothers are problem bears. Proactive mitigation measures that prevent female bears from becoming problem individuals will likely help to prevent the perpetuation of conflicts through social learning, and will help to reduce grizzly bear-agricultural conflicts in southwestern Alberta.

Preface

This thesis is an original work by Andrea Timmons Morehouse. Field methods were in accordance with the Canadian Council on Animal Care guidelines and approved by the University of Alberta BioSciences Animal Care and Use Committee (Protocol # AUP00000008).

A version of Chapter 2, 3, and 4 have been submitted for publication to *Animal Conservation*, *Journal of Wildlife Management*, and *Wildlife Biology* (respectively) with Mark S. Boyce as a co-author. For these manuscripts A. T. Morehouse designed and implemented the field program, analyzed the data, and wrote the majority of the manuscript. M. S. Boyce provided valuable input and feedback throughout the implementation of field work, data analysis, and writing of the manuscripts.

A version of Chapter 5 has been submitted for publication to *PloS ONE*. For this manuscript Tabitha A. Graves, Nate Mikle, and M. S. Boyce are co-authors. T. A. Graves and N. Mikle completed the parentage analysis used in this chapter and provided feedback on the manuscript. All other field work, data analysis, and writing were completed by A. T. Morehouse. M. S. Boyce provided feedback on analysis and writing.

Acknowledgements

The data I used in this research were collected in a truly collaborative fashion. Although I use the term "I" throughout this dissertation, the work was in many cases collaborative, and the term "we" is more appropriate. This thesis would not have been possible without the efforts and support of numerous individuals and organizations. I have done my best to sincerely acknowledge and thank all those that have contributed (while staying within FGSR's 2 page limit!). I apologize to anyone I may have missed.

First, I would like to thank my supervisor Mark Boyce for this incredible opportunity. I have learned a tremendous amount from working with Mark for the last several years, and have benefited from his mentorship and support. I greatly appreciate his enthusiasm and dedication to the field of wildlife ecology. I would like to thank my committee members Naomi Krogman and Stan Boutin for feedback throughout my degree, and for challenging me to think critically.

I would like thank the Grizzly Bear Monitoring Project working group, which included Bill Dolan, Paul Frame, Greg Hale, Barb Johnston, and Nate Webb. This group was instrumental in initiating the DNA monitoring work, and laid the foundation for that component of my thesis well before I began my PhD. They helped secure resources and funding, provided feedback and government agency perspective, and had the trust and confidence in me to let me run with it; I am thankful for their support. Additionally, Barb Johnston and her summer field staff assisted in the collection of field data and helped coordinate field logistics within Waterton Lakes National Park.

Within my study area, 60% of the land is privately owned. Over 70 landowners participated in this project by allowing continued access for data collection, sharing information on grizzly bears, and/or collecting opportunistic hair samples. I am continually impressed by the southwestern Alberta community and have learned a tremendous amount from this group of people. This project would not have been possible without community support. Additionally, the Waterton Biosphere Reserve Association's Carnivore Working Group provided support, feedback, and helped facilitate communication with landowners. The dedication and commitment of this group to mitigate conflicts between agriculture and large carnivores is truly amazing. Thank you for sharing your knowledge and expertise. It has been a pleasure working with this group the last several years. In particular, Nora Manners and Jeff Bectell have continually gone above and beyond in their efforts. It is because of people like Jeff, Nora, and the rest of the CWG members, that I feel confident that both people and large carnivores will continue to share the landscape of southwestern Alberta for years to come.

Numerous people assisted with data collection. Approximately 7,000 km were covered on foot each field season. The work would not have been possible without hard-working field staff, including: Ellen Crocket, Peter Drobny, Samantha Dunbar, Cameron Eddy, Ian Ford, Elise Galuska, Axel Honneycutt, Shannon Lawrence, Anna Lello-Smith, Adelaide Lindseth, Kara MacAulay, Peter Manners, Megan McCrae, Michelle Mjolness, Jason Olsen, Matthew Roberts, Lucy Rogers, Ethan Rubenstein, Josh Sutherby, Anneka Sutton, Kaitlin Weber, Sarah Weed, and Ryan Wilbur. Matthew Urmson, Spencer Rettler, and Troy Malish worked on the project for multiple seasons; your assistance and dedication were greatly appreciated. I would also like to thank Annie Loosen who worked tirelessly to ensure that the field seasons went as smoothly as possible, and helped fix things quickly when they didn't. Annie, you have been a tremendous support to me in a variety of ways throughout the project – thank you. Thanks to Tabitha Graves and Nate Mikle for their work on the parentage analysis, and also Lori Roberts for providing Montana bear conflict histories used in Chapter 5. Also, thanks to Murray Efford to assistance with all things SECR.

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Thanks to my fellow Boyce-Merrill lab-mates for helpful discussions and feedback over the past several years. I would like to thank my friends and family, new and old, near and far for keeping me going throughout this process. You've been a sounding board, a place to vent, and a great distraction. Thank you for believing in me even when I didn't believe in myself. I am fortunate to have such wonderful people in my life. Finally, thank you to Jesse Tigner for assistance with everything – field work, reviewing writing, and all around support. Looking forward to the next adventure!

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Chapter 1

1 General Introduction

Large carnivores can have profound impacts on ecosystems beyond the direct effects of predation. In the 1920s, Charles Elton, a founder of animal ecology, speculated that wolf removal would result in unsustainable increases in the deer population (Elton 1927). A couple decades later, Paul Errington showed that predators sometimes killed "doomed surplus" – prey that were destined not to survive regardless of predation (Errington 1945, 1946), and Aldo Leopold noted the damaging effects deer could have on vegetation in the absence of wolves (Leopold 1949). Carnivores can drive trophic cascades (Hairston et al. 1960, Paine 1980, Schmitz et al. 2000, Ripple et al. 2014a, Ripple et al. 2014b), indirectly affect prey species (Brown et al. 1999, Peckarsky et al. 2008), affect biodiversity (Crooks and Soulé 1999), and alter ecosystem processes (Estes et al. 2011). Further, for many people, wildlife, including carnivores, have intrinsic value (Leopold 1943, Kellert 1980, Bruskotter et al. 2015, Vucetich et al. 2015). Carnivores frequently feature prominently in stories and traditions (Kellert et al. 1996, Dickman 2010), and often are used as flagship species for conservation efforts (Carroll et al. 2001, Dickman et al. 2011).

However, large carnivores also pose many real and perceived threats to people and communities that live within carnivore home ranges. Carnivores can kill livestock and pets (e.g. Naughton-Treves et al. 2003, Morehouse and Boyce 2011, Miller et al. 2015), cause property damage (e.g. Wilson et al. 2006, Treves 2009), affect cattle weight gain (Ramler et al. 2014) and pose a risk to human safety (e.g. Corbett 1944, Treves and Naughton-Treves 1999, Ratnayeke et al. 2014). Consequently, opinions on large carnivore conservation and management are diverse and often opposing. Because of their ecological importance coupled with their threats to human communities, facilitating coexistence between humans and large carnivores is a pressing challenge to global conservation efforts and those tasked with managing such conflicts (Decker and Chase 1997, Ripple et al. 2014b). Indeed, as Paul Errington (1967) wrote, "*Of all the native biological constituents of a northern wilderness scene, I should say that the wolves present the greatest test of human wisdom and good intentions.*"

In North America, national parks and wilderness areas often were designated with scenic grandeur and tourism in mind rather than ecological processes (Newmark 1985), and these protected landscapes are typically limited to "rock and ice" type habitats (Joppa and Pfaff 2009). Few protected areas provide enough space to adequately provide resources for the wide-ranging carnivores that use them (Noss et al. 1996, Hansen and Rotella 2002). Consequently, large carnivores use habitats outside of protected areas, and this potentially brings them in contact with human-settled lands. In the North American West, such lands often are privately owned rangelands that provide valuable habitats for large carnivores (Northrup et al. 2012, Sayre et al. 2012, Jenkins et al. 2015).

Once significantly reduced from much of their range, large carnivore populations are now rebounding across much of Europe and North America (Chapron et al. 2014, Ripple et al. 2014b). While populations in some areas remain tenuous, North American populations of cougar (*Puma concolor*), wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) are re-establishing and even increasing in many areas (Garshelis et al. 2008, Mace et al. 2012, Knopff et al. 2014, U.S. Fish and Wildlife Service et al. 2015). An increase in the number of people both living and recreating in carnivore habitat (Flather and Cordell 1995; Federal, Provincial and Territorial Governments of Canada 2014), combined with increasing carnivore populations, means the potential for conflict between humans and large carnivores is high.

Understanding and mitigating conflicts depends on accurate documentation regarding the type and distribution of conflicts over time as well as an evaluation of the biological drivers of those conflicts. Numerous ideas exist for reducing conflicts between people and large carnivores (e.g. Table 1, Dickman, 2010), and while the empirical evaluation of these tools can be challenging, monitoring and evaluation is necessary to improve outcomes (Sutherland et al. 2004, Redpath et al. 2012). As both carnivore and human populations increase, so does the potential for conflict between people and large carnivores. Accurate and precise estimates of large carnivore populations are an informative component to wildlife management (Dice 1938), and provide a scientific basis for target population size, which is often a component of species management/recovery plans (e.g. Schultz and Gerber 2002). Further, understanding the mechanism in which a particular behaviour is acquired can provide insight into conflict reduction as well as species' management (e.g. Whitehead 2010).

In Alberta, the southwestern corner of the province is a hot-spot of conflicts between large carnivores and human activities (Morehouse and Boyce 2011, Alberta Government 2013). In this region, protected public lands are sparse, and there is a sharp contrast between the mountainous public lands in the west and private agricultural lands to the east. It is a multi-use landscape with strong human influences on ecosystem dynamics; here, human activity strengthens bottom-up trophic cascades, displaces predators resulting in prey refuges, and creates ecological traps (Muhly et al. 2011, Northrup et al. 2012, Muhly et al. 2013). Populations of grizzly bears, black bears, wolves, and cougars overlap substantially with the human population and agricultural activities. In Chapter 2, using 16 years of complaint records for all four large carnivore species, I provide an overview of large carnivore conflicts in southwestern Alberta. I document the types of conflicts and the temporal patterns within those conflicts, which is an important first step for future work on conflict mitigation. I discuss species-specific behaviours and life history traits that promote those conflicts. Of the large carnivores in Alberta, only grizzly bears have a provincially threatened status; all other species (black bears, wolves, and cougars) are considered stable in Alberta. Grizzly bear conflicts in Alberta have increased over the last 16 years, and my remaining chapters focus on empirically evaluating a sub-set of hypotheses explaining the increased grizzly bear conflicts along with a behavioural mechanism that might be amplifying the observed pattern of increasing conflicts. Certainly, there are alternative hypotheses beyond those outlined below (e.g. non-biological variables), and while I acknowledge alternative explanations, a full analysis of all possible alternate hypotheses is beyond the scope of my thesis.

Grizzly bear conflicts may be increasing because the grizzly bear population is increasing. Estimating density and abundance is a central tenant of population ecology, and the estimation of these parameters has challenged ecologists (Andrewartha and Birch 1954, Southwood 1966, Caughley 1977, Krebs 1989). Estimation methods have often relied on capture-recapture sampling methods that assume a closed population (Peterson 1896, Lincoln 1930, Otis et al. 1978). Open population models circumvent this assumption (e.g. Jolly 1965, Seber 1965, Seber 1982, Seber 1986, Pollock et al. 1990), but the challenge remains as to how to explicitly define the sampling area in question to estimate density. Relatively recent spatially explicit capture recapture models (SECR) directly estimate density thereby eliminating the need for defining the sampling area post-hoc (Efford et al. 2004, Borchers and Efford 2008, Efford and Fewster 2013). The last population estimate for grizzly bears in southwestern Alberta occurred in 2007 and estimated a population size of 51 grizzly bears using traditional non-spatial capture-recapture methods. (Alberta Grizzly Bear Inventory Team 2008). In Chapter 3, I use SECR models to provide an updated population density and abundance estimate of grizzly bears in southwestern Alberta.

Further, provincial conflict mitigation programs providing access to high-quality food resources might help to inflate the local carrying capacity of grizzly bears – potentially resulting in increased conflicts due to a higher number of bears. Supplemental feeding programs can result in increases in abundance (e.g. Sullivan and Sullivan 1982, Moris et al. 2011), survival (e.g. Cole and Batzli 1978, Seward et al. 2013), and productivity (e.g. Angerbjörn et al. 1991, Robb et al. 2008). Carrion is an important spring food resource for grizzly bears (Servheen 1983), and the proportion of meat in a grizzly bear's diet is correlated with body mass, litter size, and population density (Hilderbrand et al. 1999). Access to high-quality food resources is particularly important for sows with cubs (Farley and Robbins 1995, Ben-David et al. 2004). However, dominance hierarchies (e.g. Craighead et al. 1995, Elfstrom et al. 2014) and the risk of intra-specific killing to which females with cubs are particularly vulnerable (Swenson et al. 2001a, Swenson et al. 2001b, McLellan 2005), might limit the use of high-quality supplemental food sources by subordinate individuals. In Chapter 4, I evaluate the efficacy of the provincial intercept-feeding program. The goal of this program was to reduce spring predation of livestock by grizzly bears. In the intercept feeding program, road-killed ungulates were placed in remote areas each spring to "intercept" grizzly bears after they emerge from hibernation, thereby preventing them from moving to lower-elevation areas and killing cattle during the spring calving season.

In addition to an increased grizzly bear population, social learning might be escalating the acquisition of conflict behaviours, and subsequently conflicts, by allowing individuals to short cut the trial and error process (Galef and Laland 2005). Animals can acquire behaviours through genetic inheritance, asocial learning, or social learning or a combination thereof (Fuller and Scott 1954, Heyes 1994, Laland 2004). In Chapter 5, I evaluate evidence for genetic inheritance and social learning in the acquisition of conflict behaviour in grizzly bears. If conflict behaviour is learned socially from mother to offspring, this behaviour might perpetuate the observed pattern of increasing conflicts. Finally, in Chapter 6 I synthesize the ideas from the preceding chapters and provide recommendations for management and future research.

Chapter 2

2 Omnivores are Troublemakers: Conflicts with Humans in a Diverse Assemblage of Large Carnivores

2.1 Introduction

Human-wildlife conflict is a global conservation challenge involving a myriad of species including, but not limited to rodents (Kloskowski 2011, McGrann et al. 2014), ungulates (e.g., Chomba et al. 2012, Duarte et al. 2015, Massei et al. 2015), primates (e.g., Dutta et al. 2015, Saraswat et al. 2015), marine carnivores (e.g., Graham et al. 2011, Tixier et al. 2014), and several terrestrial large carnivores (e.g., Can et al. 2014, Dondina et al. 2015, Hiller et al. 2015). Large carnivores have been shown to have important influence by structuring ecological communities (Ripple and Beschta 2004, Estes et al. 2011, Wilson and Wolkovich 2011, Ripple et al. 2014b, Hollings et al. 2015). Access to human-provided foods, however, may alter the behaviour and ecological role of large carnivores (Newsome et al. 2015). Where carnivore ranges and human land uses overlap (e.g., Woodroffe 2000, Ripple et al. 2014b), facilitating coexistence of people and carnivores can be challenging. Some biologists advocate a separation model whereby humans and wildlife are kept apart, e.g., fenced reserves in Africa (Packer et al. 2013). While separating people and carnivores at small scales (e.g., exclusion from calving pastures or yard sites) might be desirable, the separation model is unrealistic at larger scales where there is not enough space for carnivores if they are restricted from human-settled lands (e.g., Woodroffe and Ginsberg 1998, Chapron et al. 2014). Indeed, private-land conservation is an important component to protecting biodiversity and ecological systems (Knight 1999, Selinske et al. 2015). In heavily developed landscapes with insufficient wilderness areas, coexistence of people and predators is possible and necessary for carnivore persistence (Chapron et al. 2014).

In the Rocky Mountain ecosystem of the North American West, protected areas often are comprised of "rock and ice" (Joppa and Pfaff 2009), while adjacent privately owned rangelands offer habitats for many species, including large carnivores (Northrup et al. 2012b, Sayre et al. 2012, Jenkins et al. 2015). To promote coexistence, it is necessary to reduce negative interactions between people and large carnivores. Large carnivores present numerous challenges for people living within their home ranges: they can kill livestock (e.g., Morehouse and Boyce 2011, Miller et al. 2015), cause property damage (e.g., Wilson et al. 2006, Treves 2009), destroy crops and stored grain (e.g., Northrup and Boyce 2012, Wong et al. 2015), and present a human-safety concern (e.g., Treves and Naughton-Treves 1999, Ratnayeke et al. 2014). The definition of human-wildlife coexistence varies among individuals and is influenced by human values, attitudes, and tolerance, but in a general sense, human-wildlife coexistence occurs when viable populations of wildlife inhabit the same landscape as humans without infringing on the safety, rights, and property of humans. Recognizing conflict existence, documenting conflict type, and considering mechanisms behind conflicts are first steps prior to developing and implementing conflict mitigation measures (Linnell 2011).

In Alberta, conflicts between people and carnivores are prominent in the southwestern corner of the province (Morehouse and Boyce 2011, Alberta Government 2013). In this region, human-settled lands overlap with the geographical ranges of the full assemblage of native large carnivores including wolves (*Canis lupus*), cougars (*Puma concolor*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). Agriculture is the predominant human land use in southwestern Alberta (Statistics Canada 2006), and many conflicts with carnivores are related to agricultural attractants such as livestock, grain, silage, standing crops, and dead stock (Morehouse and Boyce 2011, Northrup and Boyce 2012).

Here, I review 16 years of large-carnivore conflicts and examine the spatial distribution and temporal patterns of those conflicts. Because of variation in foraging strategies (omnivory vs. carnivory), I predict that conflicts for the bears will be more varied than for wolves and cougars that are strictly carnivorous. I discuss species-specific reasons for the observed conflict patterns as well as human factors influencing reporting rates. My data represent a unique long-term case study that provides insights into global conservation challenges of human-wildlife coexistence.

2.2 Study Area

I studied large carnivore conflicts in a 23,700 km^2 area of southwestern Alberta (Fig. 2.1). The area was bounded by the Highwood River to the north, British Columbia to the west, and Montana to the south. The eastern boundary was defined by the eastern extent of the Wildlife Management Units in the area. Highway 3 bisected the study area; this 2-lane highway is the major east-west transportation corridor in the region. A sharp transition from agricultural land and prairie habitats to the east to mountainous forested areas to the west characterizes the region. The landscape is shaped by strong winds; cold winters follow warm, dry summers. The study area was a mix of public land (20%) including Waterton Lakes National Park and provincial Crown lands. The remaining 80% of land within my study area was privately owned. The largest towns within the area were Pincher Creek (population 3,685), Cardston (population 3,580), and the Muncipality of Crowsnest Pass (population 5,565) (Statistics Canada, 2011).

All native large carnivores occur including black bear, grizzly bear, cougar, and wolf. With the exception of grizzly bears, all large carnivore species are considered "secure" within the province and have a hunting season (Table 2.1). Registration is compulsory for harvested wolves and cougars, but not for black bears (Alberta Government 2014). Ungulates include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*) and moose (*Alces alces*). Domestic cattle (*Bos taurus*), and a small number of sheep (*Ovis aries*) and goats (*Capra hircus*) also are present. Cattle are grazed seasonally from June through October on public forest reserve grazing allotments. Oil and gas activity as well as forestry also are present; widespread linear features include roads, trails, and seismic lines. Agriculture is the predominant land use on private lands (Statistics Canada 2006).

2.3 Methods

I reviewed and categorized Government of Alberta enforcement occurrence records for grizzly bears, black bears, wolves, and cougars from the Blairmore, Cardston, Claresholm, and Pincher Creek Fish and Wildlife Districts from 1999 (date of creation of electronic occurrence database) through 2014. These occurrence records represent complaint data. When someone in Alberta makes a complaint to their local Fish and Wildlife office about large carnivores, the details of the complaint are recorded as text summaries in the provincial enforcement database. Thus, it was necessary to individually review each record to extract the pertinent information. I retained only those records reporting an actual interaction with a large carnivore; all non-carnivore records were excluded from the final database. I used the following terms (Hopkins et al. 2010) to classify each carnivore occurrence:

1) Sighting: seemingly unaware of the person, no observable stress related response during the interaction;

2) *Incident:* property damage, obtained anthropogenic food, killed or attempted to kill livestock or pets, or involved in a vehicle collision; or

3) *Human Conflict:* physical contact with person or was intentionally harmed or killed by the person. Human conflict records can include both legal and illegal harvest of carnivores.

I focus on incidents and human conflicts rather than sightings because they represent actual interactions between people and carnivores. I subdivided categories to provide more insight regarding potential driving factors. Incident type was identified as property damage, livestock, attractant, and other; specific attractants were identified as grain, dead stock and boneyard, bee yard, silage, vegetation, garbage, bird feed, campsite, pet food, and other (e.g., horse pellets, pig feed, wildlife hide). I excluded records that did not fit into the above categories. For example, enforcement records occasionally contained requests for information (e.g., request for bear safety information or officer presentation) or situations where a large carnivore was not actually involved (e.g., coyote mistaken for wolf). I removed these records from my database. Additionally, I excluded any records that were outside my study area.

When geographic coordinates were provided, I mapped complaint locations in a GIS (ArcMap 10.2, ESRI, Redlands, CA). However, some records provided only a legal land description (i.e., quarter section) or address. In these cases, I derived GPS coordinates using the physical address or by calculating the centroid of the quarter section. Thus, mapped locations are accurate to the quarter section scale (800 × 800m). If I could not identify a location to the quarter-section (65 ha), I excluded the event from my maps. However, I retained all records for my summary statistics.

I summarized occurrence frequency by species and year. For incidents, I described incident type for each species, and summarized attractant type for grizzly bears and black bears. To evaluate the change in distribution patterns I calculated the distance of each occurrence from the edge of public land and compared means using a single-factor ANOVA, and plotted mean distances over time.

2.4 Results

In total, I reviewed and categorized 6,365 records over the 16-year period (1,855 for grizzly bears, 2,531 for black bears, 859 for wolves, and 1,120 for cougars). Of these, locations were provided or derived for 5,853 records. Cougar incidents stayed relatively constant, as have wolf incidents with the exception of a peak in 2008 and 2009 (Fig. 2.2, A and B). Black bear incidents varied over time, but have generally increased and peaked in 2014 (Fig. 2.2C). Grizzly bear incidents have increased, primarily since 2006 (Fig. 2.2D).

Incident type was predominantly livestock for wolves (97.1%) and cougars (84.4%) (Fig. 2.3). For black bears, attractant was the most common incident type (80.4%) (Fig. 2.3). The most common attractants for black bears were garbage (37.5%), vegetation (19.4%), and birdfeeders (11.1%) (Fig. 2.4A). The majority of grizzly bear incidents were related to attractants (55.3%) followed by livestock (39.5%) (Fig. 2.3). For grizzly bears, the main attractant was grain (43.1%) followed by boneyards/deadstock (37.1%) (Fig. 2.4B).

The mean distance from public land of grizzly bear, black bear, and cougar occurrence records differed significantly among years (grizzly bear: F = 5.060, df = 15, $p < 0.001$; black bear: F = 3.843, df = 15, $p < 0.001$; cougar: F = 2.092, df = 15, $p = 0.009$). Mean distances from public land for grizzly bear and cougar occurrences records have increased from 1999 – 2014 with increasing occurrences in eastern sections of the study area (Fig. 2.5B and D, Fig. 2.6). Black bear occurrences records had a slight negative trend and average distance from public land has decreased (Fig. 2.5C). Wolf mean distance to public land did not differ significantly across years (F = 1.246, df = 15, *p* = 0.231) (Fig. 2.5A).

In total for all species, I classified 522 occurrences as human conflicts. Of these, 414 resulted in human-caused death of the carnivore (grizzly bear *n* = 28, black bear *n* = 50, wolf *n* = 135, cougar *n* = 201). In Alberta reporting harvested animals is only compulsory for wolves and cougars (Alberta Government 2014). The most common reasons for humans killing carnivores were legal hunter harvest (46.4%) and defense of property (30.4%).

2.5 Discussion

Human-wildlife conflicts are a global conservation challenge. Patterns of human-carnivore conflicts in human-influenced landscapes reveal how access to anthropogenic food resources can alter the ecological role of predators (Newsome et al. 2015). Documenting conflict type and distribution helps target conflict resolution; such data can serve as a baseline against which to measure future conflict mitigation program success. Within my study area, the human population is stable to decreasing (Statistics Canada 1996-2011), and land tenure has remained constant at a landscape level (i.e., no change in the proportion of private land). The municipalities in southwestern Alberta are characterized by remote properties with little subdivision; the area is not experiencing the same urban sprawl as municipalities closer to Calgary (the major urban center of southern Alberta) (Miistakis Institute for the Rockies 2003). Demographic data suggests an aging population with little mobility; the majority of the population lived at the same address 5 years ago for each of the 3 census years considered

(Statistics Canada 1996-2011), suggesting that changes in reporting rates are not driven by new residents unaccustomed to living with carnivores. Therefore, I eliminate human population increase and changes in demographics as the main reasons behind increasing carnivore conflicts, and focus instead on explanations pertinent to each species, as well as human factors that influence reporting rates.

Responses to human activity have been documented for all 4 large carnivore species (e.g., Dickson et al. 2005, Whittington et al. 2005, Northrup et al. 2012a, Stillfried et al. 2015). Within my study area, high levels of recreational activity occur on public lands (Ciuti et al. 2012, Northrup et al. 2012a), and this use of public lands is increasing (Alberta Community Development 1996, Alberta Tourism Parks and Recreation 2008, Alberta Government 2014b, Parks Canada 2015). By comparison, vehicle traffic is lower on private lands (Northrup et al. 2012a), and carnivores might seek out (or are displaced to) these areas to avoid high levels of human use. Indeed, much of southwestern Alberta has been identified as an ecological trap for grizzly bears (Northrup et al. 2012b). In the Crowsnest Pass region, resource selection functions for both cougars and grizzly bears predict high probability of occurrence within close proximity to human-developed areas because of selection for resources and/or habitats in that area (Chetkiewicz and Boyce 2009). Further, climate change also might play a role in bear-human conflicts; climate models predict an upslope movement of important grizzly bear food items, and lower-elevation areas are projected to lose species richness by as much as 50% for certain species (Roberts et al. 2014). Thus, for bears living in low-elevation areas, a decrease in food availability might result in increased use of anthropogenic resources and an increase in conflicts (Roberts et al. 2014).

Beyond human-caused environmental changes, species-specific life history traits and behaviors likely provide additional explanations to the observed patterns in the occurrence records. Cougar incidents were the lowest of all carnivores despite an expanding and increasing population (Knopff et al. 2014), and of the incidents that did occur most were related to depredation or injury of livestock. Although cougars occasionally kill livestock, cougar diet in southwestern Alberta, as in many regions of North America, is primarily deer (Anderson and Lindzey 2003, Knopff et al. 2009, Bacon et al. 2011, Banfield 2012). The preferred mass for prey taken by cougars is 70-165 kg (Murphy and Ruth 2009), which is lower than cattle weights (predominant livestock in my study area). Even in areas of high cougar and livestock density, deer are preferred prey (Bacon et al. 2011). Indeed, despite the widespread global availability of livestock, Newsome et al. (2015) found that livestock comprised on average only 17% of food items in felid diets. If cougar range in Alberta expands to areas where smaller livestock such as sheep are more common, it will become increasingly important to monitor complaints to address concerns as they arise.

Similarly, wolf incidents were almost exclusively related to livestock. However, wolf-livestock incidents occurred more frequently than for cougars. Wolves are opportunistic, flexible hunters with diets depending on availability and vulnerability of prey (Huggard 1993, Cressman and Garay 2011, Morehouse and Boyce 2011, Metz et al. 2012). Prey have evolved varying predator-avoidance strategies. For example, in the presence of wolves, elk move to less-risky habitats (Fortin et al. 2005, Laporte et al. 2010), and increase path sinuosity (Laporte et al. 2010). Cattle, however, lack consistent, predictable, and timely predator-avoidance strategies (Laporte et al. 2010, Muhly et al. 2010a), making them potentially more vulnerable to predation. The frequency of wolf-livestock incidents has stayed fairly constant over the 16-year time period.

The 2008 and 2009 peaks coincide with my previous research in the area when I identified wolf kill sites using GPS radiocollars (Morehouse and Boyce 2011). Missing livestock (i.e., animals not located at the end of the grazing season) are a concern for ranchers, and previous research indicates that these missing livestock often were depredated by wolves (Morehouse and Boyce 2011). However, without the use of GPS radiocollars to locate wolf kill sites many depredated livestock are not found. Thus, data from 2008 and 2009 are likely more representative of the true number of incidents in the area rather than the outliers they appear to be. Wolf population size has not been monitored within my study area, but research in other areas of Alberta indicates wolf populations are stable (Webb et al. 2011).

Previously, the provincial government incrementally reduced wolf packs known to depredate livestock (Pym et al. 2014), but that program was discontinued in southwestern Alberta in 2009. However, even in the absence of government wolf control, wolf incidents have stayed fairly constant in my study area, probably because landowners legally can shoot or trap wolves and do not need to rely on government staff to remove a problem animal. In Montana, full wolf pack removal successfully reduced future livestock depredation events in a local area (Bradley et al. 2015), but lethal control is not always socially acceptable (Bruskotter et al. 2009). Non-lethal options such as electric fencing and fladry have been successful in deterring wolves under certain circumstances and for short (e.g., 60 days) time duration (Musiani et al. 2003, Shivik 2006). Disruptive stimuli (e.g., shots, flares, strobes, etc.) also can be effective in deterring wolves from an area (Shivik and Martin 2000, Shivik 2006). When cattle are free ranging, however, the wolf-cattle depredation problem is more complex. During the Alberta grazing season, cattle graze freely on public land, often in high densities, with little to no monitoring (Bjorge and Gunson 1983, Gunson 1983, Fritts et al. 1992). Further, grazing season timing coincides with the wolf pup-rearing season when the nutritional demands of wolves are considerable, due to the need to satisfy growing pups. This potentially heightens the risk of predation on cattle throughout the grazing season (Fritts et al. 2003). Although increased human presence (e.g., range-riding: horseback riders monitoring livestock), livestock guardian dogs, changes in cattle age classes, and changing calving dates have all helped reduce livestock depredation in certain situations (Smith et al. 2000, Bradly and Pletscher 2005, Muhly et al. 2010b, Breck et al. 2011, Barnes 2015), wolf predation of livestock remains a challenging problem.

