Black Bear Density and Resource Partitioning with Grizzly Bears

by

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ABSTRACT

American black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) have similar habitat requirements, relying on seasonally available grasses, forbs, fruiting shrubs and trees, and neonate ungulates. To avoid aggressive encounters with grizzly bears, black bears partition habitats spatially and temporally. For example, black bears avoid areas with high-quality resources like spawning salmon (*Oncorhynchus* spp.) and ungulate carcasses when grizzly bears are present. We used non-invasive genetic sampling to identify unique individuals, sex, and species. We calculated resource-selection functions for each sex and species, contrasting bear 'use' locations with 'available,' to document seasonal habitat partitioning in southwestern Alberta, Canada. Using covariates from top RSF models, we made all pair-wise combinations of male and female black and grizzly bears (6 total) in a latent selection difference function. We collected bear hair during 7 sample occasions in early summer, late summer, and autumn in 2013 and 2014 in southwestern Alberta. From the top models, black bears avoided recently burned areas (<20 years old) relative to grizzly bears, grizzly bears selected public (Crown) lands, and black bears selected private lands. Western lands in our study area are primarily Crown land and eastern lands are primary private. For all seasons, male and female black bears showed the most overlap in resource selection. In early summer, female grizzly bears and female black bears showed the most overlap. In late summer, male and female black bears showed the most overlap. In autumn, male and female black bears, as well as male grizzly bears and female black bears showed higher overlap relative to other groups. Our results indicate habitat partitioning occurred in southwestern Alberta and clarify how grizzly bears, which are listed as a *Threatened* species in Alberta, are co-existing with a subordinate, but higher-density species.

There has never been an empirical estimate of black bear density and abundance in southwestern Alberta. We used non-invasive genetic sampling and indices of habitat productivity and human disturbance to estimate black bear population density. We used spatially explicit capture-recapture (SECR) and resource-selection functions (RSF) to estimate density and abundance for each year and sex. SECR-derived black bear abundance estimates for males were 149.4 (95% CI: 124.6-179.2) in 2013 and 132.2 (95% CI: = 110.9-157.5) in 2014. SECR-derived abundance estimates for females were 261.4 (95% CI:199.9-341.8) in 2013 and 210.7 (95% CI: 159.3-278.6) in 2014. RSF-derived abundance estimates in the area of inference were 116.1 male black bears (95% CI: 82.3 – 163.9) in 2013 and 134.39 male black bears (95% CI: 98.9 – 182.6) in 2014 (Figure 6). For females in 2013, abundance in the area of inference was 159.5 (95% CI: 120.3 – 211.6) in 2013 and 147.54 (95% CI: 96.0 – 226.8) in 2014. Density estimates were highest on federally and provincially protected lands, followed by private land, and densities were lowest for both sexes on Crown land. With current plans to create two new Provincial Parks on Crown land in our study area, we speculate this could decrease mortality rates, and increase black bear densities on Crown land.

PREFACE

This thesis is an original work by Anne Elizabeth Loosen. Field data were collected during a PhD project (Andrea T. Morehouse and Mark S. Boyce; 2011-2016) and 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). The project presented in this thesis was granted official AUCU exemption (2015.002; current through Aug 2017).

To date, no manuscripts have been submitted for publication. Chapter 2 co-authors include T. Avgar, M. Boyce, and A. Morehouse. For this manuscript, A. Loosen analyzed the data, and wrote most of the manuscript. T. Avgar and M. Boyce provided valuable feedback during the analysis and writing process. A. Morehouse provided grizzly bear data and manuscript edits.

Chapter 3 co-authors include M. Boyce and A. Morehouse. A. Loosen analyzed the data, and wrote most of the manuscript. M. Boyce and A. Morehouse provided input throughout the analysis and writing process.

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CHAPTER 1 – GENERAL INTRODUCTION

At the turn of the 20th century, North American government policies were liberal with their removal of wildlife, particularly large carnivores. Large carnivores posed an economic threat to already tenuous existences (Geist 1988) and wide-spread hunting led to range-wide contractions for large carnivores, particularly bears. In North America, American black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) were removed from many landscapes to reduce damage to human settlements (e.g., agriculture), to mitigate the perceived threat to human safety, and to sell at fur markets (Mattson and Merrill 2002).

As certain wildlife populations dwindled, such as grizzly bears, the foundations of modern North American wildlife management began to form. Early conservation pioneers established networks of parks and wildlife refuges that have become the cornerstone of wildlife conservation and research in contemporary North America (Geist 1988). In addition, these conservation pioneers helped to establish a North American model of wildlife management that recommended wildlife management be based on science and that species protection requires habitat preservation and conservation (Geist 1988).

The North American model of wildlife conservation continues today, and many large carnivores are moving well beyond the boundaries of parks and protected areas and are recolonizing multi-use landscapes (Treves and Karanth 2003, Treves et al. 2006). The social tolerance of large carnivores has increased since the late 19th century (Treves and Karanth 2003), but hunting continues to be used to manage wildlife densities, disease, and human-wildlife conflict.

In Alberta, black and grizzly bears share a similar harvest policy history. In 1927, the province required hunting permits with an annual harvest maximum of 2 black or grizzly bears

(Gunson 1993). In 1928, the Game Act established a hunting season from June 15 to September 1 and the following year brought protection to females with cubs-of-the-year. Through the 1930-40s, low pelt values de-incentivized bear harvests and the province noted an increase in livestock predation. In the 1950s, a single black bear was diagnosed with rabies and the province implemented a poisoning program that killed over 4,000 black bears (Gunson 1993). The following decade, biologists noted a decrease in bear populations. In the 1980's, the government made their first province-wide estimate of black bear populations.

Similarities in black and grizzly bear hunting history in Alberta ended in the 21st century. In 2006, the province enacted a grizzly bear hunting moratorium, followed by listing the species as provincially threatened in 2010 (Alberta Sustainable Resource Development 2010). In contrast, a no-quota black bear hunt is allowed in the spring and fall (Gunson 1993). Much like black bear management elsewhere in North America (Garshelis and Hristienko 2006), biologists in Alberta have incomplete and unreliable data on which to make management decisions: harvest reporting is not required, private landowners can lethally remove offending black bears without reporting, and funds are lacking for black bear research and monitoring.

Where black bear range overlaps with grizzly bears, competitive interactions with the more dominant grizzly bear may shape black bear habitat selection. For large mammals, directly measuring competition can be difficult because they are long-lived, occur at low densities, and experimental manipulation is challenging for logistical and ethical reasons (Connell 1980, Creel 2001). Black bears and grizzly are both generalist omnivores with similar digestive capabilities where, in the absence of abundant protein sources such as anadromous salmon (*Oncorhynchus* spp.), they have high dietary overlap (Mattson et al. 2005). From a population perspective, black bears are more resilient to perturbations because they have a higher reproductive rate, higher tolerance for human disturbance, smaller body size, and naturally occur at higher densities than grizzly bears (Craighead 1974, Herrero 1978). However, black bear movements and behaviors can be altered by grizzly bears where sympatric, because they are the more-dominant species (Holm et al. 1999, Schwartz et al. 2010). With no empirical baseline population data for black bear populations in southwestern Alberta, and anecdotal observations that black bears appear to be shifting spatio-temporal use of the landscape, I studied black and grizzly bear resource use in the study area (Chapter 1).

In southwestern Alberta, there has never been an abundance and density estimate for black bears. To address this knowledge gap in Chapter 2, I used spatially explicit capture-recapture and resource-selection function models to estimate density, abundance, and spatial drivers thereof (Efford 2004). In Chapter 3, I synthesize the concepts and information from the two preceding chapters and provide recommendations for management and future research.

CHAPTER 2 – RESOURCE OVERLAP VARIES SEASONALLY BETWEEN BLACK AND GRIZZLY BEARS IN A HUMAN-DOMINATED LANDSCAPE

INTRODUCTION

Grizzly bears (*Ursus arctos*) are dominant over black bears (*U. americanus*) due to higher aggression levels and larger body size (Herrero 1978). Black bears are thought to have evolved in forested habitats and grizzly bears in open habitats (Herrero 1978). More recently, black bears have expanded into open terrain such as agricultural areas (Ditmer et al. 2016) and tundra (Jonkel and Miller 1970) where grizzly bears are allopatric. However, where these species are sympatric, black bears are restricted primarily to forested cover (Herrero 1978, Apps et al. 2006). Interspecific competition and intra-guild predation are mechanisms by which grizzly bears can alter feeding behaviour, activity patterns, and home range sizes of black bears (Aune 1994, Holm et al. 1999, Jacoby et al. 1999, Schwartz et al. 2010). To avoid direct encounters with grizzly bears, black bears separate themselves spatially and temporally from grizzly bears. Consequently, where abundant protein sources (e.g., anadromous salmon (*Oncorhynchus* spp.) or ungulate carcases) are available, grizzly bears are known to dominate these resources, whereas black bears remain largely herbivorous (Jacoby et al. 1999, Mattson et al. 2005, Belant et al. 2006). In Alaska, for example, black bears have diets similar to grizzly bears, except for adult males during salmon spawning (Jacoby et al. 1999). While grizzly bears are the superior competitor during interference competition, smaller-bodied bears can more efficiently exploit alternative food sources, and generally have lower nutritional requirements than larger-bodied grizzly bears. This suggests that black bears could out-compete grizzly bears during exploitation competition (i.e., scramble competition) when resources are dispersed (Mattson et al. 2005).

Despite these differences, black bears and grizzly bears are both opportunist omnivores with similar digestive capabilities (Pritchard and Robbins 1990). Both species rely on seasonally available neonate ungulates, grasses, forbs, and hard (e.g., white bark pine (*Pinus albicaulis*); (Hamer and Pengelley 2015)) and soft masts. In the southern Canadian Rockies, soft-mast plants such as huckleberry (*Vaccinium* spp.), buffalo berry (*Shepherdia canadensis*), and Saskatoon berry (*Amelanchier alnifolia*) provide high-calorie foods during hyperphagia, a period of intense eating in the autumn to gain mass in preparation for winter denning (Hamer et al. 1991, Holcroft and Herrero 1991, Aune 1994, Northrup et al. 2012*b*). As different foods become available, bears show seasonal variation in selection (Nielsen et al. 2002, Boyce and Waller 2003, Munro et al. 2006). In general, as snow melts and vegetation emerges, spring and early summer is a food-limiting time of year for bears. Late summer corresponds to berry ripening, and thus a time of food abundance. In the fall, productivity decreases with cold temperatures and snow and food again becomes limited. As a result of seasonal variation in food availability, we would expect intraspecies and interspecies competition to vary seasonally (Miller 1967). When food availability is low, we would expect competition (i.e., resource overlap) to be greater within species (Horn 1968, Reynolds and Beecham 1980, McLoughlin and Ferguson 2000) and resource overlap to be lower between species. For example, Belant et al. (2006) found black bears did not exploit salmon during below-average spawning numbers (i.e., low food availability), likely due to interspecific exclusion by grizzly bears. This example illustrates that when food is scarce, the potential for competition for resources increases. When food is abundant, resource partitioning offers no advantage and competition is less likely to occur.

As human activities continue to alter the natural landscape, wildlife space-use is increasingly being influenced by people. Human-dominated landscapes such as agriculture, oil and gas development, residential, urban, and suburban areas can provide alternative food resources such as stored and standing grain, dead livestock (deadstock), fruit-trees, garbage, and bird seed, but bear habituation can reduce individual bear survival (Wilson et al. 2006, Baruch-Mordo et al. 2014) and increase the propensity for human-wildlife conflicts. In particular, the effect of roads have been identified as a primary driver in the distributions and habitat selection of many species (Forman 2000, Fahrig and Rytwinski 2009, Prokopenko et al. 2017). For bears, roadsides can offer early-spring foraging opportunities (Roever et al. 2010), but in contrast, can contribute to functional habitat loss through road avoidance (McLellan and Shackleton 1988, Nielsen et al. 2006, Duquette et al. 2017). Roads pose a mortality risk because of vehicle collisions and increased access for hunters and poachers. In the Flathead Valley, BC, the majority of grizzly bears are shot within 500 m of roads (McLellan and Shackleton 1988) as was true in the central East Slopes of Alberta (Nielsen et al. 2004). In general, black bears are found closer to roads and human-dominated landscapes relative to grizzly bears (Kasworm and Manley 1990, Apps et al. 2006), likely due in part to dominance by grizzly bears. Male grizzly bears are thought to be more sensitive to human disturbance than black bears and female grizzly bears (Knight and Eberhardt 1985, Rode et al. 2006). While larger males are expected to maximize their foraging opportunities, females often select habitats to minimize predation risk to their offspring (Main et al. 1996, Ruckstuhl and Neuhaus 2002, Rode et al. 2006).

To evaluate habitat selection by sympatric black and grizzly bears, we used resource selection functions (RSFs) to contrast positional data with available habitats (Johnson et al. 2006). Selection, defined as the probability that an animal will use a resource unit if it is encountered, is driven by bottom-up forces such as food availability and top-down forces such as mortality risk (Abrahams and Dill 1989, Lele et al. 2013). Many studies employing RSFs rely on so-called “presence-only” data (Pearce and Boyce 2006), where animal locations are typically determined from telemetry data. This design provides information on where an animal was (presence) but not where the animal was not (absence), and defining habitat availability represents one of the primary challenges for RSF studies (Hirzel et al. 2002, Soberon and Peterson 2005, Basille et al. 2008; Avgar et al. 2016). In our study area in southwestern Alberta, Canada, we established a network of rub ‘objects’ (trees, fence posts, power poles) that black and grizzly bears naturally rub on as a form of communication (Green and Mattson 2003, Sato et al. 2014). To mitigate the issues in defining the available domain, we limited our use and availability domains to resource units where we found rub objects. Further, we used bear rub objects to evaluate seasonal change in black and grizzly bear resource overlap, which is poorly documented, particularly for interior populations.

Using non-invasive genetic sampling (NGS), our objective was to examine how black and grizzly bear habitat selection varied seasonally by species and sex in southwestern Alberta, Canada. The grizzly bear population is growing (Morehouse and Boyce 2016), while little is known about the black bear population. Understanding how black and grizzly bears partition resources will yield insight into how two putative competitors co-exist in an area with a high human footprint. Further, information on resource use and overlap is essential to understand community structure (Rosenzweig 1966). To meet this objective, we first identified the primary covariates associated with habitat selection for male and female black and grizzly bears. Next, we used the covariates from the top sex- and species-specific models to quantitatively compare male and female grizzly and black bear selection. Because of grizzly bear dominance and fitness consequences associated with human-dominated landscapes, we hypothesized there would be resource partitioning occurring and black bears would select human-dominated landscapes as a refuge from grizzly bears. Seasonally, we predicted that resource overlap within species would be greatest in the spring and fall when resources are limited. In contrast, we predicted that resource overlap between species would be greatest in summer when resources are abundant. Last, because male grizzly bears are the largest among the cohort of bears, we predicted males would exhibit the most dissimilar resource-selection patterns compared to female grizzly bears and male and female black bears.

STUDY AREA

The 3,600-km^2 study area lies on the east side of the continental divide in the southern Canadian Rocky Mountains (Figure 1) and is bounded by Highway 3 to the north, British Columbia to the west, the United States-Canada border to the south, and follows Highway 2 to the east. Elevation ranges from 1,030 m to 2,910 m. Important vegetation-based foods for bears in this area include Saskatoon berry, huckleberry, buffalo berry, cow parsnip (*Heracleum maximum*), horsetail (*Equisetum* spp.), and dandelion (*Taraxacum* spp.) (Hamer et al. 1991, Holcroft and Herrero 1991, Northrup et al. 2012*b*). The area is conifer forest (29%), agricultural (22%), grassland (16%) including native grassland and cultivated fields, shrub land (16%), and deciduous forest (11%). Agriculture, including cattle production, is the primary industry (Statistics Canada, MD of Pincher Creek 2011 Community Profile).

The area is managed provincially for grizzly bears as ‘Bear Management Area 6’ (http://aep.alberta.ca/). Land management includes public and Crown land (hereafter “Crown”), private land, and provincially and federally protected land (hereafter “protected”). Crown land has a lower road density than private land, and licensed black bear hunting occurs in the spring (1 Apr–31 May) and autumn (1 Sep–30 Nov). Crown land is characterized by alpine, sub-alpine, montane, and aspen-parkland eco-regions (Aune 1994, Northrup et al. 2012*b*). Parks and protected areas, namely Waterton Lakes National Park (WLNP) and Beauvais Provincial Park, have the lowest road density and hunting is prohibited. Like Crown lands, park land is characterized by alpine, sub-alpine, montane, and aspen-parkland eco-regions. Private land in the study area has the highest road density (Northrup et al. 2012*a*) and is characterized by rough fescue grasslands and agriculture (e.g., grazing pastures, hay, grain, and oil-seed). On private land, black bears can be removed by landowners year-round without restriction. Black bear baiting is prohibited in the study area (Ministry of Environment and Parks 2016). Grizzly bear hunting has been prohibited in Alberta since 2006 (Alberta Sustainable Resource Development 2008).

METHODS

We used non-invasive genetic sampling to identify individual grizzly and black bears in southwestern Alberta. We surveyed for rub objects based on known travel corridors, roads and trails, local knowledge (e.g., biologists, landowners), and grizzly bear resource-selection maps (Northrup et al. 2012*b*). Bears naturally rub on trees and other surfaces, and while the specific mechanisms behind rubbing are poorly understood, it is thought that rubbing is a form of communication (Green and Mattson 2003, Sato et al. 2014); rubs may be used to advertise for mates (Lamb et al. 2016) or to communicate dominance (Clapham et al. 2012). Rub trees are generally found on travel routes, in proximity to water, and in low-elevation terrain (Green and Mattson 2003, Sato et al. 2014, Morgan Henderson et al. 2015). We established rub 'objects' where we observed fresh bear sign, primarily bear hair, on rub trees, power poles, and fence posts. Rub objects were set up with 4 barbed-wire segments. We also surveyed barbed-wire fence-lines, and where we observed fresh bear hair on a portion of a fence we followed methods used by Kendall et al. (2009) and marked stretches of fence for resurvey.

In 2011 and 2012, we surveyed and set up rub objects on Crown and private land, respectively (Morehouse and Boyce 2016). All rub objects were sampled 8 times a year, once every 21 days from May to November in 2013 and 2014 (Table 1). During the first visit of each year we removed old hair from the barbed wire and the remaining 7 visits were collection events (Morehouse and Boyce 2016). We considered a barb or end of a barbed-wire segment a discrete sampling unit, resulting in multiple discrete sampling units from the same rub object (Kendall et al. 2009, Stetz et al. 2010). Hair was collected from wire only, not from adjacent bark. After hair collection, we burned remnant hairs using butane torches to prevent future contamination (Kendall et al. 2009, Stetz et al. 2010).

Hair samples were sent to Wildlife Genetics International (WGI; Nelson, BC) to determine species, individual, and sex via multi-locus analysis of nuclear DNA (Paetkau 2003, 2004). WGI extracted DNA from samples with ≥ 1 guard hair root or 5 underfur hairs. In the Rocky Mountains, only one individual was typically identified during a sampling period for any given rub object (Sawaya et al. 2012, Stetz et al. 2014). We employed the same sub-sampling strategy outlined by Morehouse and Boyce (2016) where every third hair sample was analyzed.