Unlike wolves and cougars that are strictly carnivorous, bears are omnivores resulting in more varied incident types. Indeed, crops, food waste, and livestock carcasses feature prominently in the diet of ursids across the globe; killing of livestock occurs less frequently (Newsome et al. 2015). Black bear incidents were predominately attributable to attractants including garbage, birdfeeders, and vegetation. The provincial government's BearSmart program, active in the Crowsnest Pass since 2006, (www.bearsmart.alberta.ca) focuses on reducing attractants within local communities (e.g., removal of birdfeeders during summer, replacing fruiting trees with non-fruiting trees, etc.), and aversive conditioning programs discourage black bears from visiting these communities. These initiatives should be effective based on previous studies (e.g., Huygens and Hayashi 1999, Mazur 2010, Papworth et al. 2014). In Wisconsin, Voyles et al. (2015) found that providing technical assistance to an individual experiencing black bear problems was a more effective long-term solution than relocation of the problem black bear. A recent survey in the Crowsnest Pass indicated 80% of survey participants "currently engage in or would be willing to engage in BearSmart practices" (Crowsnest Conservation Society and Alberta Government 2014). Additionally, recently implemented bylaws require garbage to be stored in a secure location until the morning of pick-up unless in an "animal-proof container" (Solid Waste Collection and Disposal Bylaw 863, 2013), and the number of bear-proof garbage bins in use by Crowsnest Pass residents has increased (Anderson 2015). Despite these proactive initiatives, black bear incidents increased markedly in 2014. Although 92% of survey participants agreed that attractant management on their property was their responsibility (Crowsnest Conservation Society and Alberta Government 2014), it is possible that human behaviors have not yet changed (e.g., Campbell 2012). While there are no current estimates of black bear abundance, this increase in incidents could be due to a black bear population increase, or an ongoing effort by the BearSmart program encouraging residents to report interactions with bears. Black bear use of human-settled areas often increases when natural foods are scarce (Howe et al. 2010, Baruch-Mordo et al. 2014, Lewis et al. 2014). Although berries have not been monitored, 2014 appeared to have been a poor berry year in southwestern Alberta, and black bears may have increased their use of the Crowsnest Pass region because of decreased natural foods, and its proximity to preferred forested habitats. Despite the high number of incidents in 2014, only 1 black bear was euthanized that year by Fish and Wildlife Officers as compared to an average of 2.8 black bears since 2006 (Anderson 2014).

Additionally, the spatial distribution of black bear and grizzly bear occurrences differed. For black bears, the mean distance from public land was stable to decreasing, which is driven largely by an increase in occurrence records in the Crowsnest Pass region of my study area. Crowsnest Pass contains a series of small towns along the Highway 3 corridor, all of which are in close proximity to public land (Fig. 2.1). As the less dominant of the two bear species, black bears might be excluded from more remote higher-quality areas by an expanding grizzly bear population (Chapter 3) and subsequently pushed into developed town sites (Belant et al. 2010, Elfström et al. 2014). Comparatively, grizzly bear occurrences are spreading further east each year into private lands used for agriculture.

Grizzly bears typically occupy a wider range of habitats than do black bears; in particular, grizzly bears are more likely to occur in open habitats than black bears (Apps et al. 2006). Grizzly bears are not only exposed to different attractants, but in some instances their physical strength and long claws allowed them to better access these attractants. For example, grizzly bears will dig at the base of a grain bin, ripping through a wooden floor until grain is exposed (Fig. 2.7). In my study area, grizzly bears use agricultural lands (Northrup et al. 2012b) and most attractants were agricultural – primarily grain and boneyards. Additionally, they are the more carnivorous of the two bear species (Fortin et al. 2013) and grizzly bear depredation and/or injury of livestock was documented in the occurrence records.

Grizzly bear incidents increased most markedly since 2006 when Alberta suspended grizzly bear hunting (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). The resulting incident increase could be due to changes in bear behaviour in the absence of hunting (Swenson 1999, Ordiz et al. 2012, Penteriani et al. 2016), or an increase in reporting rates (Howe et al. 2010), which could be a reflection of increased frustration from the community because of the loss of a sense of control (i.e., landowners can no longer remove a problem bear). Alternatively, the increase in grizzly bear incidents could be due to the increasing population of grizzly bears (Chapter 3). Grizzly bears have been listed as a threatened species in Alberta since 2010 and the hunting moratorium and access management may have helped to increase the population. Grizzly bears in southwestern Alberta are part of a larger international grizzly bear population that includes Montana and British Columbia (Proctor et al. 2012). Montana recently estimated that their grizzly bear population has been growing at approximately 3% per year (Mace et al. 2012); grizzly bears in southwestern Alberta have undergone similar population growth (Chapter 3).

Aside from species-specific reasons, temporal trends in occurrence records might be due to changes in reporting rates (Howe et al. 2010). One limitation of complaint data is that they are restricted to occurrences reported by the public; I do not know how many carnivore occurrences go unreported. An increase in complaint data might be due to a change in human attitudes and tolerance towards large carnivores. Various factors can affect attitudes including, but not limited to, personal experience with carnivores, economic circumstances, socio-demographic parameters, knowledge, and the location of the carnivore interaction (e.g., Lindsey et al. 2013, Kansky and Knight 2014, Kansky et al. 2014). As grizzly bear distribution expands eastward, more people are encountering bears for the first time. Because the experience of encountering grizzly bears is new, people on this eastern front might be more inclined to report an issue than a landowner who has been experiencing bears for decades. Further, reporting rates might reflect an individual's frustration with regulations. For example, in Alberta, it is within a landowner's legal right to kill a black bear, wolf, or cougar that is depredating livestock; but he/she has no such ability for grizzly bears, and must instead rely on the provincial government to relocate a problem bear. Past research has found that individuals are 1,000 times more likely to accept voluntary risks than those imposed on them externally (Starr 1969). Reporting rates might be affected if individuals blame government agencies for imposing the risks of large carnivores on them (Dickman 2010).

Numerous tools are available to help mitigate conflicts (e.g., Table 1, Dickman 2010). The majority of such mitigation efforts focus on restricting access to attractants. Attractant management is a powerful tool for separating people and carnivores (e.g., Wilson et al. 2005, Bino et al. 2010). For example, fencing, grain-bin retrofits, noise/light stimuli, livestock guardian dogs, aversive conditioning, and fladry have been used to restrict access/deter large carnivores (e.g., Bangs and Shivik 2001, Breck et al. 2002, Musiani et al. 2003, Wilson et al. 2005, Van Bommel and Johnson 2012). The Waterton Biosphere Reserve's Carnivore Working Group is working within the study area to reduce conflicts with grizzly bears (e.g., electric fencing projects, grain bin retrofits, etc.). In southwestern Alberta and Montana, there has been a focus on removing dead livestock from the landscape, which can be an attractant for large carnivores and potentially bring them into close proximity to other attractants (e.g., live livestock) (Morehouse and Boyce 2011, Northrup and Boyce 2012, Wilson et al. 2014). Long-term solutions to human-wildlife issues, however, must address both scientific and non-scientific considerations (Clark 2011). For example, the dead stock removal project in Montana was initially met with concern from ranchers because they did not want to disclose their calf losses out of fear they would be stigmatized as having poor animal husbandry practices (Wilson et al. 2014). Once this concern was addressed, the program enjoyed high participation and numerous carcasses were removed from the landscape (Wilson et al. 2014). Similarly, in Alberta, the Waterton Biosphere Reserve's Deadstock Removal Program offers free deadstock pick-up for producers on over 500,000 ha (Manners and Bectell 2014); over 140 landowners have participated and at least 2,500 livestock carcasses have been removed since the program started in 2009 (Manners and Bectell 2014, Waterton Biosphere Reserve unpublished data).

By engaging landowners, ranchers, biologists, and managers the Waterton Biosphere Reserve is working on numerous conflict-reduction projects. For example, 32 attractant management projects have been completed from 2008 – spring 2013 in conjunction with the Waterton Biosphere Reserve's Carnivores and Communities program (Loosen et al. 2014, Waterton Biosphere Reserve unplublished data). Personal interviews with landowners indicate that not only have these projects been successful at reducing conflicts at the site level, but also that these projects an important component to promoting coexistence between people and large carnivores (Loosen et al. 2014). These interviews also highlight the need for multiple mitigation options because there no single solution to the complex problem of carnivore conflict. These projects require extensive time, financial resources, and often a change in ranch management; their completion is indicative of the community's commitment to reducing conflicts between grizzly bears and agricultural activities (Loosen et al. 2014). Indeed, over 70% of residents within the Waterton Biosphere Reserve believe that people and large carnivores can share the landscape if managed properly (Quinn and Alexander 2011). While I have not observed a large scale decrease in grizzly bear conflicts, such local efforts are promising; continued tracking of complaint records can be used to help evaluate the efficacy of mitigation efforts once implemented.

2.6 Conclusion

Carnivore life histories influence conflict patterns. Omnivorous species like bears are involved in more varied conflicts than carnivorous species such as wolves and cougars. Bear incidents were more frequently reported than wolf and cougar incidents even though bears den for several months of the year. Over four times more grizzly bear incidents were reported than cougar incidents despite a higher density of cougars than grizzly bears (Webb et al. 2012, Chapter 3), and incidents involving bears ranged from livestock killing to destroying property, while incidents involving cougars and wolves were almost exclusively killing or injuring livestock. However, incidents involving livestock might be underrepresented in the occurrence reports because of difficulty locating carcasses, particularly in forested, mountainous terrain. Thresholds for human-carnivore coexistence vary among regions depending on the characteristics of the human and carnivore populations present (Oriol-Cotterill et al. 2015). Changing attitudes and tolerance towards large carnivores might influence the reporting of conflicts and understanding this human dimension of conflicts will likely help direct future mitigation work (Oriol-Cotterill et al. 2015).

Resolving large-carnivore human conflicts is a challenging problem beyond the scope of biology; successful mitigation programs will integrate concepts and ideas from biology, ecology, economics, agricultural sciences, rangeland ecology, sociology, and anthropology both in program design and evaluation (Redpath et al. 2013, Kansky and Knight 2014). For example, attractant management is a powerful tool for reducing human conflicts with bears, but requires methods that are realistic to implement and economically viable for the human communities experiencing conflicts (e.g., Huygens and Hayashi 1999, Barrett et al. 2014, Papworth et al. 2014). Current attractant management work in southwestern Alberta provides a successful example of such an interdisciplinary collaboration by drawing on expertise from ranchers, biologists, and wildlife managers. These site-specific mitigation measures can serve as a case study for other regions of the world in how to match mitigation strategies to the species, conflicts, and human communities present. An interdisciplinary approach together with continued monitoring of complaint data is necessary to identify problem areas, improve mitigation efforts, and facilitate long-term coexistence between people and large carnivores.

Table 2.1 Provincial status and hunting information for each large carnivore species in southwestern Alberta. Information current as of May, 2015 (Alberta Government 2014).

Species	Provincial Status	Hunting Season	Hunting for Control of Livestock Predation[c]
Grizzly Bear	Threatened	no[a]	no
Black Bear	Secure	yes	yes[d]
Wolf	Secure	yes[b]	yes[e]
Cougar	Secure	yes	yes[d]

[a] Hunting season for grizzly bears suspended in 2006

[b] There is also a trapping season for wolves

[c] Heading under Alberta Hunting regulations, but there is no stipulation that evidence of livestock predation must be provided

[d] Any owner or occupant of private land, anyone authorized to keep livestock on public land, or any resident authorized by the preceding may hunt on described lands without a license at all times of the year.

[e] Any owner or occupant of private land, anyone authorized to keep livestock on public land, or any resident authorized by the preceding may hunt on described lands, or any lands within 8km, without a license at all times of the year.

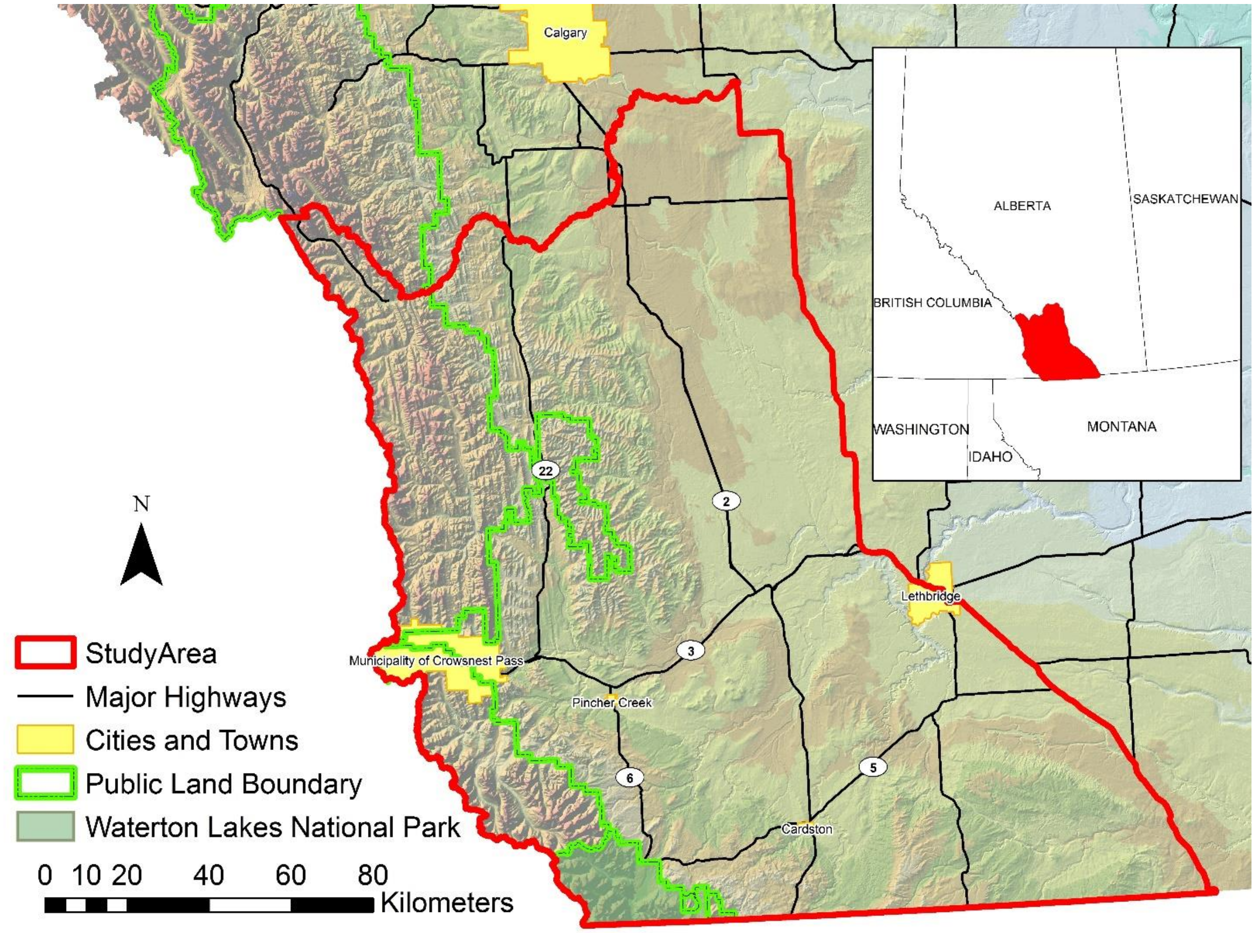

Figure 2.1 Map of study area in southwestern Alberta. The Municipality of Crowsnest Pass is a linear series of small towns along the Highway 3 transportation corridor.

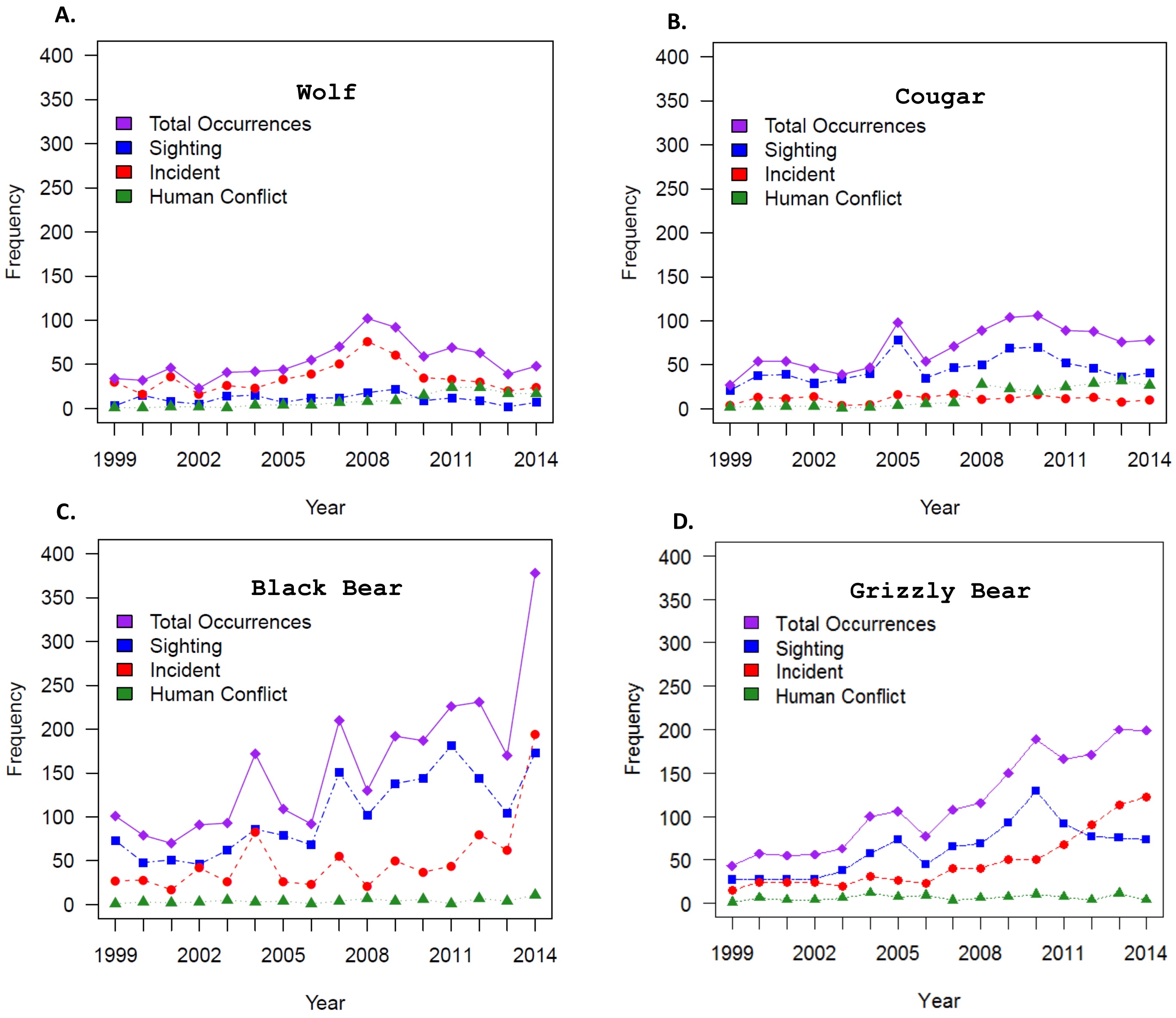

Figure 2.2 Wolf (A), cougar (B), black bear (C), and grizzly bear (D) occurrences by type from 1999 through 2014 in southwestern Alberta, Canada.

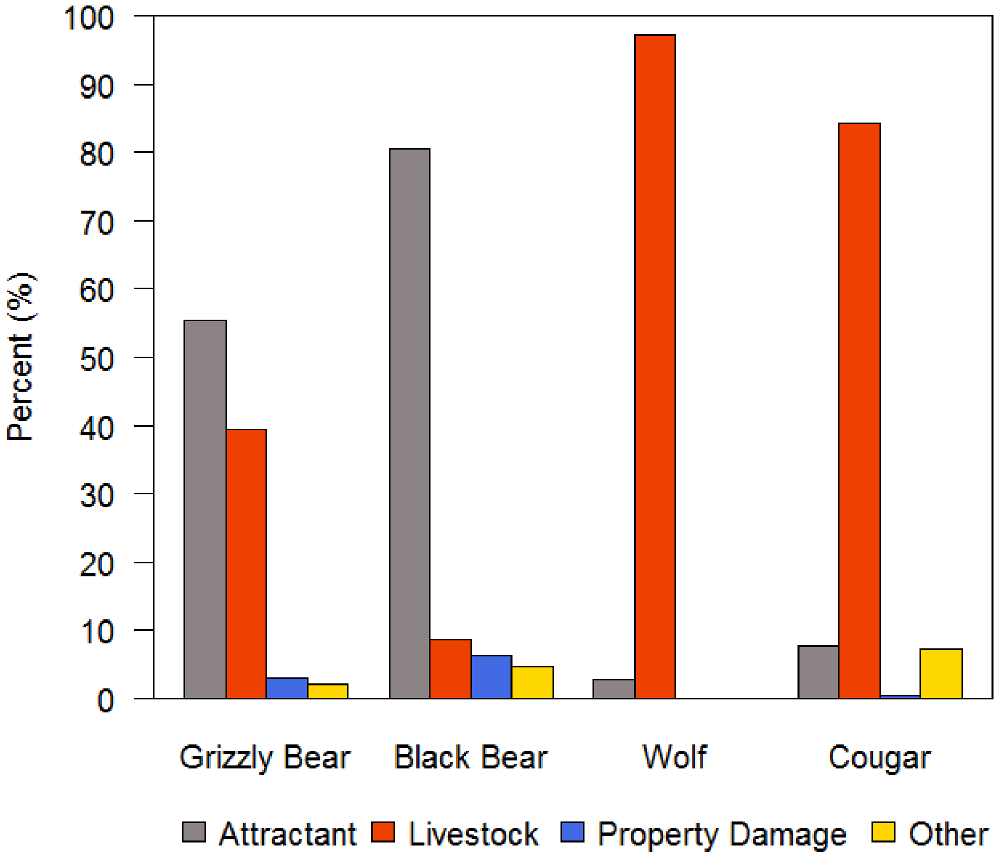

Figure 2.3 Large carnivore incidents by species and type. Percentages are cumulative over 1999 through 2014.

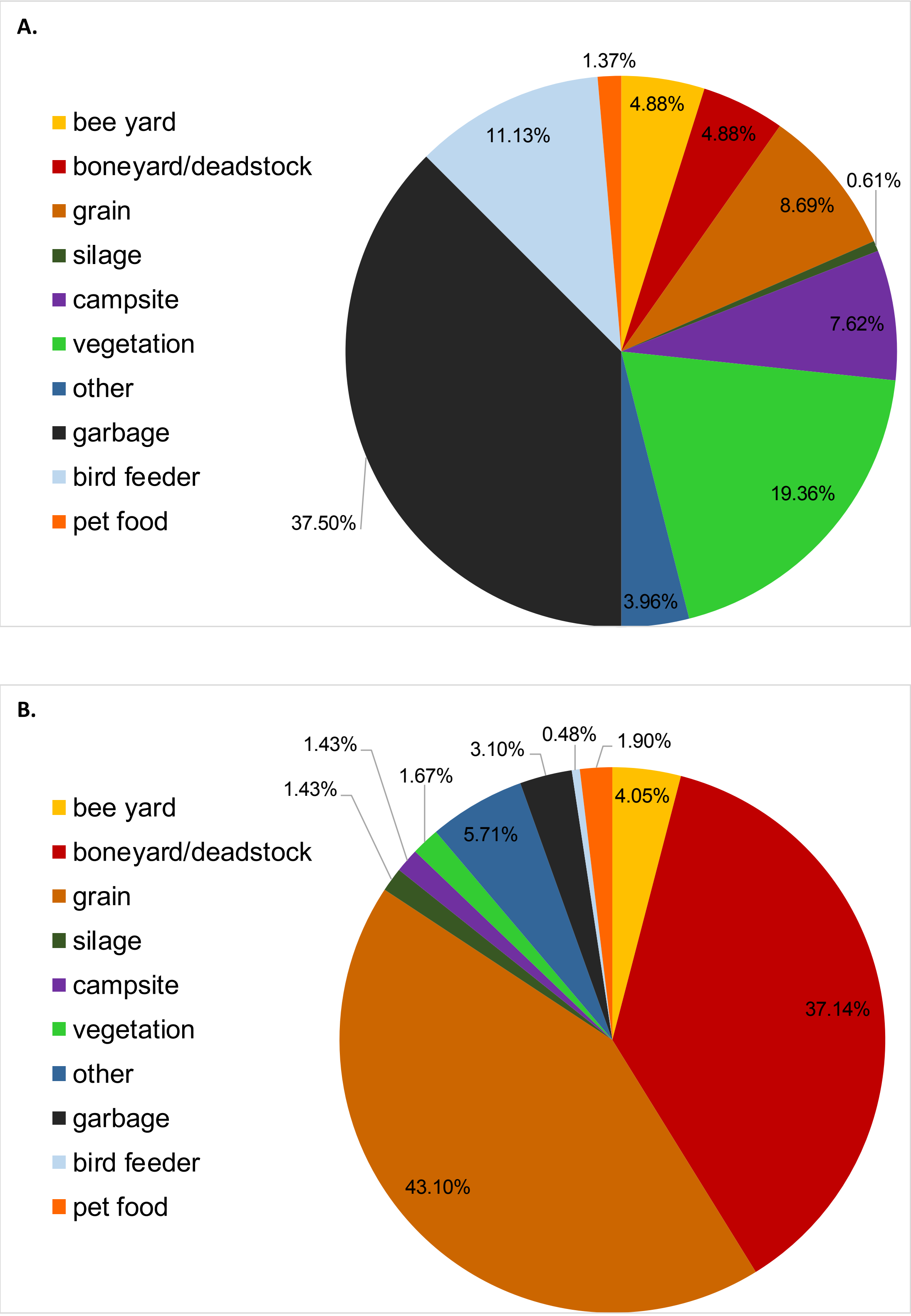

Figure 2.4 Primary attractants for (A) black bear (n = 816) and (B) grizzly bear incidents (n = 420) in occurrence records in southwestern Alberta 1999 – 2014.

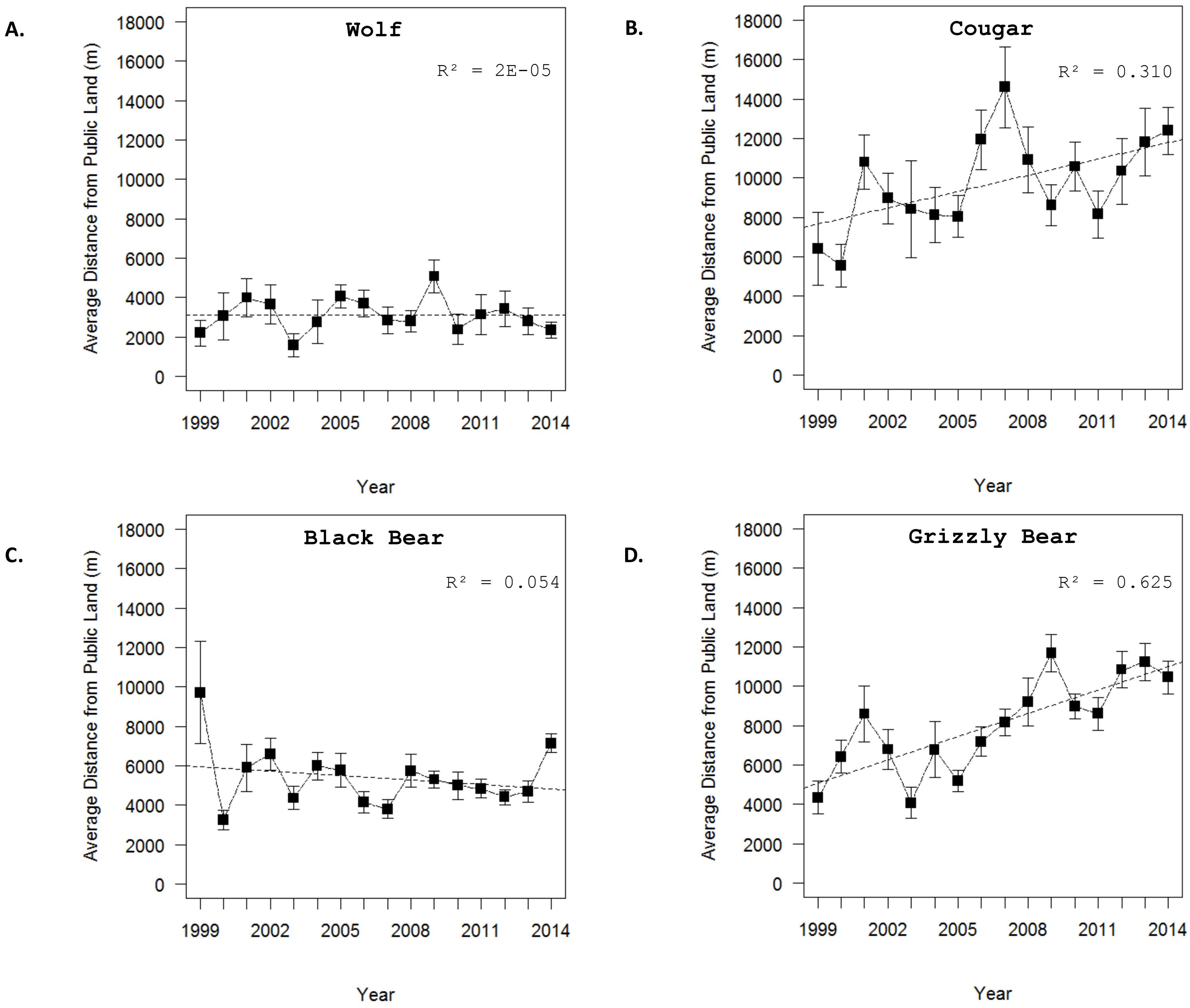

Figure 2.5 Average distance in meters of occurrence records from the public land boundary by species and year.

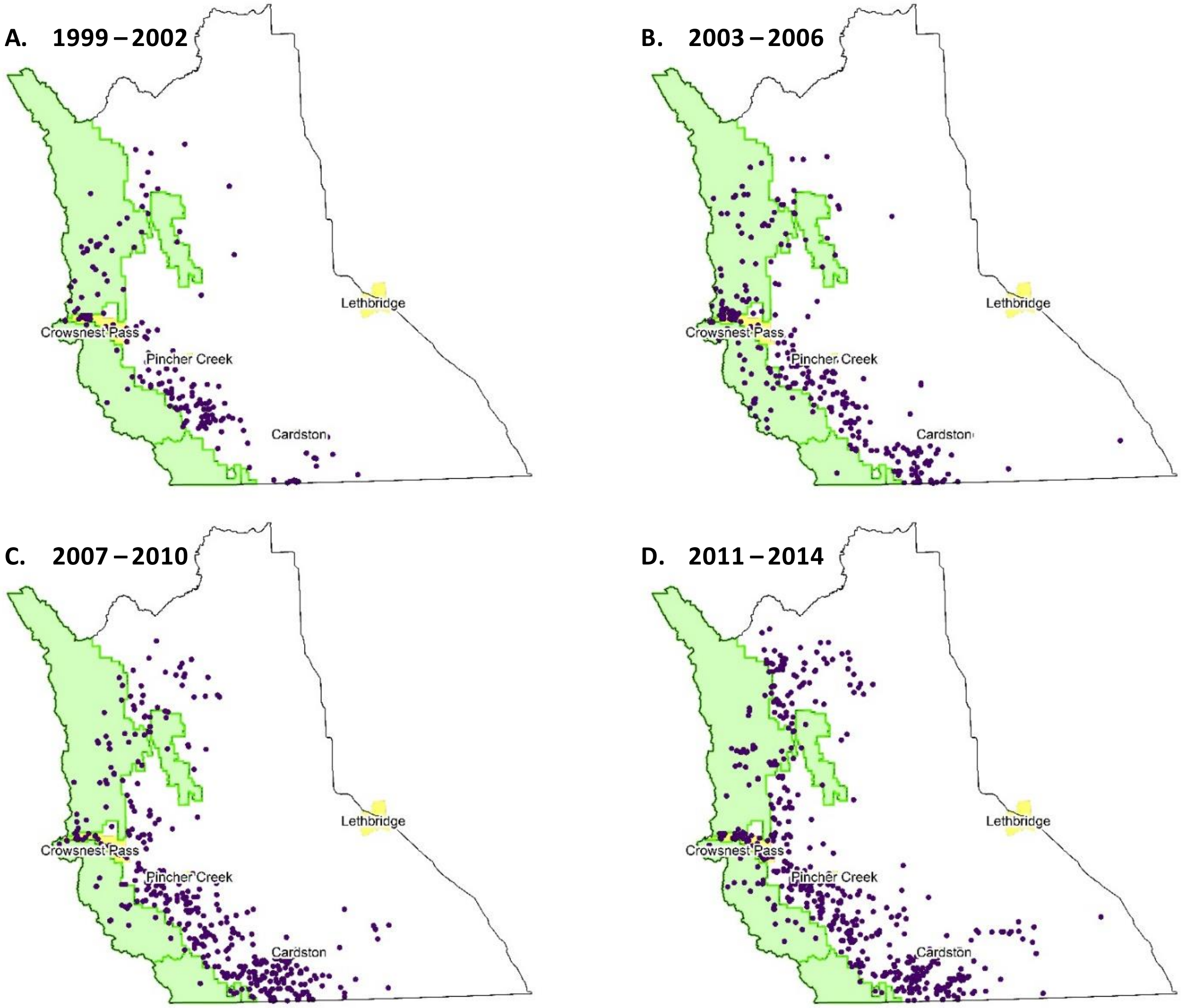

Figure 2.6 Spatial locations of grizzly bear occurrences records in southwestern Alberta 1999 through 2014 grouped in four-year increments. The shaded green area represents the public land portion of the study area.

Figure 2.7 Examples of grain bin damage caused by grizzly bears in my study area. Photo credits clockwise from top left are Andrea Morehouse, Nora Manners, Alberta Environment and Parks/Waterton Biosphere Reserve Association remote trail camera, Spencer Rettler

Chapter 3

3 Grizzly Bears without Borders: Spatially Explicit Capture Recapture in southwestern Alberta

3.1 Introduction

Facilitating coexistence between people and large carnivores in human-settled landscapes is a challenge of contemporary conservation. Reserves and protected areas rarely provide adequate space for wide-ranging carnivores (Hansen and Rotella 2002, Hilty et al. 2006), resulting in substantial overlap between carnivore ranges and human-settled lands (e.g., Woodroffe 2000, Laliberte and Ripple 2004). While this overlap of people and carnivores can be detrimental to the carnivore population and create challenges for humans (e.g., Laliberte and Ripple 2004, Estes et al. 2011, Ripple et al. 2014b), experience in Europe demonstrates that large carnivores can indeed persist and expand in highly developed landscapes given supportive public opinions, protective legislation, and effective conflict mitigation to promote coexistence (Chapron et al. 2014).

In some regions of North America, as in Europe, populations of grizzly bears (also *Ursus arctos*) overlap human-settled and developed areas (e.g., Dood et al. 2006, Alberta Sustainable Resource Development 2008). In Alberta, Canada, grizzly bear home ranges along the Rocky Mountain front overlap multiple land uses creating potential for human-bear conflicts. The last population estimate in Alberta was conducted from 2004 to 2008. Using DNA-based, capture-mark-recapture methods as well as habitat modeling, the Provincial Government estimated a grizzly bear population of 691 in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Based largely on this low estimated population size, increasing human activity and continued development associated with natural resource extraction within grizzly bear habitats, in 2010 Alberta listed the grizzly bear as provincially threatened.

However, public perception of grizzly bear numbers in some regions of Alberta differs from the government's estimate. For example, the last population estimate of 51 grizzly bears in southwestern Alberta occurred in 2007 (Alberta Grizzly Bear Inventory Team 2008). Local residents, however, believe that this estimate is low and they often are encountering grizzly bears in new areas (Quinn and Alexander 2011). Further, grizzly bear conflicts in this region have been increasing for the last 16 years (Chapter 2), and one possible explanation for this increase is an increasing grizzly bear population. This apparent disconnect between local perceptions and provincial-level wildlife management has resulted in frustration within local communities. To most effectively manage the grizzly bear population, a robust, transparent monitoring framework and updated population density and abundance estimates are crucial not only from an ecological standpoint, but also for gaining local confidence in the data – which in turn may ensure more support for management actions.

Estimating grizzly bear population size in southwestern Alberta is challenging for two main reasons. First, the bears are part of a much larger regional population that includes southeastern British Columbia and northern Montana (Proctor et al. 2012). This lack of population closure has confounded the ability to provide meaningful abundance and density estimates. Partitioning an Alberta portion of this inter-jurisdictional grizzly bear population as a separate management unit has no ecological basis. However, because grizzly bears are managed according to provincial and state jurisdictions (Ministry of Environment, Lands and Parks 1995, Dood et al. 2006, Alberta Sustainable Resource Development 2008), there is a need to have population estimates specific to Alberta. Second, grizzly bear life histories and dominance hierarchies (e.g., Craighead et al. 1995, Elfström et al. 2014) also might confound our ability to estimate population size using mark-recapture methods. Mark-recapture estimators assume that marked and unmarked animals are captured randomly (Krebs 2009). Sampling only high-quality habitats (e.g., high resource selection function [RSF] scores) might be biased towards dominant individuals if dominant individuals show higher recapture rates (Fretwell 1969, Kendall and McKelvey 2008). Additionally, seasonal variation in density will not be captured by the typically short survey windows of mark-recapture designs that are used to minimize violation of the closure assumption (Otis et al. 1978, Carretta et al. 1998, Harris et al. 2013). Failure to account for behavioural differences between sexes also could influence population estimates. For example, rub trees are commonly used to estimate abundance (e.g., Stetz et al. 2010, Sawaya et al. 2012), and male bears rub more frequently than do females (Harting et al. 1987).

Here, I use non-invasive genetic sampling across a range of habitats and seasons to estimate grizzly bear density and abundance. I use spatially explicit capture-recapture models (SECR) to estimate the density and abundance of grizzly bears with home range centers in Alberta (i.e., “Alberta bears”) because these numbers are necessary for regional management. However, because southwestern Alberta is a small part of a larger international population, I am interested not only in the number of “Alberta bears,” but also desire an estimate of the total number of grizzly bears using the area. When animals move in and out of the study area, this larger “superpopulation” can be of greater ecological interest than the number of animals estimated to be within the trapping array (Kendall 1999). I wanted to estimate the number of animals using the study area because that number might better represent the bears that local residents are encountering. To do this I use the Chao capture-mark-recapture models (Chao 1987, 1989) to estimate the number of grizzly bears that used the study area at some point during my field surveys, recognizing that this design expands the sampled population substantially into adjacent jurisdictions. Together, these 2 metrics provide updated population information for southwestern Alberta and help to reconcile some of the discrepancies between the past population estimate and local perceptions of grizzly bear numbers.

3.2 Study Area

I studied the grizzly bear population in a 3,600 km^2 area of southwestern Alberta bounded by Highway 3 to the north, British Columbia to the west, Montana to the south, and the approximate edge of current grizzly bear range to the east (Fig. 3.1). Provincially, my study area is known as Bear Management Area 6 (BMA6), and was comprised of two zones, the Recovery Zone (1814 km^2) and the Support Zone (1774 km^2). The Recovery Zone was comprised of predominately public lands and represents the area in which the provincial government explicitly intends to recover grizzly bears (Alberta Environment and Parks 2016). The Support Zone was intended to help maintain grizzly bears with home ranges that were not exclusively contained within the Recovery Zone; road density thresholds that applied in the Recovery Zone (0.6 km/km^2) were relaxed for the Support Zone (0.75 km/km^2) (Alberta Environment and Parks 2016). Grizzly bears in southwestern Alberta also occur outside of the Recovery and Support Zones, but their presence in those areas was not required to meet the objectives of the provincial grizzly bear recovery plan (Alberta Environment and Parks 2016). BMA6 boundaries were modified during the course of my study (Alberta Sustainable Resource Development and Alberta Conservation Association 2010, Alberta Environment and Parks 2016), and as a consequence my sampling included a small area outside of the southeastern corner of the provincial Support Zone.

The study area was a mix of privately owned (60%) and public lands (40%) under the jurisdiction of the Alberta provincial government (Crown land) and the Canadian federal government (Waterton Lakes National Park). A sharp transition from prairies and agricultural land in the east to mountainous terrain in the west characterized the study area; there are limited foothills. Heavy winds, cold winters, and warm dry summers characterized the climate. In addition to grizzly bears, wolves (*Canis lupus*), cougars (*Puma concolor*), and black bears (*Ursus americanus*) also were present. Available native ungulate prey include white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). Domestic cattle (*Bos taurus)* and to a lesser extent domestic sheep (*Ovis aries*) also were present. The region is a multiple-use landscape with uses that include recreation, forestry, and oil and gas production. The predominant land use, however, was agriculture including both livestock and crop production (Statistics Canada, MD of Pincher Creek 2006 Community Profile).

3.3 Methods

3.3.1 Field Methods

I used non-invasive genetic methods to monitor the grizzly bear population in BMA6. Non-invasive genetic sampling for grizzly bears typically involves collecting hair samples from either baited hair-snag corrals (e.g., Woods et al. 1999, Mowat and Strobeck 2000) or bear rub objects (e.g., Kendall et al. 2008, Stetz et al. 2010, Kendall et al. 2015). A rub object is an object such as a tree, power pole or fence post that a bear has rubbed on. As a result of repeated rubbing, the rub object often develops distinguishing characteristics such as a smooth or discolored rub surface, presence of a bear trail, and/or presence of bear hair (Stetz et al. 2010, Sato et al. 2014). Rubbing is a natural bear behaviour; bears will rub on such objects apparently as a form of communication (Green and Mattson 2003, Sato et al. 2014). All rub objects used in my study were either naturally occurring rubs or stretches of barbed wire fence through which bears naturally travelled. I did not use any lures or attractants.

From 2011 through 2014, I identified 899 rub objects across the study area. I trained field crews to identify and survey for rub objects along existing trail networks. On private lands without an existing trail network, I prioritized lands for sampling in a GIS to identify areas with high bear use based on existing RSF models (Northrup et al. 2012b), grizzly bear conflict records, and by working with landowners to identify known travel corridors. I use the term "rub object" loosely because it includes not only objects on which bears rubbed, but also stretches of barbed wire fence that bears traveled along or through. Each rub site was uniquely numbered, and I attached four-pronged barbed wire to the rub object with fencing staples to facilitate hair collection. On fence crossings I marked the specific stretch of fence line to be sampled. I ensured that I had sampling stations within each 7 × 7 km cell of the sampling grid used in the previous 2007 BMA6 grizzly bear population estimate (Alberta Grizzly Bear Inventory Team 2008). Field crews visited rub objects every 3 weeks from approximately late May through mid-November for a total of 8 visits per field season (1st visit to clean, 7 subsequent visits to sample). Each barb/wire end represented a unique sample collection point, and I removed all hairs from barbs/wire ends to ensure that I knew the deposition period for the sample (Kendall et al. 2009, Stetz et al. 2010). I passed a flame over each barb after hair collection to prevent contamination in the next collection cycle (Kendall et al. 2009, Stetz et al. 2010).

Further, to ensure that no hair collection opportunities were missed, to provide a second data source to improve precision of the estimate (Boulanger et al. 2008), and to engage the public, I also allowed for opportunistically collected hair samples (e.g., samples from bears trapped for management purposes, samples collected at bear-conflict sites). I focused opportunistic hair collection on private agricultural lands within the Support Zone. Opportunistic hair samples were collected by field crews, landowners, and Fish and Wildlife Officers who were trained in proper hair-collection methods. Opportunistic samples allowed me to detect bears not detected by my rub-object methods.

The first 2 years of my study (2011 and 2012) were primarily set-up years, and hair samples were collected less frequently. Here, I report on 2013 and 2014 genetic data only.

3.3.2 Genetic Methods

I stored all hair samples in paper coin envelopes with silica desiccant at room temperature until the end of each field season. After each field season, I sent hair samples to Wildlife Genetics International (WGI) to identify species, individual identity, and sex via analysis of nuclear DNA extracted from hair follicles following protocols outlined by Paetkau (2003, 2004). WGI used the G10J marker for species assignment to black bear vs. grizzly bear (Mowat et al. 2005, Kendall et al. 2015). Multi-locus genotyping followed Paetkau's (2004) 3-phase process of first pass, error check, and clean-up using the established 8-locus marker system (7 microsatellites plus the amelogenin marker for sex) for grizzly bears in the southern Rocky Mountain region (Paetkau et al. 1995, Paetkau 2003). After individuals were identified, 1 high-quality sample from each individual was extended to 2 additional microsatellite markers (CXX110 and MU50); these 10-locus genotypes were used for comparisons with South Rockies database to ensure no 1 or 2 mismatch pairs (pairs of samples with genotypes that match at all but 1 or 2 microsatellite markers) were found (Paetkau 2003, Kendall et al. 2008, D. Paetkau, Wildlife Genetics International, unpublished report).

In 2011, I analyzed all hair samples from my project and used these data to evaluate various sub-sampling strategies because analyzing all hair samples from future (2012-2014) field seasons would have been cost prohibitive. In 2011, I found that I most typically detected only 1 bear per rub/date combination. Based on my 2011 data and the recommendation of WGI, I sub-sampled hairs from 2013 and 2014 by genetically analyzing every 3rd hair sample from a given rub/date combination. This sub-sampling strategy allowed me to maximize detections of individuals, while working within my funding constraints. I did not sub-sample opportunistic hair samples. I analyzed samples with ≥ 1 guard hair root or 5 underfur hairs.

3.3.3 Analysis Methods

I used DNA-based grizzly bear encounter histories and spatially explicit capture-mark-recapture (SECR) models to estimate density of grizzly bear home range centers across the study area (Efford et al. 2004, Borchers and Efford 2008, Efford and Fewster 2013, Whittington and Sawaya 2015). SECR models offer advantages over conventional capture-mark-recapture methods because they automatically allow for capture heterogeneity, are more robust to the violation of the population-closure assumption, and derived abundance estimates relate to a specified geographical region (Obbard et al. 2010, Efford and Fewster 2013). SECR fits an observation model and a state model to individual spatial-detection histories (Efford et al. 2009, Efford and Fewster 2013). The observation model describes the decaying probability of detection as a function of the distance between trap (i.e., rub object) location and an animal's home range center. The state model uses a spatial Poisson point process to describe the intensity of animal home range centers in space. I fit each model using a binomial distribution and a hazard half-normal detection function; the parameter λ_0 is the cumulative hazard of detection and is related to the probability of detection at the home-range center via the following equation: $g(d) = 1 - \exp(-\lambda(d))$, where is g is the probability of detection and d is the distance between trap location and an animal's home range center (Efford et al. 2004, Efford et al. 2009).

The parameter σ is the spatial scale parameter of the observation model (Efford et al. 2004, Efford et al. 2009). The state model consists of a single parameter *D* (density) (Efford et al. 2004, Efford et al. 2009). I used the *secr* (version 2.9.5, http://www.otago.ac.nz/density/SECRinR.html, accessed 1 July 2015) package in program R (R Version 3.2.1, https://cran.r-project.org, accessed 1 July 2015) for all data analyses; functions described in the following paragraphs are specific to that package.

I incorporated my opportunistic hair samples into grizzly bear detection histories following procedures similar to the unstructured spatial sampling described by Thompson et al. (2012), and Russell et al. (2012). I considered a grid cell searched if it was visited by my survey crews, Fish and Wildlife Officers, or landowners. Because I could not quantify variation in search effort, I analyzed opportunistic hair samples as though there was a uniform chance that they would arise in each grid cell. In other words, I assumed that the observation process leading to the opportunistic hair samples was approximately uniform, and similar to Mollet et al. (2015), I did not include a covariate for search effort associated with the opportunistic hair samples. I believe this to be a justifiable assumption because field crews traveled consistently within the Support Zone on survey routes. Also, the increased effort represented by the opportunistic samples will affect precision, but not accuracy of SECR estimates (Mollet et al. 2015). All opportunistic hair samples were grouped into a single, separate (8^{th}) occasion as is often done with incidental samples in a traditional capture-mark-recapture design (e.g., Kendall et al. 2009, Kendall et al. 2015) and overlaid on a 7 × 7-km grid that overlapped the Support Zone and a small portion of areas further east that were prone to grizzly bear agricultural conflicts (65 grid cells in total). I used a 7 × 7-km grid because that was the grid cell size determined to be optimal for the 2007 estimate (Alberta Grizzly Bear Inventory Team 2008), and because Thompson et al.

(2012) found that grid cell size did not substantially influence density estimates. I excluded grid cells that were not visited (47 grid cells searched in 2013, and 54 grid cells searched in 2014). Similar to the unstructured spatial sampling methods used by Thompson et al. (2012), Russell et al. (2012), and Mollet et al. (2015), each opportunistic hair sample was assigned to the centroid location of the grid cell in which it fell. Thus, grid centroids became trap locations and were added to my rub object locations in the trap layout file. Rub objects retained their original point locations.

Because there is a male bias in use of rub trees (Harting et al. 1987, Kendall et al. 2008, Clapham et al. 2012) and to allow for complete sex-specificity in all model parameters (Kendall et al. 2015), I estimated abundance of each sex separately, and then combined the estimates to provide a total density and home-range-center abundance estimate for BMA6. I analyzed the 2013 and 2014 data in two ways. First, because I was interested in year-specific estimates of model parameters, I considered each year separately to provide a density estimate for each year. Second, I combined the two years into a single model framework and considered each year a separate session. In the case of the multi-session analysis, I did not allow density to vary across sessions (i.e., years), but rather estimated a single density for the study area. I truncated the capture histories for known dead bears in the appropriate occasion. I did not truncate capture histories for bears relocated long distances (i.e., outside of BMA6) because I have observed that 4 out of 13 of these bears returned to the study area; additional bears might have returned but were not redetected by my sampling. Additionally, I allowed observation model parameters to vary by trap type (*traptype*), time trend (*T*), a trap-specific behavioural response (*bk*), and, in the multi-session analysis, session (*session*). Trap type (*traptype*) was included as a covariate to account for differences in behaviour/sampling; I considered 3 categories for trap type: rub, fence, and opportunistic samples. Because the frequency of rubbing varies between males and females throughout the season (Claphman et al. 2012), I included time trend (*T*) as a linear covariate.

Although I did not use any lure or bait, I included a trap-specific behavioural response (*bk*) because I believed that individual bears might have tree preferences and/or that the decision of a bear to rub might be influenced by the dominance/social hierarchy of other bears in the area. I included *session* in the multi-session analysis to account for differences between years in movements and detection probabilities. Finally, because management agencies were interested in differences in grizzly bear density across public (Recovery Zone) and private (Support Zone) lands, I allowed *D* to vary between the 2 zones (*Zone2*).

I defined the area of integration (i.e., state space) as the area in which my rub objects were located and a surrounding buffer zone; home-range centers can be distributed over this area of integration (Fig. 3.2). The buffer zone needed to be large enough that animals outside the buffer had a low probability of being detected, and thus were unlikely to influence density estimates (Efford and Fewster 2013, Royle et al. 2014). Density estimates are robust to changes in the area of integration provided it is sufficiently large to encompass all animals with a non-negligible probability of capture (Efford and Fewster 2013, Royle et al. 2014). Within *secr,* the mask defines the outer limit to the area of integration (Efford 2016); I used a mask with a buffer of 33 km for males and 18 km for females, or approximately 3 times the Root Pooled Spatial Variance (RPSV), which is a measure of the 2-dimensional dispersion of animal detection locations, around all trap locations. I used the *mask.check* command to ensure that I had selected an appropriate buffer size.

I compared 17 *a priori* models with varying effects on λ_0, σ, and *D* as discussed above for the single year data sets; for the multi-session analysis I compared 28 models. I used Akaike's

Information Criterion corrected for small samples (AIC_c) to identify the most parsimonious model (Burnham and Anderson 2002), and used the AIC_c-weighted average from all models to estimate model parameters (Burnham and Anderson 2004, Burnham et al. 2011). Using the *fxi.contour* command, I plotted the estimated 50% probability density functions and modes for each individual grizzly bear for the 2013 and 2014 AIC_c identified top models (Borchers and Efford 2008). The probability density function of estimated animal home range centres is given by: $f(X_j|\omega_i) = \Pr(\omega_i|X_j)\pi(X_j)$, where $\pi(X)$ is the probability density of range centers across the mask (Borchers and Efford 2008). The plots generated by the *fxi.contour* describe only the likely positions of the home range centers of bears that were detected; they do not include estimated home range centers of the non-detected bears. Additionally, *fxi.contour* plots can be prone to artefacts such as concentric clustering of estimated home range centers around the traps themselves (Efford 2014). I include these plots, however, to illustrate the relationship between estimated home range centers and my study area boundaries as well as differences in estimated home range center locations between years. Finally, I used the model-averaged density estimates from both the year-specific and multi-session models to calculate expected grizzly bear home range center abundance for each sex within the Recovery and Support Zones by multiplying the density estimate (D) by the area of interest. I summed Recovery and Support Zone estimates to provide a total abundance estimate for BMA6.

SECR-derived abundance estimates are representative of the number of bears with home range centers within the study area only and do not represent the number of bears using the study area. When an estimated home range center fell outside the study area, that animal was not counted in the density estimate; thus, it was possible to detect more animals than the estimated population size. I, however, was interested in both the number of resident bears and the number of bears using the study area because bears in my study area are part of a much larger population that includes bears in both British Columbia and Montana. To estimate the number of bears using the study area, I used a traditional capture-mark-recapture (CMR) population model to estimate the population of grizzly bears using the study area at some point during my field sampling. I used Chao's Mh model (Chao 1987) because it has been justified for use in Alberta and British Columbia to estimate bear abundance (e.g., Boulanger et al. 2002, Boulanger et al. 2004, Alberta Grizzly Bear Inventory Team 2008), and has performed well in terms of confidence interval coverage and bias, even with sparse data (Chao 1989, Boulanger et al. 2002, Boulanger et al. 2004). I used the Mh Chao model to estimate the number of male and female grizzly bears that used the study area at some point during each year. I then combined these sex-specific estimates for a total year-specific estimate of the number of grizzly bears using my study area. The area of integration (Fig. 3.2) for my SECR models identifies the area over which home range centers can be distributed. Bears outside the area of integration have a negligible probability of detection, and as such, I might expect that my CMR estimate samples bears from within this area. However, because I cannot explicitly define the area for which the CMR estimate applies, I cannot estimate density from my CMR models.

3.4 Results

In 2013, I sent 4,554 hair samples (4,179 rub object and 375 opportunistic) to WGI for analysis. I collected, but did not send to WGI, an additional 93 hair samples because they were clearly not bear hair (e.g., ungulate or cattle). Of the 4,554 hair samples sent, WGI excluded 38.5% (*n* = 1755) based on my sub-selection rules and 16.1% (*n* = 732) due to inadequate material. Of the 2,067 hair samples remaining, 45.6% (*n* = 942) were black bear, 25.1% (*n* = 518) failed either during the G10J pre-screen or mutli-locus analysis, 0.7% (*n* = 14) were non-bear, and 0.05% (*n* = 1) produced mixed results. WGI assigned the remaining 592 hair samples to 118 individual grizzly bears (66 males, 52 females).

In 2014, I sent 3,912 hair samples (3,597 rub object and 315 opportunistic) to WGI for analysis (42 additional non-bear hairs were collected but not sent). WGI excluded 38.3% (*n* = 1499) of my hair samples based on my sub-selection rules, and 4.4% (*n* = 562) due to inadequate material. Of the 1,851 hair samples remaining, 41% (*n* = 758) were black bear, 29.4% (*n* = 544) failed either during the G10J pre-screen or multi-locus analysis, 0.6% (*n* = 12) were non-bear, and 0.2% (*n* = 3) produced mixed results. WGI assigned the remaining 534 hair samples to 103 individual grizzly bears (62 males, 41 females). Between 2013 and 2014 I identified 164 grizzly bears; I detected 64 of these bears in both years. Of these 164 grizzly bears, 84 had previously been detected through past projects in either British Columbia or Montana (D. Paetkau, Wildlife Genetics International, unpublished report).

In 2013, I had 902 sampling stations (855 operational rub objects, and 47 opportunistic grid cells). In 2014, I had 927 sampling stations (873 operational rub objects, and 54 opportunistic grid cells). I detected grizzly bears at 40.1% (*n* = 369) and 36.8% (*n* = 341) of my sampling stations in 2013 and 2014 respectively (Table 3.1). I detected male grizzly bears more frequently than females, and male detections were highest in the early part of my sampling season in both years (Table 3.1). I had 301 detections of 66 male grizzly bears in 2013, and 280 detections of 62 males grizzly bears in 2014 (Table 3.1, Fig. 3.3). I had 114 detections of 52 female grizzly bears in 2013 and 84 detections of 41 female grizzly bears in 2014 (Table 3.1, Fig. 3.3).

For the 2013 data, the top model for females included effects of trap type and a trap-specific behavioural response on λ_0 and was 2.6 times more supported than the next best model

(Table 3.2). For males, the top-supported model included effects of trap type on both λ_0 and σ, and a trap-specific behavioural response on λ_0, and was 1.55 times more supported than the next best model (Table 3.2). In 2014, the top female model included a trap-specific behavioural response and trap-type effects on λ_0 and trap-type effect on σ; the top model was 3.89 times more supported than the next-best model (Table 3.3). The 2014 top model for males included time trend over occasions for both σ and $\lambda_{0,}$ and effects of trap type and a trap-specific behavioural response on λ_0 (Table 3.3). For both sexes, although I allowed density to vary across Recovery and Support Zones, the inclusion of this covariate explained little additional variance (Table 3.2, Table 3.3), and density estimates were generally similar between zones.

My model-averaged estimate of female grizzly bear density in 2013 was 14.9 per 1,000 km^2 (95% CI 10.8 – 20.6) in the Recovery Zone and 13.6 per 1,000 km^2 (95% CI 9.3 – 19.9) in the Support Zone (Table 3.4). My 2014 model-average female grizzly bear density estimate was 9.0 per 1,000 km^2 (95% CI 6.5 – 12.5) in the Recovery Zone and 8.5 per 1,000 km^2 (95% CI 5.9 – 12.3) in the Support Zone (Table 3.4). Male grizzly bear density was 9.2 per 1,000 km^2 (95% CI 6.9 – 12.3) in the Recovery Zone and 8.1 per 1,000 km^2 (95% CI 5.5 – 12.0) in 2013 (Table 3.4). In 2014, the model-averaged male grizzly bear density estimate was 7.2 per 1,000 km^2 (95% CI 5.3 – 9.8) in the Recovery Zone and 5.7 per 1,000 km^2 (95% CI 3.5 – 9.3) in the Support Zone (Table 3.4). Expected total number of home-range centers within BMA6 was 82.4 (95% CI 58.5 – 116.2) in 2013 and 54.6 (95% CI 38.0 – 78.7) in 2014 (Table 3.5).