All samples sent to WGI were pre-screened at the G10J microsatellite to differentiate between grizzly and black bear samples and to screen out low-quality DNA samples. All hair samples were subjected to a 3-phase process of first pass, cleanup, and error-check (Paetkau 2003). Hair sample collection was approved by University of Alberta's Animal Care and Use Committee (AUP00000008). Possession of hair samples was permitted by Alberta Environment and Parks (Research Permit #56014 and Collection Licence #56015).

Landscape Covariates

We used GIS-based habitat, terrain, and human-use covariates to account for variation in landscape characteristics in ArcMap (v. 10.3.1, Environmental Systems Research Institute, Redlands, CA). For habitat, we included the presence or absence of burned areas ≤ 20 years old (Apps et al. 2006), ln-transformed distance (m) to higher-order streams and lakes, and percent canopy cover. We also included a quadratic term for canopy cover, because mid-level canopy cover could provide security while offering a more diverse understory for foraging. We included MODIS Normalized Difference Vegetation Index (NDVI; https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1), which is a time-varying index of greenness and proxy for vegetation quality, and has been associated with grizzly bear habitat selection (Northrup et al. 2012*b*), though NDVI does not predict understory growth in closed-canopy areas (Hebblewhite et al. 2008). Open areas correlate with mid-level NDVI values and closed canopy deciduous and coniferous cover correlate with high-level NDVI values. We included NDVI in time-varying and time-static models by calculating the mean values during the time period of interest. We included 5 land cover types (shrub, grass, agriculture, conifer, and deciduous).

For terrain covariates, we included elevation (m) in linear and quadratic forms, and terrain ruggedness index (Riley et al. 1999). For human use covariates, we used ln-transformed distance to primary, secondary, and tertiary roads (m). Road classifications were derived from camera-based traffic data (Northrup et al. 2012*a*) and road features (Prokopenko et al. 2017). We combined tertiary roads with motorized trails for a singular low-traffic motorized road class. We also included ln-transformed distance (m) to houses and land tenure (private, Crown, and protected land). Since land tenure is a categorical variable, protected land was used as the reference category. See Table 2 for a complete list of covariates, resolution, and data sources.

We tested for collinearity using Pearson's r coefficient and excluded covariates from the same model when |r| > 0.6 (Dormann et al. 2007). For all non-distance covariates, we extracted the mean values within a 90-m radius buffer around all unique rub object locations. This patch scale was three times the minimum mapping unit, and captures the habitat characteristics of the object's surroundings while minimizing overlap with adjacent buffered objects.

Habitat Models

Species and Sex-Specific Habitat Selection – Using species-specific detection locations, we identified important correlates of habitat selection for each sex and species. We used the rub object as the sampling unit and compared locations where we detected each species and sex (used) anytime in 2013 and 2014, to the full set of unique rub objects (available; *n* = 873). We used an exponential RSF, fitted using logistic regression:

$$RSF(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \cdots + \beta_n x_n)$$

where β_i represents the selection coefficient for covariate x_i in a vector, $\boldsymbol{x}$, of *n* covariates. We estimated habitat-selection models for each species and sex independently for 15 candidate models, which included linear, non-linear, and interaction terms (Table 3). We scaled all continuous covariates and used Akaike information criterion (AIC) to identify the most parsimonious model (Burnham and Anderson 2002, Burnham et al. 2011).

Latent Selection Difference Function – We used a latent selection difference function (LSDF) to directly compare selection coefficients for grizzly and black bears (Fischer and Gates 2005, Czetwertynski 2008, Latham et al. 2011, 2013, Erickson et al. 2014). An LSDF takes the same exponential form as a resource selection function, except we assume both bear species can access the same habitats (i.e., a common ‘available’ distribution), and we directly compare habitats selected by the two species. An LSDF takes the following form:

$$LSDF\ (xX, \beta_{gb}, \beta_{bb}\Delta B) = \frac{\pi(xX, \beta B_{gb})}{\pi(xX, \beta B_{bb})} = \exp(\Delta\beta_0 + \Delta\beta_1 x_1 + \cdots + \Delta\beta_m x_m)$$

where $\boldsymbol{X}$ is a vector of m landscape covariates and $\Delta\beta$ represents the difference in habitat selection by the two species. In this analysis, we retained multiple visits by unique bears during the same occasion. We used covariates with a strong effect size (e.g., standard errors did not overlap zero) from the top RSF models for each species and sex described previously. Although we considered all candidate covariates to be important for bears, those included in the top RSF models were interpreted as more important and were included in subsequent LSDF models.

Using the suite of covariates defined from the RSFs, we compared all possible combinations of male and female grizzly and black bears (6 total: grizzly bear male x black bear male; grizzly bear male x grizzly bear female; black bear male x black bear female; grizzly bear female x black bear female; grizzly bear female x black bear male; grizzly bear male x black bear female). For all comparisons, the (presumably) dominant group was coded as ‘1’ and the other group coded as ‘0’ (e.g., male grizzly bears = 1, male black bears = 0). To examine seasonal variation in selection, we defined 3 seasons for LSDF modelling. We defined ‘early summer’ as June 17–July 28 (occasions 1–2), ‘late summer’ as July 29–September 29 (occasions 3–5), and ‘autumn’ as September 30–November 9 (occasions 6–7; Table 1). Our season cut-offs coincided with pre-berry, berry, and post-berry season outlined by Hamer et al. (1991) in WLNP. Because LSDF models are a relative selection difference, positive beta coefficients mean the group coded as ‘1’ select more strongly for resource units relative to group coded as ‘0’. A negative coefficient means the group coded as ‘0’ selected more strongly for resource units relative to the group coded as ‘1’. We interpreted LSDF beta coefficients indistinguishable from zero (i.e., standard error bars overlap zero) as having similar selection.

We used generalized linear models fit by maximum likelihood in program R (R Development Core Team 2008). Because RSF data are not two discrete sets of data (i.e., use data are a sub-set of the available data), we used k-fold cross validation to measure the predictive ability of the RSF (Fielding and Bell 1997, Boyce et al. 2002). We partitioned the data into 10 folds and tested the association between the frequency of presence observations in 10 RSF bin ranks. We did this 10 times and used the averaged Spearman’s rank correlation coefficient ($\bar{r}_s$) to evaluate the predictive success of each RSF model (Boyce et al. 2003). For LSDF models we assessed model performance using area under the receiver operating curve (AUROC; Hanley and McNeil 1982). The AUROC is the probability that model predictions match observed values, where AUROC equals one means the prediction model is perfect.

RESULTS

In 2013, we sampled 855 rub objects and submitted 4,179 hair samples to WGI for analysis. The following year, we sampled 873 rub objects and submitted 3,597 hair samples for analysis. Across 2013 and 2014, we identified 331 individual black bears (180 males, 151 females) and 143 individual grizzly bears (83 males, 60 females). For details on grizzly bear genetic sampling results, see Morehouse and Boyce (2016). For details on black bear genetic sampling results, see Appendix 3.

For male grizzly bears, we had 338 presence locations from 2013 and 2014. In the RSF top model, male grizzly bears avoided private land, the proximity of primary roads, and selected mid-lower elevations, deciduous cover, and Crown land (Figure 2; Appendix 1 Table A 1; $\bar{r}_s$ = 0.72). For female grizzly bears, we had 101 presence locations in 2013 and 2014. In the top RSF model, female grizzly bears selected deciduous cover, recently burned areas, and avoided the proximity of primary roads (Figure 2; Appendix 1 Table A 1; $\bar{r}_s = 0.90$). We had 407 presence locations for male black bears in 2013 and 2014. In the top RSF model, male black bears selected higher NDVI, avoided burned areas, Crown and private land relative to protected land (Figure 2; Appendix 1 Table A 1; $\bar{r}_s = 0.68$). We had 323 presence locations for female black bears in 2013 and 2014. In the top RSF model, female black bears selected higher canopy cover, and avoided private and Crown land relative to protected land (Figure 2; Appendix 1 Table A 1; $\bar{r}_s = 0.73$).

For the LSDF models, we combined covariates from the top sex and species-specific RSF models, and ran 6 pair-wise comparisons for male and female black and grizzly bears in early summer (grizzly: $n = 242$ male, $n = 27$ female; black bear: $n = 360$ male, $n = 96$ female), late summer (grizzly: $n = 155$ male, $n = 70$ female; black bear: $n = 151$ male, $n = 162$ female), and autumn (grizzly: $n = 123$ male, $n = 51$ female; black bear: $n = 60$ male, $n = 66$ female).

Male and female black bears showed the most resource-selection overlap for all seasons (Figure 3; Appendix 1 Table A 2). In early summer, female grizzly bear and female black bears showed the most overlap in resource-selection. In late summer, male and female black bears showed the most overlap (Figure 3; Appendix 1 Table A 2). In autumn, male and female black bears, as well as male grizzly bears and female black bears showed greater overlap (Figure 3; Appendix 1 Table A 2). On average, interspecies overlap was highest in early summer and autumn, intraspecific overlap was highest in autumn, and overall resource overlap was lowest in late summer (Figure 3; Appendix 1 Table A 2).

In early summer, relative to male black bears, male grizzly bears selected burned areas (< 20 years old), deciduous cover, and lower NDVI values, but avoided park lands (Figure 4;

Appendix 1 Table A 2). In late summer, male grizzly bears selected deciduous cover, burned areas, higher NDVI values (Figure 5), and Crown land, but avoided park lands, relative to male black bears (Figure 4; Appendix 1 Table A 2). In autumn, male grizzly bears selected deciduous cover and Crown land, but avoided park lands and high NDVI, relative to male black bears (Figure 4; Appendix 1 Table A 2).

Female grizzly and black bears showed similar selection patterns for canopy cover, distance to primary roads, and land tenure in early summer (Figure 4; Appendix 1 Table A 2). In late summer, female grizzly bears selected Crown and private lands and to be farther from primary roads relative to black bears (Figure 4Figure 4; Appendix 1 Table A 2). In autumn, female grizzly bears selected Crown and private lands relative to black bears (Figure 4; Appendix 1 Table A 2). Female grizzly bears avoided park lands relative to female black bears across all three seasons.

In early summer, male grizzly bears selected for deciduous cover and Crown land relative to female black bears, and lower NDVI values relative to female black bears (Figure 4; Appendix 1 Table A 2). In late summer, male grizzly bears selected for Crown land, private land, higher NDVI, deciduous cover, higher elevation, and to be farther from primary roads relative to female black bears (Figure 4; Appendix 1 Table A 2). In autumn, female black bears selected private land relative to those selected by male grizzly bears (Figure 4; Appendix 1 Table A 2).

In early summer, female grizzly bears selected burned areas, deciduous cover, higher elevation, and to be farther from primary roads relative to male black bears (Figure 4; Appendix 1 Table A 2). In late summer, female grizzly bears selected private and Crown land, to be further from primary roads, lower NDVI, and in burned areas relative to male black bears (Figure 4; Appendix 1 Table A 2). In autumn, female grizzly bears selected private and Crown land, deciduous cover, lower NDVI values, and higher elevations relative to male black bears (Figure 4; Appendix 1 Table A 2).

In early summer, male black bears selected deciduous cover, higher elevations, closer proximity to primary roads relative to habitats selected by female black bears (Figure 4; Appendix 1 Table A 2). In late summer, females selected higher elevations relative to male black bears (Figure 4; Appendix 1 Table A 2). In autumn, males selected higher elevations relative to female black bears, and females selected deciduous cover relative to male black bears (Figure 4; Appendix 1 Table A 2).

In early summer, male grizzly bears selected Crown land, lower NDVI, avoided burned areas, and lower elevation relative to female grizzly bears (Figure 4; Appendix 1 Table A 2). In late summer, males selected Crown land, higher NDVI, lower elevation, deciduous cover, and to be further from primary roads relative to females (Figure 4; Appendix 1 Table A 2). In autumn, males selected higher NDVI, lower elevation, and burned areas relative to females (Figure 4; Appendix 1 Table A 2).

DISCUSSION

Our results demonstrate that resource partitioning occurred between black and grizzly bears. During all seasons, Crown lands were selected by grizzly bears. Northrup et al. (2012*a*) found grizzly bear primary habitat was on Crown land in southwestern Alberta, while private lands acted as ecological traps. In contrast to grizzly bears, black bears selected park and private land (Figure 4). This finding is in contrast to many studies where grizzly bears are more likely to be found in National Parks. For example, Apps et al. (2006) found grizzly bears occurred more than predicted in National Parks, whereas black bears were found in closer proximity to roads. In Banff, Kootenay, and Yoho National Parks in the Canadian Rockies, Rogala et al. (2011) found as human activity on trails increased above 2 persons per hour, wolves (*Canis lupus*) and elk (*Cervus elaphus*) mutually avoided areas 50–400 m from hiking trails. Given the small area of WLNP (500 km^2), prohibition on black bear hunting, and high human visitation rates (410,910 average annual visitors 2013-2014; Parks Canada, *unpublished data*), and black bears' higher tolerance for human disturbance may result in stronger selection of the Park by black bears than by grizzly bears.

The covariate showing the largest selection differences by season for all pair-wise combinations was NDVI. We used NDVI as a proxy for vegetation quality (Pettorelli et al. 2011), and found that male black bears selected higher NDVI values during early summer and autumn relative to grizzly bears, while male grizzly bears selected higher NDVI values in late summer (Figure 5). Female grizzly bears, however, showed the opposite relationship with NDVI compared to males (Figure 5). Open areas have lower NDVI values relative to closed-canopy areas (Figure 6) and similar to other research, relative to black bears, grizzly bears are more often found in open areas digging for ground squirrels, roots, and tubers (McLellan and Hovey 1995).

NDVI is often used for grazing species like elk (e.g., Prokopenko et al. 2017) where grassland green-up can be tracked by satellites because there is no interfering forest canopy. But for bears, both understory and open-area foraging are important, and understory productivity is not captured in NDVI (Hebblewhite et al. 2008). For example, Nielsen et al. (2017) found no correlation between buffalo berry, an understory-species, and NDVI in central Alberta. As in many other wildlife studies, NDVI appears to be important but there is inadequate interpretation of its ecological meaning. In our study, NDVI was helpful for distinguishing temporal switching between coniferous and deciduous forests, and pulses of green-up (Figure 6; Avgar et al. 2013).

For all pair-wise comparisons and all seasons, male grizzly bears and male black bears had the lowest resource overlap (Figure 3). Immediately south of our study area in Montana, Aune (1994) found grizzly bear home ranges were on average over 5 times larger than male black bear home ranges. Due to larger home ranges, male grizzly bears have a greater range of available habitats compared to male black bears. In a heterogenous landscape such as southwestern Alberta, a larger home range would equate to a greater diversity of available habitats (e.g., both alpine and agriculture). Also, grizzly bears kill black bears (Mattson et al. 1992). Black bears could thus be mitigating predation risk by avoiding areas that are highly selected by grizzly bears, such as Crown lands.

Rub trees could be a problematic method to identify habitat selection patterns. First, bear rub trees are known to be found on travel routes, in proximity to water, and at lower elevations (Green and Mattson 2003, Sato et al. 2014, Morgan Henderson et al. 2015). Although not included in our results, we examined our study-specific bias for rub tree placement (Appendix 2). In general, rub tree locations were in lower elevations, park land, and closer to water (streams, lakes), and tertiary roads and motorized trails relative to available (i.e., random sampling). Our inference is thus only relevant within this environmental envelope and we specifically identified the area of inference (Appendix 2). A second potential issue could be a result of dominance hierarchies. In our study area, dominant individuals rub more than subordinates (Morehouse et al. *in prep*). However, there is no evidence that bears are making long-distance movements to rub, so rub trees are representative locations of their used habitat. If researchers clearly identify the area of inference and control for habitat covariates, we believe that valid inferences can be made from rub tree detections about resource-selection where telemetry data are limited.

During direct competition for resources (i.e., interference competition; Miller 1967), black bears are inferior competitor to grizzly bears due to their smaller body size and lower aggression levels (Herrero 1978, Begon et al. 1990). While both species use similar food resources, black bears typically have reduced nutritional requirements because of reduced body size (with an exception being lactating females), a higher tolerance for human-disturbed landscapes relative to grizzlies (Apps et al. 2006), and can more efficiently exploit dispersed resources (i.e., scramble competition; McLellan 1993, Mattson et al. 2005). For example, Fortin et al. (2013) found that as spawning cutthroat trout (*Oncorhynchus clarki*) numbers dwindled in Yellowstone National Park, grizzly bears switched to alternative food sources while black bears utilized the high-protein but low-density spawning grounds. Black bears in southeastern British Columbia (Flathead Valley), which has the highest recorded interior grizzly bear densities (55/1,000 km^2), have higher fat content than their larger-bodied competitors (black bears 20% fatter; McLellan 2011). Because black bears can more efficiently exploit dispersed resources, and gain mass faster than larger-bodied grizzly bears, black bears could negatively affect recovering grizzly bear populations (Mattson et al. 2005).

Private lands in our study are more typical of grizzly bear habitat, with large, natural, open areas (e.g., south-facing slopes, grasslands) and man-made open areas (e.g., crop and pasture land). Our results indicate, however, that black bear selection for private land was higher relative to grizzly bear selection. These findings suggest that as human disturbance increases, the likelihood of black bear selection for these areas increased even in typical grizzly bear habitat. Given that grizzly bears are listed as a *Threatened* species in Alberta, this should be cause for concern that black bears could potentially out-compete (scramble competition) grizzly bears, especially during food-poor years where foods are dispersed and of low quality.

Advances in non-invasive genetic sampling have increased the efficiency of sampling a high number of individuals, particularly large carnivores, which are often elusive, wide-ranging, and occur at low densities. Additionally, there has long been a call for a shift from single to multi-species research and management (Simberloff 1997). Multi-species studies remain rare but are increasing with changes in technology. This study highlights the flexibility in mark-recapture data in understanding black and grizzly bear habitat selection.

MANAGEMENT IMPLICATIONS

Using non-invasive genetic sampling, we found evidence for resource partitioning, where the most prominent drivers of resource partitioning were NDVI and land tenure, which may reflect spatial population structuring in the multi-use landscape of southwestern Alberta. Seasonal shifts in resource selection could have population-level implications. For example, if grizzly bears, which are listed as a *Threatened* species in Alberta, strongly select for Crown land during autumn, increased human visitation by hunters (e.g., for elk, black bear) could exacerbate fine-scale avoidance of roads and motorized trails. As outlined by the International Union for the Conservation of Nature’s Bear Specialist Group, elevated levels of human disturbance and human-wildlife conflicts could threaten otherwise stable grizzly bear populations (McLellan et al. 2008). While protected areas are designed to protect a range of species, small parks such as WLNP may not be of the appropriate spatial scale for wide-ranging species like grizzly bears, and may give advantage to more human-tolerant species like black bears.