In 2013, probability density functions for detected females indicated smaller confidence intervals for detected females than detected males, and estimated home-range centers for these detected females were located throughout the study area (Fig. 3.4A). Estimated home-range centers for detected males were often outside my study area (Fig. 3.4A). In 2014, detected female home-range center estimates were primarily on the western or eastern edge of my study area (Fig. 3.4B).

For the multi-session models where I did not allow density to vary between years, the top female model included the covariate trap type on both λ_0 and σ, as well as a trap-specific behavioural response and effect of zone on λ_0 (Table 3.6). The top multi-session model for male bears included the covariates trap type, time trend over occasions, session and a trap-specific behavioural response on λ_0. Model-averaged female density was estimated to be 12.4 grizzly bears per 1,000 km^2 (95% CI 9.3 – 16.5) in the Recovery Zone and 10.0 per 1,000 km^2 (95% CI 6.8 – 14.7) in the Support Zone (Table 3.4). Model-averaged estimated male grizzly bear density was 8.0 per 1,000 km^2 (95% CI 6.5 – 9.9) in the Recovery Zone and 7.1 per 1,000 km^2 (95% CI 5.3 – 9.7) in the Support Zone (Table 3.4). The expected number of grizzly bear home range centers within BMA6 was 67.4 (95% CI 50.0 – 91.1) (Table 3.5).

Using the traditional CMR model, I estimated 68.9 (95% CI 58.4 – 97.2) female and 102.6 (95% CI 81.2 – 154.2) male grizzly bears used the study area in 2013. In 2014, I estimated that 63.0 (95% CI 48.9 – 102.6) female and 108.6 (95% CI 80.8 – 177.0) male grizzly bears used the study area (Table 3.7).

3.5 Discussion

My density and abundance estimates of grizzly bears with home range centers in Alberta varied between 2013 and 2014; density estimates for both males and females were higher in 2013 than in 2014. Using the model-averaged multi-session models I estimate a density of 20.4 grizzly bears/1,000 km^2 (95% CI 15.7 – 26.4 grizzly bears/1,000 km^2) in the Recovery Zone and 17.1 grizzly bears/1,000 km^2 (95% CI 12.1 – 24.4 grizzly bears/1,000 km^2) in the Support Zone within the Bear Management Area encompassing southwestern Alberta (BMA6). The multi-session density estimate assumes a constant density between years and translates to an abundance estimate of 67.4 (95% CI 50.0 – 91.1) grizzly bears with home range centers located within BMA6 (i.e., resident "Alberta bears"). When density was modeled for each year, I estimated 82.4 (95% CI 58.5 – 116.2) resident "Alberta bears" in 2013 and 54.6 (95% CI 38.0 – 78.7) resident "Alberta bears" in 2014.

My estimates of the number of grizzly bears using the study area, however, varied little between years and were much larger because Alberta is a small portion of a larger international population of grizzly bears. I estimated approximately 172 grizzly bears used the study area each year (2013 females 68.9 (SE = 9.0), males 102.6 (SE = 17.3); 2014 females 63.0 (SE = 12.4), males 108.6 (SE = 22.7)). These numbers better represents exposure to the number of individual bears that local communities could encounter; these estimates also represent the total number of grizzly bears with the potential to become involved in conflicts with human land practices in southwestern Alberta.

Prior to my research, the most recent population information for BMA6 came from a 2007 study in which 27 individual bears were detected and the estimated population size was 51 grizzly bears, or a density of 18.1 bears/1,000 km^2 (95% CI 12.1 – 30.6) (Alberta Grizzly Bear Inventory Team 2008). It should be noted, however, that these density estimates were derived rather than directly estimated as is done in SECR. If I assume that the 2007 abundance estimate of 51 grizzly bears is comparable to my model-averaged multi-session SECR abundance estimate of 67 resident bears, this would indicate a 4% per year population increase since 2007 – though there is overlap of the confidence intervals. Detection probability, however, was low in the 2007 estimate and the majority of grizzly bear detections were spatially clustered along the British

Columbia Border (Fig. 2 in Alberta Grizzly Bear Inventory Team 2008). From other data sources (Chapter 2), I know that grizzly bears were present across the study area during the 2007 sampling period indicating that the 2007 estimate might have been affected by false absences (MacKenzie et al. 2002). False absences can influence model and parameter estimates (MacKenzie 2006), and low detection probabilities can increase standard errors (Mackenzie et al. 2002). Indeed, the 95% confidence interval for the 2007 estimate was 34 to 87 grizzly bears in BMA6 (Alberta Grizzly Bear Inventory Team 2008), and detection probability in this BMA was the lowest in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association 2010).

CMR and SECR estimators are likely to give different estimates of density and abundance (Obbard et al. 2010, Gerber and Parmenter 2015, Whittington and Sawaya 2015). Ad-hoc CMR estimates of density can be higher than SECR density estimates likely because of a failure to fully account for animal movement off the sampling gird (Obbard et al. 2010, Gerber et al. 2012, Noss et al. 2012, Rich et al. 2014). For example, in 2007 Alberta and British Columbia were simultaneously sampled, and the CMR density estimate for the British Columbia portion of the grid was 55 bears/1,000 km^2 (Alberta Grizzly Bear Inventory Team 2008). However, when these data were reanalyzed using SECR, the density estimate was 40% lower and estimated to be only 33 bears/1,000 km^2 (Efford and Mowat, 2014). The Alberta 2007 abundance estimate was completed using a lured design and traditional CMR methods corrected for closure, whereas I estimated resident bear abundance using rub objects and SECR. Thus, I would expect uncertainty around my estimate of per annum growth because of differences in the analysis methods.

Regardless of the potential error in the 2007 estimate or alternative estimation methods, it is apparent that the grizzly bear population in southwestern Alberta has not declined since the

2007 estimate, and is instead stable to increasing. Because southwestern Alberta grizzly bears are part of a larger international population, the dynamics of the bear population is influenced by adjacent jurisdictions. Indeed, over 50% of the grizzly bears that I detected had been detected previously in either British Columbia or Montana, highlighting the international and inter-provincial connectivity of this population. The bordering Flathead Population Unit in British Columbia, for example, had an estimated grizzly bear density of 33 grizzly bears per 1,000 km^2 (Efford and Mowat 2014). Grizzly bear density in Glacier National Park was estimated to be 30 bears per 1,000 km^2 (Kendall et al. 2008). In Montana, estimates indicate that the grizzly bear population in the Northern Continental Divide Ecosystem (NCDE) is growing approximately 3% per year (Mace et al. 2012). My results suggest that the population is growing at a rate similar to Montana (Mace et al. 2012), which helps to explain the large number of grizzly bears that local residents are encountering and the increased abundance estimates since the previous 2007 survey.

The Alberta grizzly bear recovery plan requires BMA-specific population estimates; bears, however, do not respect such boundaries. I believe that the decrease in my resident bear density estimates between 2013 and 2014 reflects a shift in habitat use by grizzly bears. Clearly the population of grizzly bears did not decline by 34% from 2013 to 2014, but rather the home range centers of the animals shifted. Because SECR estimates the density of animal home range centers and not the density of animals, when a home range center falls outside the area of interest the density estimate will be lower. This is not the case for traditional CMR models; indeed, my CMR model estimates were remarkably similar between 2013 and 2014. The home range centers of individual bears vary over time; animal home ranges can change in response to changes in food supply and environmental conditions (e.g., Ferguson et al. 1999, McLoughlin and Ferguson 2000, McLoughlin et al. 2003). Relative to 2013, berry production in 2014 appeared to be poor in southwestern Alberta. Conversely, the adjacent Flathead Valley of British Columbia had its first good huckleberry crop after over a decade of poor productivity (McLellan 2015, and Bruce McLellan, British Columbia Ministry of Natural Resource Operations, unpublished data). Although I do not have sufficient data to verify that changes in berry crop were the cause, grizzly bears in my study spent more outside Alberta during 2014. Grizzly bear home range size is often related to food availability; home ranges tend to be smaller in more productive areas (McLoughlin and Ferguson 2000, McLoughlin et al. 2003, Nilsen et al. 2005). In times of food shortage, bears may increase their movement and space use to acquire the necessary caloric intake (Craighead 1976, Gittleman and Harvey 1982, Blanchard and Knight 1991). If this shift in habitat use resulted in the bear's home range center being located in a neighboring jurisdiction that lowers the density estimate for my study area, while simultaneously increasing density estimates in neighboring jurisdictions.

I believe the shifting of home range centers is an important result emerging from my analysis that needs to be brought to the attention of people using SECR models. Failure to account for such trans-border movements can have serious implications for population monitoring and management (Bischof et al. 2015). Recent work in Norway, for example, found that failing to account for detections of non-resident bears (i.e., double counting across jurisdictions) inflated abundance estimates by as much as 119% (Bischof et al. 2015). My results highlight the importance of multi-year monitoring at an ecologically appropriate scale.

In this region, however, the ecologically appropriate scale is quite large. Recent genetic work by Proctor et al. (2012) revealed interbreeding among grizzly bears in the southern Rocky Mountain subpopulation within an area defined by Highway 3 to the north, the Rocky Mountain

Trench to the west, the southern end of the Bob Marshall Wilderness to the south, and the eastern edge of grizzly bear range to the east (Proctor et al. 2012, Fig. 19). In recent years, Alberta, Montana, and British Columbia have all used similar non-invasive genetic methods to monitor grizzly bears (e.g., Alberta Grizzly Bear Inventory Team 2008, Kendall et al. 2009, Stetz et al. 2010). Ideally, monitoring methods and timing would be standardized across jurisdictions so that the population could be monitored collaboratively at a larger scale relevant to the biology of the bears (Proctor et al. 2012). From a management perspective, however, such boundaries might be considered too large and impractical.

Under the current management plans, there is still a need for area managers to have information that is specific to the bear management area of interest. In this context, I believe SECR offers a useful tool. Monitoring and analyzing the data at a larger scale would allow for more informed models of density and abundance. Because SECR is a spatial model, jurisdiction-specific information could be extracted after the regional analysis was complete. Monitoring at an ecologically appropriate scale would help overcome some of the issues that have plagued past population models (e.g., lack of closure, incomplete detection histories, etc.), while an inter-jurisdictional SECR analysis would allow for better informed information to be obtained.

Animal behaviour and life history traits have the potential to influence how likely an individual is to be detected (O'Connell et al. 2006). For example, dominant individuals might have higher recapture rates (Fretwell 1969, Kendall and McKelvey 2008); this problem could be exacerbated in baited designs, or those sampling exclusively in highest-quality habitats. Thus, rather than attempting to lure bears into a specific location, I let bear presence dictate my sampling locations. However, not every bear uses rub objects, and male grizzly bears are more likely to rub than female grizzly bears, particularly in the early season. Thus, I also included opportunistically collected hair samples, providing an important second data source and allowed me to detect 39 bears that were not detected at my rub objects. Additionally, opportunistic hair samples provided an opportunity to directly engage the community and regional Fish and Wildlife agency staff in my research.

Local knowledge was important not only in the collection of opportunistic hair samples, but also in helping to identify areas of bear activity and presence on private lands. Detection probabilities can be influenced by habitat, site-specific conditions, sampling effort, and density (Bailey et al. 2004, Gu and Swihart 2004, Smith et al. 2007, Haynes et al. 2013); the best (i.e., accurate and precise) results are obtained when capture probability is high (Lukacs and Burnam 2005). If sampling stations are placed in areas not frequented by bears, I would expect fewer bears to be detected. My surveys on private land were done largely in consultation with the landowner and this information supplemented survey areas I had *a priori* identified through use of various GIS data layers; I believe my surveys were improved by the incorporation of local knowledge. Local ecological knowledge can provide valuable insights to contemporary field ecology (Berkes 2004, Moller et al. 2004, Service et al. 2014), and engaging communities in research and management can help to facilitate long-term coexistence between people and large carnivores (Redpath et al. 2013). Not only can local knowledge improve data collection (e.g., Huntington 2000, Zukowski et al. 2011, Service et al. 2014), but engaging stakeholders in the collection of data also helps to establish mutual trust – which is an important component to the successful conceptualization of ecosystem conservation and management (Berkes 2004).

3.6 Management Implications

Alberta's BMA6 is small in area (3,600 km^2) relative to the area of the larger Rocky Mountain population including Alberta, British Columbia, and Montana (~35,000 km^2) in which this international grizzly bear population lives (Proctor et al. 2012); grizzly bears move freely across these geographical boundaries. Because SECR estimates the density of home range centers in an area, changes from one year to another can reflect a shift in animal home range centers rather than a change in overall population density – particularly in areas where the boundaries of the monitoring area do not align with the ecological boundaries of the population being monitored. Thus, I recommend multi-year monitoring at an ecologically appropriate scale. Further, both resident and non-resident bears have the potential to be involved in conflict. Several tools are available to help mitigate conflict between grizzly bears and human land-use activities (e.g., electric fencing, bear-proof grain bin doors, etc.). When making management decisions regarding the allocation of resources to help prevent conflicts, both the number of resident bears and the number of bears using the area should be considered.

Finally, because the ecological boundaries of the grizzly bear population are large, I recommend increased coordination across jurisdictions. Currently, three management plans govern the same grizzly bear population (Ministry of Environment, Lands and Parks 1995, Dood et al. 2006, Alberta Environment and Parks 2016). In British Columbia, there is a limited-entry hunting season on grizzly bears (Ministry of Environment, Lands and Parks 1995). By contrast, in Montana, the grizzly bear is listed as threatened under the United States Endangered Species Act, and has been since 1975 (United States Fish and Wildlife Service 1993), and likewise the species is classified as threatened under the provincial Wildlife Act in Alberta. Clearly, inter-jurisdictional grizzly bear management would be more pertinent for this trans-boundary grizzly bear population.

Table 3.1 Grizzly bear detections from non-invasive genetic sampling in 2013 and 2014 within southwestern Alberta, Canada.

Year	Occasion	Number of Sampling Stations[a]	# of Sampling Stations Detecting a Grizzly Bear		Hair Collection Dates[b]	Number of New Grizzly Bears		Number of Individuals Detected		Number of Detections	
			M	F		M	F	M	F	M	F
2013	1	804	58	1	June 17 – July 7	21	1	21	1	61	1
	2	813	52	13	July 8 – July 28	8	13	17	13	52	14
	3	809	31	16	July 29 – August 18	7	9	17	14	32	16
	4	828	13	11	August 19 – September 8	4	2	12	9	16	11
	5	836	34	14	September 9 – September 29	3	5	16	13	36	17
	6	846	37	10	September 30 – October 20	7	6	18	8	37	11
	7	776	25	18	October 21 – November 8	1	4	15	14	25	18
	8[c]	47	20	16	March 18 – November 19	15	12	32	24	42	26
			270	99		66	52			301	114

Table 3.1 Continued

2014	1	861	76	4	June 16 – July 6	30	3	30	3	80	4
	2	871	50	8	July 7 – July 27	5	6	19	6	50	8
	3	869	36	8	July 28 – August 17	3	7	15	9	36	9
	4	869	13	4	August 18 – September 7	3	2	11	3	13	4
	5	870	23	13	September 8 – September 28	6	4	15	9	23	13
	6	872	35	12	September 29 – October 19	6	2	21	9	36	12
	7	867	23	10	October 20 – November 9	1	2	11	9	24	10
	8[c]	54	14	12	April 1 – October 28	8	15	17	21	18	24
			270	71		62	41			280	84

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[a] Number of sampling stations varied for a variety of reasons including: tree fell due to wind, new rub object was set-up, rub object inaccessible due to flooding (particularly in 2013), rub object inaccessible due to avalanche, etc.

[b] Rub objects were visited 8 times over the field season for a total of 7 sampling occasions. The first visit cleaned the rub objects and started May 25th. Hair could have been deposited any time during the 3-weeks prior to the listed collection dates.

[c] Occasion 8 includes only opportunistic hair samples; all opportunistic samples were pooled into a single occasion.

Table 3.2 Model selection results for 17 fitted models ranked by Akaike's Information Criterion corrected for small samples (AIC_c) for 2013 grizzly bear density in southwestern Alberta. I fit models using the hazard half-normal detection function. Effects on λ_0 and σ included trap type (traptype), time (T), and a trap-specific behavioural response (bk). Density (D) was allowed to vary across Recovery and Support Zones (Zone2).

Sex	Model	K[a]	LL[b]	AIC_c	ΔAIC_c[c]	w_i[d]
Female	D~1 λ_0~traptype + bk σ~1	6	-604.97	1223.81	0.00	0.52
	D~Zone2 λ_0~traptype + bk σ~1	7	-604.60	1225.74	1.93	0.20
	D~1 λ_0~traptype + bk + T σ~T	8	-603.85	1227.05	3.24	0.10
	D~1 λ_0~traptype + bk σ~traptype	8	-604.05	1227.44	3.63	0.09
	D~Zone2 λ_0~traptype + bk σ~traptype	9	-603.05	1228.40	4.58	0.05
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-603.45	1229.19	5.37	0.04
	D~1 λ_0~traptype σ~1	5	-624.45	1260.21	36.40	0.00
	D~1 λ_0~traptype σ~traptype	7	-622.11	1260.77	36.96	0.00
	D~1 λ_0~T * traptype σ~T * traptype	13	-619.24	1274.06	50.25	0.00
	D~1 λ_0~1 σ~traptype	5	-635.62	1282.55	58.74	0.00
	D~1 λ_0~T σ~1	4	-664.52	1337.90	114.09	0.00
	D~1 λ_0~T σ~T	5	-664.42	1340.15	116.34	0.00
	D~1 λ_0~1 σ~T	4	-668.89	1346.62	122.81	0.00
	D~1 λ_0~bk σ~1	4	-670.87	1350.60	126.79	0.00
	D~Zone2 λ_0~bk σ~1	5	-669.98	1351.26	127.45	0.00

Table 3.2 Continued

	D~1 λ_0~1 σ~1	3	-687.27	1381.04	157.23	0.00
	D~Zone2 λ_0~1 σ~1	4	-686.46	1381.77	157.96	0.00
Male	D~1 λ_0~traptype + bk σ~traptype	8	-1716.70	3451.94	0.00	0.45
	D~Zone2 λ_0~traptype + bk σ~traptype	9	-1715.82	3452.85	0.92	0.29
	D~1 λ_0~traptype + bk + T σ~T	8	-1717.52	3453.56	1.63	0.20
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-1717.36	3455.93	3.99	0.06
	D~1 λ_0~traptype σ~traptype	7	-1729.82	3475.57	23.63	0.00
	D~1 λ_0~traptype + bk σ~1	6	-1731.31	3476.05	24.11	0.00
	D~1 λ_0~T * traptype σ~T * traptype	13	-1721.76	3476.52	24.59	0.00
	D~Zone2 λ_0~traptype + bk σ~1	7	-1731.30	3478.54	26.60	0.00
	D~1 λ_0~1 σ~traptype	5	-1743.21	3497.43	45.49	0.00
	D~1 λ_0~traptype σ~1	5	-1747.48	3505.96	54.02	0.00
	D~1 λ_0~bk σ~1	4	-1816.35	3641.36	189.43	0.00
	D~Zone2 λ_0~bk σ~1	5	-1815.30	3641.61	189.67	0.00
	D~1 λ_0~T σ~T	5	-1825.74	3662.48	210.54	0.00
	D~1 λ_0~1 σ~T	4	-1827.23	3663.12	211.19	0.00
	D~1 λ_0~1 σ~1	3	-1830.16	3666.71	214.78	0.00
	D~Zone2 λ_0~1 σ~1	4	-1829.18	3667.02	215.08	0.00
	D~1 λ_0~T σ~1	4	-1829.65	3667.96	216.03	0.00

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[a] Number of model parameters.

[b] Log likelihood

[c] Difference in AIC$_c$ score compared with smallest AIC$_c$ score

[d] AIC$_c$ model weight.

Table 3.3 Model selection results for 17 fitted models ranked by Akaike's Information Criterion corrected for small samples (AIC$_c$) for 2014 grizzly bear density in southwestern Alberta. I fit models using the hazard half-normal detection function. Effects on λ_0 and σ included trap type (traptype), time (*T*), and a trap-specific behavioural response (*bk*). Density (*D*) was allowed to vary across Recovery and Support Zones (*Zone2*).

Sex	Model	K^a	LL^b	AIC$_c$	ΔAIC$_c^c$	w_i^d
Female	D~1 λ_0~traptype + bk σ~traptype	8	-440.41	901.32	0.00	0.74
	D~Zone2 λ_0~traptype + bk σ~traptype	9	-440.12	904.04	2.72	0.19
	D~1 λ_0~traptype σ~traptype	7	-444.67	906.74	5.43	0.05
	D~1 λ_0~1 σ~traptype	5	-448.54	908.80	7.49	0.02
	D~1 λ_0~traptype + bk + T σ~T	8	-450.55	921.60	20.29	0.00
	D~1 λ_0~T * traptype σ~T * traptype	13	-441.76	923.00	21.69	0.00
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-450.52	924.85	23.54	0.00
	D~1 λ_0~traptype + bk σ~1	6	-455.39	925.25	23.94	0.00
	D~Zone2 λ_0~traptype + bk σ~1	7	-455.38	928.16	26.84	0.00
	D~1 λ_0~traptype σ~1	5	-464.73	941.17	39.86	0.00
	D~1 λ_0~1 σ~T	4	-496.10	1001.31	100.00	0.00
	D~1 λ_0~T σ~T	5	-495.82	1003.35	102.04	0.00
	D~1 λ_0~T σ~1	4	-499.20	1007.51	106.19	0.00
	D~Zone2 λ_0~bk σ~1	5	-512.95	1037.62	136.31	0.00
	D~1 λ_0~bk σ~1	4	-514.76	1038.64	137.32	0.00

Table 3.3 Continued

	D~Zone2 λ_0~1 σ~1	4	-519.65	1048.42	147.11	0.00
	D~1 λ_0~1 σ~1	3	-521.30	1049.24	147.93	0.00
Male	D~1 λ_0~traptype + bk + T σ~T	8	-1695.05	3408.81	0.00	0.52
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-1693.77	3408.99	0.18	0.48
	D~1 λ_0~T * traptype σ~T * traptype	13	-1697.80	3429.19	20.38	0.00
	D~1 λ_0~traptype + bk σ~traptype	8	-1719.00	3456.71	47.90	0.00
	D~Zone2 λ_0~traptype + bk σ~traptype	9	-1717.63	3456.72	47.91	0.00
	D~1 λ_0~traptype + bk σ~1	6	-1725.87	3465.27	56.46	0.00
	D~Zone2 λ_0~traptype + bk σ~1	7	-1724.98	3466.03	57.22	0.00
	D~1 λ_0~1 σ~traptype	5	-1728.16	3467.39	58.58	0.00
	D~1 λ_0~traptype σ~traptype	7	-1726.01	3468.09	59.28	0.00
	D~1 λ_0~traptype σ~1	5	-1733.70	3478.47	69.66	0.00
	D~1 λ_0~T σ~T	5	-1738.50	3488.08	79.27	0.00
	D~1 λ_0~T σ~1	4	-1744.00	3496.70	87.89	0.00
	D~1 λ_0~bk σ~1	4	-1746.73	3502.17	93.36	0.00
	D~Zone2 λ_0~bk σ~1	5	-1746.61	3504.30	95.49	0.00
	D~1 λ_0~1 σ~1	3	-1753.85	3514.12	105.31	0.00
	D~1 λ_0~1 σ~T	4	-1752.72	3514.15	105.34	0.00
	D~Zone2 λ_0~1 σ~1	4	-1753.71	3516.11	107.30	0.00

[a] Number of model parameters. [b] Log likelihood

[c] Difference in AIC_c score compared with smallest AIC_c score [d] AIC_c model weight.

Table 3.4 Model-averaged real parameter estimates for 2013, 2014, and multi-session models for male and female grizzly bears in southwestern Alberta (BMA6). Expected number of detections at the home-range center (λ_0) is given for initial detection (bk_0) and for previously detected individuals (bk_1) for each trap type. The spatial scale parameter (σ) is reported in kilometers. Time trend over occasions (T) is T = 0 for reported values of λ_0 and σ.

Year	Sex	Zone	Density (bears/1000 km^2)	SE	95% CI	λ_0 (SE)[a]	σ (SE)
2013	F	Recovery	14.9	2.5	10.8 – 20.6	traptype$_r$bk$_0$: 0.008 (0.003)	traptype$_r$: 4.4 (0.6)
		Support	13.6	2.7	9.3 – 19.9	traptype$_r$bk$_1$: 0.115 (0.052)	traptype$_f$: 4.7 (0.9)
						traptype$_f$bk$_0$: 0.012 (0.006)	traptype$_o$: 4.6 (0.9)
						traptype$_f$bk$_1$: 0.181 (0.107)	
						traptype$_o$bk$_0$: 0.312 (0.164)	
						traptype$_o$bk$_1$: 4.657 (3.167)	
2013	M	Recovery	9.2	1.4	6.9 – 12.3	traptype$_r$bk$_0$: 0.016 (0.004)	traptype$_r$: 7.7 (0.4)
		Support	8.1	1.6	5.5 – 12.0	Traptype$_r$bk$_1$: 0.069 (0.030)	traptype$_f$: 10.2 (2.4)
						traptype$_f$bk$_0$: 0.010 (0.008)	traptype$_o$: 12.3 (4.1)
						traptype$_f$bk$_1$: 0.042 (0.043)	

Table 3.4 Continued

						traptype$_{o}$bk$_{0}$: 0.166 (0.253)	
						traptype$_{o}$bk$_{1}$: 0.728 (1.405)	
2013	Total	Recovery	24.2		17.8 – 32.9		
		Support	21.7		14.8 – 31.9		
2014	F	Recovery	9.0	1.5	6.5 – 12.5	traptype$_{r}$bk$_{0}$: 0.027 (0.008)	traptype$_{r}$: 3.2 (0.3)
		Support	8.5	1.6	5.9 – 12.3	traptype$_{r}$bk$_{1}$: 0.108 (0.056)	traptype$_{f}$: 8.0 (3.2)
						traptype$_{f}$bk$_{0}$: 0.004 (0.005)	traptype$_{o}$: 10.8 (2.2)
						traptype$_{f}$bk$_{1}$: 0.015 (0.025)	
						traptype$_{o}$bk$_{0}$: 0.086 (0.039)	
						traptype$_{o}$bk$_{1}$: 0.350 (0.305)	
2014	M	Recovery	7.2	1.1	5.3 – 9.8	traptype$_{r}$bk$_{0}$: 0.030 (0.005)	traptype$_{r}$: 9.4 (0.6)
		Support	5.7	1.4	3.5 – 9.3	traptype$_{r}$bk$_{1}$: 0.124 (0.036)	traptype$_{f}$: 9.4 (0.6)
						traptype$_{f}$bk$_{0}$: 0.036 (0.011)	traptype$_{o}$: 9.4 (0.6)
						traptype$_{f}$bk$_{1}$: 0.146 (0.060)	
						traptype$_{o}$bk$_{0}$: 0.733 (0.286)	
						traptype$_{o}$bk$_{1}$: 2.99 (1.450)	

Table 3.4 Continued

2014	Total	Recovery	16.2		11.8 – 22.3		
		Support	14.2		9.4 – 21.6		
Multi-Session	F	Recovery	12.4	1.8	9.3 – 16.5	session$_{13}$traptype$_{r}$bk$_{0}$: 0.015 (0.003)	session$_{13}$traptype$_{r}$: 3.5 (0.3)
		Support	10.0	2.0	6.8 – 14.7	session$_{13}$traptype$_{r}$bk$_{1}$: 0.137 (0.034)	session$_{13}$traptype$_{f}$: 7.2 (1.3)
						session$_{13}$traptype$_{f}$bk$_{0}$: 0.007 (0.003)	session$_{13}$traptype$_{o}$: 8.4 (1.2)
						session$_{13}$traptype$_{f}$bk$_{1}$: 0.058 (0.031)	session$_{14}$traptype$_{r}$: 3.5 (0.3)
						session$_{13}$traptype$_{o}$bk$_{0}$: 0.123 (0.038)	session$_{14}$traptype$_{f}$: 7.2 (1.3)
						session$_{13}$traptype$_{o}$bk$_{1}$: 1.085 (0.484)	session$_{14}$traptype$_{o}$: 8.4 (1.2)
						session$_{14}$traptype$_{r}$bk$_{0}$: 0.154 (0.003)	
						session$_{14}$traptype$_{r}$bk$_{1}$: 0.136 (0.034)	
						session$_{14}$traptype$_{f}$bk$_{0}$: 0.006 (0.003)	
						session$_{14}$traptype$_{f}$bk$_{1}$: 0.057 (0.031)	
						session$_{14}$traptype$_{o}$bk$_{0}$: 0.122 (0.038)	
						session$_{14}$traptype$_{o}$bk$_{1}$: 1.077 (0.479)	

Table 3.4 Continued

Multi-Session	M	Recovery	8.0	0.9	6.5 – 9.9	session$_{13}$traptype$_{r}$bk$_{0}$: 0.027 (0.004)	session$_{13}$traptype$_{r}$: 8.1 (0.5)
		Support	7.1	1.1	5.3 – 9.7	session$_{13}$traptype$_{r}$bk$_{1}$: 0.127 (0.026)	session$_{13}$traptype$_{f}$: 8.1 (0.5)
						session$_{13}$traptype$_{f}$bk$_{0}$: 0.031 (0.007)	session$_{13}$traptype$_{o}$: 8.1 (0.5)
						session$_{13}$traptype$_{f}$bk$_{1}$: 0.147 (0.042)	session$_{14}$traptype$_{r}$: 8.6 (0.5)
						session$_{13}$traptype$_{o}$bk$_{0}$: 0.933 (0.231)	session$_{14}$traptype$_{f}$: 8.6 (0.5)
						session$_{13}$traptype$_{o}$bk$_{1}$: 4.454 (1.381)	session$_{14}$traptype$_{o}$: 8.6 (0.5)
						session$_{14}$traptype$_{r}$bk$_{0}$: 0.025 (0.003)	
						session$_{14}$traptype$_{r}$bk$_{1}$: 0.118 (0.024)	
						session$_{14}$traptype$_{f}$bk$_{0}$: 0.029 (0.007)	
						session$_{14}$traptype$_{f}$bk$_{1}$: 0.137 (0.039)	
						session$_{14}$traptype$_{o}$bk$_{0}$: 0.869 (0.221)	
						session$_{14}$traptype$_{o}$bk$_{1}$: 4.148 (1.304)	
Multi-Session	Total	Recovery	20.4		15.7 – 26.4		
		Support	17.1		12.1 – 24.4		

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^{a}traptype$_{r}$ refers to rub, traptype$_{f}$ refers to fence, traptype$_{o}$ refers to opportunistic.