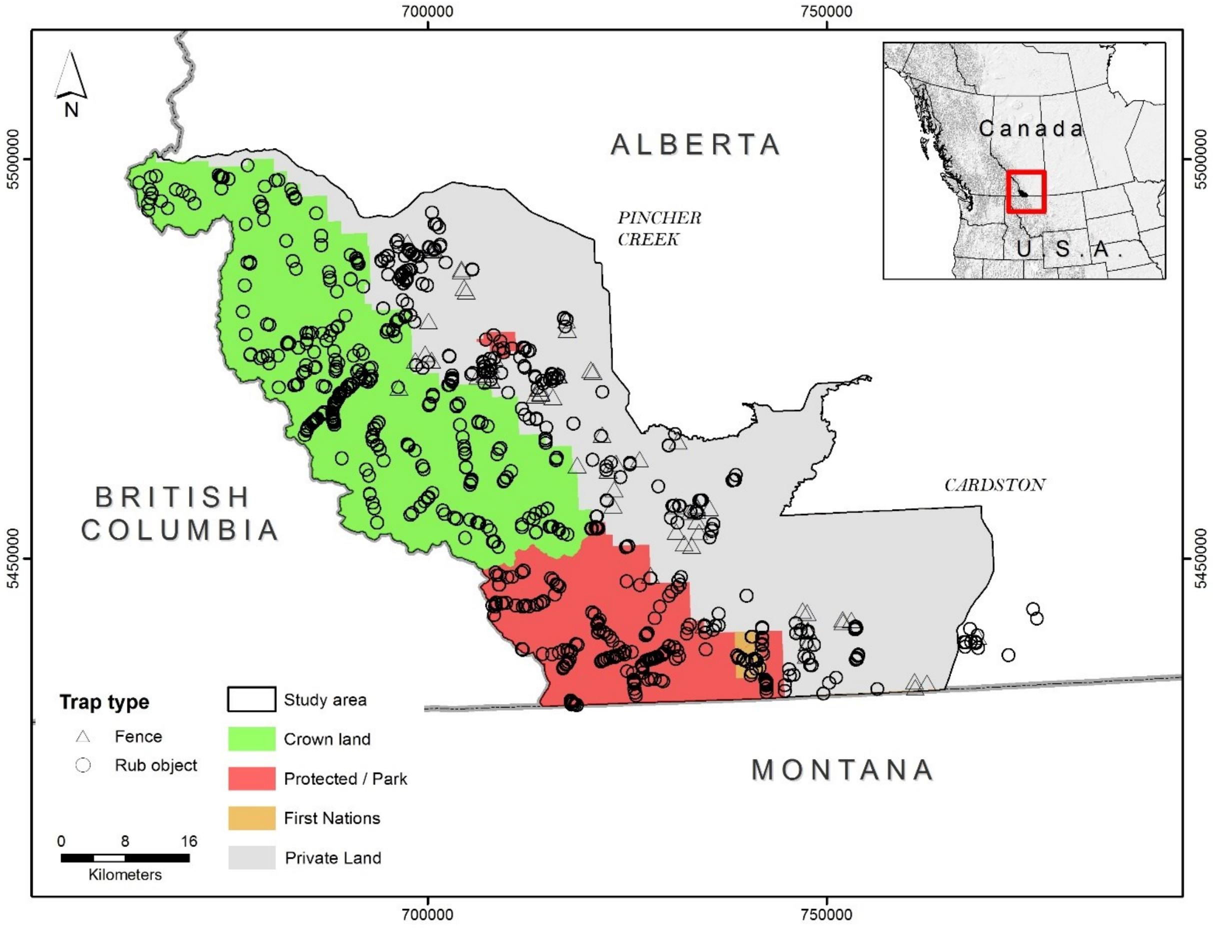

Figure 1. The study area in southwestern Alberta, Canada. Rub objects included rub trees, power poles, and fence posts. Fence lines (fence) included sections of barbed-wire fences that bears frequently traveled through. All fence lines and rub objects were sampled 7 times in 2013 and 2014 (14 total sample occasions).

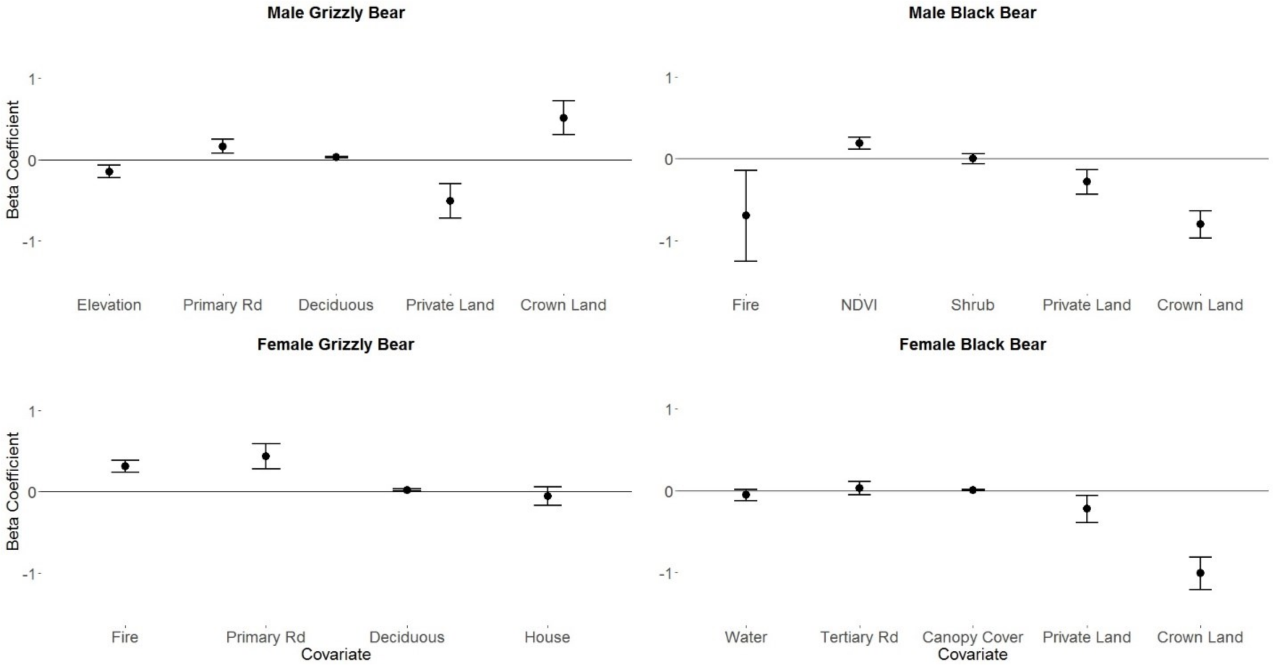

Figure 2. Scaled beta coefficients from top-RSF models for each species and sex comparing presence data for each species and sex to all rub tree locations (*n* = 873) in southwestern Alberta, Canada. Presence data were from black and grizzly bear non-invasive genetic sampling data collected in 2013 and 2014. Error bars represent standard error.

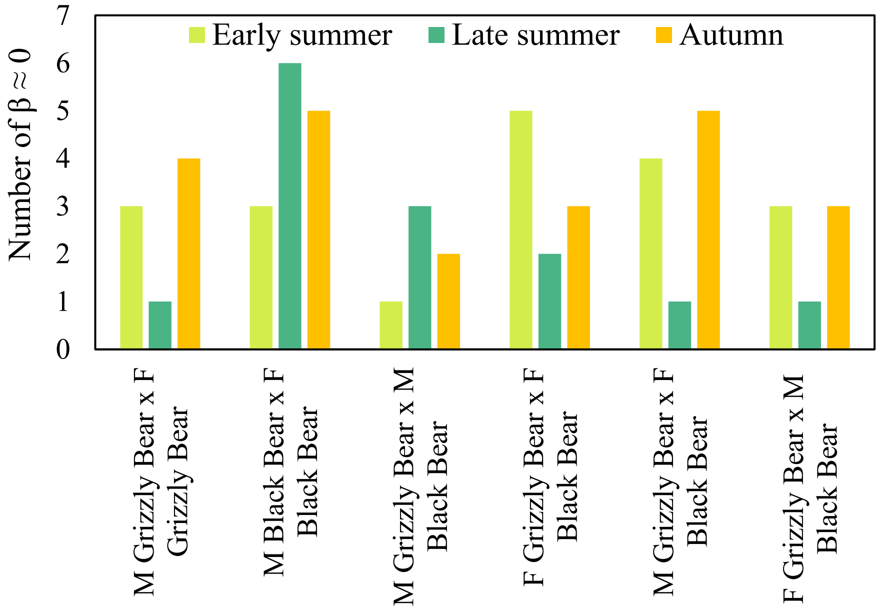

Figure 3. Seasonal variation in resource-selection overlap where the number of beta coefficients in each model were indistinguishable from zero (i.e., number of β ≈ 0) are displayed on the y-axis. Larger values indicate greater resource overlap and smaller values indicate lesser resource overlap. For early summer (June 17-July 28), late summer (July 29- September 29), and autumn (September 30-November 9), male and female black bears showed the highest resource-selection overlap. In contrast, male grizzly bears and male black bears showed the lowest resource-selection overlap for all seasons.

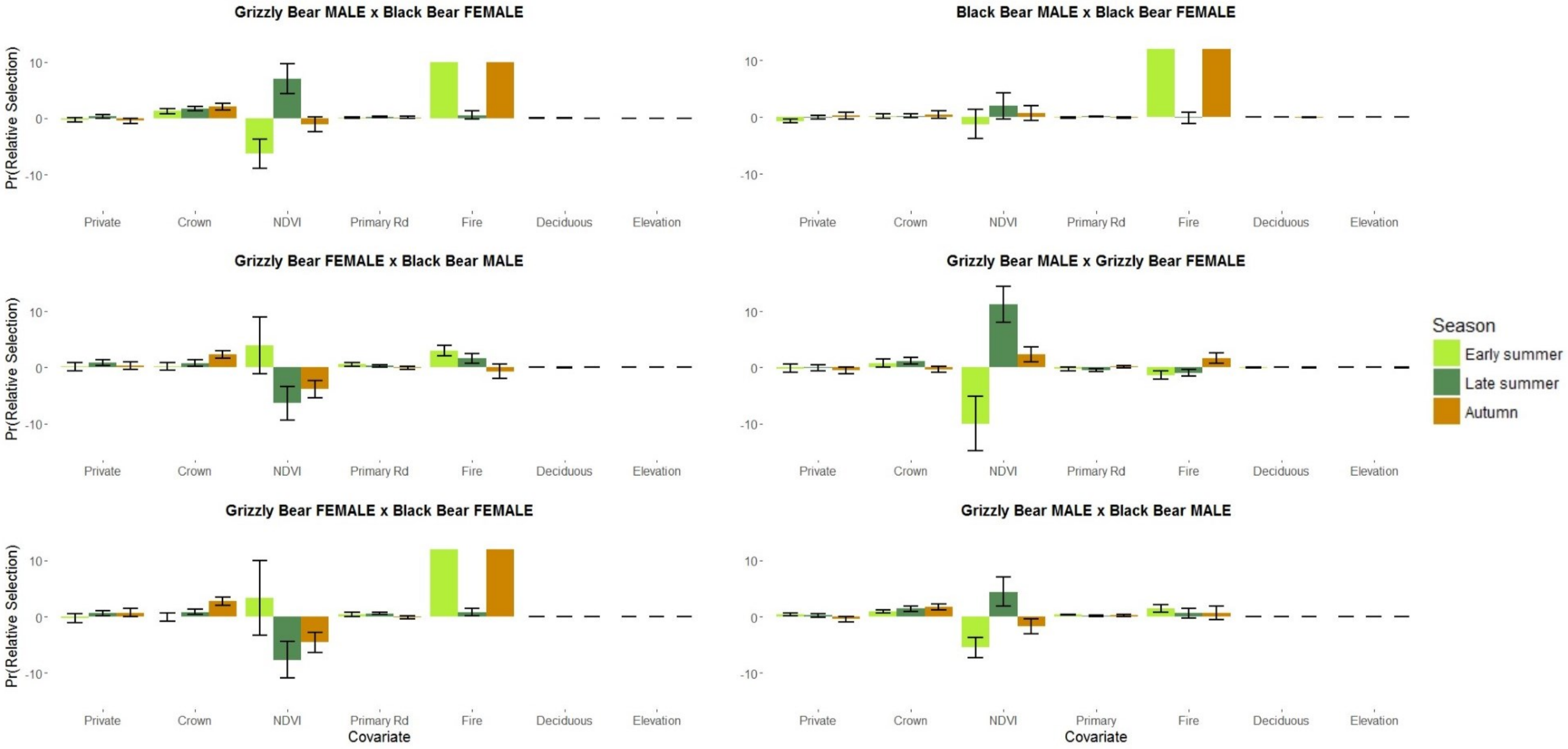

Figure 4. Seasonal variation in relative selection coefficients in LSDF models for male and female black and grizzly bears in southwestern Alberta, 2013-2014. In all cases, the more dominant sex/species were coded as 1. High probability values relate to high probability of grizzly bear selection and low probability values relates to high probability of black bear selection. We defined ‘early summer’ as June 17 – July 28, ‘late summer’ as July 29 – September 29, and ‘autumn’ as September 30 to November 9. Error bars

represent standard error. For graphs that include comparisons with female black bears, few detections within burned areas (Fire) resulted in high error rates; actual values and associated error bars were excluded from the graph.

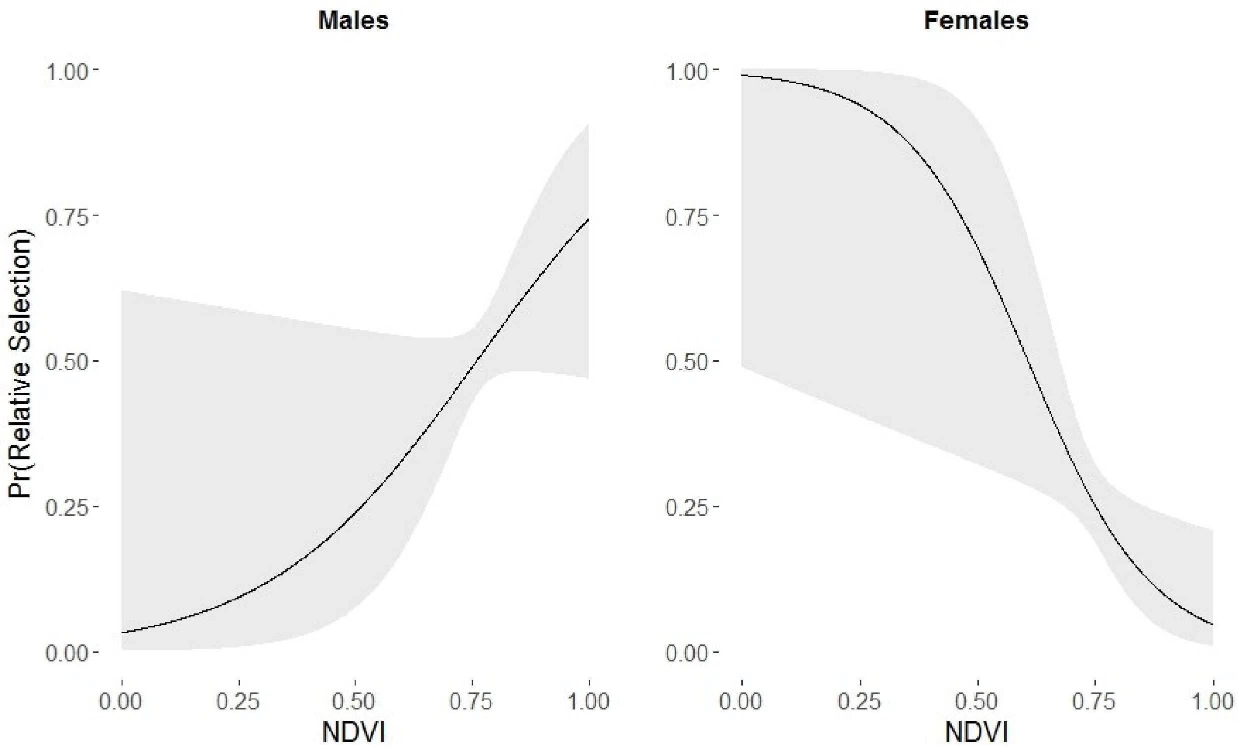

Figure 5. Relative selection coefficients for NDVI in late-summer LSDF models for male (left) and female (right) black and grizzly bears in southwestern Alberta, 2013-2014. Grizzly bears were coded as 1. High probability values relate to high probability of grizzly bear selection and low probability values relates to high probability of black bear selection. Late summer was defined as July 29–September 29. Error bars represent 90% confidence intervals.

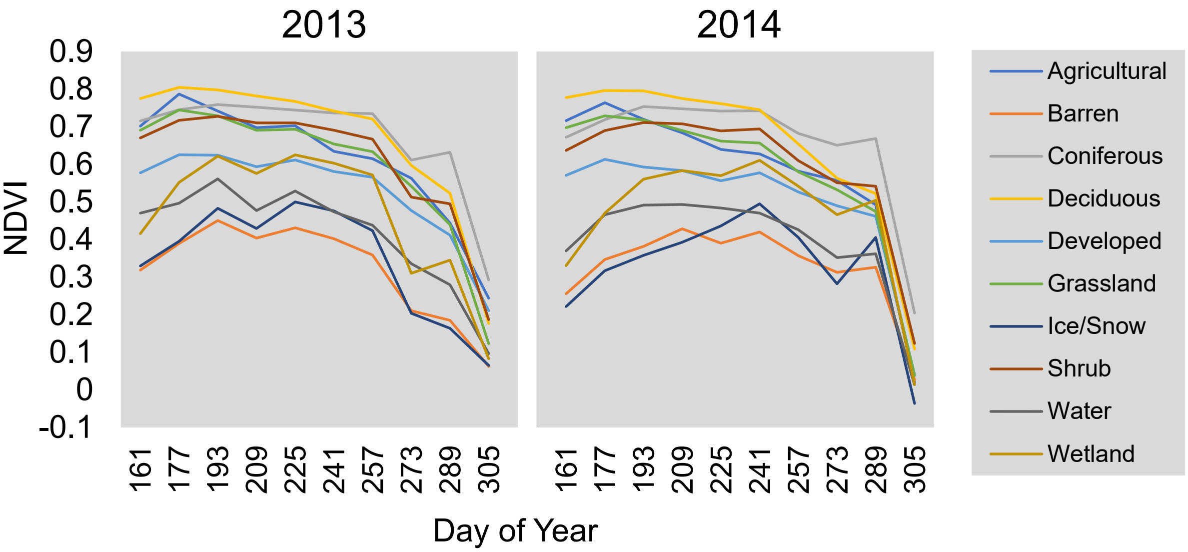

Figure 6. Mean normalized difference vegetation difference (NDVI) by land cover type in 2013 and 2014 in southwestern Alberta. Mean MODIS NDVI data (250 m spatial and 16-day temporal resolution) from June (Day 161 = 10 June) to November (Day 305 = 1 Nov) were extracted to landcover types. Peaks in early summer primary productivity are seen in 2013 but are delayed in 2014. A sharp decline in NDVI values in the fall 2014 reflect persistent early-season snow.

Table 1. Black and grizzly bear non-invasive genetic sampling (NGS) at rub objects occurred from June to November in 2013 and 2014 in southwestern Alberta, Canada. We used NGS samples to associate use and available locations for resource selection and latent selection difference functions.

Year	Occasion	Hair Collection Dates
2013	1	June 17 - July 7
	2	July 8 - July 28
	3	July 29 - Aug 18
	4	Aug 19 - Sep 8
	5	Sep 9 - Sep 29
	6	Sep 30 - Oct 20
	7	Oct 21 - Nov 8
2014	1	June 17 - July 6
	2	July 7 - July 27
	3	July 28 - Aug 17
	4	Aug 18 - Sep 7
	5	Sep 8 - Sep 28
	6	Sep 29 - Oct 19
	7	Oct 20 - Nov 9

Table 2. Covariates used for RSF and LSDF habitat models. Covariates were extracted using a 90m buffer around rub object point locations using 3 data themes: habitat, topography, and human-use.

Covariates	Resolution	Data source
Habitat		
Fire *(fire)*	30 m	Crown Managers Partnership
Percent canopy cover *(canopy cover)*	30 m	Crown Managers Partnership
Quadratic canopy cover *(canopy cover^2)*	30 m	Crown Managers Partnership
Shrub cover *(shrub)*	30 m	Crown Managers Partnership
Grass cover *(grass)*	30 m	Crown Managers Partnership
Agriculture cover (*agriculture)*	30 m	Crown Managers Partnership
Conifer cover *(conifer)*	30 m	Crown Managers Partnership
Deciduous cover *(deciduous)*	30 m	Crown Managers Partnership
Normalized Difference Vegetation Index *(NDVI)*	250 m spatial;16 day temporal	MODIS
Ln-distance to stream and lake *(water)*	Vector	Crown Managers Partnership, Open Government Licence – Alberta
Topography		
Terrain ruggedness *(TRI)*	30 m	Crown Managers Partnership
Elevation *(elevation)*	30 m	Crown Managers Partnership
Quadratic elevation *(elevation^2)*	30 m	Crown Managers Partnership
Human-Use		
Land tenure *(tenure)*	Vector	Alberta Environment and Parks

Ln-distance to primary rd *(primary rd)*	Vector	Prokopenko et al. 2016
Ln-distance to secondary rd *(secondary rd)*	Vector	Prokopenko et al. 2016
Ln-distance to tertiary rd and motorized trails *(tertiary rd)*	Vector	Prokopenko et al. 2016
Ln-distance to house *(house)*	Vector	Municipal data from MDs of Pincher Creek, Crowsnest Pass, and Cardston County

Table 3. Candidate models used for RSF models for black and grizzly bears in southwestern Alberta, Canada.

Model	Covariates
1	water + tertiary rd + canopy cover + tenure
2	fire + NDVI[a] + shrub + tenure
3	TRI + primary rd + house + canopy cover
4	TRI + primary/secondary rd + house + canopy cover^2
5	water + fire + canopy cover + tertiary rd
6	elevation + primary rd + house + canopy cover
7	NDVI^2 + primary/secondary rd + house + canopy cover^2
8	elevation + primary rd + deciduous + tenure
9	elevation^2 + primary rd + shrub + tenure
10	fire + tertiary rd + shrub + house
11	fire + primary rd + deciduous + house
12	fire + primary rd + agriculture + house
13	primary rd * shrub + house + GB
14	tertiary rd * conifer + water
NULL	~1

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[a] NDVI = Normalized Difference Vegetation Index (MODIS)

CHAPTER 3 – LAND TENURE SHAPES BLACK BEAR DENSITY AND ABUNDANCE ON A MULTI-USE LANDSCAPE

INTRODUCTION

Across the globe, parks and protected areas are often preserved for scenic beauty and not for biodiversity or connectivity (Newmark 1985, Jenkins et al. 2015). Many mountain parks in North America have a high proportion of rock and ice, which for many species does not provide adequate foraging opportunities (Joppa and Pfaff 2009). Further, parks and protected areas are commonly of low soil fertility, which in turn, can result in nutrient-poor areas and increased chances of food shortages (Rogers 1987). In contrast, private lands are often working landscapes, such as agricultural farming and ranching. These lands are often highly-productive and attractive to animals for their high-quality forage (Sayre et al. 2012), as well as food subsidies from agricultural products such as stored and standing grain and hay, silage, livestock, dead livestock (deadstock), and bee-yards (Wilson et al. 2006, Northrup et al. 2012*b*, Loosen 2016, Morehouse and Boyce 2017). In southwestern Alberta (AB), private lands are dominated by agricultural areas for cattle ranching, cereal grain and oil-seed farming. These private lands are attractive to bears, but can act as an ecological trap as a result of human-wildlife conflicts (Northrup et al. 2012*b*).

Human disturbance, such as infrastructure, roads, and land-use practices can pose a mortality risk to wildlife and can reduce functional habitat caused by avoidance of these areas (Dyer et al. 2001, Nielsen et al. 2006). In hunted areas, roads provide access for hunters and poachers, and black bears (*Ursus americanus*; Stillfried et al. 2015) and other wildlife (e.g., elk (*Cervus elaphus*); Paton et al. 2017) avoid roads even more during hunting season. For some species, hunting can disrupt social structure (Gosselin et al. 2017) and in most populations hunting will reduce wildlife populations below carrying capacity (Caughley 1979), although this is more complex in seasonal environments (Boyce et al. 1999). In North America, the estimated annual black bear harvest totals 40,000–50,000 individuals (Garshelis et al. 2008). In our study area, black bear hunting pressure and human disturbance differs among land tenures with highest road density on private land and lowest density on National Park land, and highest average harvest pressure is on Crown land.

In hunted populations, population estimates are needed to calculate sustainable harvest levels (Williams et al. 2002). Despite low precision and power to detect trends, harvest data often are the only information biologists have to assess black bear population trends or to set harvest objectives (Garshelis and Hristienko 2006). In southwestern Alberta, the most recent black bear abundance estimates were extrapolated from capture-recapture (1980–1983) and telemetry (1984–1985) studies conducted 150 km to the north (Gunson 1993). These data were used to derive a minimum number of black bears in permanently occupied habitats in southwestern Alberta (52.9 bears/1,000 km^2, excluding Waterton Lakes National Park), which at that time was low density relative to other management units in Alberta (Gunson 1993).

In addition to land tenure, human disturbance, and harvest pressure influencing black bear space use, interspecific interactions can influence population density and abundance. Interspecific competition and intraguild predation predict subordinate species would be forced into lower-quality habitats and high-quality habitats would be occupied by the dominant species (Miller 1967). Pertinent to our study, grizzly bears (*U. arctos*) are dominant over black bears (Herrero 1978) and can attack and kill subordinate black bears (Boyd and Heger 2000). For example, black bears in British Columbia (BC) avoid large, open-canopy huckleberry (*Vaccinium* spp.) patches when berries are ripe and where grizzlies are common (McLellan

2011). Likewise, grizzly bears also have been shown to exclude black bears from high-quality resources like salmon (*Oncorhynchus* spp.) spawning grounds in coastal areas (Jacoby et al. 1999). Recent grizzly bear estimates for our study area indicate densities are slightly higher on public lands (Recovery Zone: 20.4 grizzly bears per 1,000 km^2, 95% CI: 15.7–26.4) relative to private lands (Support Zone: 17.1 grizzly bears per 1,000 km^2, 95% CI: 12.1–24.4), but the addition of the management zones (Recovery and Support) did not significantly improve model fit (Morehouse and Boyce 2016). Further, a portion of private land within the Support Zone does not provide suitable wildlife habitat (e.g., large swaths of canola); therefore, actual grizzly bear density on suitable habitat on private land may be higher than reported.

In areas where grizzly bears and black bears are sympatric, non-invasive genetic sampling (NGS) provides an opportunity to sample both grizzly and black bears, at reduced cost compared to radiotelemetry studies. Bears are thought to rub on trees as a means of communication (Green and Mattson 2003) and the hair left behind can be sampled and the DNA extracted (Woods et al. 1999). Because rubbing behavior is male biased (Kendall et al. 2008) and rub trees have lower detection probabilities than other sampling methods like scent-lured hair corrals (Stetz et al. 2010, but see Sawaya et al. 2012), we used two methods to estimate density and abundance. First, we used spatially explicit capture-recapture (SECR) methods to estimate density and abundance (Efford 2004, Royle et al. 2014). SECR models allow the incorporation of covariates to account for spatial variation in habitats and directly incorporate spatial information associated with detections. Second, because animal densities are usually related to habitat selection (Boyce et al. 2016), we estimated resource selection functions (RSFs; Manly et al. 2002, Johnson et al. 2006) for male and female black bears in Waterton Lakes National Park (i.e., a protected area with no hunting and low road density). We assumed black bear densities in

Waterton Lakes National Park (WLNP) were at carrying capacity and used RSF estimates to extrapolate densities across the sampled area to estimate the population size within the study area (Mladenoff and Sickley 1998, Boyce and McDonald 1999, Boyce and Waller 2003).

Our objectives were to (1) estimate black bear abundance and density; (2) identify spatial covariates that best explain variation in density and abundance using SECR models; and (3) compare SECR abundance estimates to abundance estimated by extrapolation based on habitat selection (i.e., RSF values) from an area assumed to be at carrying capacity. We used data from non-invasive genetic sampling in southwestern Alberta (2013–2014), habitat and human disturbance covariates, and grizzly bear presence data to account for spatial variation in density. We predicted that black bear densities would be highest in protected areas where mortality risk is lowest (low road density and no hunting) and where forested escape terrain from grizzly bears is more abundant. Conversely, we predicted the lowest black bear densities would be on private lands where mortality risk is highest (high road density and hunting allowed), where patchy tree cover limits escape terrain, and land cover is predominantly pasture and crop land. Because black bears are hunted in our study area and hunters disproportionately select males (Bunnell and Tait 1980, Miller 1990), we predicted higher female densities relative to males.

STUDY AREA

The 3,600-km^2 study area lies east of the continental divide in the southern Canadian Rocky Mountains and is bounded by Highway 3 to the north, BC to the west, the USA-Canada border to the south, and roughly follows Highway 2 to the east (Figure 7). The area includes WLNP, which shares its border with a portion of Glacier National Park, Montana (MT), USA. Elevation ranges from 1,030 m to 2,910 m. Important vegetation-based foods for black bears include Saskatoon berry (*Amelanchier alnifolia*), huckleberry (*Vaccinium* spp.), buffaloberry

(*Shepherdia canadensis*), cow parsnip (*Heracleum maximum*), horsetail (*Equisetum* spp.), and dandelion (*Taraxacum* spp.) (Hamer et al. 1991, Holcroft and Herrero 1991, Northrup et al. 2012*b*). The area is a mix of land-cover types: conifer forest (29%), agricultural (22%), grassland (16%) including native grassland and cultivated fields, shrub land (16%), and deciduous forest (11%). Agriculture, including cattle production, is the primary industry (Statistics Canada, MD of Pincher Creek, 2011 Community Profile).

Land management in southwestern Alberta is varied. Private land (1,872 km^2; 52% of area) has the highest road density (Northrup et al. 2012*a*), and is characterized by rough fescue grasslands and agriculture (e.g., grazing pastures, hay, grain, and oil-seed). Crown land (1,204 km^2; 34% of area) has lower road density relative to private land, and licensed black bear hunting occurs in the spring (1 April–31 May), and fall (1 September–30 November). Crown land is characterized by alpine, montane, and aspen-parkland habitat (Aune 1994, Northrup et al. 2012*b*). National park land (511 km^2; 14% of area) has the lowest road density and hunting is prohibited within the Park. Like Crown land, the park is characterized by alpine, montane, and aspen-parkland vegetation. Bear baiting is not allowed in the study area.

METHODS

Hair Collection and Analysis

We used non-invasive genetic methods to identify individual black bears from hair samples (Woods et al. 1999). In 2011 and 2012, we surveyed for and set up rub objects on Crown and private land, respectively (Figure 7). We searched for rub objects based on known bear travel corridors, roads and trails, local knowledge (e.g., biologists, landowners), and grizzly bear resource-selection maps (Northrup et al. 2012*b*). We established rub objects on power poles, fence posts, and rub trees where we observed fresh bear sign, primarily bear hair. We attached four barbed-wire segments to each rub object (Figure 8). We also surveyed barbed-wire fence-lines and if we observed fresh bear hair on a portion of a fence, we followed methods used by Kendall (2009) and marked start and end points for resurvey during each sample occasion.

By 2013, we established 873 rub objects. All rub objects were sampled once every 21 days from May to November in 2013 and 2014, for a total of eight sampling occasions (Table 4). During the first visit of each year we removed old hair from the wire and the remaining seven visits were collection events. We considered a barb or end of a wire segment a discrete sampling unit (Kendall et al. 2009, Stetz et al. 2010). Hair was collected only from the wire (e.g., not from adjacent bark). After hair collection, we burned remnant hairs using butane torches to prevent future contamination (Kendall et al. 2009, Stetz et al. 2010). A second data source included 'opportunistic' hair samples collected by field technicians walking collection routes, landowners, and Fish and Wildlife officers visiting conflict sites (Morehouse and Boyce 2016). Opportunistic samples were collected throughout the bear season and were not time-restricted (See Morehouse and Boyce 2016).

Hair samples were stored in coin envelopes on silica desiccant and were sent to Wildlife Genetics International (WGI; Nelson, BC) for genetic analysis to determine species, identify individuals, and sex via multi-locus analysis of nuclear DNA (Paetkau 2003, 2004). WGI extracted DNA from samples with ≥ 1 guard hair root or 5 underfur hairs. In the Rocky Mountains, research has indicated that typically only one individual is identified during a sampling period for any given rub object (Sawaya et al. 2012, Stetz et al. 2014). For each rub/date combination, we sub-sampled every third hair sample for genetic analysis because previous research indicated that sub-selection protocol maximized detections while staying within funding constraints (Morehouse and Boyce 2016).

All hair samples were subjected to a 3-phase process of first pass, cleanup, and error-check to establish an 8-locus marker system common to the Rocky Mountains (microsatellites: G10J, G1A, G10B, G1D, G10H, G10M, G10P plus amelogenin sex marker) (Ennis and Gallagher 1994, Paetkau 2003). In 2013, WGI prescreened samples at the G10J microsatellite to differentiate between grizzly and black bear samples and to remove low-quality DNA samples. Samples identified as black bear, either visually (i.e., jet black from tip to follicle) or genetically (G10J), were analyzed. In 2014, all samples meeting quality control and sub-sampling rules were assigned a first-pass multi-locus score. Additionally, WGI used the genetic clustering program Genetix (Belkhir et al. 2004) to confirm species differentiation at 6 microsatellites other than G10J. Hair sample collection was approved by University of Alberta's Animal Care and Use Committee (AUP00000008). Possession of hair samples was permitted by Alberta Environment and Parks (Research Permit #56014 and Collection Licence #56015).

Spatially Explicit Capture-Recapture

Spatially explicit capture-recapture (SECR; Efford 2004, Royle et al. 2014) relates two detection parameters, $g_{0,}$ the probability of detection if the trap is located at the animal's home range center, and sigma (σ), the spatial scale parameter, to the estimation of population density (*D*) (Efford 2004, Efford et al. 2009). The distance between successive recapture events informs σ, which increases with home-range size (Efford 2004). Instead of g_0, we used λ_0, the cumulative hazard of detection, and the equation relating λ_0 and g_0 is $g(d) = 1 - \exp(\lambda(d))$ where *g* is the probability of detection and *d* is the distance between trap location and an animal's home-range center (Efford 2004, Efford et al. 2009). We used a binomial distribution and a hazard half-normal function with a full likelihood to estimate density *D*, σ, and λ_0 (Efford 2004, Efford et al. 2009).

The area of integration, or state space, sets the outer spatial limits for which home ranges can be assigned and should be large enough to encompass all individuals that could have been exposed to the trap array (Sollmann et al. 2012). For both males and females, we calculated the area of integration using 3 times the root pooled spatial variance (RPSV), which is a 2-D measure of dispersion of detections around trap locations (Efford 2016). We calculated RPSV separately for each sex and used the largest value for each sex as the area of integration (18 km for males, 13 km for females). We tested varying buffer sizes using predicted animal densities as the response variable (secr package version 2.10.3; Efford 2016) in program R v.3.2.1 (R Development Core Team 2008).

Each year, we grouped opportunistic samples into an eighth sampling occasion and associated each sample with the center of a 7×7 km grid cell overlaid on the study area. We used a 7x7 km grid because it is the approximate radius of a female black bear home range (137 km^2) on the eastern front of the Rocky Mountains (Aune 1994). It has also been reported as an optimal grid size for non-invasive genetic sampling of black bears (Sawaya et al. 2012). Similar to unstructured scat dog searches with non-fixed trap locations, we created a grid based on locations searched by technicians, participating landowners, and Fish and Wildlife Officers (Thompson et al. 2012, Morehouse and Boyce 2016). We overlaid each opportunistic hair sample location onto the grid and the grid centroid was used as the new opportunistic location. Thus, each grid cell became a trap location for opportunistic samples. This method assumes a uniform observation process for encountering hair samples within each grid cell (Mollet et al. 2015). See Morehouse and Boyce (2016) for details.

Because SECR models are computationally intensive to run, we designed a 2-step modeling approach to minimize processing time. In step 1, we created 18 *a priori* single-session observation models (σ and λ_0) for males and females in 2013 and 2014 and used Akaike information criterion corrected for small sample sizes (AICc) to identify the most parsimonious model (Burnham and Anderson 2002). Models used in step 1 were designed using the covariates listed in Table 4 (see Tables A 4-7 for step 1 candidate models). In lured or baited designs, an animals' previous capture can increase or decrease the probability of recapture (e.g., trap happy or trap shy). While rub trees offer no lure or bait, there is a potential for individual trees to be favored based on proximity to habitats or travel paths. As well, we assumed variation in detection probabilities among the three trap types (rub object, fence, and opportunistic) and included a 'trap specific learned response' (*bk*) covariate. A bear's decision to rub could be influenced by the bear that rubbed previously. Using grizzly bear detection data from Morehouse and Boyce (2016), we created a time-varying index of grizzly bear detection (*GB*; 1 = detected during previous occasion, 0 = not detected during previous occasion) at each trap for each sampling occasion. Last, bear use of rub objects is known to vary seasonally, which can influence detection probabilities, we included time trend (*T*) as a covariate for σ and λ_0.

Next, because we were interested in variables that influence black bear density, we created 8 *a priori* single-session, sex-specific density models in 2013 and 2014 (Table 5). We used the most parsimonious model from step 1 as the base model in step 2. We included annual MODIS Normalized Difference Vegetation Index (NDVI; https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1) data as in indicator of vegetation greenness, or vegetation quality (Pettorelli et al. 2011). NDVI has been associated with grizzly bear habitat selection (Northrup et al. 2012*b*). In our study area, high linear NDVI values correspond to conifer and aspen forests. We created a per-cell-average (250 m x 250 m cell) NDVI layer for data collected June to November in 2013 and 2014 using the cell statistics tool in ArcMap (v. 10.3.1, Environmental Systems Research Institute, Redlands, CA).

Density covariates also included land tenure (Crown, private, park), recently burned areas (< 20-year-old; Apps et al. 2006), canopy cover (0-100%), ln-transformed distance to lakes and major streams, ln-transformed distance to water (higher-order streams, lakes), ln-transformed distance to tertiary roads, and road density. We calculated road density (km roads / km^2) using a 7-km search radius. Last, we estimated harvest per unit area for BC, MT, and AB. We defined harvest density as the estimated number of reported number of bears killed by hunters during the year prior to sampling, divided by the wildlife management unit. In all jurisdictions, spring and fall black bear hunting is allowed. Montana harvest data were downloaded from the MT Fish, Wildlife and Parks data portal (http://fwp.mt.gov/hunting/planahunt/harvestReports.html). British Columbia and Alberta harvest data were shared by government personnel.