Table 3.5 Expected N and associated CI's of the expcted number of home range centers within each management zone. Estimates are derived from model-averaged density estimates.

		Recovery Zone		Support Zone		BMA6	
Year	Sex	Expected N	95% CI	Expected N	95% CI	Expected N	95% CI
2013	F	27.0	19.6 - 37.3	24.1	16.5 - 35.2	51.2	36.1 - 72.5
	M	16.8	12.6 - 22.3	14.4	9.7 - 21.3	31.2	22.3 - 43.6
	Total	43.8	32.2 - 59.6	38.6	26.3 - 56.6	82.4	58.5 - 116.2
2014	F	16.3	11.7 - 22.6	15.1	10.4 - 21.8	31.4	22.2 - 44.4
	M	13.1	9.6 - 17.9	10.1	6.2 - 16.4	23.2	15.8 - 34.3
	Total	29.4	21.4 - 40.5	25.2	16.6 - 38.3	54.6	38.0 - 78.7
Multi-Session[a]	F	22.4	16.8 - 30.0	17.7	12.1 - 26.1	40.2	28.9 - 56.1
	M	14.5	11.7 - 17.9	12.7	9.4 - 17.1	27.2	21.1 - 35.1
	Total	36.9	28.5 - 47.9	30.4	21.4 - 43.2	67.4	50.0 - 91.1

[a] The multi-session model uses data from both 2013 and 2014, but density was not allowed to vary across years

Table 3.6 Model selection results for 28 fitted multi-session models ranked by Akaike's Information Criterion corrected for small samples (AICc) for 2013 and 2014 grizzly bear density in southwestern Alberta. I fit models using the hazard half-normal detection function. Effects on λ_0 and σ included trap type (traptype), time (*T*), session (*session),* and a trap-specific behavioural response (*bk*). Density (*D*) was allowed to vary across Recovery and Support Zones (*Zone2*).

Sex	Model	K[a]	LL[b]	AIC$_c$	ΔAIC$_c$[c]	w_i[d]
Female	D~Zone2 λ_0~traptype + bk σ~traptype	9	-1050.25	2120.68	0.00	0.50
	D~1 λ_0~traptype + bk σ~traptype	8	-1051.75	2121.21	0.53	0.38
	D~1 λ_0~traptype + bk + session σ~traptype	9	-1051.70	2123.58	2.90	0.12
	D~1 λ_0~traptype + bk + T σ~T	8	-1059.88	2137.47	16.80	0.00
	D~1 λ_0~traptype + bk σ~1	6	-1063.09	2139.15	18.48	0.00
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-1059.61	2139.40	18.72	0.00
	D~1 λ_0~traptype + bk + T + session σ~1	8	-1060.91	2139.53	18.85	0.00
	D~1 λ_0~traptype + bk + session σ~1	7	-1062.84	2140.99	20.31	0.00
	D~Zone2 λ_0~traptype + bk σ~1	7	-1062.92	2141.16	20.49	0.00
	D~1 λ_0~traptype + bk + T + session σ~session	9	-1060.90	2141.97	21.30	0.00
	D~1 λ_0~traptype + bk + T + session σ~T + session	10	-1059.70	2142.08	21.41	0.00

Table 3.6 Continued

D~Zone2 λ_0~traptype + bk + session σ~1	8	-1062.68	2143.06	22.39	0.00
D~1 λ_0~traptype σ~traptype	7	-1072.88	2161.08	40.41	0.00
D~1 λ_0~T * traptype σ~T * traptype	13	-1067.71	2166.02	45.35	0.00
D~1 λ_0~1 σ~traptype	5	-1089.59	2189.86	69.19	0.00
D~1 λ_0~traptype σ~1	5	-1092.02	2194.72	74.05	0.00
D~1 λ_0~traptype + session σ~1	6	-1091.91	2196.80	76.13	0.00
D~1 λ_0~T σ~T	5	-1164.36	2339.42	218.74	0.00
D~1 λ_0~T σ~1	4	-1165.55	2339.55	218.87	0.00
D~1 λ_0~T + session σ~1	5	-1165.53	2341.75	221.07	0.00
D~1 λ_0~1 σ~T	4	-1167.37	2343.19	222.51	0.00
D~1 λ_0~T + session σ~T + session	7	-1164.08	2343.47	222.79	0.00
D~Zone2 λ_0~bk σ~1	5	-1184.89	2380.46	259.79	0.00
D~1 λ_0~bk σ~1	4	-1187.56	2383.57	262.90	0.00
D~Zone2 λ_0~1 σ~1	4	-1207.78	2424.01	303.34	0.00
D~1 λ_0~1 σ~1	3	-1210.21	2426.68	306.01	0.00
D~1 λ_0~session σ~1	4	-1210.16	2428.78	308.10	0.00

Table 3.6 Continued

	D~1 λ_0~1 σ~session	4	-1210.20	2428.86	308.19	0.00
Male	D~1 λ_0~traptype + bk + T + session σ~T + session	10	-3423.33	6868.54	0.00	0.44
	D~Zone2 λ_0~traptype + bk + T σ~T	9	-3424.85	6869.23	0.69	0.31
	D~1 λ_0~traptype + bk + T σ~T	8	-3426.24	6869.70	1.16	0.2471
	D~1 λ_0~traptype + bk + T + session σ~session	9	-3432.53	6884.59	16.045	0.00
	D~1 λ_0~traptype + bk + T + session σ~1	8	-3435.90	6889.01	20.47	0.00
	D~1 λ_0~T * traptype σ~T * traptype	13	-3436.76	6902.72	34.18	0.00
	D~Zone2 λ_0~traptype + bk σ~traptype	9	-3445.21	6909.95	41.41	0.00
	D~1 λ_0~traptype + bk σ~traptype	8	-3447.66	6912.534	43.99	0.00
	D~1 λ_0~traptype + bk + session σ~traptype	9	-3447.56	6914.65	46.11	0.00
	D~1 λ_0~traptype σ~traptype	7	-3467.46	6949.86	81.32	0.00
	D~1 λ_0~traptype + bk σ~1	6	-3469.50	6951.70	83.15	0.00
	D~Zone2 λ_0~traptype + bk σ~1	7	-3468.88	6952.70	84.16	0.00
	D~1 λ_0~traptype + bk + session σ~1	7	-3469.28	6953.49	84.95	0.00
	D~Zone2 λ_0~traptype + bk + session σ~1	8	-3468.65	6954.51	85.97	0.00
	D~1 λ_0~1 σ~traptype	5	-3481.03	6972.55	104.01	0.00

Table 3.6 Continued

D~1 λ_0~traptype σ~1	5	-3493.00	6996.50	127.96	0.00
D~1 λ_0~traptype + session σ~1	6	-3492.63	6997.96	129.42	0.00
D~1 λ_0~bk σ~1	4	-3569.93	7148.19	279.65	0.00
D~Zone2 λ_0~bk σ~1	5	-3569.67	7149.83	281.29	0.00
D~1 λ_0~T + session σ~T + session	7	-3574.91	7164.75	296.21	0.00
D~1 λ_0~T σ~T	5	-3578.17	7166.83	298.29	0.00
D~1 λ_0~1 σ~session	4	-3586.42	7181.16	312.62	0.00
D~1 λ_0~T σ~1	4	-3587.79	7183.91	315.37	0.00
D~1 λ_0~T + session σ~1	5	-3587.27	7185.04	316.50	0.00
D~1 λ_0~1 σ~1	3	-3590.59	7187.37	318.83	0.00
D~1 λ_0~session σ~1	4	-3590.08	7188.48	319.94	0.00
D~Zone2 λ_0~1 σ~1	4	-3590.38	7189.08	320.53	0.00
D~1 λ_0~1 σ~T	4	-3590.39	7189.11	320.57	0.00

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[a] Number of model parameters.

[b] Log likelihood

[c] Difference in AIC$_c$ score compared with smallest AIC$_c$ score

[d] AIC$_c$ model weight.

Table 3.7 Sex-specific estimates of the number of grizzly bears using the study area in southwestern Alberta as estimated from Chao's Mh traditional capture-mark-recapture population model for 2013 and 2014.

Year	Sex	$\hat{N}$	SE	LCL	UCL
2013	F	68.9	9.0	58.4	97.2
	M	102.6	17.3	81.2	154.2
Total		171.5			
2014	F	63.0	12.4	48.9	102.6
	M	108.6	22.7	80.8	177.0
Total		171.6			

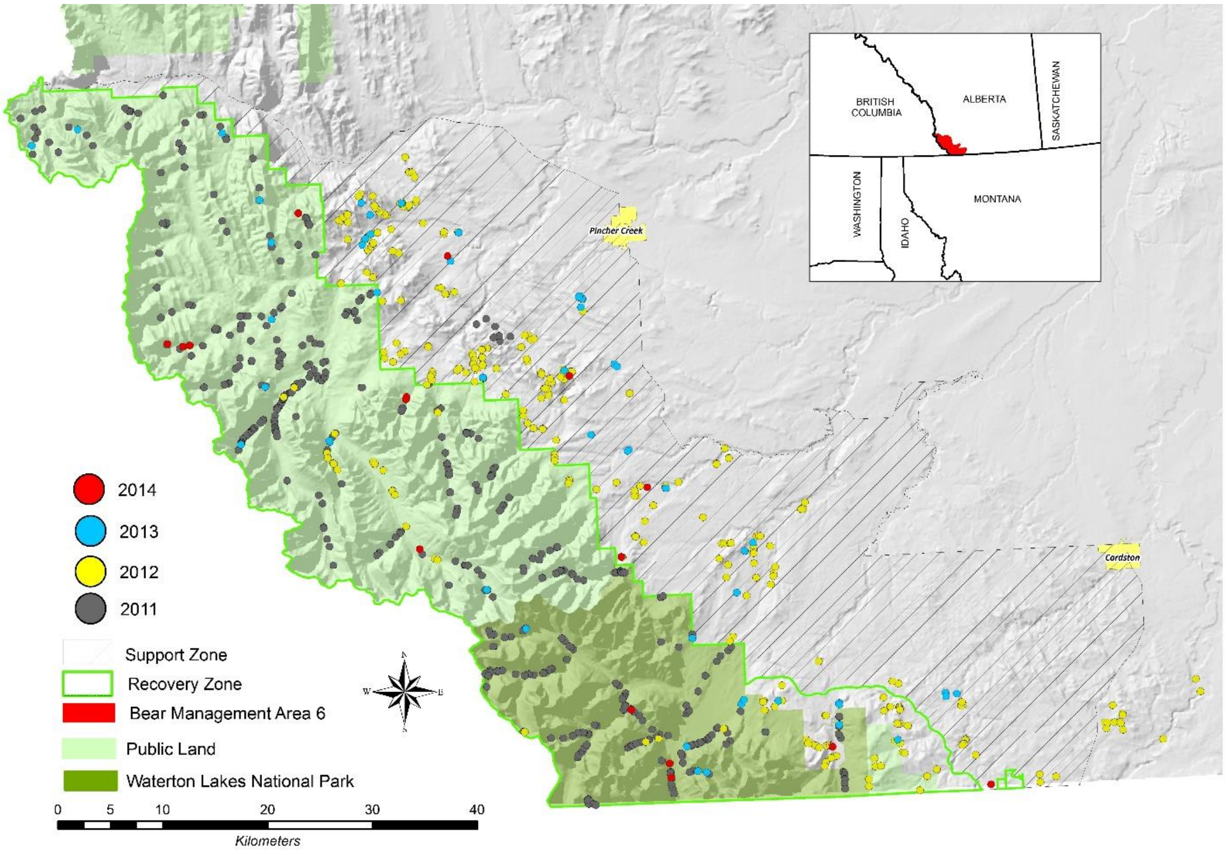

Figure 3.1 The study area for non-invasive genetic monitoring of grizzly bears in southwestern Alberta, Canada. Colors correspond to the year in which the rub object was set-up for inclusion in my project. Together, the Recovery Zone and Support Zone comprise Bear Management Area 6 (BMA6) (i.e., the study area).

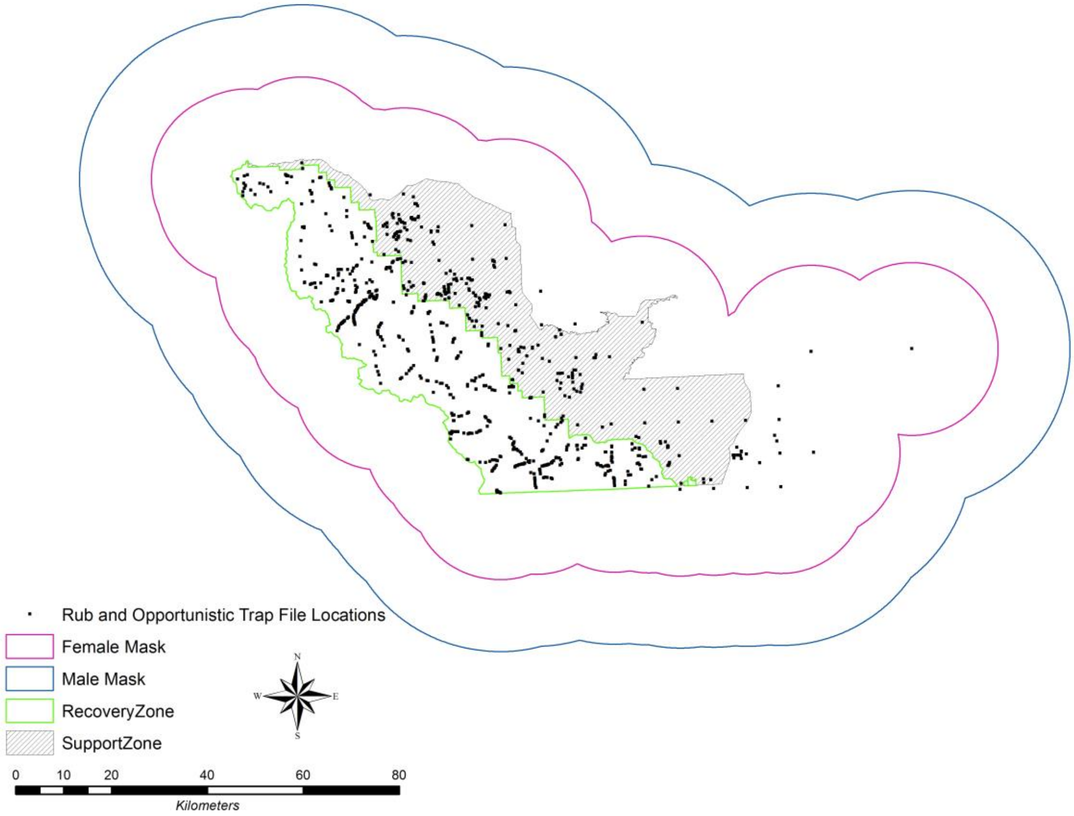

Figure 3.2 The area of integration used for males and females in the year-specific and multi-session SECR models of grizzly bear density in southwestern Alberta.

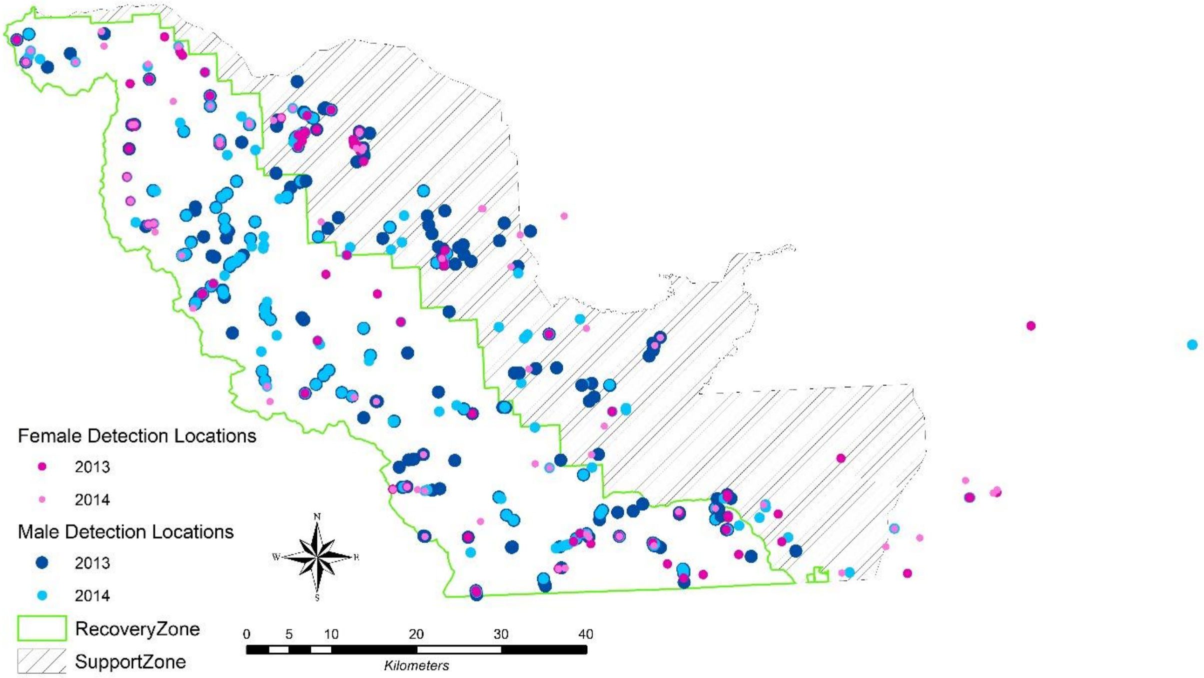

Figure 3.3 Detection locations of female and male grizzly bears in southwestern Alberta by year. There were 301 detections of 66 male grizzly bears and 115 detections of 52 female grizzly bears in 2013, and 280 detections of 62 male grizzly bears and 84 detections of 41 female grizzly bears in 2014.

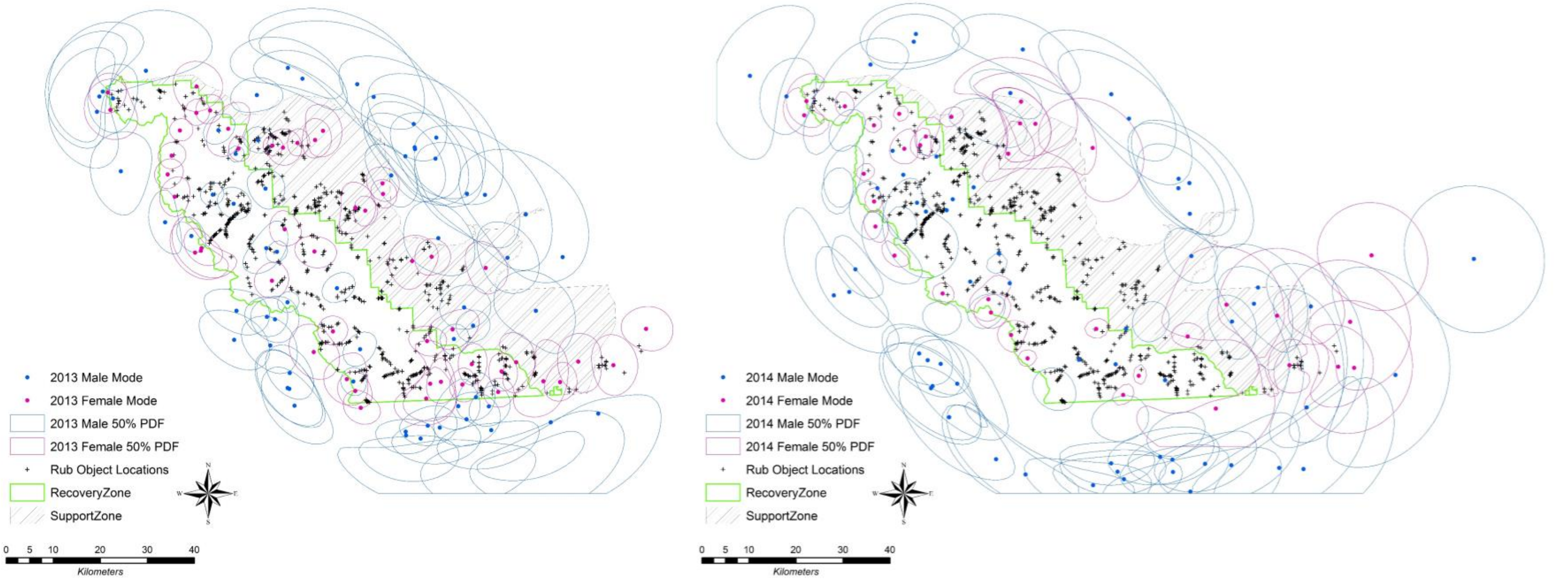

Figure 3.4 Estimated 50% probability density functions and home range center modes for the top AIC$_c$ selected model for detected female (pink) and male (blue) grizzly bears in southwestern Alberta for 2013 (A) and 2014 (B). Estimated home range centers for non-detected grizzly bears are not included in these plots.

Chapter 4

4 Male Dominance Interferes with Intercept Feeding of Grizzly Bears

4.1 Introduction

Supplemental feeding programs have been used globally for a variety of species to reduce damage to crops (e.g., Geisser and Reyer 2004) and forestry operations (e.g., Ziegltrum 2006, Sullivan and Klenner 1993), decrease collisions with vehicles and/or trains (e.g., Andreassen et al. 2005, Milner et al. 2014), and as a conflict mitigation tool (e.g., Mason and Bodenchuk 2002, Kavčič et al. 2013). For bears, the most controversial use of supplemental feeding has been for conflict mitigation (Kavčič et al. 2015). Previous research has found mixed results regarding supplemental feeding and human-bear conflicts; some studies report decreased damages and conflicts (e.g., Partridge et al. 2001, Mason and Bodenchuk 2002, Rogers 2011), while others have suggested that it is an ineffective conflict mitigation tool (e.g., Kavčič et al. 2013, Steyaert et al. 2014) because conflicts persisted despite supplemental food sources.

Supplemental provisioning can be intentional (e.g., roe deer feeding stations, Rauer et al. 2003) or unintentional consequences of management (e.g., bear use of roe deer feeding stations, Rauer et al. 2003). Such programs can result in increases in abundance (e.g., Moris et al. 2011), survival (e.g., Seward et al. 2013), and productivity (e.g., Angerbjörn et al. 1991, Robb et al. 2008), which, if the goal is to reduce human-bear conflicts, might be contrary to the program's intent. Additionally, social structure within bear populations might further complicate the intent of supplemental provisioning. For example, males are the dominant sex among grizzly bears (*Ursus arctos*) and they typically use the highest-quality habitats and food resources, excluding less-dominant bears such as females and sub-adults (Craighead et al. 1995). Indeed, dominant male grizzly bears are known to defend food resources excluding subordinate individuals from these sites (e.g., Gende and Quinn 2004, Elfström et al. 2014).

Alternatively, females often avoid areas frequented by dominate males because of the risk of intra-specific killing, to which females with cubs are particularly vulnerable (Swenson et al. 2001a, Swenson et al. 2001b, McLellan 2005). Sexually selected infanticide (SSI) is well documented for some carnivore species (e.g., Packer et al. 2009), but its existence amongst grizzly bears is debated (e.g., Miller et al. 2003, Swenson 2003, McLellan 2005). If SSI operates in grizzly bears it is most likely to occur where male grizzly bears kill cubs to gain breeding opportunities with their mother (McLellan 2005). Females, particularly sows with cubs, might avoid supplemental feeding sites because of the risk of predation of their cubs by males (e.g., Rode et al. 2006, Steyaert et al. 2013). Thus, dominance hierarchies and the potential influence of SSI predict that supplemental provisioning sites are likely to be used primarily by a small number of dominant male bears.

Access to high-quality food resources, however, is particularly important for sows with cubs (Farley and Robbins 1995, Ben-David et al. 2004). Thus, females must continue to search for nutrient-rich food resources outside of supplemental feeding sites. Low-elevation areas typically offer the first available food resources for bears in the spring (Hamer and Herrero 1987, Mace et al. 1999). In southwestern Alberta, Canada, low-elevation areas are predominately human-settled lands used for agriculture that host a variety of attractants, potentially resulting in grizzly bear-agricultural conflicts (Chapter 2). Bears are commonly believed to frequent human-settled areas because of habituation and food conditioning (McCullough 1982, Beckmann and Berger 2003, Herrero et al. 2005). However, these might be proximate rather than ultimate mechanisms underlying grizzly bear-human conflicts (Elfström et al. 2014). Species rely on multiple cues to assess habitat quality, and species distribution patterns are, in part, a result of habitat selection decisions by individuals to maximize their fitness (Gaillard et al. 2010). For example, Fretwell and Lucas (1970) defined two alternative models of species distribution: the ideal free (IFD) and ideal despotic distributions (IDD). The IDD model predicts the exclusion of subordinate individuals from the highest-quality resources (Fretwell 1972). In combination, the IDD and SSI hypotheses could result in a biased sex/age ratio in lower-quality habitats. If human-settled areas represent lower-quality habitats (e.g., Elfström et al. 2014), the IDD would predict a higher proportion of females and young males occupying these habitats accounting for a higher proportion of human-grizzly bear conflicts.

In southwestern Alberta, conflicts between grizzly bears and agriculture are primarily related to attractants, and the predominant attractants are grain and boneyards (i.e., dead stock piles) (Chapter 2). The increased prevalence of boneyards is an unintentional consequence of changes in dead stock disposal regulations (Northrup and Boyce 2012), and has resulted in an abundance of high-quality food available to bears. While boneyards are an unintended food source, an intentional provisioning program also exists in southwestern Alberta. In an effort to keep grizzly bears in the mountains to reduce spring livestock predation, the provincial government initiated a diversionary feeding program wherein road-killed ungulate carcasses were slung via helicopter to locations where bears were likely to encounter them upon emergence from their dens - thereby “intercepting” bears and keeping them off lower-elevation agricultural lands during the livestock-calving season. Carrion can be an important spring food resource for grizzly bears (Servheen 1983), and the proportion of meat in a grizzly bear’s diet is correlated with body mass, litter size, and population density (Hilderbrand et al. 1999). Because grizzly bear population density is affected by the availability of high-quality food sources

(McLellan 2011), the intercept-feeding program, along with access to boneyards, might be acting to inflate the local grizzly bear carrying capacity. The grizzly bear population in southwestern Alberta is growing (Chapter 3), and an increased population might result in increased conflicts.

Alberta's intercept-feeding program was initiated in 1998, but the effectiveness in reducing spring grizzly bear predation of livestock remains unknown. Other regions of the world have found supplemental feeding of bears to be expensive and might not ultimately reduce depredation events (Kavčič et al. 2013). Here, I evaluate the efficacy of the provincial intercept-feeding program for reducing spring grizzly bear depredation of livestock. Specifically, I evaluate the following predictions: 1) intercept-feeding sites are predominately used by males, whereas spring grizzly bear-agricultural conflicts are female dominated; 2) because of dominance hierarchies, the intercept-feeding sites will be used by only a few individuals relative to the entire population of grizzly bears; and 3) grizzly bears using the intercept-feeding sites should not be the same individuals detected at spring grizzly bear-agricultural conflict locations.

4.2 Study Area

I evaluated the provincial intercept-feeding program in the southwestern corner of Alberta. The program occurs within the area known provincially as Bear Management Area 6 (BMA6). BMA6 is bounded by Highway 3 to the north, British Columbia to the west, and Montana to the south. The eastern extent was loosely defined by the edge of grizzly bear range. This region of the province is characterized by a stark interface between forested mountainous terrain to the west and private agricultural lands to the east, and is home to the highest grizzly bear density in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association 2010, Chapter 3). Strong winds shape the landscape; cold winters and warm dry summers describe the climate. In addition to grizzly bears, other large carnivores include, black bears (*U. americanus*), cougars (*Puma concolor*), and wolves (*Canis lupus*). Aside from grizzly bears, which are provincially threatened, populations of the other large carnivores are considered to be secure within the province. Wild ungulates include mule deer, (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*). Agriculture is the predominant land use on private lands (Statistics Canada, MD of Pincher Creek 2006 Community Profile). Domestic cattle (*Bos taurus*) are the predominant livestock in the area, and calving is typically between January and May.