Resource-Selection Functions

To estimate abundance using RSFs, we conducted a 4-step process. We (1) defined the area of inference, (2) calculated RSFs for male and female black bears in the reference area, (3) associated estimated density with habitat selection in the reference area, and (4) extrapolated *N* across the remaining area of inference (Boyce and McDonald 1999).

We anticipated that the location of our rub objects was biased because surveys for rub objects were limited to existing linear features (e.g., roads, trails, seismic lines, game trails). To quantify this bias, we first compared habitat covariates associated with all sampled rub object locations to random locations. We re-defined the study area as a minimum convex polygon (MCP) bounding all unique rub object locations (n = 873). We buffered the MCP by 2.4 km so random points could be located in all cardinal directions from rub objects. Because our original sampling design was intended for grizzly bears (see Morehouse and Boyce 2016), our buffer distance represents the average daily linear movement of grizzly bears in the neighbouring Flathead Valley, BC (Apps et al. 2006), which we assumed was similar to bear movements in our study area because they are part of the sample population (Proctor et al. 2012). We generated 17,460 random points (20:1 random:used) within the MCP and used an exponential RSF, fitted using logistic regression:

$$RSF(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \cdots + \beta_n x_n)$$

where β_i represents the selection coefficient for covariate x_i in a vector, $\boldsymbol{x}$, of n covariates (Manly et al. 2002, Johnson et al. 2006). We used a single global model that included all non-correlated covariates from Table 6. We standardized ($\bar{x} = 0$, SD = 1) all continuous predictor covariates. From the global model (i.e., the model including all covariates), we created a raster layer from unscaled beta coefficients in ArcMap. We reclassified RSF values in ArcMap to 10 groups with natural breaks (Jenks) and removed the lowest 3 groups to re-define our area of inference.

Second, we used detection locations (i.e., confirmed positive black bear detections) to calculate RSFs for male and female black bears. We used the rub object as the sampling unit and compared locations where we detected each sex (used) anytime in 2013 and 2014, to the full set of unique rub objects (available). Although these data were derived from the same dataset used for SECR, RSF data are simple presence/available data (e.g., was a bear ever at the rub tree?) whereas time-varying data were used for SECR (e.g., what was the frequency of detection at the rub tree?). Thus, SECR and RSF datasets represent differently structured data, making this comparison possible. We used used AIC to identify the most parsimonious model for each sex among 15 candidate models (Table 6). We calculated RSFs only within the area of inference defined in Figure 10.

Next, we used SECR-derived estimates of $\widehat{N}$ for males and females in WLNP and related $\widehat{N}$ to habitat quality (i.e., RSF score) following Boyce and McDonald (1999). We assumed WLNP was at carrying capacity because of a low human footprint, hunting restriction, and proximity to Glacier National Park (i.e., source area; Stetz et al. 2014). From the top RSF model in WLNP within the area of inference, we reclassified scaled RSF scores (0–1) into 10 quantile bins (Nielsen 2007). Because selection is proportional to the probability of use, we calculated the relative probability of use as:

$$U(x_i) = \frac{w(x_i)A(x_i)}{\sum_j w(x_j)A(x_j)}$$

where $w(x_i)$ is the midpoint probability for an RSF bin and $A(x_i)$ is the area for a vector of i habitat variables. For the i^{th} habitat class, we calculated the expected number of bears as $\widehat{N}_i = \widehat{N} * U(x_i)$ where $\widehat{N}$ is the estimated population size for WLNP, and density is $\widehat{D}_\iota = \widehat{N}_\iota / A_i(x_i)$.

Lastly, based on abundance and habitat associations in WLNP, we extrapolated across the remaining area of inference to estimate $\widehat{N}$ for the entire study area. We compared $\widehat{N}$ and 95% CIs from SECR and RSF methods. We used k-fold cross validation to measure the predictive ability of the RSF (Fielding and Bell 1997, Boyce et al. 2002). We partitioned the data into 10 folds and tested the association between the frequency of presence observations in 10 RSF bin ranks. We did this 10 times and used the averaged Spearman's rank correlation coefficient ($\bar{r}_s$) to evaluate the predictive success of each RSF model (Boyce et al. 2003).

RESULTS

In 2013, we sampled 855 rub objects and 49 opportunistic grids and submitted 4,554 hair samples (4,179 rub object; 375 opportunistic) to WGI for analysis. Data from the visual and genetic data sets were combined and resulted in 306 detections of 126 males and 177 detections of 101 female black bears over 8 occasions in 2013 (Table 7). We detected black bears at 52% of the traps (*n* = 466). In 2014, we sampled 873 rub objects and 54 opportunistic grids and submitted 3,912 hair samples (3,597 rub object and 315 opportunistic) for analysis in 2014. This resulted in 294 detections of 122 males and 168 detections of 100 females in 2014 (Table 7). We detected black bears at 48% of the traps (*n* = 444). Across both years, 1,236 samples were assigned individual multi-locus genotypes to 347 black bears (186 males, 161 females). Of these, 107 individuals were detected in both years (see Appendix 3 for more details).

SECR Models

The top model from step 1 for males in 2013 and 2014 included lambda$_0$ (λ_0) covariates traptype, *bk* (trap-specific learned response), and within-season linear time trend (Table A 4; Table A 5). The σ covariate included within-season linear time trend. The top models for males from step 2 in 2013 and 2014 allowed density to vary by land tenure (Table A 4; Table A 5). Male beta coefficients for Crown land were negative relative to park land, the reference level (2013: $\beta_{private}$= -0.48, SE = 0.26; β_{public} = -0.93, SE = 0.27; 2014: $\beta_{private}$= -0.86, SE = 0.26; β_{public} = -1.29, SE = 0.28; Figure 9).

The top model from step 1 for females in 2013 included λ_0 covariates traptype and *bk*, and σ covariates traptype and previous grizzly bear detection (Table A 6). The top model from step 1 for females in 2014 included λ_0 covariates traptype and *bk*, and σ covariate was traptype (Table A 7). To be consistent among years, we selected the second-top observational model (ΔAICc = 3.17) in 2013 for further modeling.

The top model for females from step 2 in 2013 included hunter harvest as the density covariate (Table A 6). There was a negative relationship between harvest and black bear density for females (β_{hunt} = -0.27, SE = 0.07; Figure 9). The top model from step 2 for females in 2014 included land tenure as a density covariate (Table A 7). Results suggested a negative relationship between Crown land and female black bear density in 2014. (β_{Crown} = -1.20, SE = 0.34; β_{private} = -0.21, SE = 0.28; Figure 9).

Male black bear density was 46.8/1,000 km^2 (SE = 12.4; Table 8) in 2013 and 45.8/1,000 km^2 (SE = 17.9; Table 8) in 2014. Female black bear density was 72.1 bears/1,000 km^2 (SE = 21.8; Table 8) in 2013 and 62.3 bears/1,000 km^2 (SE = 18.5; Table 8) in 2014. In all cases, density is reported at mean covariate levels. Sigma (σ) and λ_0 were lower for females than males in both years (Table 8).

Resource Selection Functions

The global 'rub tree' RSF indicated rub trees were located in areas with high NDVI values, low to mid-elevations, and rub trees were not selected in agricultural areas such as crop land and year-round cattle pastures (Figure 10). When the lowest 3 RSF bins were excluded, the area of inference was reduced to 2751.6 km^2 (Figure 10).

Across our study area, we detected male black bears at 407 locations in 2013 and 2014. Male black bears selected higher NDVI, avoided burned areas, and avoided Crown and private land relative to park land (Figure 11, $\bar{r}_s$ = 0.70; Table A 8). We had 323 locations for female black bears in 2013 and 2014. Female black bears selected higher canopy cover and grizzly bear intensity of use, and avoided private and Crown land (Figure 11, $\bar{r}_s$ = 0.74; Table A 9).

Using WLNP as the reference area, RSF-derived abundance in the area of inference was 116.1 male black bears (95% CI: 82.3 – 163.9) in 2013 and 134.4 male black bears (95% CI: 98.9 – 182.6) in 2014 (Figure 12). For females in 2013, abundance in the area of inference was 159.5 (95% CI: 120.3 – 211.6) in 2013 and 147.5 (95% CI: 96.0 – 226.8) in 2014 (Figure 12).

DISCUSSION

We estimated density and abundance of a black bear population where there has never been an empirical estimate. As expected, there were more females than males in our study area, which was supported by both SECR and RSF methods. Hunted bear populations often have a higher proportion of females than males, a result of disproportionate harvest pressure on males (Bunnell and Tait 1980, 1981, O'Pezio et al. 1983, Garshelis 1990, Miller 1990). For females in our study area, harvest density in 2012 was the top SECR model-covariate driving spatial variation in density in 2013. In 2012, female harvest exceeded 30% (33%; *n* = 14) of the total reported harvest (*n* = 43) in southwestern Alberta. A high proportion of females harvested (e.g., >30%) can be an indicator of over harvest (Miller 1990, McLellan et al. 2017). For example, Kolenosky (1986) found few females were harvested in Ontario when hunting pressure was low, but were more vulnerable to harvest as pressure increased. The proportion of females harvested during 2010-2014 in southwestern Alberta averaged 29% (SE = 0.07; 2 years exceeded 30% female harvest 2011 (50% F) and 2012 (33% F)). However, Garshelis (1990) points out that interpreting changes in sex ratios can be misleading because age is strongly tied to harvest vulnerability, and without an understanding of age structure of the population, changes in sex ratios could be misinterpreted as a population decline when the population is dominated by a specific age cohort (e.g., subadults).

For all top SECR models except one (females 2013), land tenure was the density covariate that explained the most variation. In addition, black bears showed reduced densities on Crown lands in both SECR and RSF models. A large-scale covariate like land tenure can be confounding because it may be describing more than just 'land tenure'. However, we speculate that lower black bear densities on Crown land can be related to the multiplicative effect of road density and harvest intensity, which would explain why the individual covariates ‘roads’ and ‘harvest density’ in the density models did not perform better than land tenure. For example, vegetation types in WLNP and Crown land were similar and if land tenure did not have an effect, we would expect densities to be similar. Yet, densities are 1.5 times higher for males and 2.7 times higher for females in WLNP than Crown land.

Land tenure encompasses habitat differences such as road density, with park land having the lowest road density and private with the highest road density. Roads provide the potential for human-wildlife vehicle collisions, reduce functional habitat, and increase access for hunters and poachers. Harvest rates are higher on Crown land than private land (Alberta Environment and Parks, *unpublished data*). Differences in perceived risk by land tenure type have been documented for elk (*Cervus elaphus*) in our study area. From radiocollared elk, Ciuti et al. (2012) found the highest level of group vigilance occurred on public land during the hunting season, and the lowest levels of group vigilance were recorded in WLNP during summer (i.e., non-hunting season). Increased time spent being vigilant, in turn, resulted in decreased time spent foraging, implying a fitness consequence. Indeed, Ciuti et al. (2012) found the lowest elk calf/cow ratios on public lands, relative to park and private lands. Land tenure also encompasses differences in grizzly bear density and selection. Loosen (2017) found that grizzly bears selected Crown land over private and park lands. Because habitat selection is tied with animal density (Boyce et al. 2016), grizzly bears’ preference for Crown land may discourage high black bear densities via interspecific competition.

In southwestern Alberta, the primary industry is agriculture and many producers maintain patches of treed cover, primarily aspen parkland. There is variation in landowners who give hunters access to their property (e.g., some allow hunter access, some do not), thus maintaining a grid-based matrix of bear habitat with spatial variation in hunting. Smaller-scale spatial variation in hunting pressure on private land is in contrast to Crown land where the entire land unit is open to hunting in the spring and fall. This is congruent with McCullough's (1996) description of harvest whereby high harvests can be maintained when there is a matrix in hunted/non-hunted areas that can serve as spatial refuges. Moreover, the indirect effects of hunting have myriad effects on bear populations. For example, Gosselin et al. (2017) found the distribution of harvested male brown bears in Sweden to be the primary influence on cub survival, suggesting source-sink dynamics in areas of heterogeneous hunting pressure. Hunting pressure is spatially heterogenous (Lebel et al. 2012, Steyaert et al. 2016) and areas with high mortality and low recruitment would then contribute less to population growth (Novaro et al. 2005).

The primary link between habitat selection and abundance is movement. Interestingly, our SECR and RSF-derived abundance produced comparable abundance estimates (Figure 12), though there were some differences. Variance estimates differed between the two methods; the RSF-derived abundance estimate had smaller 95% CIs than the SECR-derived abundance estimate. This likely stems from the high variance of ratio estimators (Czaplewski et al. 1983), including capture-recapture estimators. SECR models also estimate density, and thus abundance, using two additional parameters, sigma (σ) and lambda$_0$ (λ_0). In contrast, RSFs do not account for errors in detection and simply compare used locations to locations where they could have been. Of course, we know that we did not detect all bears that were near a hair trap. For example, Boulanger et al. (2004) found that only 37% of GPS-collared grizzly bears visited hair traps when in the vicinity of a trap (hair corrals) and rub objects typically have lower detection probabilities than lured hair corrals (Stetz et al. 2010). However, SECR models account for animals we did not detect by estimating un-observed bear home ranges and generally the accuracy of density estimates depends on the factors affecting detection probability (Whittington and Sawaya 2015). The accuracy of SECR abundance and density estimates depend on the ability to model factors influencing σ and λ_0 (Whittington and Sawaya 2015). Thus, it would make sense that with low detection probabilities, SECR would generate larger variance estimates than the RSF.

The majority of applications of the Boyce and McDonald (1999) method of relating animal populations to habitats have been applied to theoretical (e.g., Boyce and Waller 2003) or expanding populations. For example, Mladenoff and Sickley (1998) predicted the potential population of gray wolves (*Canis lupus*) in northeastern US based on habitat suitability metrics from existing populations in Wisconsin and Michigan. They calculated a continuous area of more than 33,500 km^2 could support 1,070 wolves. Population projections are important, particularly for species at risk, to anticipate how habitats could shape population expansions. Rarely, however, has the RSF method for extrapolation been applied to a population with concurrent mark-recapture data to compare results. In this paper, we used our SECR-derived density as an anchor point for RSF bins so our estimates are not fully independent. However, the data and model structure were different so we could expect different estimates of density and abundance. Surprisingly, we found comparable results (broadly overlapping confidence intervals), which suggests the validity of the RSF method for estimating animal populations, even for a generalist species such as the black bear.

The only previous estimate for black bear abundance in southwestern Alberta (Gunson 1993) was derived without variance estimates, which precludes comparison and therefore, inferences about population changes (Miller 1990). When compared to other black bear density estimates using similar methods, our density estimates were slightly lower, on average, than

SECR estimates in neighboring Glacier National Park (male $\widehat{D}$ = 48/1000 km^2, 95% CI = 40-57, female $\widehat{D}$ = 72/1000 km^2, 95% CI = 60-87; Stetz et al. 2014). As a coarse-level comparison, our estimates were in the range of reported interior black bear densities where sympatric with grizzly bears (mean = 164 bears/1000 km^2), although the range of densities is high (range = 9-450/1000 km^2; Mattson et al. 2005). Our black bear population lies at the eastern edge of their distributional range in southern Alberta. Animals at the edge of their range were historically thought to suffer demographic consequences (e.g., reduced immigration, emigration), and increased habitat fragmentation, and therefore we would expect to see reduced densities (Lawton and May 1995, but see Channell and Lomolino 2000). However, our study indicates a healthy population of black bears with densities higher along the range-limits than areas thought to be more typical black bear habitat.

To our knowledge, this study marks the first rub-only method to estimate black bear density. In contrast to hair corrals, which a common method for black bear mark-recapture studies (Hristienko and McDonald 2007, Gardner et al. 2010, Howe et al. 2013, Wilton et al. 2014), bear rub sampling offers several advantages because bears rub naturally (i.e., no need for bait/lure), there is a lower potential for bears to show negative trap response as interest in scent lure declines (Boulanger et al. 2004, 2008), and can be more cost-efficient (Stetz et al. 2010). If researchers are to pursue rub-object sampling for black bears, we recommend: (1) a longer than normal sampling season (this study: May – Nov) to mitigate the male bias in early spring rubbing behavior (Kendall et al. 2008); (2) deploying rub objects at high spatial densities (this study: average distance between rub objects = 500 m; Lamb et al. 2016). Despite the apparent success of this rub-only method for black bears, we recommend the collection of NGS from multiple data sources (e.g., both rub trees and hair corrals) to improve the precision of mark-recapture density estimates (Boulanger et al. 2008).

MANAGEMENT IMPLICATIONS

Black bear population monitoring studies are often spatially and temporally isolated (Beston 2011). With recent abundance and density estimates for Glacier National Park, MT (Stetz et al. 2014), our study adds demographic information to a shared population of black bears but on a multi-use landscape. While rub-object sampling for black bears proved successful in this study, we believe that estimates could be improved with a secondary data source, particularly for females, because detection probabilities are on average lower than for males. Interestingly, our parallel methods for estimating density and abundance yielded comparable results, and support the use of multiple methods to give credence to results, particularly when exploring a new method of data sampling. For both males and females, density estimates were lowest and harvest densities were highest on Crown land. In 2015, the Alberta government released plans for a new Castle Provincial Park and Castle Wildland Provincial Park that encompasses most of the Crown land within our study area (https://talkaep.alberta.ca/CastleManagementPlan). Currently, draft management plans are to restrict off-highway vehicle use but continue to allow spring and fall black bear hunting. Even with no changes to hunting regulations, we would expect a decrease in hunter success due to restricted motor-vehicle access. We speculate this could reduce mortality rates, and potentially increase black bear densities on Crown lands. Finally, continued research and monitoring of both black and grizzly bears in the Castle Parks after the implementation of access restrictions could provide an excellent opportunity to evaluate changes to black and grizzly densities and spatial interactions.

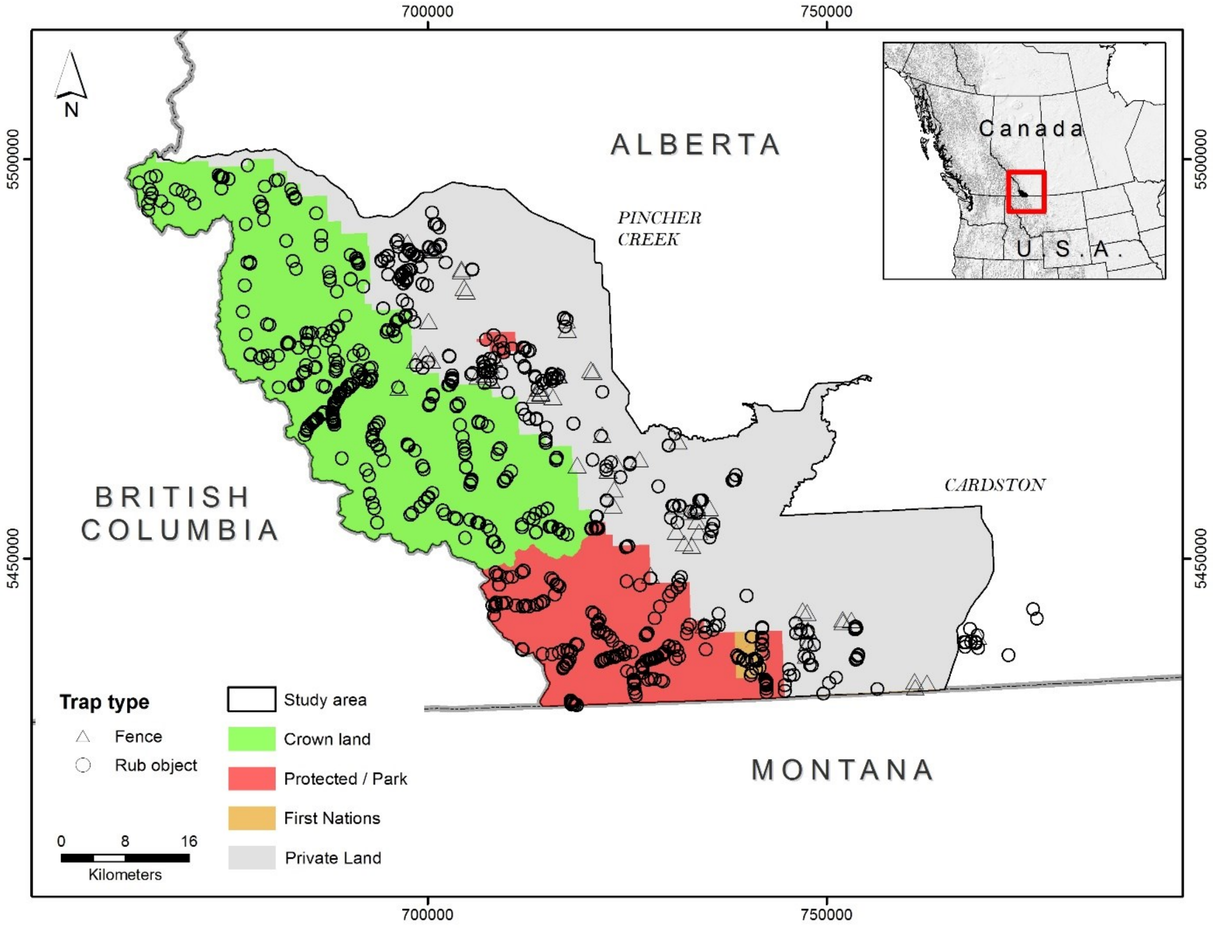

Figure 7. Black bear hair samples were collected from rub objects in 2013 and 2014 in southwestern Alberta, Canada. Rub objects included trees, fence posts, and power pole. Rub objects were sampled east of the study area boundary. Parks and protected areas (red) include Waterton Lakes National Park and Beauvais Provincial Park. Other provincial parks within the study area were too small spatially to include as park.

Figure 8. We affixed 4 short segments of barbed wire to bear rub trees. The barbed wire facilitated collection of bear hair and provided discrete sampling units for field technicians to clean after sampling. Photo credit: Annie Loosen

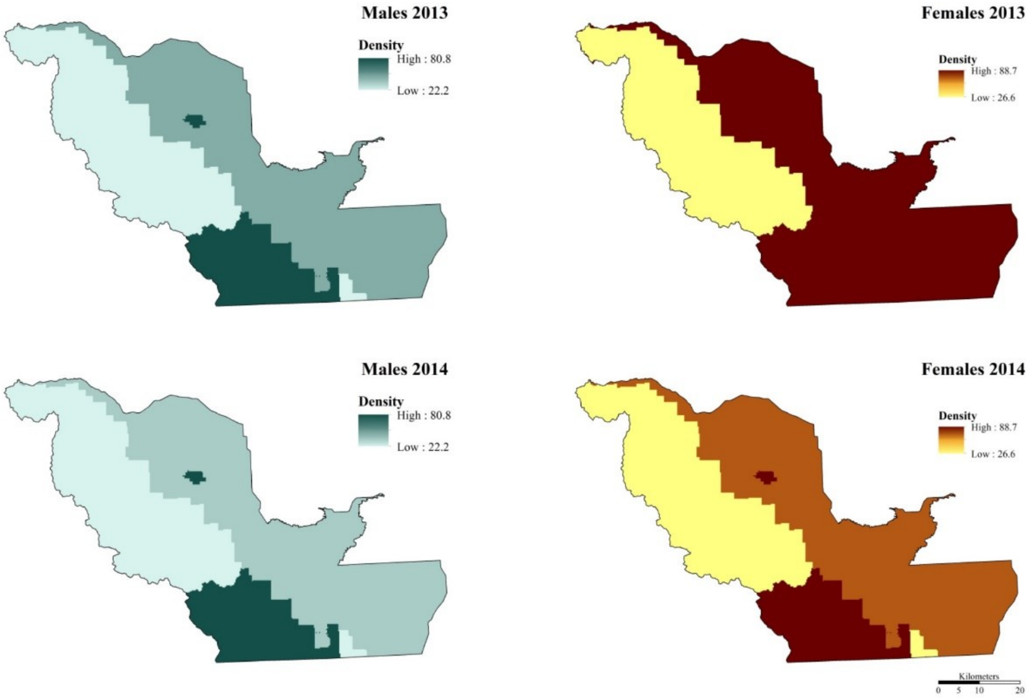

Figure 9. Surface densities derived from top-performing male and female black bear SECR models in southwestern Alberta. For males in both years and females in 2014, the density varied by land tenure (Crown, private, park). Densities were highest on park land and lowest on Crown land. For females in 2013, density varied by harvest density. Densities are reported in bears per 1,000 km^2.

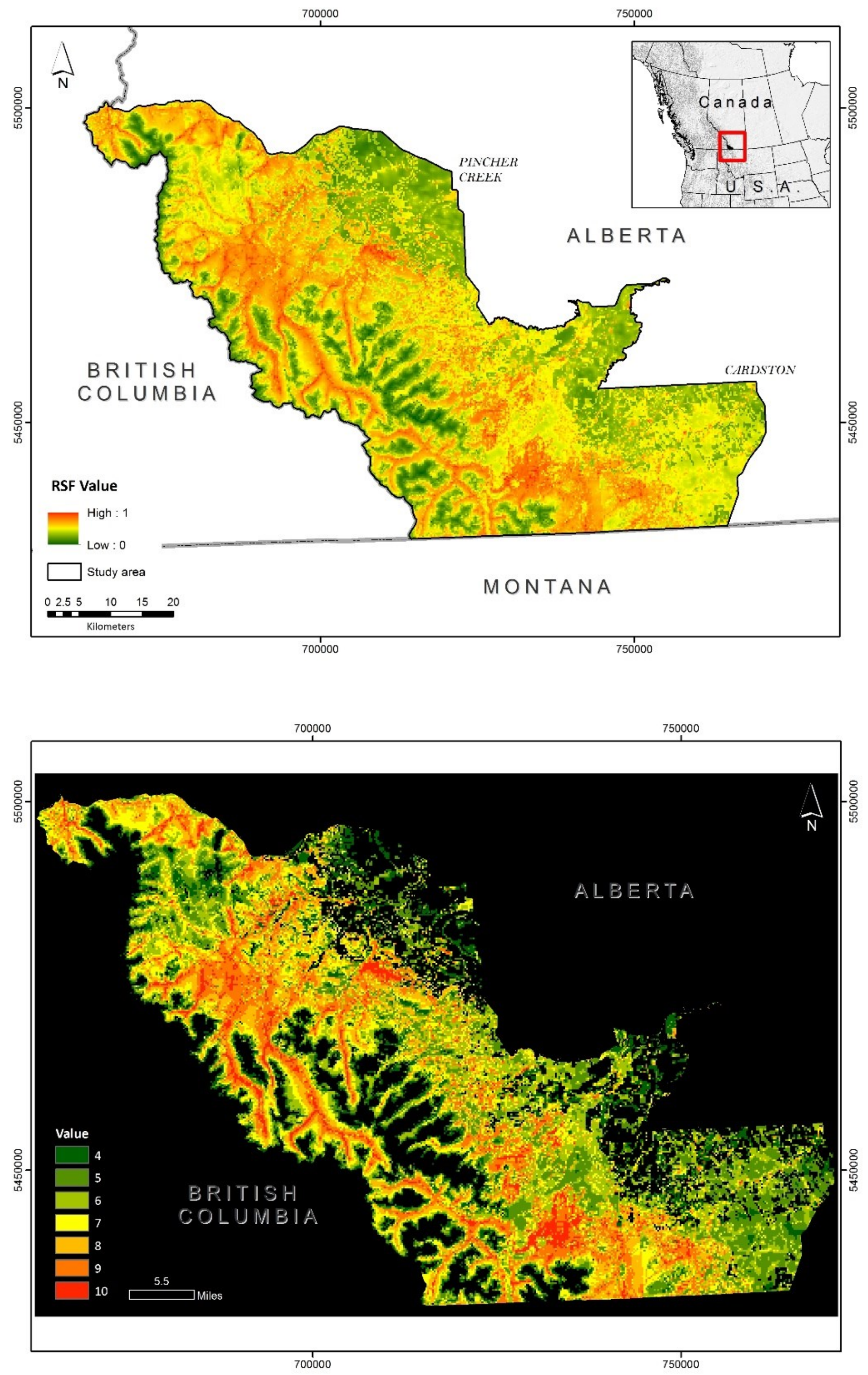

Figure 10. RSF for rub object selection (top) with areas we had a low probability of sampling removed (bottom). Our inference from habitat selection is restricted to discussion in the bottom

map. We reclassified RSF values in the top map to 10 groups with natural breaks (jenks) and removed the lowest 3 groups. Black cells represent areas outside our area of inference.

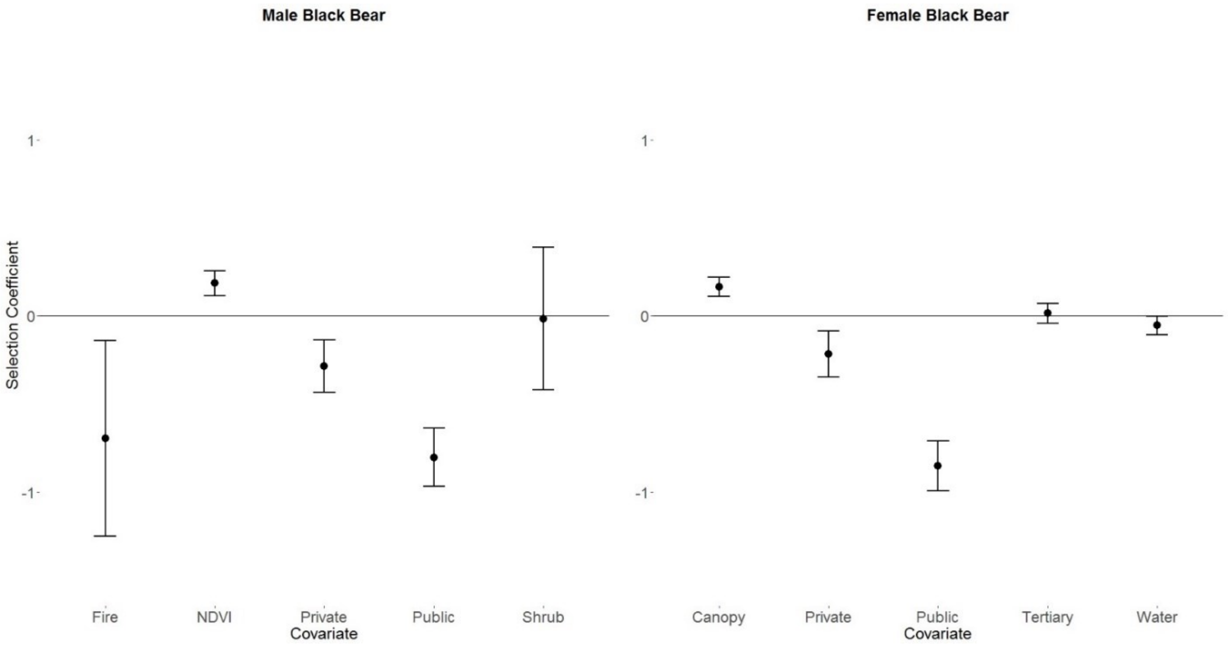

Figure 11. Scaled beta coefficients for top RSF-models for male and female black bears in southwestern Alberta, Canada. We compared detection locations (use), and associated habitat covariates, to the full set of rub objects (available) in 2013 and 2014.

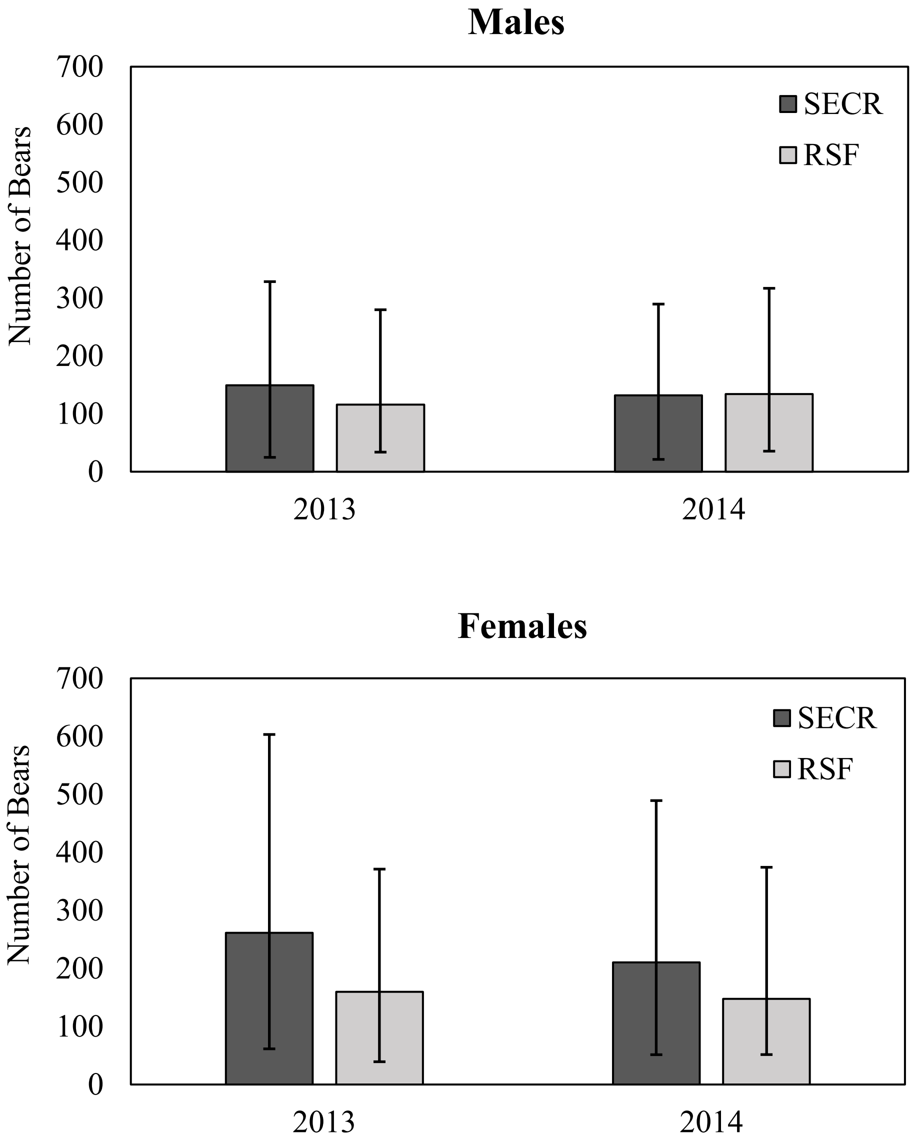

Figure 12. Comparison of SECR and RSF methods to estimate the number of male (top) and female (bottom) black bears in the southwestern Alberta. Error bars represent 95% CI.

Table 4. Covariates used in the observation and state models for hierarchical SECR models for black bears in southwestern Alberta in 2013 and 2014.

Covariate	Name	Resolution	Notes
Step 1			
Trap-specific learned response	bk		1 = individual was detected previously at specific trap, 0 = individual was not detected previously
Time trend	T		Within-season linear time trend
Type of non-invasive hair trap	traptype		Rub object, fence, and opportunistic
Previous grizzly bear detection	GB		1 = Grizzly bear detected during previous occasion, 0 = Grizzly bear not detected during previous occasion
Step 2			
Land management	tenure	Vector	Crown, private, and park land
Harvest density	hunt	Vector	Number of individuals harvested divided by area of wildlife management unit for year prior to sampling
Distance to tertiary rd	tertiary	30 m	Ln-transformed distance to tertiary roads and motorized trails (30 m)
Road density	rddens	30 m	Road density calculated for 6 km moving window

Burned	fire	30 m	Binary; 1 = area was burned < 20 year ago, 0 = area not burned
Normalized difference vegetation index	NDVI	250 m	Average NDVI values for Jun-Nov, calculated separately for 2013 and 2014
Distance to water	water	30 m	Ln-transformed distance to lakes and higher-order streams
Canopy cover	canopy	30 m	Percent canopy cover

Table 5. Candidate SECR models for male and female black bears in southwestern Alberta. We ran single-session models for 2013 and 2014.

Sex	Model Number	Model Name	Model
MALE	1	Fire	D~fire λ_0[a]~traptype + bk σ[b]~traptype
	2	Tenure	D~tenure λ_0~traptype + bk σ~traptype
	3	Hunt	D~hunt λ_0~traptype + bk σ~traptype
	4	Tertiary Rd	D~tertiary rd λ_0~traptype + bk σ~traptype
	5	Canopy	D~canopy λ_0~traptype + bk σ~traptype
	6	Water	D~water λ_0~traptype + bk σ~traptype
	7	NDVI	D~ndvi λ_0~traptype + bk σ~traptype
	8	Rd Dens	D~rddens λ_0~traptype + bk σ~traptype
FEMALE	1	Fire	D~fire λ_0~traptype + bk σ ~traptype
	2	Tenure	D~tenure λ_0~traptype + bk σ ~traptype
	3	Hunt	D~hunt λ_0~traptype + bk σ ~traptype
	4	Tertiary Rd	D~tertiary rd λ_0~traptype + bk σ ~traptype
	5	Canopy	D~canopy λ_0~traptype + bk σ ~traptype
	6	Water	D~water λ_0~traptype + bk σ ~traptype
	7	NDVI	D~ndvi λ_0~traptype + bk σ ~traptype
	8	Rd Dens	D~rddens λ_0~traptype + bk σ ~traptype

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[a] λ_0 = Cumulative hazard of detection

[b] σ = Spatial scale parameter

Table 6. Candidate models used for RSF models for black and grizzly bears in southwestern Alberta, Canada. Covariates from the top RSF models for each sex were used in SECR models.

Model	Covariates
1	Water + Tertiary Rd + Canopy Cover + Tenure
2	Fire + NDVI[a] + Shrub + Tenure
3	TRI[b] + Tertiary Rd + Building + Canopy Cover
4	TRI + Primary/Secondary Rd + Building + Canopy Cover^2
5	Water + Fire + Canopy Cover + Tertiary Rd
6	Elevation + Primary Rd + Building + Canopy Cover
7	Elevation + Primary/Secondary Rd + Building + Canopy Cover^2
8	Elevation + Primary Rd + Deciduous + Tenure
9	Elevation^2 + Primary Rd + Shrub + Tenure
10	Fire + Tertiary Rd + Shrub + Building
11	Fire + Primary Rd + Deciduous + Building
12	Fire + Primary Rd + Agriculture + Building
13	Primary Rd * Shrub + Building
14	Tertiary Rd * Conifer + Water
15	Water + Tertiary Rd + Canopy Cover + Tenure + GB IOU
NULL	~.