4.3 Methods

4.3.1 Grizzly Bear Intercept-Feeding Sites

Grizzly bear intercept-feeding locations were chosen by the provincial government and were to meet the following conditions: more than 400m from 2 wheel-drive roads, more than 5km from residences, and relatively high elevation (Government of Alberta, unpublished data). However, these conditions were not always met. For example, in 2012 and 2013, 4 of the 12 sites were less than 5km from residences. Average site elevation in 2012 and 2013 was 1676 m (SE = 37 m). Road-killed ungulates were collected starting in October and stored in sea-can shipping containers until the spring carcass drops. Deer were the most frequent road-killed ungulate, but elk and moose were used also. Road-killed ungulate carcasses were slung via helicopter to specified locations, and these drops of carcasses were made once in March and once in April.

In 2012 and 2013, I collected grizzly bear hair samples non-invasively at 12 intercept-feeding sites (Fig. 4.1). Two additional sites were used as carcass drop sites, but due to difficult access could not be monitored safely. At each site, I attached barbed wire using fencing staples to two trees that were in close proximity to the drop site. Prior to the first drop, I sprayed each tree with WD40 to elicit a rub response. Hair accumulated until the second drop, at which point hair was collected, and the tree sprayed again. Hair was allowed to accumulate for approximately 5 weeks after the second carcass drop and then collected for a second time. I used nuclear DNA extracted from hair follicles to identify species, individual identity, and sex following protocols outlined by Paetkau (2003, 2004). Because age cannot be determined from hair samples and I cannot distinguish an old male bear from a young male bear, I am making the assumption that male grizzly bears are more dominant than female grizzly bears. I tracked the number of carcasses distributed at each site in 2012 and 2013. I used average live weights of Alberta ungulates from the literature (Schladweiler and Stevens 1973, Renecker and Samuel 1991, Stelfox 1993, Cook 2002, Hudson and Haigh 2002, Schwartz 2007) to estimate the biomass of carcasses distributed.

I compared the number of bears detected at intercept-feeding sites to those detected at natural rub objects throughout the study area from my concurrent grizzly bear monitoring program (Chapter 3). The number of bears detected in my larger monitoring program represents the number of bears that used BMA6 at some point over the sampling period of May through mid-November. A full explanation of sampling methods for the larger monitoring program can be found in Chapter 3.

Additionally, at each site I deployed up to 3 remote trail cameras. Trail cameras were pointed at each artificial rub tree as well as the carcass drop site. I reviewed trail cameras to identify grizzly bear presence at each feeding site as well as family groups (i.e., sows with cubs). Male grizzly bears are more likely to exhibit rubbing behaviour than females (Harting et al. 1987, Kendall et al. 2008, Clapham et al. 2012), and I used the trail cameras to determine if my genetic sampling methods were missing females with cubs. I used a combination of Reconyx (PC900 HyperFire, PC85 Rapidfire Pro, Silent Image), Bushnell (Trophy Cam 119405), and UWAY (Vigilant Hunter VH200B, HCO Scoutguard SG550) cameras.

4.3.2 Tracking Grizzly Bear Conflicts

I tracked grizzly bear conflicts using the provincial database of complaint records maintained by the Solicitor General of Alberta. When an individual has a complaint about a grizzly bear, the record is recorded as a text summary in an electronic database. I read through 16 years of grizzly bear complaint records from 1999 (beginning of the electronic database) through spring 2015, and used the following terms (Hopkins et al. 2010, Chapter 2) to classify each occurrence:

1) Sighting: seemingly unaware of the person, no observable stress related response during the interaction;

2) *Incident:* property damage, obtained anthropogenic food, killed or attempted to kill livestock or pets, or involved in a vehicle collision; or

3) *Human Conflict:* physical contact with person or was intentionally harmed or killed by the person. Human conflict records can include both legal and illegal harvest of carnivores.

Further details on my categorization of complaint data can be found in Chapter 2. Here I consider not only total occurrences, but also specifically spring grizzly bear complaint records, which I defined as March 1st through June 15th. I included only those records with location information, and mapped all occurrence records in a GIS. I excluded any records that fell outside my study area. I focused my analysis on grizzly bear incidents because those represent true interactions between grizzly bears and human activities. Incident records were grouped as property damage, livestock, attractant, and other (Chapter 2).

I tracked spring grizzly bear incidents and compared them to non-spring (June 16th – February 28th) grizzly bear incidents for each year. I evaluated incident type (i.e., attractant, livestock, property damage, other) (Chapter 2) for the spring vs. non-spring. Because the intercept-feeding program was designed to reduce spring grizzly bear predation on livestock, I also specifically tracked livestock incidents for both spring and non-spring for each year. Additionally, I tracked the number of spring livestock incidents per bear from 2007 through 2015; I assumed a resident grizzly bear population of 51 grizzly bears in 2007 (Alberta Grizzly Bear Inventory Team 2008) and a 4% per year population increase (Chapter 3). I used the years 2007 through 2015 because population estimates were completed in 2007 and 2015. As noted in Chapter 3, there is variability around my estimate of 4% per year population increase, but it is apparent the population has not declined. Thus, the number of incidents per bear might be higher than reflected by my assumption of 4% per year grizzly bear population growth.

Sex is not always reported in the occurrence records, but was available for a small subset of the complaint data from 1999 through 2014. When possible, I evaluated the sex of grizzly bears involved in incidents; I included only those occurrences where a Fish and Wildlife Officer visited the location and was able to confirm the sex (e.g., visual, animal captured, photographed, etc.). I compared the sex of grizzly bears involved in spring incidents to the sex of bears involved in non-spring incidents over the last 16 years.

Further, I evaluated historical grizzly bear occurrence records prior to the implementation of the intercept-feeding program from 1982 to 1995. Records from 1996 through 1998 were not available. No text summaries are provided in the 1982 to 1995 records, but location, date, and a general descriptive category were included. Thus, I was still able to extract pertinent information. I considered records labeled as "personal/property damage – livestock harassment/kill/mauling" as similar to my category "livestock incident" described above and in Chapter 2. I tracked frequency only in the historic records because insufficient details prevented me from classifying all occurrences in the same manner I did for the 1999-spring 2015 data; thus, I did not evaluate the proportion of incidents that were livestock related. Locations were provided to the quarter section scale (800 × 800m), and I included only those records that fell within BMA6. I compared the average number of livestock incidents prior to and after the implementation of intercept-feeding.

Finally, I opportunistically targeted conflict locations within BMA6 to collect hair samples that were used to identify individuals via the extraction of nuclear DNA from hair follicles (Chapter 3). I compared individuals detected from hair samples at conflict locations to those individuals detected at intercept-feeding sites to test my prediction that individuals observed at intercept-feeding sites differed from those involved in spring conflicts.

4.3.3 Program Suspension

In 2014, the government of Alberta temporarily suspended the intercept-feeding program for 2 years (2014 and 2015). Funds that had previously been allocated to helicopter costs for intercept feeding were redirected to a local non-profit (Waterton Biosphere Reserve Association) working on grizzly bear-agricultural conflict mitigation. I continued to track grizzly bear complaint records and I collected opportunistic hair samples in 2014 after the suspension of intercept-feeding. I tracked spring grizzly bear complaint records in 2015.

Grizzly bear occurrences in southwestern Alberta have spread further east over the last 16 years (Chapter 2), and it is possible that more recent spring livestock incidents involve bears that den in the eastern regions of the study area as opposed to the mountains, and are thus not encountering the intercept-feeding sites. I plotted all spring livestock incidents pre (1982 – 1995), during (1999 – 2013), and post (2014 – 2015) intercept-feeding in a GIS. I calculated the distance between each spring livestock incident and the nearest intercept-feeding site, and compared mean distance between pre, during, and post years using multiple two-tailed t-tests.

4.3.4 Program Costs

Finally, I estimated program costs in collaboration with biologists within the provincial government responsible for the program. Costs were based on 2012/2013 operational costs, recognizing that costs likely varied over the 16 years of the program. I used the broad categories of personnel, helicopter time, and equipment (annual vs. initial). I reported funds in Canadian dollars (CAD) rounded to the nearest $50 increment.

4.4 Results

In 2012, carcass drop dates were April 3 and April 25. A drop date in March was not possible because high winds did not allow for safe flying conditions. In total, the Alberta government distributed 149 carcasses over the 2 drops (3 moose, 139 deer, and 7 elk) for a total estimated biomass of approximately 14,700 kilograms. In 2013, drop dates were March 19 and April 18. In total, the Alberta government distributed 159.5 carcasses (5 moose, 149 deer, and 5.5 elk) for a total estimated biomass of approximately 16,000 kilograms over the 2 drops.

Using DNA extracted from collected hair samples I detected a total of 18 grizzly bears using the intercept-feeding sites in 2012 (15 males, 3 females) (Table 4.1). In 2013, I detected 11 males using the sites but no females. In total, 22 grizzly bears were detected at the intercept-feeding sites over the two years of sampling (19 males, 3 females). By comparison, within BMA6 I detected 117 grizzly bears in 2012 (70 males, 47 females), and 118 grizzly bears in 2013 (66 males, 52 females). Cumulatively, 165 grizzly bears have been detected at some point over the two years of sampling (May through November) in BMA6 (92 males, 73 females) (Table 4.1).

Of the bears detected at the intercept-feeding sites, only 2 bears also were detected at a spring conflict site (both in 2012 during the intercept-feeding program). All 3 female grizzly bears were detected at the same site; there were no intercept-feeding sites in which both a male and female grizzly bear were detected based on my DNA sampling (Table 4.2). The number of males detected from DNA ranged from 0 to 3 individuals per site (Table 4.2). Remote trail cameras, however, detected grizzly bear presence at all intercept-feeding sites. In particular, females with cubs were detected at 3 different intercept-feeding sites by remote trail cameras (Table 4.2).

I reviewed 64 historical records of spring grizzly bear occurrences. In the historical data set from 1982 through 1995, the frequency of spring grizzly bear livestock incidents was variable and ranged from 0 to 3 per year (Fig. 4.2). I reviewed and classified 1,140 occurrence records for grizzly bears in BMA6 from 1999 through spring 2015 (516 incidents, 587 sightings, and 52 human conflicts). Livestock incidents as well as non-livestock incidents have increased in both the spring and non-spring seasons since 1999 (Fig. 4.3). Spring livestock incidents increased at a rate of 64.8% per year from 2007 through 2013. Grizzly bear livestock incidents were on average lower before the initiation of intercept-feeding (1982 – 1995, $\bar{x}$ =0.8 livestock incidents/year, SE=0.3) than during feeding (1999 – 2013, $\bar{x}$ =3.3 livestock incidents/year, SE=1.3).

There were 12 spring livestock incidents each year in 2014 and 2015, which was actually lower than occurred during the last year (2013) of intercept-feeding (Fig. 4.3). The number of spring livestock incidents per bear increased from 2007 through 2013, but then decreased in 2014 and 2015; there is unaccounted for uncertainty around the number incidents per bear because of variability around the estimate of population growth (Fig. 4.4). Incidents from 1999 through spring 2015 were predominately attractant based for the non-spring season (67.03%), but split almost equally between livestock (48.03%) and attractants (46.71%) during spring (Fig. 4.5). Livestock incidents represented 27.75% of all non-spring incidents (Fig. 4.5). Slightly more females than males were involved incidents in both the spring (54.5%) and non-spring (55.9%) (Fig. 4.6).

Spring livestock incidents were historically closer to the mountainous region of my study area (Fig. 4.7). Eastern spring livestock incidents became more common beginning in 2008 (Fig. 4.7a). The mean distance between spring livestock incident locations and the nearest intercept-feeding site was higher during ($\bar{x}$ =14.77 km, SE=1.06) and after ($\bar{x}$ =16.58 km, SE=1.79) intercept feeding as compared to prior to ($\bar{x}$ =9.76 km, SE=1.25) intercept feeding (during vs. prior to intercept feeding: t = 3.05, df = 27, p = 0.005; after vs. before intercept feeding: t = 3.12, df = 33, p = 0.004). The mean distance was not significantly greater after intercept feeding was stopped as compared to during intercept feeding (t = 0.87, df = 40, p = 0.390).

Finally, I estimated annual operating costs to be conservatively $43,850 CAD, and initial capital equipment costs to be $19,000 CAD (Table 4.3). Thus, in total, approximately $720,600 has been spent on the intercept-feeding program since its inception in 1998.

4.5 Discussion

Diversionary and supplemental feeding programs have been a successful tool in a variety of situations such as reducing crop damage and decreasing vehicle collisions (Geisser and Reyer 2004, Ziegltrum 2006, Milner et al. 2014). For bears, however, the use of supplemental feeding as a conflict mitigation tool remains controversial because some studies have found supplemental feeding has no effect on the frequency of human-bear conflicts, and in some cases might actually increase conflicts (Kavčič et al. 2013, Kavčič et al. 2015). Because of the existence of dominance hierarchies (Craighead et al. 1995) and the potential role of SSI and/or the risk of interspecific killing (e.g., Ben-David et al. 2004, Swenson et al. 2001a), I predicted that the intercept-feeding sites would be used disproportionately by males, dominated by a few individual bears, and used by different individuals than those detected at spring grizzly bear-agricultural conflict locations. My data supported all three predictions, and my results indicate that the intercept-feeding program is not meeting its goal of reducing spring livestock predation by grizzly bears.

Indeed, few individuals used the spring intercept-feeding sites relative to the number of grizzly bears using the study area indicating that this food resource is only available to a select group of individuals, primarily dominate males. I am not able to determine age from hair samples, so have made the assumption that male bears are more dominant than female bears. The majority of bears using southwestern Alberta, are not being intercepted by the feeding sites and need to seek out food resources outside of the spring intercept-feeding sites, potentially in the form of agricultural food sources. I identified 22 unique grizzly bears using the spring feeding locations, and when the program was suspended in 2014, I did not detect any of these bears at a spring conflict site. Thus, while these 22 bears might have been being intercepted during the program, the absence of the program did not result in these 22 bears being associated with a spring livestock conflict site. Additional bears might have been involved in agricultural conflicts, but not detected. However, to increase my hair collection and subsequent ability to detect bears at agricultural conflict sites, I worked extensively with local Fish and Wildlife officers (provincial staff responsible for responding to grizzly bear conflicts) and numerous landowners (over 70 individuals and 4 livestock grazing co-operatives) to collect hair samples.

Even though intercept-feeding benefited almost exclusively male bears, the feeding involves supplemental provisioning of high-quality food for the bears at a crucial stage in their annual cycle, thus probably increasing survival and contributing to a positive growth rate. Indeed, the grizzly bear population in southwestern Alberta is estimated to be stable to increasing at 4% per year since 2007 (Chapter 3). The observed increase in grizzly bear livestock incidents could be partly attributable to an increasing grizzly bear population (Chapter 3). However, spring livestock incidents continued to increase despite the supplemental provisioning, and increased at a rate (64.8% per year) that far exceeded the increase in the grizzly bear population (4% per year). If the program were effective, I would have expected the rate of increase in spring livestock incidents to be more similar to the rate of increase in the grizzly bear population. The mean number of spring livestock depredations per year was higher after the program implementation than prior to the program starting. Further, I did not see an increase in spring livestock incidents associated with the closure of the feeding sites. I note, however, that it is likely that improved records were kept with the implementation of the electronic enforcement database in 1999. Thus, improved record keeping might account for some of the increase in conflict records. However, with or without the intercept-feeding program, conflicts are likely to have increased because there are more bears.

Not only has the grizzly bear population increased, but grizzly bear occurrences also have been spreading further east into lands used primarily for agriculture (Chapter 2). Similarly, spring livestock incidents have also spread further east. In Montana, grizzly bears have recently been documented denning in prairie habitats far from the mountains (Puckett 2013). If some grizzly bears in Alberta also are denning in the prairies, they would not encounter the spring intercept-feeding stations when they emerge from hibernation. DNA relocation data from my larger monitoring program indicate that bears detected in the southeastern portion of my study area are rarely also detected in the mountainous public lands. Thus, alternative mitigation measure are likely necessary to reduce spring predation of livestock in eastern portions of BMA6, which is where a large portion of spring livestock predation events by grizzly bears are occurring.

The eastern portions of BMA6 are lands primarily used for agriculture, and dominance hierarchies and SSI predict that these habitats should be used by subordinate individuals. Sex often is not reported in grizzly bear incidents, but when it is, incidents tend to involve more females than males (though yearly variation occurs). Females with cubs often are more conspicuous than a single bear, which could lead to biased reporting of sex by the general public. For this reason, I included only those records in which a Fish and Wildlife officer confirmed the sex of the bear involved in the incident, which should substantially reduce any potential reporting bias. Alternatively, incident reports might be female dominated not because of dominance hierarchies or potential bias in reporting, but because of Alberta's current grizzly bear management policy. The provincial grizzly bear response guide mandates that at a first offence, captured females with cubs be relocated within the same bear management area, whereas males are more likely to be relocated long distances (Alberta Government 2009). Because male bears can be essentially removed from the population, females could be reported more frequently.

Further, when I evaluated program cost, I estimated that the program costs approximately $43,850 annually. Given that spring livestock predation incidents have increased at a rate exceeding the rate of grizzly bear population increase, I suggest that these funds might be better spent elsewhere, such as on electric fencing of calving pastures or removal of dead stock (i.e., boneyards) from the landscape. Electric fencing has been shown to be a powerful tool separating attractants and large carnivores (e.g., Wilson et al. 2005, Otto and Roloff 2015). Costs of electric fencing are highly variable, but recent projects in my study area where calving pastures were electrified ranged in costs from approximately $2,500 up to $14,405 (Loosen et al. 2014). Personal interviews with the landowners implementing electric fencing indicate that it was highly successful in reducing livestock losses to large carnivores.

Finally, boneyards are a major attractant for grizzly bears in this area (Northrup and Boyce 2012, Chapter 2). Recent work in Poland found that an indirect effect of supplementary feeding was an increase in predation on nesting birds in close proximity to feeding stations (Selva et al. 2014). Similarly, it is possible that bears using boneyards that are in close proximity to live cattle, might increase their predation on livestock; grizzly bear-human conflict hotspots are strongly associated with the presence of boneyards (Wilson et al. 2005). Consequently, there has been a major effort to remove dead stock from the landscape in southwestern Alberta (Chapter 2). Locally, the Waterton Biosphere Reserve's Deadstock Removal Program offers free deadstock pick-up for producers over 500,000 ha (Manners and Bectell 2014). The cost of removing dead stock increased in February, 2015, and the Deadstock Removal Program currently costs approximately $75,000 annually (Waterton Biosphere Reserve, unpublished data). Continued support of programs such as electric fencing and deadstock removal might be a more effective solution than intercept feeding to spring livestock predation by grizzly bears.

4.6 Conclusion

Spring intercept-feeding sites in southwestern Alberta were used almost exclusively by dominant male grizzly bears. The majority of other grizzly bears using the study area had to seek out spring food resources elsewhere. Livestock predation events by grizzly bears increased even during the spring-intercept feeding program, and increased at a rate that far exceeded the estimated increase in the grizzly bear population. The program benefitted a small number of grizzly bears, but I did not see an increase in conflicts by these bears in the absence of the intercept feeding program. Given the cost of the program and the increase in spring livestock incidents during the program I suggest that efforts might be more effectively focused on other conflict mitigation strategies - particularly in the eastern portion of the study area.

Table 4.1 Number of grizzly bears by sex that were detected within Bear Management Area (BMA) 6 and at intercept-feeding sites (GBIF) in southwestern Alberta from 2012 – 2013.

	Detections					
	GBIF			BMA6		
Year	M	F	Total	M	F	Total
2012	15	3	18	70	47	117
2013	11	0	11	66	52	118
Total[a]	19	3	22	92	73	165

[a] Total is not a sum of 2012 and 2013 but rather the cumulative number of bears that were detected between both years of sampling

Table 4.2 Number of individual grizzly bears detected by DNA at each intercept-feeding site in southwestern Alberta 2012 – 2013.

	Number of Individuals Detected per Site					
Site Name	2012		2013		Cumulative	
	Male	Female	Male	Female	Male	Female
Gladstone	3	0	0	0	3	0
L.C.	2	0	3	0	5	0
Mill Creek 1	0	0	1	0 [a]	1	0
NCC B	1	0	1	0 [a]	2	0
North Drywood	1	0	0	0	1	0
Pincher	1	0	0	0 [a]	1	0
South Drywood	0	3[a]	0	0	0	3
Spionkop	3	0	1	0	4	0
WLNP- Belly River	2	0	1	0	3	0
WLNP- Oil Basin	3	0	1	0	4	0
WLNP- Sofa	3	0	0	0	3	0
Yarrow	1	0	0	0	1	0

[a] Female with cubs detected by remote trail camera. Individual identify cannot be determined by remote trail camera.

Table 4.3 Estimated operational costs by broad category to run 13 intercept-feeding stations in southwestern Alberta. All costs are reported in CAD ($) and are rounded to the nearest $50. All costs are annual except where otherwise stated.

Item	Estimated Cost ($CAD)
Personnel Time	$20,000
Helicopter Costs	$19,000
Vehicle Costs	$3,100
Equipment and Repair Costs	$1,750
Total Annual Costs	**$43,850**
Equipment Costs - Non-Annual	$19,000

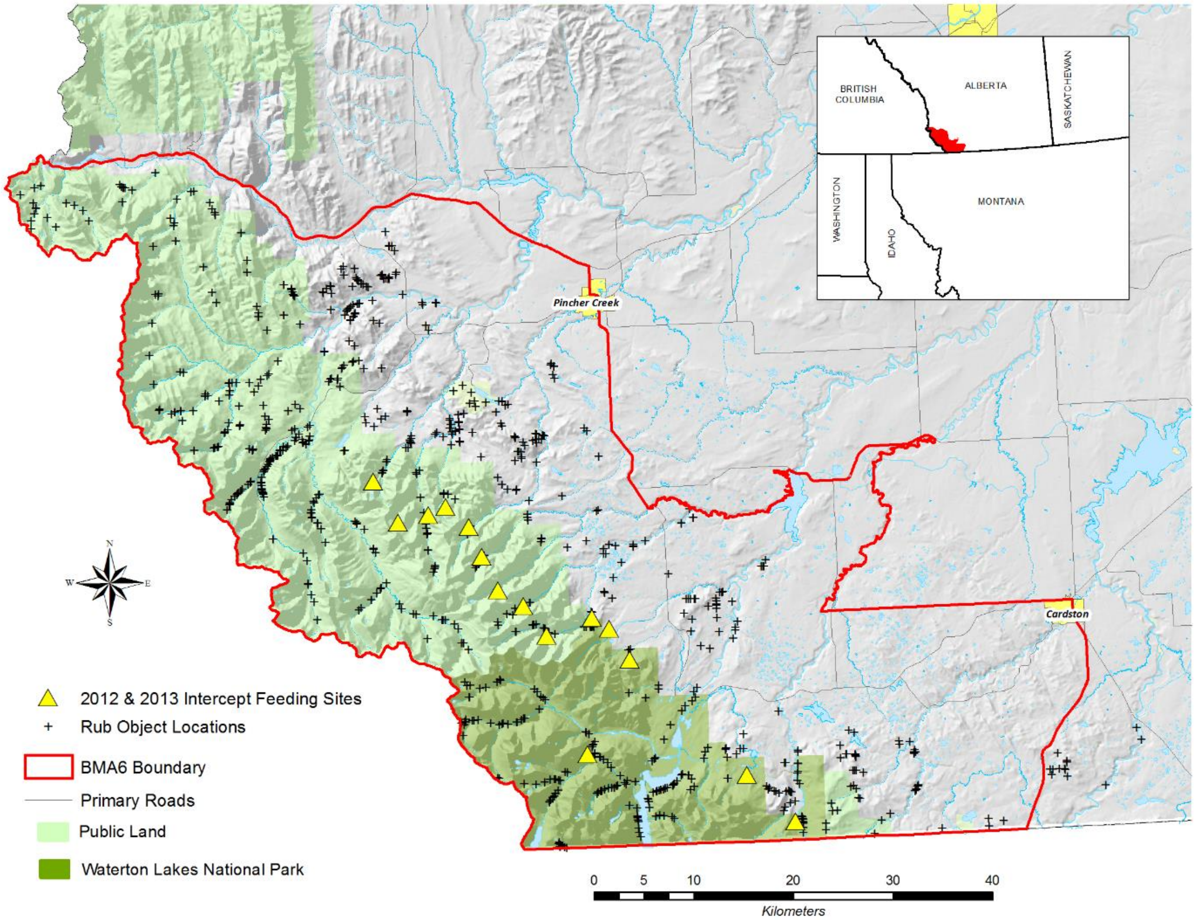

Figure 4.1 Map of study area in southwestern Alberta. Yellow triangles are the intercept-feeding sites monitored in 2012 and 2013. The black crosses are the sampling stations from my larger non-invasive genetic grizzly bear monitoring program.

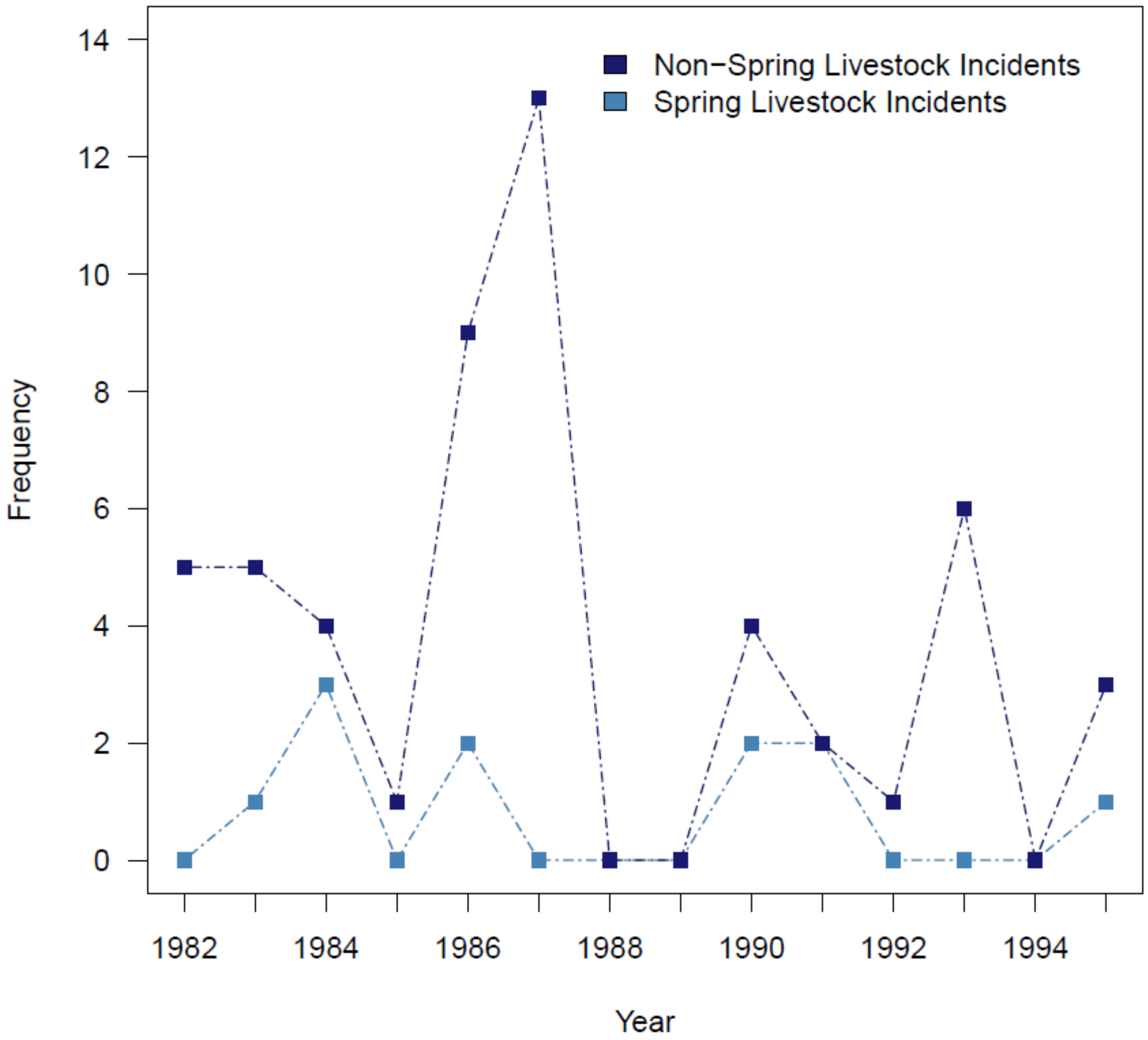

Figure 4.2 Non-spring (n = 53) and spring (n = 11) grizzly bear livestock incidents in BMA6 in southwestern Alberta from 1982 through 1995.

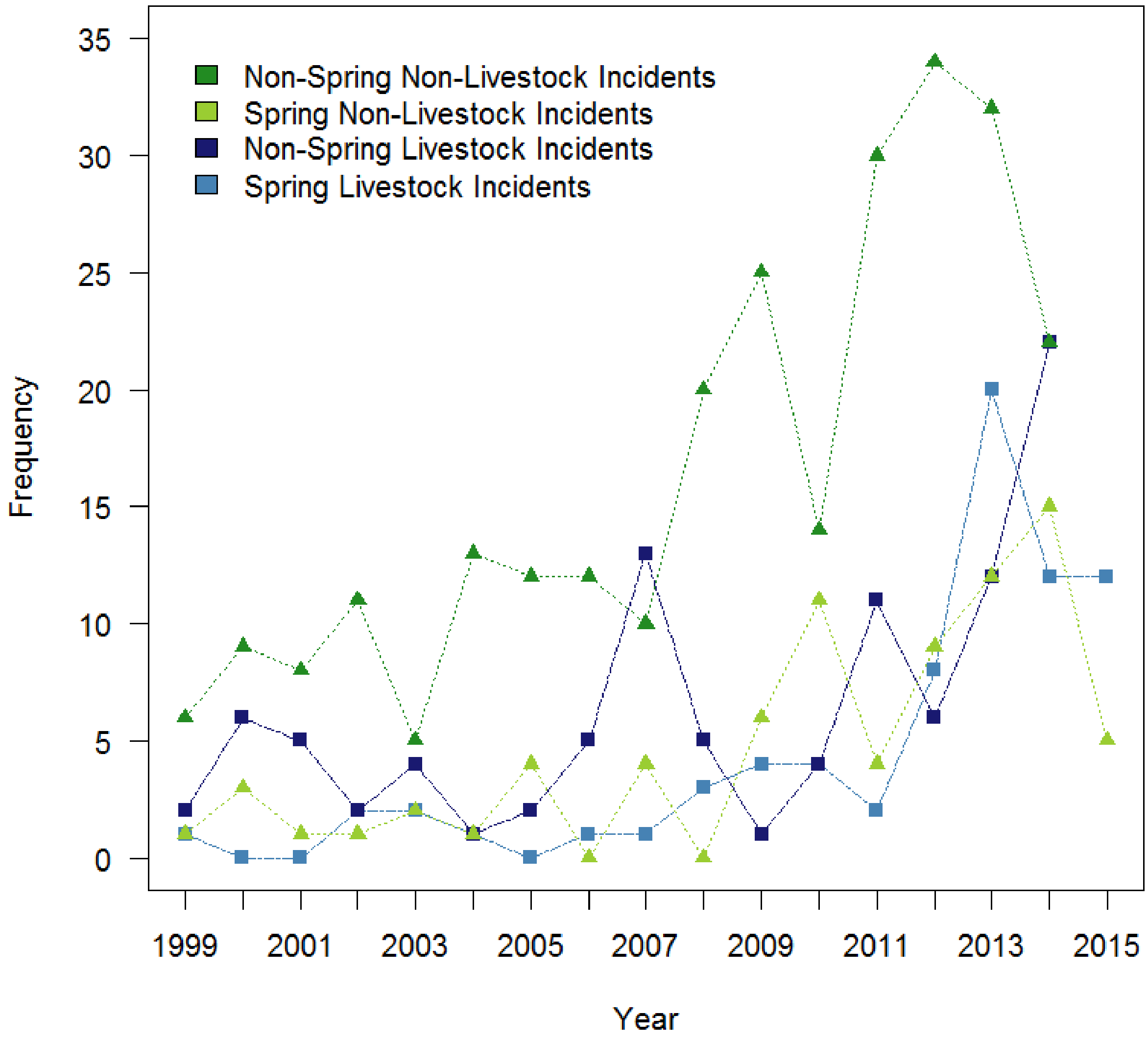

Figure 4.3 Non-spring (n = 101) and spring (n = 73) grizzly bear livestock incidents in BMA6 in southwestern Alberta (blue lines), and non-spring (n = 263) vs. spring (n =79) non-livestock incidents in BMA6 in southwestern Alberta (green lines).

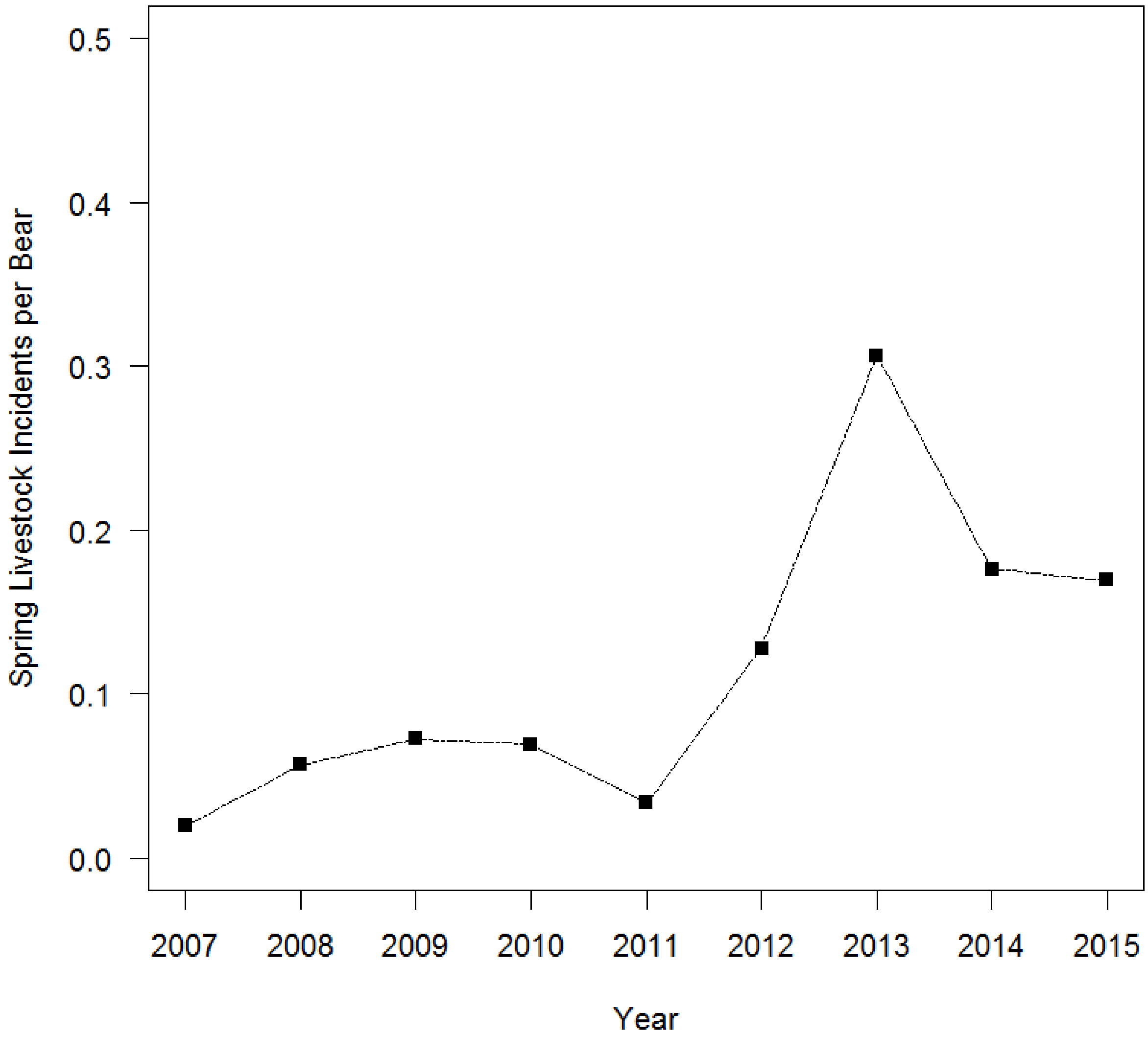

Figure 4.4 Number of spring livestock incidents (n = 73) per grizzly bear from 2007 through 2015. The resident grizzly bear population is assumed to be 51 grizzly bears in 2007 and increasing at a rate of 4% per year (note that there is uncertainty around the estimate of population growth that is not reflected in this graph).

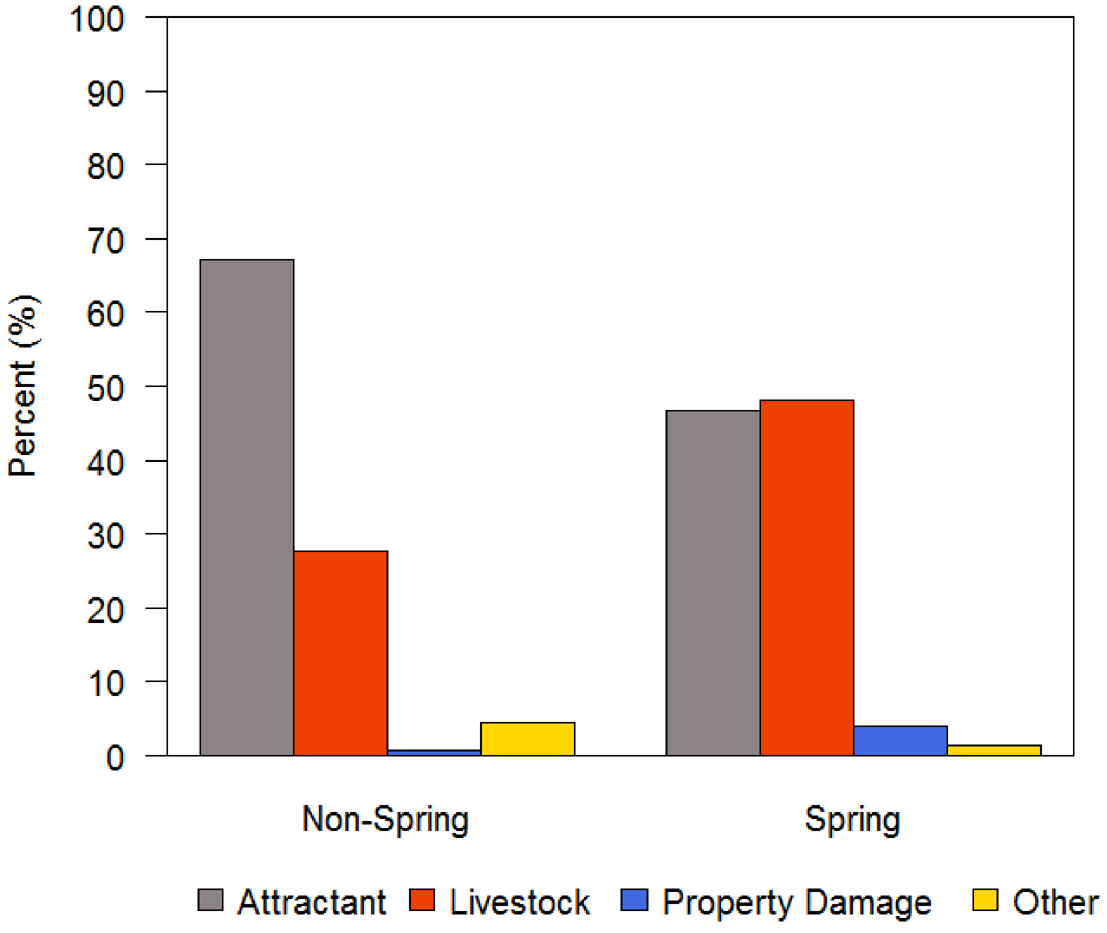

Figure 4.5 Percentages of incident type for grizzly bears in BMA6 for the non-spring (n = 364) vs. the spring (n = 152) from 1999 through spring 2015.

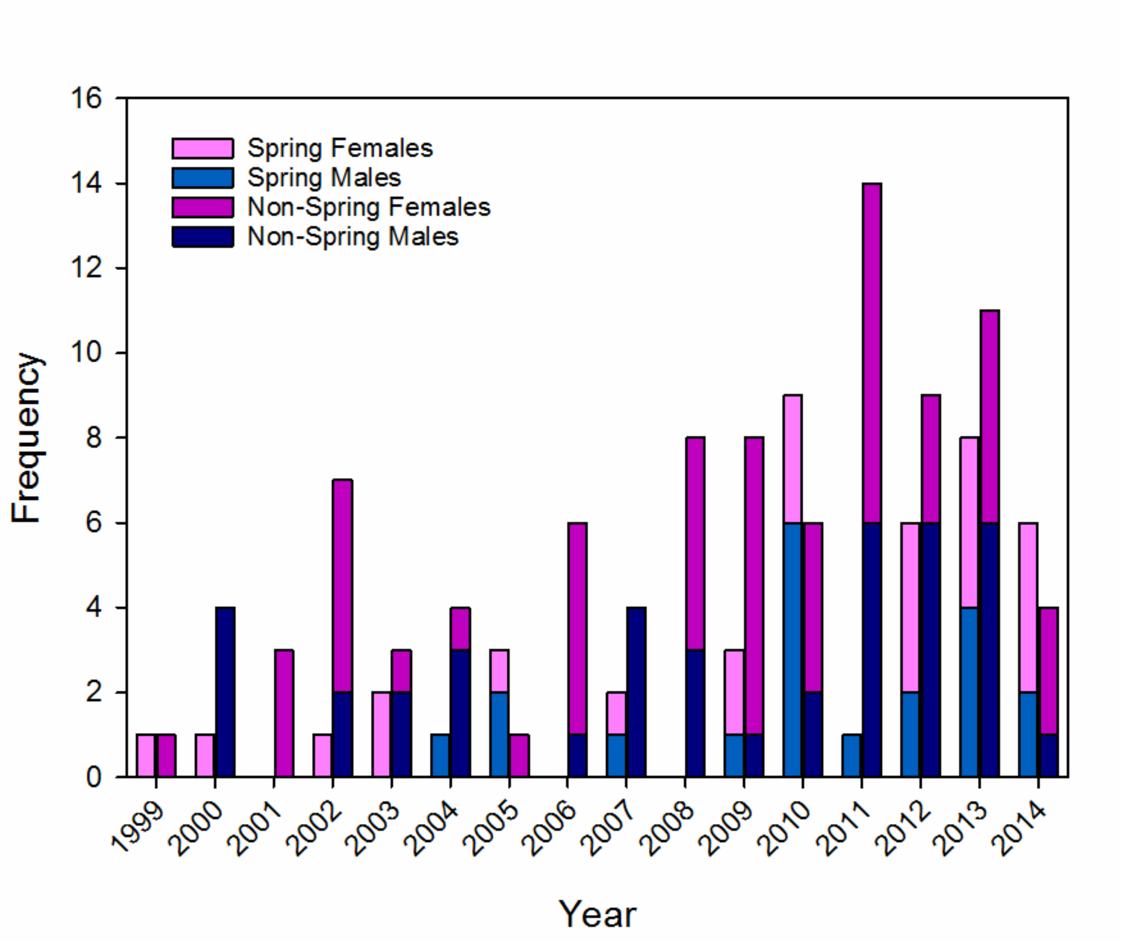

Figure 4.6 Sex of grizzly bear incidents in southwestern Alberta 1999 through 2014. Only incidents where sex was confirmed by a Fish and Wildlife officer are included. Spring (n = 44) vs. non-spring incidents (n = 93).

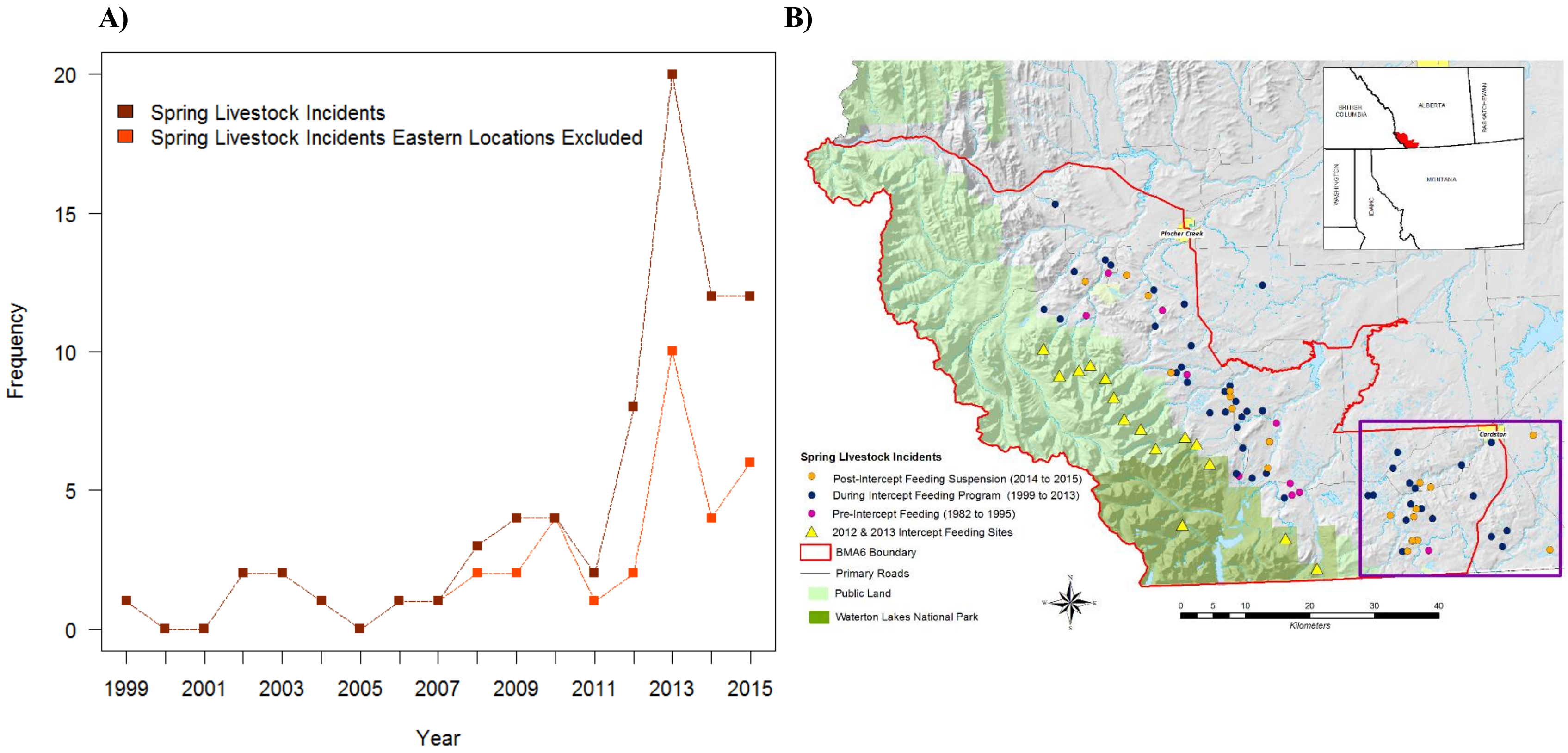

Figure 4.7 A) Spring livestock incident in southwestern Alberta 1999 through 2014 including (n = 73) and excluding eastern locations (n = 39) (those within purple square in B); **B)** Spring livestock incidents in southwestern Alberta pre, during, and post intercept-feeding. Yellow triangles are the locations of intercept-feeding sites.

Chapter 5

5 Nature versus Nurture: Evidence for Social Learning in Grizzly Bears

5.1 Introduction

"*The ideal criminal has marked peculiarities of character: his conscience is almost deficient, his instincts are vicious, his power of self-control is very weak…It is, however, easy to show that the criminal nature tends to be inherited"* (Galton 1883). Francis Galton, a pioneer of behavioural genetics, believed that criminal tendencies, among many other behavioural traits, were inherited, and his work sparked the long-standing nature versus nurture debate (Galton 1874). While it is now recognized that behavioural development and criminal behaviour is a complex interaction between both genes and the environment (Breed and Sanchez 2010, Sameroff 2010), the question of how behaviours are developed and acquired remains an important question in behavioural ecology.

Behaviour involves decision making which results in costs and benefits to individuals. Selecting favorable habitats, acquiring suitable food, and finding mates are all critical to an individual animal's survival and reproduction. The acquisition of such behaviours can occur through inheritance, asocial learning, social learning, or some combination of inheritance and learning (Laland 2004, Galef and Laland 2005, Hopkins 2013). Asocial learning occurs independently through trial and error, whereas social learning occurs as a result of interacting with or observing others, usually allowing animals to acquire adaptive behaviours faster than asocial learning (Heyes 1994, Galef and Whiskin 2001, Galef and Laland 2005).

Studies of both captive and free-ranging animals have found learning to be correlated with opportunism, curiosity, behavioural plasticity, large brain size, and developed memory

(Lefebvre and Giraldeau 1996, Reader and Laland 2002, Mazur and Seher 2008, Pokrovskaya 2015). Bears (Ursidae) possess each of these traits along with high maternal investment in offspring, making them predisposed to social learning (Gittleman 1986, Gilbert 1999). Grizzly bear (*Ursus arctos*) cubs typically stay with their mother for 2-3 years (McLellan 1994) giving cubs opportunity for social learning from their mothers. While there is some evidence that cub behaviours are influenced by their mother's behaviour and the habitats in which she reared her young (Mazur and Seher 2008, Hopkins 2013, Nielsen et al. 2013), the literature is inconclusive on this subject and other studies did not support such relationships (Breck et al. 2008). Bears are opportunistic and flexible foragers (Gilbert 1999, Bojarska and Selva 2012); for a non-specialized species we might not expect strong evidence for social learning because a variety of options are available to meet nutritional demands – particularly in human-settled areas where anthropogenic resources are readily and easily obtained (e.g. Beckmann and Berger 2003, Breck et al. 2008, Baruch-Mordo et al. 2014). If a behaviour is easily developed, social learning might not be essential to the acquisition of that behaviour (Breck et al. 2008).

After removal from much of their range, several populations of grizzly bears in both the United States and Canada are now increasing (Mace et al. 2012, van Manen et al. 2014, Chapter 3). As grizzly bear populations expand, they are increasingly overlapping with human-settled lands where they come into conflict with human land uses such as agriculture and ranching (e.g. Wilson et al. 2006, Northrup et al. 2012, Chapter 2). Despite the potential for conflict, recent work indicates that with supportive public opinion and effective mitigation measures, co-existence between people and large carnivores such as grizzly bears is possible (Chapron et al. 2014). Understanding how bears acquire conflict behaviours can have important management implications, especially where conflicts limit public support and the palatability of co-existence in human-settled landscapes.

In southwestern Alberta grizzly bears have been listed as a provincially threatened species under the provincial Wildlife Act since 2010. Conflicts between grizzly bears and agricultural activities in the region are prevalent, increasing, and typically involve either agricultural attractants or livestock predation (Chapter 2); these incidents are slightly (55%) female biased (Chapter 4). Within Alberta, grizzly bear management frequently is reactive; Fish and Wildlife Officers often relocate problem grizzly bears in response to public complaints of conflicts (Alberta Sustainable Resource Development 2008, Alberta Government 2009). Adult females have the highest elasticity in grizzly bear populations (Garshelis et al. 2005, Harris et al. 2006); because the death of a breeding-age female has a more significant impact on population size than the death of a cub or sub-adult male, the provincial government has focused on reducing female mortality and keeping females with cubs within their local bear management area (BMA) to promote population growth – even if the bear has been identified as a problem individual (Alberta Sustainable Resource Development 2008, Alberta Government 2009, Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Thus, the current response guidelines mandate that at a first incidence of conflict, a female with cubs will be relocated within the same BMA as opposed to males that are likely to be translocated long distances (Alberta Government 2009).

If conflict behaviour in grizzly bears is a result of social learning, then the current grizzly bear management paradigm in Alberta might perpetuate the problem; by keeping problem females with cubs on the same landscape in which they have been involved in conflict, cubs might be exposed to additional opportunities to learn conflict behaviours from their mother.

Further, Alberta's bear management policy might be altering demographic structure by enforcing a different mortality risk for males versus females on agricultural landscapes because translocated bears typically suffer higher mortality rates than non-translocated bears (Riley et al. 1994, Blanchard and Knight 1995, Linnell et al. 1997). Thus, acquiring conflict behaviours might be particularly maladaptive for male grizzly bears.

Here, I evaluate evidence for social learning and genetic inheritance of conflict behaviour in grizzly bears in southwestern Alberta. Using a parentage analysis, I test the prediction that if conflict behaviour is genetically inherited, there will be a significant relationship between paternal conflict behaviour and offspring conflict behaviour. Conversely, if a cub learned conflict behaviour from its mother, I would predict significantly more offspring (males and females) to be involved in conflict behaviours if their mother was a problem bear, but I should see no such effect for paternal conflict behaviour because male grizzly bears are not involved in rearing offspring.

5.2 Study Area

My study area was located in southwestern Alberta, in an area known provincially as Bear Management Area 6 (BMA6) (Fig. 5.1). BMA6 was bounded by Highway 3 to the north, British Columbia to the west, Montana to the south, and the approximate edge of grizzly bear range to the east. BMA6 includes two zones, the Recovery Zone and the Support Zone (Alberta Environment and Parks 2016). The Recovery Zone is the area in which the province explicitly intends to recover the grizzly bear population, and is predominately public land. The Support Zone in southwestern Alberta is exclusively private land, and is intended to support grizzly bears with home ranges that do not fall entirely within the Recovery Zone. While the provincial BMA6 boundary is the combination of the Recovery and Support Zones, grizzly bears occur outside the eastern boundary, and I included bears detected outside this eastern boundary in my analysis. Bears in BMA6 are a small part of the much larger international Rocky Mountains subpopulation as identified by Proctor et al. (2012), which includes the Northern Continental Divide Ecosystem (NCDE) in the U.S. (United States Fish and Wildlife Service 1993).

There is an abrupt transition between public forested mountainous land to the west, and private agricultural land to the east. Agricultural land is used for both livestock and crop production. In addition to grizzly bears, other large carnivores include cougar (*Puma concolor*), black bear (*U. americanus*), and wolves (*Canis lupus*). Available native prey species include mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*). With the exception of grizzly bears, all native carnivores and prey are considered secure within the province. Domestic prey cattle (*Bos taurus*), and a small number of sheep (*Ovis aries*) and goats (*Capra hircus*) also are present.

5.3 Methods

I used DNA extracted from hair samples to identify individual grizzly bears. I collected hair samples from natural rub objects established within the study area during 2011 – 2014. Rub objects included trees, power poles, fence posts, as well as stretches of barbed-wire fence the bears traveled along or through. The first two years of the project, 2011 and 2012, were primarily set-up years and included fewer visits to rub objects (2011: 2 visits Recovery Zone only, 2012: 8 visit Recovery Zone, 2 visits Support Zone). Then, during 2013 and 2014 rub objects in both the Recovery and Support Zones were visited 8 times (7 sampling occasions). Additionally, I opportunistically collected hair samples from agricultural lands within the Support Zone. Specifically, I worked with over 70 landowners as well as provincial Fish and Wildlife Officers to collect hair samples at grizzly bear incident sites. A full description of field sampling methods can be found in Chapter 3.

I sent hair samples to Wildlife Genetics International (WGI) in Nelson, B.C. where samples were used to identify species, individual identity, and sex via analysis of nuclear DNA extracted from hair follicles following the protocols outlined by Paetkau (2003, 2004). WGI used the G10J marker for species assignment to black bear vs. grizzly bear (Mowat et al. 2005). Multi-locus genotyping followed Paetkau's (2004) 3-phase process of first pass, error check, and clean-up using the established 8-locus marker system (7 microsatellites plus the amelogenin marker for sex) for grizzly bears in the southern Rocky Mountain region (Paetkau et al. 1995, Paetkau 2003). Because an insufficient number of loci is one of the primary causes of incorrect assignment in a parentage analysis (Marshall et al. 1998, Jones et al. 2010, Harrison et al. 2013, Wang and Scribner 2014), I extended the genotypes of the known individuals to 24 microsatellite loci in 2014 after I had finished adding to my genetic dataset. In total, I genotyped 213 unique grizzly bears (118 male, 95 female) from southwestern Alberta at 24 microsatellite loci, plus the amelogenin marker for sex.

In addition to insufficient loci, the other primary cause of incorrect parent assignment is incomplete sampling of candidate parents (Marshall et al. 1998, Jones and Arden 2003, Harrison et al. 2013). Because grizzly bears in southwestern Alberta are a small part of a larger international population that includes Montana and British Columbia (Proctor et al. 2012, Chapter 3), I collaborated with biologists in neighboring jurisdictions to increase the likelihood of identifying complete triads (mother, father, offspring) in my parentage analysis. Over 50% of grizzly bears detected by my sampling methods had been previously genotyped by projects in Montana and British Columbia (Chapter 3), and 16 bears had been previously genotyped by the

2007 Alberta inventory project (Alberta Grizzly Bear Inventory Team 2008). Montana grizzly bear genetic data were obtained from previous non-invasive genetic sampling projects throughout the NCDE (Kendall et al. 2008, 2009). British Columbia grizzly bear genetic data were obtained from the B.C. Ministry of Forests, Lands, and Natural Resource Operations (Mowat et al. 2013). Additionally, I also obtained data on bears genotyped under a previous Alberta inventory (Alberta Grizzly Bear Inventory Team 2008). Individuals were genotyped at 6 to 24 microsatellite loci (mean loci = 15.91, mode = 24). In total, I used 2043 individual grizzly bears (977 males, 1072 females) from the Rocky Mountains subpopulation (Proctor et al. 2012) in my parentage analysis. In 6 cases, sex was unknown and I analyzed these bears as both potential fathers and potential mothers.

I used program COLONY to assign parentage (Jones and Wang 2010). COLONY uses full pedigree likelihood methods to simultaneously infer sibship and parentage among individuals (Jones and Wang 2010). The likelihood is considered over the entire pedigree rather than for pairs of individuals. Simultaneously accounting for parent-offspring pairs as well as full- and half-sibs, increases accuracy of assignments (Wang and Sancture 2009, Wang and Scribner 2014), and in a recent review the full pedigree likelihood method implemented in COLONY outperformed other parentage methods (Harrison et al. 2013). I set the estimated proportion of parents in the dataset at 0.4 for each sex, and specified genotyping error at 0.001 based on WGI published error rates (Kendall et al. 2009); COLONY is robust to these parameters provided sufficient information is contained in the data (Wang 2004, Wang and Santure 2009). Other specified parameters included: polygamous males and females, long run length (~1.9 billion iterations), full-likelihood analysis, and medium-likelihood precision. Ages were known for some bears (i.e. bears that were physically handled and age determined by cementum annuli), and I used this information to rule out potential parents if they were not at least 2 years older than other bears at that bear's birth (n = 42). For example, if a bear was born in 2000 it was excluded as a parent for a bear born in 1995.