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[a] NDVI = Normalized Difference Vegetation Index (MODIS)

[b] TRI = Terrain Ruggedness Index (Riley et al. 1999)

Table 7. Black bear detections from non-invasive genetic sampling in southwestern Alberta, Canada. Data were collected from rub objects (*n* = 873) in 2013 and 2014.

Year	Occasion	Number of Active Sampling Stations[a]	Number of Sampling Stations Detecting a Black Bear		Hair Collection Dates	Number of New Black Bears		Number of Individuals Detected		Number of Detections	
			M	F		M	F	M	F	M	F
2013	1	808	96	16	June 17 - July 7	56	15	56	15	99	16
	2	816	78	25	July 8 - July 28	25	21	53	23	78	26
	3	809	44	24	July 29 - Aug 18	11	17	29	21	46	24
	4	828	13	39	Aug 19 - Sep 8	8	25	13	35	16	41
	5	836	20	22	Sep 9 - Sep 29	9	8	15	19	20	22
	6	846	22	29	Sep 30 - Oct 20	10	7	22	23	23	29

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[a] Number of active sampling stations may vary depending on destruction of a rub tree from windfall or avalanche, access issues as a result of snow or flooding, or discovery and set up of new rub tree.

	7	777	12	10	Oct 21 - Nov 8	5	3	10	10	12	11
	8	48	8	8	Apr 30 - Oct 31	2	5	12	8	12	8
		Total	*293*	*173*		*126*	*101*			*306*	*177*
2014	1	861	103	25	June 17 - July 6	62	22	62	22	108	27
	2	871	75	26	July 7 - July 27	25	19	49	24	77	27
	3	869	32	19	July 28 - Aug 17	10	12	30	18	34	20
	4	869	19	23	Aug 18 - Sep 7	4	12	15	18	19	23
	5	870	16	32	Sep 8 - Sep 28	7	19	15	26	16	32
	6	872	18	16	Sep 29 - Oct 19	8	4	14	13	18	16
	7	867	7	10	Oct 20 - Nov 9	4	4	7	8	7	10
	8	54	12	11	May 20 - Oct 14	2	8	13	11	15	13
		Total	*282*	*162*		*122*	*100*			*294*	*168*

Table 8. Top density models and parameter estimates for male and female black bears in southwestern Alberta in 2013 and 2014. Top models were selected based on AICc values. Densities are reported in bears per 1,000 km^2.

Year	Sex	Covariate	Levels	Density	SE[a]	95% CI	λ_0 [b](SE)	σ[c] (SE)
2013	Male	Tenure	Park	43.2	7.1	31.4 - 59.5	$\mathrm{traptype}_{\mathrm{rub}}\ \mathrm{bk}^{d}_{0}$: 0.009 (0.001)	$\mathrm{traptype}_{\mathrm{rub}}$: 4.69 (0.22)
			Private	69.78	12.5	49.3 - 98.7	$\mathrm{traptype}_{\mathrm{rub}}\ \mathrm{bk}_{1}$: 0.030 (0.007)	$\mathrm{traptype}_{\mathrm{fence}}$: 2.85 (0.99)
			Crown	27.4	5.3	18.8 - 39.9	$\mathrm{traptype}_{\mathrm{opp}}\ \mathrm{bk}_{0}$: 0.0001 (0.0004)	$\mathrm{traptype}_{\mathrm{opp}}$: 61.81 (1998.70)
							$\mathrm{traptype}_{\mathrm{opp}}\ \mathrm{bk}_{1}$: 0.0004 (0.007)	
							$\mathrm{traptype}_{\mathrm{fence}}\ \mathrm{bk}_{0}$: 0.001 (0.007)	
							$\mathrm{traptype}_{\mathrm{fence}}\ \mathrm{bk}_{1}$: 0.034 (0.027)	
	Female	Harvest Density	Max	28.9	8.8	16.1 - 51.9	$\mathrm{traptype}_{\mathrm{rub}}\ \mathrm{bk}_{0}$: 0.018 (0.003)	$\mathrm{traptype}_{\mathrm{rub}}$: 1.94 (0.15)
			Min	98.5	14.6	73.8 - 131.4	$\mathrm{traptype}_{\mathrm{rub}}\ \mathrm{bk}_{1}$: 0.080 (0.020)	$\mathrm{traptype}_{\mathrm{fence}}$: 8.48 (3.31)
			Mean	88.8	12.5	67.5 - 116.8	$\mathrm{traptype}_{\mathrm{opp}}\ \mathrm{bk}_{0}$: 9E-05 (8E-05)	$\mathrm{traptype}_{\mathrm{opp}}$: 95.0 (763.5)
							$\mathrm{traptype}_{\mathrm{opp}}\ \mathrm{bk}_{1}$: 0.0004 (0.0004)	
							$\mathrm{traptype}_{\mathrm{fence}}\ \mathrm{bk}_{0}$: 0.0004 (0.0004)	

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[a] SE = standard error

[b] λ_0 = the cumulative hazard of detection

[c] σ = spatial scale parameter

[d] bk = previous capture of x individual (0,1)

							traptype$_{\text{fence}}$ bk$_1$: 0.002 (0.002)	
2014	Male	Tenure	Park	34.3	6.1	24.2 - 48.5	traptype$_{\text{rub}}$ bk$_0$: 0.007 (0.001)	traptype$_{\text{rub}}$: 5.0 (0.25)
			Private	80.8	12.8	59.3 – 110.0	traptype$_{\text{rub}}$ bk$_1$: 0.014 (0.004)	traptype$_{\text{fence}}$: 2.35 (0.35)
			Crown	22.2	4.8	14.6 - 33.9	traptype$_{\text{opp}}$ bk$_0$: 0.0002 (0.001)	traptype$_{\text{opp}}$: 27.70 (35.96)
							traptype$_{\text{opp}}$ bk$_1$: 0.0004 (0.001)	
							traptype$_{\text{fence}}$ bk$_0$: 0.031 (0.010)	
							traptype$_{\text{fence}}$ bk$_1$: 0.058 (0.023)	
	Female	Tenure	Park	71.6	14.1	48.9 - 104.8	traptype$_{\text{rub}}$ bk$_0$: 0.005 (0.001)	traptype$_{\text{rub}}$: 3.74 (0.31)
			Private	88.7	19.9	57.4 – 137.0	traptype$_{\text{rub}}$ bk$_1$: 0.041 (0.013)	traptype$_{\text{fence}}$: 1.38 (0.39)
			Crown	26.6	7.5	15.4 - 45.9	traptype$_{\text{opp}}$ bk$_0$: 0.0001 (9.2E-05)	traptype$_{\text{opp}}$: 113.73 (1351.37)
							traptype$_{\text{opp}}$ bk$_1$: 0.001 (0.001)	
							traptype$_{\text{fence}}$ bk$_0$: 0.027 (0.014)	
							traptype$_{\text{fence}}$ bk$_1$: 0.225 (0.101)	

CHAPTER 4 – CONCLUSION

One of the themes from Chapters 2 and 3 is the importance of private land for black bears in southwestern Alberta. Private lands in southwestern Alberta are highly productive agricultural areas for cow-calf ranching, cereal grains, and oil-seed production. Agricultural areas are attractive to bears for natural forage (Sayre et al. 2012), as well as subsidies from agricultural products just as stored and standing grain, silage, dead livestock (deadstock), and bee-yards (Wilson et al. 2006, Northrup et al. 2012*b*, Loosen 2016, Morehouse and Boyce 2017). In contrast, public or Crown land, and parks and protected areas in North America are commonly of low soil fertility, which in turn, can result in nutrient-poor areas and increased chances of food shortages (Rogers 1987). Moreover, parks are preserved often for their scenic beauty and not for biodiversity or connectivity (Newmark 1985, Jenkins et al. 2015). Many mountain parks have a high proportion of rock and ice, which for many species does not provide adequate foraging opportunities (Joppa and Pfaff 2009). Our findings support habitat restoration and preservation efforts projects on private lands. Private land habitat work is ongoing in southwestern Alberta, such as watershed groups like Drywood-Yarrow Conservation Partnership, large-carnivore attractant management programs as part of Waterton Biosphere Reserve, and land conservation with the Nature Conservancy of Canada.

In Chapter 2, we found evidence for resource partitioning. While protected areas are designed to protect a range of species, small parks such as Waterton Lakes National Park (WLNP) may not be of the appropriate spatial scale for wide-ranging species like grizzly bears, and may give advantage to more human-tolerant species like black bears. Further, as outlined by the International Union for the Conservation of Nature's Bear Specialist Group, elevated levels of human disturbance and human-wildlife conflicts could threaten otherwise stable grizzly bear populations (McLellan et al. 2008).

For future research, I recommend examining if black bears rub in higher-quality habitats. This has been explored for grizzly bears in our study area (Morehouse et al. *in prep*) and elsewhere in Canada (Clapham et al. 2012, Lamb et al. 2017), but not for black bears. More importantly, it has not been explored for sympatric black and grizzly bears, where social dynamics likely play an important role in rubbing behavior. Additionally, I recommend further investigation into the spatio-temporal aspects of black-grizzly bear partitioning in southwestern Alberta. We examined partitioning strictly from a resource-partitioning perspective. However, spatio-temporal use would add further insight into habitat use by sympatric species.

This project represents a collaboration with a grizzly bear monitoring project (GBMP), which substantially reduced project costs. The GBMP budget in 2013-2014 was approximately $370,000, with major costs including field staff time ($55,200 annually) and genetic analysis ($73,600 annually). In contrast, with no field staff required because hair samples were already collected, the 2013-2014 black bear budget was $52,000 total. Most of the costs were for genetic analysis. The current grizzly bear recovery plan outlines resurvey plans within each bear management area every 5 years (Alberta Sustainable Resource Development 2008). Given these plans, there is the potential to simultaneously learn more about black bears and spatio-temporal partitioning with grizzly bears across western Alberta.

Human-wildlife conflicts and hunter success are often used by provincial and state managers as indicators of population change (Roseberry and Woolf 1991) and to set harvest objectives (Garshelis and Hristienko 2006). However, these metrics are inextricably tied with food availability and are prone to large inter-annual variation (Noyce and Garshelis 1997), and without information on age-structure of the harvested population, trends in sex-ratio may be misleading (Garshelis 1990). In Alberta, the provincial government initiated a black bear tooth collection program to better understand the age, sex, condition, and reproductive history of harvested individuals (http://mywildalberta.com/hunting/game-species/black-bear-tooth-collection-program.aspx). We recommend the extension of this pilot project to southern Alberta, and include non-licensed hunters, as well as licensed hunters, in the pool of harvested black bears.

In this thesis, I have explored black bear density and abundance where no population study has occurred. My estimates indicate similar densities to interior black bear populations where sympatric with grizzly bears. I have also explored resource overlap with the more dominant grizzly bear. It is my hope that I have provided ecological insight into Alberta's "forgotten bear species" and given managers baseline information on which to manage black bear populations in the future.

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APPENDICES

APPENDIX 1. BETA COEFFICIENTS

Table A 1. Beta coefficients from top-performing RSF models comparing presence data versus all rub object for male and female black and grizzly bears in southwestern Alberta. We used use/availability data from non-invasive genetic data collected in 2013 and 2014.

Species / Sex	**Covariate**	**β**[1]	**SE**[2]	**df**[3]	**LL**[4]	**AIC**[5]	**ΔAIC**[6]	***w_i***[7]
Grizzly bear male	Elevation	-0.15	0.08	6	-696.50	1405.08	0.00	0.91
	Primary road	0.16	0.09					
	Deciduous	0.03	0.01					
	Private land	-0.51	0.21					
	Crown land	0.51	0.21					

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[1] β = beta coefficient

[2] SE = standard error

[3] df = degrees of freedom

[4] LL = log likelihood

[5] AIC = Akaike information criterion

[6] ΔAIC = difference in AIC value from top-performing model

[7] w_i = model weight

Grizzly bear female	Fire	0.31	0.07	5	-307.84	625.73	0	0.58
	Primary road	0.43	0.16					
	Deciduous	0.02	0.01					
	House	-0.05	0.11					
Black bear male	Fire	-0.70	0.56	6	-783.48	1579.02	0.00	0.65
	NDVI[1]	0.19	0.07					
	Shrub	-0.002	0.06					
	Private land	-0.29	0.15					
	Crown land	-0.80	0.17					
Black bear female	Water	-0.05	0.07	6	-675.07	1362.20	0.00	0.52
	Tertiary road	0.03	0.08					
	Canopy cover	0.01	0.003					
	Private land	-0.22	0.17					
	Crown land	-1.01	0.20					

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[1] NDVI = normalized difference vegetation index (MODIS)

Table A 2. Beta coefficients from seasonal LSDF models comparing male (M) and female (F) black and grizzly bears for all pariwise combinations (6 total). We defined 'early summer' as June 17-July 28, 'late summer' as July 29-September 29, and 'autumn' as September 30-November 9.

		EARLY SUMMER			LATE SUMMER			AUTUMN		
Model	**Covariate**	**β**[1]	**SE**[2]	**AUROC**[3]	**β**	**SE**	**AUROC**	**β**	**SE**	**AUROC**
					Intraspecies					
M Grizzly Bear x F Grizzly Bear	Private	-0.19	0.73	0.73	-0.08	0.51	0.77	-0.52	0.58	0.69
	Crown	0.79	0.70		1.19	0.54		-0.34	0.58	
	NDVI	-9.98	4.89		11.19	3.22		2.26	1.33	
	Primary Rd	-0.26	0.33		-0.44	0.25		0.15	0.22	
	Fire	-1.36	0.73		-0.98	0.60		1.67	0.89	
	Deciduous	-0.03	0.03		0.05	0.02		0.00	0.03	
	Elevation	0.00	0.00		0.00	0.00		-0.01	0.00	

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[1] β = beta coefficient

[2] SE = standard error

[3] AUROC = Area under the receiver operating curve

M Black Bear x F Black Bear	Private	-0.72	0.33	0.64	-0.05	0.30	0.65	0.24	0.53	0.64
	Crown	0.19	0.37		0.23	0.38		0.39	0.67	
	NDVI	-1.26	2.57		1.98	2.30		0.70	1.29	
	Primary Rd	-0.16	0.13		0.10	0.10		-0.10	0.17	
	Fire	13.71	837.81		-0.13	0.96		13.85	882.74	
	Deciduous	0.02	0.01		-0.01	0.01		-0.03	0.02	
	Elevation	0.00	0.00		0.00	0.00		0.00	0.00	
Interspecies										
M Grizzly Bear x M Black Bear	Private	0.39	0.29	0.70	0.25	0.34	0.72	-0.42	0.48	0.74
	Crown	0.93	0.27		1.41	0.40		1.75	0.55	
	NDVI	-5.49	1.75		4.44	2.56		-1.71	1.29	
	Primary	0.35	0.11		0.12	0.14		0.25	0.20	
	Fire	1.52	0.66		0.62	0.91		0.67	1.22	
	Deciduous	0.02	0.01		0.04	0.02		0.04	0.02	
	Elevation	0.000	0.001		0.002	0.001		-0.003	0.001	
	Private	-0.27	0.77	0.77	0.62	0.48	0.92	0.73	0.72	0.82

F Grizzly Bear x F Black Bear	Crown	-0.02	0.74		0.87	0.51		2.75	0.75	
	NDVI	3.34	6.64		-7.65	3.22		-4.54	1.80	
	Primary Rd	0.39	0.36		0.61	0.23		-0.13	0.21	
	Fire	18.26	1742.25		0.80	0.69		14.20	1527.08	
	Deciduous	0.03	0.03		-0.01	0.02		-0.01	0.03	
	Elevation	0.004	0.002		0.001	0.001		0.008	0.003	
M Grizzly Bear x F Black Bear	Private	-0.24	0.40	0.74	0.34	0.33	0.74	-0.47	0.46	0.76
	Crown	1.25	0.44		1.73	0.38		2.06	0.57	
	NDVI	-6.33	2.64		6.97	2.66		-1.09	1.37	
	Primary Rd	0.11	0.18		0.23	0.13		0.13	0.18	
	Fire	15.27	888.67		0.56	0.74		15.49	1178.82	
	Deciduous	0.03	0.02		0.03	0.01		0.01	0.02	
	Elevation	0.001	0.001		-0.002	0.001		-0.002	0.002	
F Grizzly Bear x M Black Bear	Private	0.17	0.73	0.77	0.85	0.51	0.76	0.36	0.66	0.76
	Crown	0.21	0.66		0.78	0.56		2.32	0.71	

NDVI	3.91	5.04	-6.36	2.97	-3.80	1.53
Primary Rd	0.56	0.30	0.26	0.22	-0.07	0.23
Fire	2.96	0.92	1.61	0.87	-0.68	1.30
Deciduous	0.05	0.03	-0.01	0.02	0.03	0.03
Elevation	0.005	0.002	0.004	0.001	0.003	0.002

APPENDIX 2. QUANTIFYING BIAS IN RUB OBJECT LOCATIONS

Because our surveys for rub objects were limited primarily to existing linear features (e.g., roads, trails, seismic lines, game trails), we anticipated a bias with our rub-object sampling. To quantify this bias, we compared the habitat covariates associated with all sampled rub object locations to those associated with randomly selected resource units. We re-defined the study area as a minimum convex polygon (MCP) bounding all unique rub object locations. We buffered the MCP by 2.4 km so random points could be situated in all cardinal directions from rub objects. This buffer distance represented the average daily linear movement of grizzly bears in the neighbouring Flathead Valley, BC (Apps et al. 2006), which we assumed to be similar to bear movements in our study area because they are part of the sampled population. We generated 17,460 random points within this MCP (20 points for each rub object), and used an exponential RSF, fitted using a logistic regression:

$$RSF(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \cdots + \beta_n x_n)$$

where β_i represents the selection coefficient for covariate x_i in a vector, x, of n covariates. We modelled this to identify attributes of researcher-identified rub objects compared to random locations. Because we were interested in precisely quantifying the habitat and landscape variables that described our bias in rub object placement, we included all non-correlated covariates in one global model. We scaled all variables so we could directly compare beta values. We excluded areas that we apparently avoided by iteratively reducing the low-value RSF habitats. In other words, we used the results from this RSF to refine our “effectively sampled area.”

For the researcher-bias model, we compared all unique rub object locations (n = 873) with random locations (n = 17,460). The global model included 13 covariates. Researchers selected areas of high NDVI value and avoided setting up rub objects in agricultural areas such as crop land and year-round cattle pastures (Table A 3, Figure A 1).

Table A 3. Beta coefficients for the top resource selection model comparing unique rub object locations (n = 873) with random locations (n = 17,460) in southwestern Alberta. Random points were drawn within a buffered minimum convex polygon at a ratio of 1:20 (use:avail). Rub object locations indicate high levels of selection and avoidance for landscape covariates.