While I used the larger genetic data set for my parentage analysis to ensure my parentage assignments were as robust as possible, my analysis of problem bears used only the Alberta offspring data because my targeted sampling of grizzly bear incident and human-bear conflict locations was limited to southwestern Alberta. I define an incident as an occurrence in which the grizzly bear caused property damage, obtained anthropogenic food, or killed or attempted to kill livestock or pets (Hopkins et al. 2010, Chapter 2). Incident occurrences were grouped as property damage, livestock, attractant, and other (Chapter 2). A few additional samples associated with an incident came from areas outside the officially designated BMA6 boundaries. I also included 4 hair samples associated with a human-bear conflict in which the bear made physical contact with a person, was killed by a person in self-defence, or, in one case, was deemed an aggressive bear and subsequently translocated by provincial Fish and Wildlife Officers to ensure public safety. I considered a bear a problem bear if it was associated with either an incident or human-bear conflict via detection by either non-invasively collected hair samples at incident sites, or from hair samples obtained by physical capture (done by provincial Fish and Wildlife Officers).

If the parent of an Alberta offspring was not contained in my Alberta data (i.e. was a bear detected only in Montana or British Columbia), I obtained conflict history from the respective state/province when possible. I classified all parent offspring relationships as within-group pairs (PP-PO, PP-NPO, NPP-PO, NPP-NPO; PP = problem parent, PO = problem offspring, NPP = non-problem parent, NPO = non-problem offspring). COLONY assigns an "inferred" parent if the most likely genotype is not included in the input of candidate parents. I excluded these inferred mothers and fathers from my analysis because they were not actually detected by my sampling methods and thus their conflict status was unknown. Although I cannot determine age from hair, I assumed that if a female and her offspring were detected together at the same location on the same date, that the offspring were cubs and traveling with their mother. Consequently, any decisions regarding resource use, were being made by their mother and not the offspring themselves. I excluded these mother-offspring detections from my analysis.

I used Barnard's test (Barnard 1945, 1947) to compare the frequency of problem and non-problem offspring from problem and non-problem parents. Barnard's test is more powerful than Fisher's exact test for moderate to small sample sizes (Lydersen et al. 2009). First, to rule out the possibility of conflict behaviour being associated with a sex-linked gene, I used 4 Barnard's tests to evaluate mother-daughter, mother-son, father-daughter, and father-son relationships. I would expect significant results in these 4 tests only if conflict behaviour is sex-linked. Second, I considered each parent sex separately (i.e., one Barnard's test for mothers, one Barnard's test for fathers) to evaluate evidence for social learning. If social learning is present, I would expect a significant relationship for mother-offspring behaviours but not for father-offspring behaviours.

To evaluate the number of bears with potential exposure to conflict situations (e.g., a bear detected only in a remote area of public land would not be involved in an agricultural conflict), I evaluated the land tenure associated with each detection for each bear. In other words, I determined how many grizzly bears were detected exclusively on private land, exclusively on public land, and on both public and private lands. I determined these detection metrics both for all bears detected and the number of individuals associated with an incident or human-bear conflict site to help interpret my results.

5.4 Results

From 2011 through 2014, I opportunistically collected 86 hair samples in Alberta that were associated with a grizzly bear incident (n = 82) or human conflict (n = 4) location; these 86 incident/human-bear conflict hair samples were assigned to 55 unique individuals (24 females, 31 males). Of the 213 identified grizzly bears from my broader sampling effort, 79 were detected exclusively on private land, 76 were detected exclusively on public land, and 58 were detected on both public and private lands. Of the 55 problem bears, 40 were detected exclusively on private land, and 15 on both public and private lands.

In my final analysis, I evaluated a total of 76 mother-offspring and 119 father-offspring relationships. My parentage analysis identified 28 unique mothers and 33 unique fathers within the Alberta data. I identified 61 mother-offspring and 88 father-offspring pairs for Alberta detected bears, but excluded 13 of the 61 mother-offspring relationships because they were situations in which the offspring were only detected with their mother. I included in my total 28 mother-offspring and 31 father-offspring relationships after obtaining parent conflict history from Montana. Montana conflict history changed the conflict status of 5 Alberta detected bears, bringing my total number of Alberta problem bears to 60 (out of 213). All offspring were bears detected in Alberta. Within the 76 mother-offspring relationships I evaluated, 30.3% of offspring were identified as problem bears regardless of their mother’s conflict status. For the father-offspring relationships I evaluated, 28.6% of offspring were identified as problem bears regardless of their father’s conflict status.

There was no evidence that conflict behaviour was associated with a sex-linked gene (Barnard's test: mother-daughter, *p* = 0.17; mother-son, *p* = 0.12; father-daughter, *p* =1.0; father-son, *p* = 0.83). There was no evidence that offspring are more likely to be involved in conflict behaviours when their fathers were problem bears (Barnard's test, *p* = 0.92, Fig. 5.2). In contrast, offspring are more likely to be involved in incidents or human-bear conflict when their mothers were problem bears (Barnard's test, *p* = 0.05, Fig. 5.3).

5.5 Discussion

My results provide evidence of a behavioural mechanism (i.e., social learning) that might be amplifying the propensity for grizzly bear-agricultural conflicts in southwestern Alberta. More offspring exhibit conflict behaviours when their mothers are problem bears, but no such effect was observed for paternal conflict behaviour. Thus, my results support the social learning hypothesis, but not the genetic inheritance hypothesis as it relates to the acquisition of conflict behaviour. If conflict was an inherited behaviour, I would have expected to see a significant relationship between paternal conflict behaviour and offspring behaviour. My results provide more direct evidence for social learning in grizzly bears than previous studies (e.g. Nielsen et al. 2013) because I used a parentage analysis rather than relatedness to examine family relationships. Relatedness analyses cannot distinguish between full-sibling and parent-offspring relationships (e.g. relatedness coefficients for full-siblings and parent-offspring are both 0.5) (Queller and Goodnight 1989). Conclusions regarding social learning from relatedness analyses are typically based on the assumption that because males are not involved in the rearing of offspring there should be a positive correlation between behaviour and relatedness in females but not males. A parentage analysis, however, allows me to explicitly examine direct mother-offspring versus father-offspring relationships, rather than inferred relationships as is done in a relatedness analysis. Thus, because my parentage analysis uses known relationships rather than relatedness coefficients, it provides more direct evidence that maternal behaviour influenced offspring behaviour.

Social learning has the potential to perpetuate grizzly bear conflicts – highlighting the importance of preventing initial conflicts, but also removing problem individuals once conflicts start. Prompt removal (i.e. culling) of grizzly bears engaged in conflict behaviour might be an effective solution for reducing conflicts (Meagher and Fowler 1989, Anderson et al. 2002), but removing females is unlikely to be a provincially approved mitigation measure in Alberta because grizzly bears have threatened status in the province. Indeed, one of the measures of success within the provincial Recovery Plan is to have no female grizzly bears killed as problem animals through agency control (Alberta Sustainable Resource Development 2008). However, problem grizzly bears in Alberta often are relocated (moved within the BMA) or translocated (moved outside the BMA), and relocation/translocation happens according to the provincial grizzly bear response guidelines (Alberta Government 2009). While male grizzly bears can be relocated long distances outside of the bear management area, it is mandatory on a first offence that a female grizzly bear with cubs stays within the same BMA (Alberta Government 2009).

Further, long-distance relocation of problem individuals often is unsuccessful (e.g. Meagher and Fowler 1989, Linnell et al. 1997, Spencer et al. 2007, Fontúrbel and Simonetti 2011), and translocated bears typically have higher mortality rates and lower survival than non-translocated bears (Blanchard and Knight 1995, Linnell et al. 1997). Within Alberta the overall success rate of translocations and relocations of problem grizzly bears is only 30.5%, with translocated individuals re-offending, homing, or suffering increased mortality (Brown et al.

2014). Thus, Alberta's bear management policy might be resulting in increased mortality risk for males versus females. Because of social learning in conflict behaviour, keeping females within the same bear management area might be providing more learning opportunities for cubs of problem females, and consequently ultimately increasing the number of problem bears.

However, not every bear that uses private lands will become a problem bear. Indeed, of the 213 grizzly bears detected, 137 were detected on private land at some point, but only 55 grizzly bears were identified as problem bears (an additional 5 bears were involved in incidents in Montana). Philopatry exists in grizzly bears, particularly females, and small sample sizes prohibited me from evaluating this potential confounding effect. However, as evidence by the numbers above, simply using private land does not mean that a bear will become a problem bear. Emphasizing proactive (e.g. attractant management) rather than reactive (e.g. relocation) mitigation measures might be a more effective long-term solution (Spencer et al. 2007), and unlike lethal removal, such proactive efforts fit within the objectives of Alberta's grizzly bear Recovery Plan. While accessing anthropogenic resources such as dead stock in a bone pile could be considered natural grizzly bear foraging behaviour, such behaviour is not desirable on private lands. Securing anthropogenic food sources through attractant management can be a powerful tool for preventing conflicts (e.g. Wilson et al. 2005, Bino et al. 2010), and local community groups in southwestern Alberta have demonstrated effective mitigation measures (e.g. electric fencing, grain bin retrofits, dead stock removal, etc.) (Chapter 2).

Additionally, aversive conditioning can be an effective strategy for preventing bears from developing undesirable behaviors (Gillin et al. 1994, Anderson et al. 2002, Mazur 2010). Aversive conditioning uses a negative stimulus to cause pain, discomfort, or irritation in an animal involved in an unwanted behaviour (Gillin et al. 1994, Shivik et al. 2003, Mazur 2010).

Aversive conditioning, however, will not be an effective management tool if unsecured attractants remain in the area (Gillin et al. 1994, Leigh and Chamberlain 2008, Mazur 2010). Thus, attractant management should likely be prioritized over aversive conditioning. Such mitigation measures are important because the area has an increasing grizzly bear population that overlaps substantially with agricultural land uses (Chapter 3). The most recent abundance estimate for my study area is 67 resident bears, and the population is estimated to be stable to increasing (Chapter 3). However, far more bears use the study area than are considered resident bears; the estimate of grizzly bears using the study area during the course of a year is 172 and this number represents the number of bears that have the potential to be involved in conflict (Chapter 3).

While Galton advocated an "inheritance of criminal tendencies" in humans (Galton 1883), I found no evidence for a genetic basis for "criminal" behaviour by bears. We might, however, be able to prevent learning of conflict behaviour by minimizing opportunities for females to become problem bears and quickly addressing and/or removing the source of the conflict once discovered. Because grizzly bears are provincially threatened, lethal removal of problem female grizzly bears is a last resort (Alberta Government 2009). Thus, preventing conflict behaviours through proactive initiatives such as electric fencing, attractant management, grain bin modifications, and potentially aversive conditioning offer more promising solutions that both reduce the economic impact of grizzly bears to producers but could also help stop the acquisition of conflict behaviours. While the sample size of problem mothers was limited (n = 8), and I might have misclassified the behaviour of some bears (e.g., Fish and Wildlife Officers could have captured a bear at a conflict site but accidentally caught the wrong bear), there was a strong pattern of non-problem mothers (n = 68 non-problem mothers) producing non-problem offspring. Thus, preventing female grizzly bears from becoming problem individuals will likely help prevent the perpetuation of conflicts through social learning.

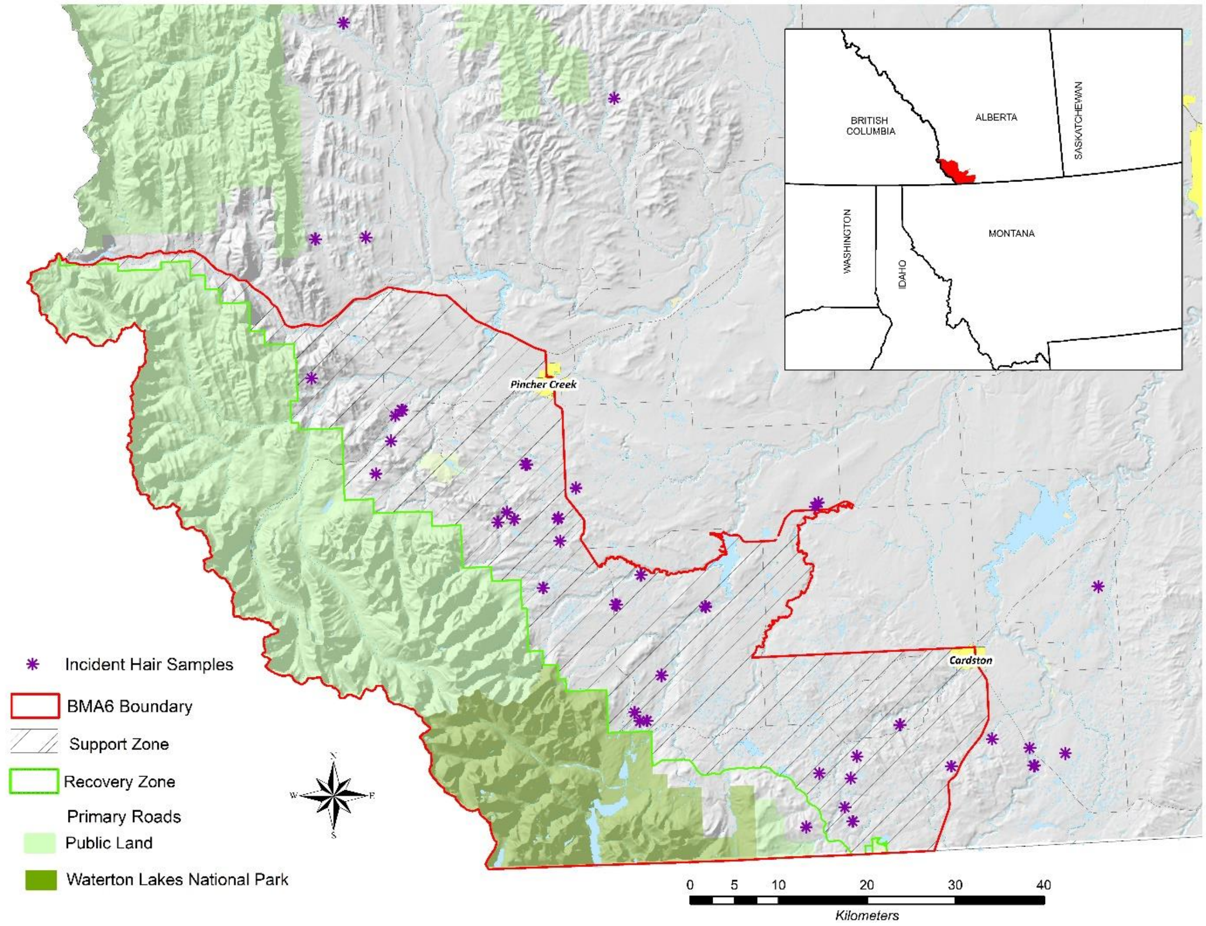

Figure 5.1 Map of the study area (BMA6) and incident hair samples in southwestern Alberta.

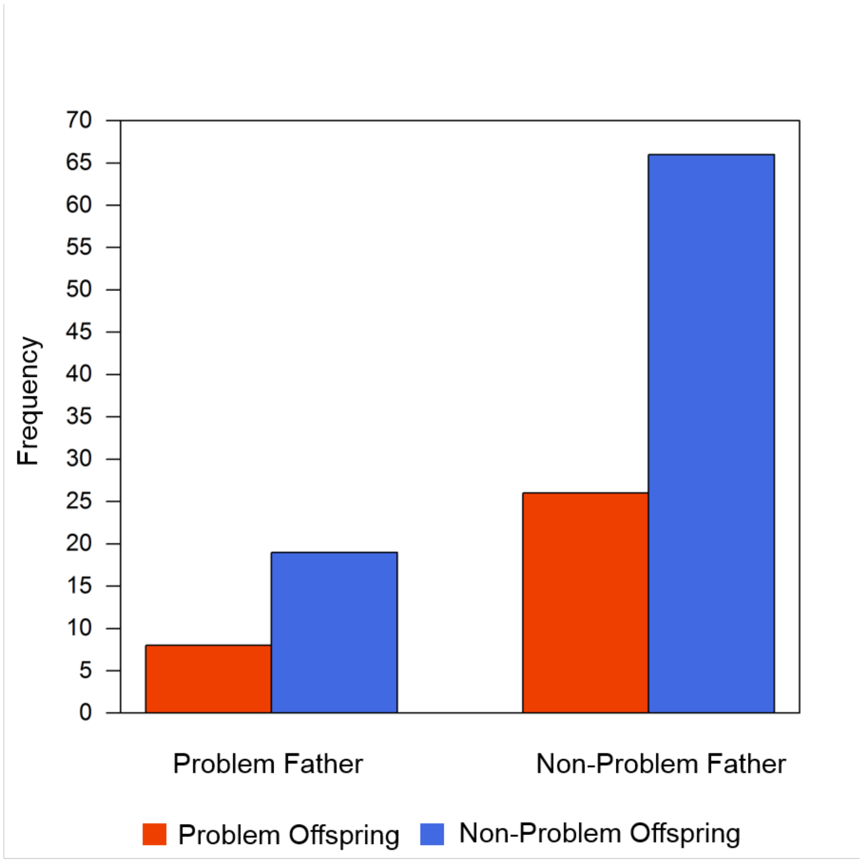

Figure 5.2 Frequency of problem and non-problem offspring grouped by behaviour type of their father.

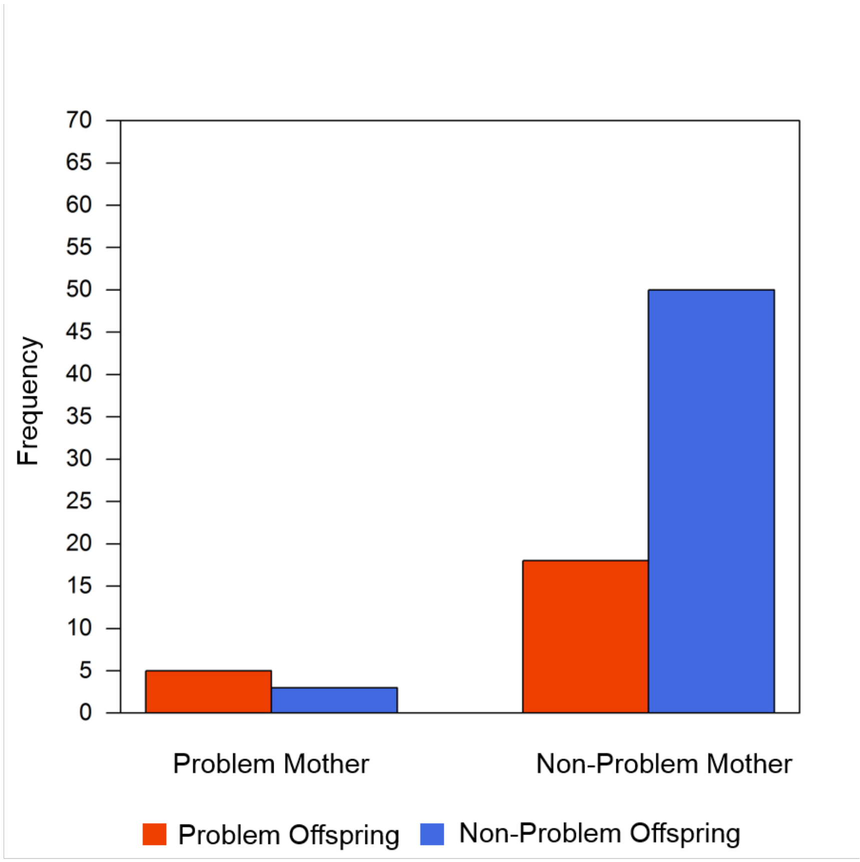

Figure 5.3 Frequency of problem and non-problem offspring grouped by behaviour type of their mother.

Chapter 6

6 Conclusion

As Aldo Leopold, a pioneer of wildlife management, famously wrote, "*A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise*" (Leopold 1949). At its core this statement is inherently simple; in practice, however, as the human population increases and human-altered landscapes become the dominant land cover type (Vitousek et al. 1997, Sanderson et al. 2002) abiding by this strict view of right and wrong becomes increasingly challenging. Wildlife often are viewed as a public good, but there is a cost to maintaining wildlife on the landscape, and this cost can be particularly high when it comes to large carnivores (e.g. Patterson et al. 2004, Baker et al. 2008, Sommers et al. 2010, Dickman et al. 2011).

Where people and large carnivores share space, there is potential for conflict – both between people and large carnivores, but also among people themselves with opposing viewpoints regarding carnivore conservation and management (Clark et al. 2014). On one hand, large carnivores such as grizzly bears, black bears, cougar, and wolves often are viewed as iconic symbols of wilderness and are often used as flagship species in conservation efforts (e.g. Carroll et al. 2001, Macdonald 2001, Dickman et al. 2011). This viewpoint, however, is relatively recent when compared to historical documentation of the persecution of large carnivores for being real and perceived threats to human safety and livelihood (e.g. Kellert et al. 1996, Treves and Naughton-Treves 1999, Naughton-Treves et al. 2003, Ratnayeke et al. 2014). Indeed, "*Among the earliest forms of human self-awareness was the awareness of being meat*" (Quammen 2003). As human land uses increasingly dominate landscapes across the globe, there is a growing need to find a balance between the needs of large carnivores and the needs of people inhabiting the same landscapes. This search for coexistence between humans and large carnivores is a fundamental challenge of contemporary conservation efforts, and I have explored these issues in my research. Within my thesis I have reviewed the types of conflicts, potential explanations for conflicts, mitigations measures to reduce conflicts, and a behavioural mechanism potentially amplifying the conflict pattern in southwestern Alberta.

In Chapter 2, I reviewed a long-term multi-species data set on large carnivore complaint records for southwestern Alberta. Analysis of these records revealed that conflicts for the omnivorous bear species are more varied and prevalent than for the strictly carnivorous wolves and cougars. Bear incidents were predominately related to attractants, and local efforts within the community have focussed on restricting carnivore access to these attractants. These proactive mitigation efforts are necessary for continued coexistence particularly as carnivore occurrences spread eastward into landscapes dominated by agricultural activities. The local community's adoption of proactive mitigation measures is promising. For example, 2015 complaint records for all large carnivore species were lower than 2014 complaint records within my study area (Alberta Environment and Parks, unpublished data).

There is, however, no "one size fits all" solution to the problem of large carnivore conflicts. Mitigation efforts must be designed in conjunction with the individual landowner to ensure success. New ideas and tools are continually being developed, and while an evaluation of mitigation measures can be challenging (and consequently rarely done despite the large volume of literature advocating such solutions), it must become a priority to document the circumstances under which various mitigation measures can be effective. I also recommend that future work involve interdisciplinary collaborations to better understand the non-biological variables that affect complaint reporting rates and adoption of conflict mitigation measures.

For example, while my research quantified the types of issues caused by large carnivores, I was not able to quantify non-biological reasons that might affect reporting rates (e.g. individual tolerance toward large carnivores, landowner satisfaction with government staff, differing opinions on the value of complaint data). Continued monitoring of complaint data are important, but will be improved by quantifying the social factors influencing reporting rates. Similarly, not every landowner participates in the deadstock removal program, and not every community member in the Crowsnest Pass engages in BearSmart – and the reasons go beyond a lack of awareness. Social sciences could help to quantify reasons for a lack of participation, and thus, subsequently improve the efficacy of such efforts. The policy sciences can offer a framework to integrate the biological and non-biological data into meaningful management and policy decisions (Clark 2011).

As I showed in Chapter 2, grizzly bear incidents have been increasing, and one potential reason is an increased grizzly bear population. In Chapter 3, I provided current grizzly bear abundance and density estimates. I estimated that the resident grizzly bear population has been stable to increasing (potentially growing at 4% per year), and that a much larger number of bears use the study area than are considered residents. This larger number of bears using the area represents the number of grizzly bears that the local community might encounter and the number of bears that have the potential to be involved in conflict. Importantly, I also demonstrated that spatially explicit capture recapture (SECR) estimates can be sensitive to shifting animal space use. This pattern is likely particularly apparent in situations such as southwestern Alberta where there is a mismatch between the monitoring boundaries (i.e. bear management area), and ecological boundaries of the population. A decrease in SECR estimates might represent a shift of animal home range centers rather than a true population decline, and I believe this is an important point that should be brought to the attention of SECR users. Further, my results highlight the importance of multi-year, interjurisdictional monitoring and management – particularly in light of the preceding comment. Recent analysis of British Columbia grizzly bear data indicate a decline in numbers (Lamb et al. 2016), yet both Alberta (Chapter 3) and Montana (Mace et al. 2012) indicate an increase; these jurisdictions are all part of the same biological grizzly bear population (Proctor et al. 2012).

To assimilate cross-jurisdictional information on the same population, I recommend increasing international and interprovincial collaborations to better monitor the population ecology of grizzly bears in this region. The monitoring framework I established in southwestern Alberta provides a robust, repeatable framework. However, my sampling effort of 7 occasions per year might be more than is required to inform management, and future work should evaluate the intensity of sampling required to provide the necessary data (e.g. changes in population abundance and density) while minimizing costs. Ideally, a monitoring program would be established collaboratively at the ecosystem scale to match monitoring boundaries with the ecological boundaries, to establish consistency in methods between jurisdictions, and to ensure that all management agencies are obtaining necessary data for sound management.

For example, the Grizzly Bear Recovery Plan outlines the criteria necessary to consider the Alberta grizzly bear population recovered and reinstitute a hunt (Alberta Sustainable Resource Development 2008). Alberta's metrics of a recovered population include a stable to increasing population and a population of at least 90% of the population target (identified by the Recovery Team) (Alberta Sustainable Resource Development 2008). Similarly, the United

States Fish and Wildlife Service has outlined demographic recovery goals for the U.S. grizzly bear population (United States Fish and Wildlife Service 1993). These goals, however, have been greatly surpassed for the Northern Continental Divide Ecosystem (NCDE) recovery zone, and the new conservation strategy includes a population goal of at least 800 grizzly bears in the NCDE recovery zone and adjacent management zone (United States Fish and Wildlife Service 2013). Monitoring data are required to document whether this international grizzly bear population has achieved a recovered status; collaborative cross-jurisdictional monitoring will ensure the most accurate data are obtained.

Because there is a substantial overlap between grizzly bears and human land uses in southwestern Alberta, there will likely always be some level of conflict. As mentioned in Chapter 2, numerous mitigation efforts are in place to reduce such conflicts. In Chapter 4, I evaluated one of Alberta's conflict mitigation programs – the intercept feeding program. I found that despite the program, spring-livestock conflicts have continued to increase and have done so at a rate that exceeds the estimated population growth rate of grizzly bears. Further, intercept feeding sites were dominated by a small number of male grizzly bears, and were thus unavailable as a food resource for the majority of the grizzly bear population. Spring livestock predation events are now occurring further from the mountains in more prairie/agricultural habitats and might be caused by bears denning in eastern areas as opposed to the mountains (i.e. bears that would never encounter the intercept feeding sites). The intercept feeding program was costly both in terms of expense (e.g. helicopter time) and manpower. Although some male grizzly bears might have been intercepted by the program, my research suggests that the costs (both financial and increasing conflicts) outweigh the benefits. I recommend continued monitoring of spring grizzly bear depredation events and an evaluation of other mitigation tools such as the electric fencing of spring calving pastures.

In Chapter 5, I evaluated a behavioural mechanism for the acquisition of conflict behaviour. Not every grizzly bear that used private lands was involved in a conflict, prompting the question of why some bears are more likely to engage in conflict than others. I evaluated evidence for genetic inheritance and social learning of conflict behaviour. I found no evidence for the genetic-inheritance hypothesis, but I did find evidence for the social-learning hypothesis. In other words, offspring of problem females were more likely to be involved in conflict behaviours than offspring from non-problem females, but there was no relationship with paternal conflict behaviour because males are not involved in the rearing of offspring.

Although my sample sizes of problem mothers were small, there was a strong pattern of non-problem mothers producing non-problem offspring. Prompt removal (i.e. culling) of a problem bear is an unlikely management recommendation given the threatened status of grizzly bears in Alberta, but it might be an option when considered in the context of the larger international grizzly bear population. I recommend future work repeat my analysis at the ecosystem scale to provide the appropriate ecological context. Further, increased samples sizes might allow for the separation of specific conflict behaviours, providing further insight into social learning by grizzly bears. For example, in my analysis, I grouped all conflict behaviours together, but it might be that social learning is more prevalent in complex behaviours (e.g. killing cattle vs. accessing unsecured garbage) (Breck et al. 2008). Proactive conflict mitigation measures will be important in preventing females from becoming problem bears – and subsequently reducing development of conflict behaviours in their offspring. I recommend resources support these proactive initiatives.

All of my research was completed in consultation and collaboration with the local community and I believe these partnerships improved my research. Where science and local perspective disagree, solutions to complex wildlife and ecological problems will be difficult (Clark 2011). I worked extensively with local communities from the inception of the project to ensure that they were engaged and informed of all project activities. For example, over 70 landowners and 4 livestock grazing co-operatives participated in the project, and I gave 55 public presentations between January 2012 and March 2016. Landowners shared information regarding grizzly bear presence and behaviours, provided continued land access, and assisted in the collection of opportunistic hair samples. I believe my research benefited from this information. Our understanding of predator ecology often is driven by studies in wildland areas, but it is not sufficient to base management of predators in human-settled lands on information acquired from remote areas (Moss et al. 2016). Further, without engaging communities within carnivore home ranges, we run the risk of missing the challenges that these communities are dealing with, and failing to develop partnerships that will be critical to facilitating coexistence between people and large carnivores.

Clearly, there is much work remaining to be done as it relates to large carnivore ecology and coexistence in human-settled landscapes. I have explored a few hypotheses explaining the observed patterns in southwestern Alberta, and it is my hope that my dissertation research advanced our understanding of carnivore ecology (particularly grizzly bears) in human-settled areas, provided further insight to population estimation techniques, improved wildlife management in Alberta, and provided an example of a successful collaboration with local communities.

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