Covariate	β[1]	SE[2]	df[3]	LL[4]	AIC[5]	ΔAIC[6]	w_i[7]
Water	-0.32	0.03	14	-2726.15	5480.33	0	1
Class 3 Road	-0.29	0.02					
Building	0.11	0.05					
Fire	-0.21	0.21					
NDVI[8]	5.17	0.75					
Private	-0.42	0.12					
Crown	-0.89	0.12					
Agriculture	-3.44	0.44					
Deciduous	0.44	0.16					
Grass	-1.21	0.22					
Shrub	0.50	0.24					
Elevation	0.00	0.00					
Canopy Cover	0.02	0.00					

---

[1] β = beta coefficient

[2] SE = standard error

[3] df = degrees of freedom

[4] LL = log likelihood

[5] AIC = Akaike information criterion

[6] ΔAIC = difference in AIC value from top-performing model

[7] w_i = model weight

[8] NDVI = normalized difference vegetation index (MODIS)

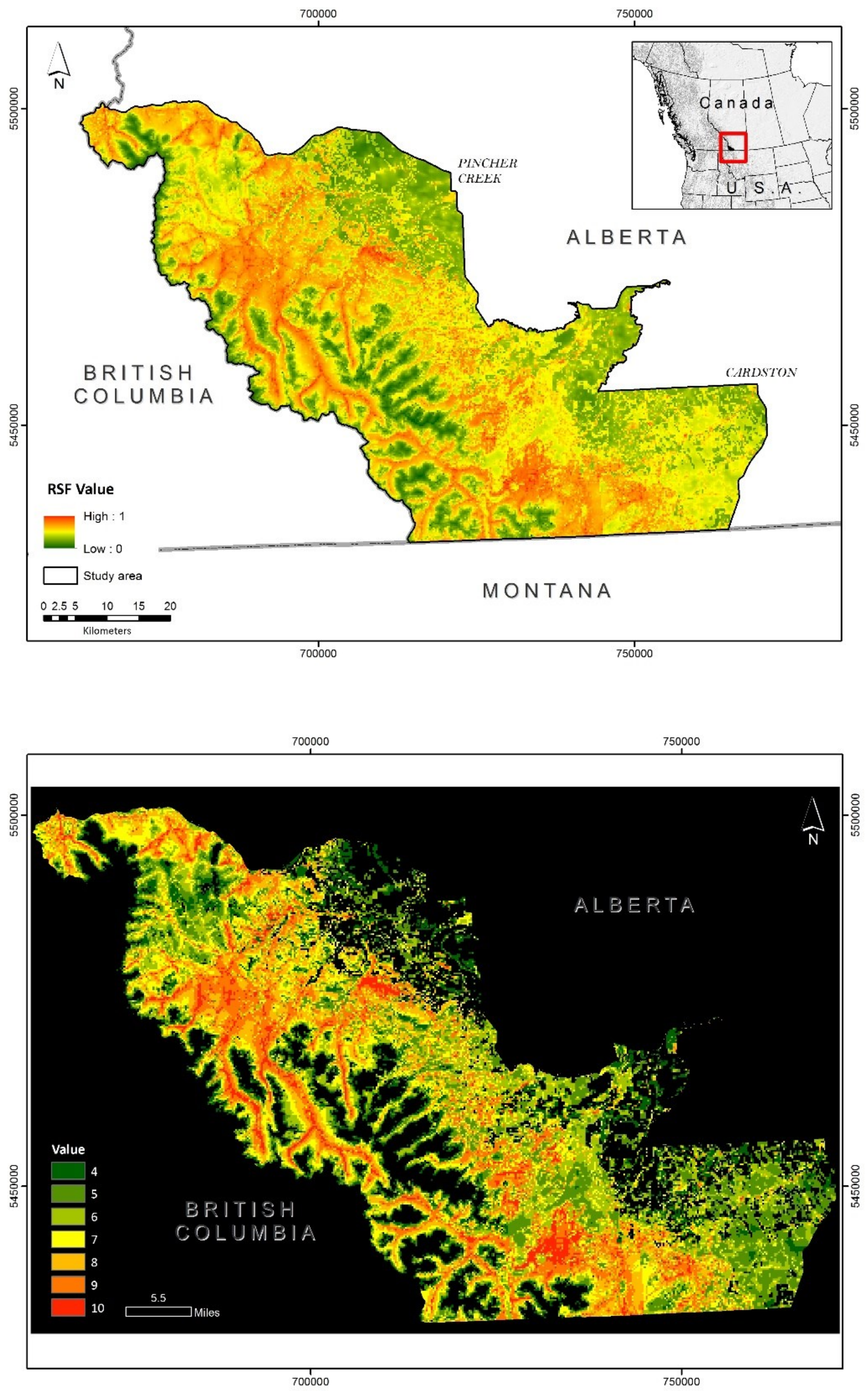

Figure A 1. RSF for rub object selection (top) with areas we had a low probability of sampling removed (bottom). Our inference from habitat selection is restricted to discussion in the bottom map. We reclassified RSF values in the top map to 10 groups with natural breaks (jenks) and removed the lowest 3 groups. Black cells represent areas we did not effectively sample.

APPENDIX 3. DETAILED GENETIC RESULTS

In 2013, we sampled 855 rub objects and 49 opportunistic grids. We submitted 4,554 hair samples (4,179 rub object; 375 opportunistic) to WGI for analysis in 2013. Genetic results were derived from two data sets. The first data set (genetic data) included individuals identified to be black bears during the single-locus pre-screen of data (G10J; 54.4%). Samples that were assigned a high-confidence G10J score had an 83% (*n* = 564) genotyping success rate, 16% (*n* = 108) of samples failed at >3 loci and were excluded from further analysis, and 1% (*n* = 4) had genetic material from >1 individual. The second data set (visual data set) included samples identified as black bear during visual inspection (i.e., jet black) before genotyping. Samples had a 74% (*n* = 67) genotyping success rate and 26% (*n* = 23) of samplings failed at >3 loci. Data from the visual and genetic data sets were combined and resulted in 306 detections of 126 males and 177 detections of 101 female black bears over 8 occasions in 2013 (Table 7). We detected black bears at 52% of the traps (*n* = 466).

In 2014, we sampled 873 rub objects and 54 opportunistic grids. Average spacing between traps was 525 m. We submitted 3,912 hair samples (3,597 rub object and 315 opportunistic) for analysis in 2014. Like 2013, samples visually identified as black bear were restricted to the visual data set. These samples had a 68% (*n* = 111) genotyping success rate, 32% (*n* = 52) failed at >3 loci, and 1% (*n* = 1) had genetic material from >1 individual. Unlike 2014, samples with odd-numbered alleles at G10J were not set aside and WGI staff conducted a simultaneous analysis of grizzly and black bear samples, using the 8-locus first pass as a quality control measure. These samples had a 96% (*n* = 494) genotyping success rate and 4% (*n* = 21) failed at >3 loci. Combined, this resulted in 294 detections of 122 males and 168 detections of 100 females in 2014. We detected black bears at 48% of the traps (*n* = 444). Across both years, 1,236 samples were assigned individual multi-locus genotypes to 347 black bears (186 males, 161 females). Of these, 107 individuals were detected in both years.

APPENDIX 4. AIC TABLES

Table A 4. Single-session SECR models for male black bears in southwestern Alberta in 2013 ranked by corrected Akaike's Information Criterion (AICc). We used a hazard half-normal detection function for all models.

Model	Model Number	K[1]	LL[2]	AICc[3]	ΔAICc[4]	w_i[5]
Step 1 - Identify top observational model						
D~1 λ_0~traptype + bk + T[6] σ ~T	11	8	-1750.67	3518.58	0.00	1.00
D~1 λ_0~T + habitat + bk σ ~1	17	11	-1760.63	3545.58	27.00	0.00
D~1 λ_0~T σ ~T	7	5	-1769.32	3549.15	30.57	0.00
D~1 λ_0~GB[7] + T + traptype σ ~1	13	7	-1773.35	3561.65	43.08	0.00
D~1 λ_0~GB + T σ ~1	12	5	-1775.64	3561.79	43.21	0.00
D~1 λ_0~T + habitat σ ~GB	14	11	-1770.97	3566.26	47.68	0.00
D~1 λ_0~T σ ~1	6	4	-1780.77	3569.87	51.29	0.00
D~1 λ_0~1 σ ~T	8	4	-1815.44	3639.22	120.64	0.00
D~1 λ_0~traptype + bk σ ~GB	15	7	-1817.39	3649.72	131.15	0.00
D~1 λ_0~traptype + bk σ ~GB + traptype	16	9	-1815.80	3651.16	132.58	0.00
D~1 λ_0~traptype + bk σ ~1	10	6	-1821.53	3655.77	137.20	0.00
D~1 λ_0~bk σ ~1	2	4	-1824.23	3656.79	138.21	0.00
D~1 λ_0~traptype + bk σ ~traptype	9	8	-1820.00	3657.24	138.66	0.00
D~1 λ_0~traptype + habitat + bk σ ~1	18	12	-1817.28	3661.32	142.75	0.00
D~1 λ_0~1 σ ~traptype	4	5	-1831.67	3673.83	155.26	0.00
D~1 λ_0~traptype σ ~1	3	5	-1831.78	3674.05	155.48	0.00
D~1 λ_0~traptype σ ~traptype	5	7	-1829.97	3674.88	156.31	0.00
D~1 λ_0~1 σ ~1	1	3	-1834.65	3675.49	156.92	0.00
Step 2 - Identify top model with density covariates						
D~tenure λ_0~traptype + bk σ~traptype	2	10	-1814.33	3650.57	0.00	0.69
D~hunt λ_0~traptype + bk σ~traptype	3	9	-1817.15	3653.86	3.29	0.13
D~tertiary rd λ_0~traptype + bk σ~traptype	4	9	-1817.26	3654.08	3.51	0.12
D~fire λ_0~traptype + bk σ~traptype	1	9	-1819.41	3658.38	7.81	0.01
D~ndvi λ_0~traptype + bk σ~traptype	7	9	-1819.66	3658.87	8.30	0.01

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[1] K = number of model parameters

[2] LL = log likelihood

[3] AICc = Akaike information criterion corrected for small sample sizes

[4] ΔAICc = difference in AICc value from top-performing model

[5] w_i = model weight

[6] T = linear time trend

[7] GB = grizzly bear detection in previous occasion

D~rddens λ_0~traptype + bk σ~traptype	8	9	-1819.80	3659.16	8.59	0.01
D~water λ_0~traptype + bk σ~traptype	6	9	-1819.93	3659.41	8.84	0.01
D~canopy λ_0~traptype + bk σ~traptype	5	9	-1819.99	3659.54	8.97	0.01

Table A 5. Single-session SECR models for male black bears in southwestern Alberta in 2014 ranked by corrected Akaike's Information Criterion (AICc). We used a hazard half-normal detection function for all models.

Model	Model Number	K[1]	LL[2]	AICc[3]	ΔAICc[4]	w_i[5]
Step 1: Identify top observational model						
D~1 λ_0~traptype + bk + T[6] σ ~T	11	8	-1710.17	3437.61	0.00	0.81
D~1 λ_0~T σ ~1	6	4	-1716.95	3442.24	4.63	0.08
D~1 λ_0~GB[7] + T σ ~1	12	5	-1716.60	3443.71	6.11	0.04
D~1 λ_0~T σ ~T	7	5	-1716.66	3443.84	6.24	0.04
D~1 λ_0~T + habitat + bk σ ~1	17	11	-1710.26	3444.92	7.31	0.02
D~1 λ_0~GB + T + traptype σ ~1	13	7	-1715.72	3446.42	8.82	0.01
D~1 λ_0~T + habitat σ ~GB	14	11	-1715.27	3454.94	17.34	0.00
D~1 λ_0~1 σ ~T	8	4	-1732.39	3473.13	35.53	0.00
D~1 λ_0~traptype + bk σ ~traptype	9	8	-1767.13	3551.53	113.92	0.00
D~1 λ_0~traptype σ ~traptype	5	7	-1768.90	3552.78	115.18	0.00
D~1 λ_0~traptype + bk σ ~GB + traptype	16	9	-1766.90	3553.41	115.80	0.00
D~1 λ_0~bk σ ~1	2	4	-1779.64	3567.62	130.01	0.00
D~1 λ_0~1 σ ~traptype	4	5	-1779.43	3569.37	131.77	0.00
D~1 lambda0~traptype + bk sigma~1	10	6	-1778.35	3569.44	131.83	0.00
D~1 lambda0~traptype + bk sigma~GB	15	7	-1777.81	3570.60	132.99	0.00
D~1 lambda0~1 sigma~1	1	3	-1782.23	3570.65	133.05	0.00
D~1 lambda0~traptype sigma~1	3	5	-1780.88	3572.29	134.68	0.00
D~1 lambda0~traptype + habitat + bk sigma~1	18	12	-1776.80	3580.45	142.85	0.00
Step 2: Identify top model with density covariates						
D~tenure λ_0~traptype + bk σ~traptype	2	10	-1756.12	3534.23	0.00	0.89
D~tertiary rd λ_0~traptype + bk σ~traptype	4	9	-1759.36	3538.32	4.09	0.11
D~hunt λ_0~traptype + bk σ~traptype	3	9	-1762.35	3544.31	10.08	0.00
D~fire λ_0~traptype + bk σ~traptype	1	9	-1764.66	3548.93	14.71	0.00
D~rddens λ_0~traptype + bk σ~traptype	8	9	-1766.10	3551.81	17.59	0.00
D~canopy λ_0~traptype + bk σ~traptype	5	9	-1766.13	3551.88	17.65	0.00

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[1] K = number of model parameters

[2] LL = log likelihood

[3] AICc = Akaike information criterion corrected for small sample sizes

[4] ΔAICc = difference in AICc value from top-performing model

[5] w_i = model weight

[6] T = linear time trend

[7] GB = grizzly bear detection in previous occasion

D~ndvi λ_0~traptype + bk σ~traptype	7	9	-1766.65	3552.91	18.69	0.00
D~water λ_0~traptype + bk σ~traptype	6	9	-1767.04	3553.70	19.47	0.00

Table A 6. Single-session SECR models for female black bears in southwestern Alberta in 2013 and 2014, ranked by corrected Akaike's Information Criterion (AICc). We used a hazard half-normal detection function for all models.

Model Number	Model	K[1]	LL[2]	AICc[3]	ΔAICc[4]	w_i[5]
	Step 1: Identify top observational model					
16	D~1 λ_0~traptype + bk σ ~GB[6] + traptype	9	-948.09	1916.17	0.00	0.83
9	D~1 λ_0~traptype + bk σ ~traptype	8	-950.88	1919.33	3.17	0.17
5	D~1 λ_0~traptype σ ~traptype	7	-961.73	1938.67	22.51	0.00
15	D~1 λ_0~traptype + bk σ ~GB	7	-975.12	1965.44	49.28	0.00
2	D~1 λ_0~bk σ ~1	4	-978.97	1966.36	50.20	0.00
10	D~1 λ_0~traptype + bk σ ~1	6	-977.88	1968.65	52.49	0.00
4	D~1 λ_0~1 σ ~traptype	5	-984.09	1978.81	62.65	0.00
17	D~1 λ_0~T[7] + habitat + bk σ ~1	11	-978.11	1981.20	65.03	0.00
18	D~1 λ_0~traptype + habitat + bk σ ~1	12	-977.09	1981.72	65.56	0.00
12	D~1 λ_0~GB + T σ ~1	5	-989.92	1990.46	74.30	0.00
13	D~1 λ_0~GB + T + traptype σ ~1	7	-988.89	1992.98	76.81	0.00
7	D~1 λ_0~T σ ~T	5	-991.56	1993.75	77.59	0.00
1	D~1 λ_0~1 σ ~1	3	-995.19	1996.63	80.46	0.00
6	D~1 λ_0~T σ ~1	4	-995.04	1998.50	82.33	0.00
3	D~1 λ_0~traptype σ ~1	5	-994.12	1998.86	82.70	0.00
14	D~1 λ_0~T + habitat σ ~GB	11	-990.55	2006.06	89.90	0.00
8	D~1 λ_0~1 σ ~T	4	-1000.47	2009.36	93.19	0.00
11	D~1 λ_0~traptype + bk + T σ ~T	8	-1000.84	2019.24	103.07	0.00
	Step 2: Identify top model with density covariates					
3	D~hunt λ_0~traptype + bk σ ~traptype	9	-940.50	1900.97	0.00	0.61
2	D~tenure λ_0~traptype + bk σ ~traptype	10	-939.72	1901.89	0.92	0.39
1	D~fire λ_0~traptype + bk σ ~traptype	9	-946.04	1912.06	11.09	0.00

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[1] K = number of model parameters

[2] LL = log likelihood

[3] AICc = Akaike information criterion corrected for small sample sizes

[4] ΔAICc = difference in AICc value from top-performing model

[5] w_i = model weight

[6] GB = grizzly bear detection in previous occasion

[7] T = linear time trend

8	D~rddens λ_0~traptype + bk σ ~traptype	9	-948.53	1917.05	16.07	0.00
7	D~ndvi λ_0~traptype + bk σ ~traptype	9	-949.37	1918.71	17.74	0.00
4	D~tertiary rd λ_0~traptype + bk σ ~traptype	9	-949.68	1919.35	18.37	0.00
6	D~water λ_0~traptype + bk σ ~traptype	9	-950.53	1921.04	20.06	0.00
5	D~canopy λ_0~traptype + bk σ ~traptype	9	-950.53	1921.04	20.07	0.00

Table A 7. Single-session SECR models for female black bears in southwestern Alberta in 2014, ranked by corrected Akaike's Information Criterion (AICc). We used a hazard half-normal detection function for all models.

Model Number	Model	K[1]	LL[2]	AICc[3]	ΔAICc[4]	w_i[5]
	Step 1: Identify top observational model					
9	D~1 λ_0~traptype + bk σ ~traptype	8	-950.88	1919.33	0.00	1.00
5	D~1 λ_0~traptype σ ~traptype	7	-961.73	1938.67	19.34	0.00
16	D~1 λ_0~traptype + bk σ ~GB[6] + traptype	9	-964.72	1949.44	30.11	0.00
17	D~1 λ_0~T[7] + habitat + bk σ ~1	11	-965.65	1956.29	36.96	0.00
2	D~1 λ_0~bk σ ~1	4	-974.34	1957.10	37.77	0.00
11	D~1 λ_0~traptype + bk + T σ ~T	8	-969.79	1957.16	37.83	0.00
18	D~1 λ_0~traptype + habitat + bk σ ~1	12	-965.43	1958.45	39.12	0.00
10	D~1 λ_0~traptype + bk σ ~1	6	-973.56	1960.02	40.69	0.00
15	D~1 λ_0~traptype + bk σ ~GB	7	-973.53	1962.28	42.95	0.00
7	D~1 λ_0~T σ ~T	5	-990.69	1992.02	72.69	0.00
1	D~1 λ_0~1 σ ~1	3	-993.48	1993.22	73.88	0.00
14	D~1 λ_0~T + habitat σ ~GB	11	-984.98	1994.97	75.63	0.00
6	D~1 λ_0~T σ ~1	4	-993.30	1995.02	75.69	0.00
8	D~1 λ_0~1 σ ~T	4	-993.47	1995.36	76.02	0.00
4	D~1 λ_0~1 σ ~traptype	5	-992.44	1995.51	76.18	0.00
3	D~1 λ_0~traptype σ ~1	5	-992.82	1996.29	76.95	0.00
12	D~1 λ_0~GB + T σ ~1	5	-993.21	1997.06	77.73	0.00
13	D~1 λ_0~GB + T + traptype σ ~1	7	-992.54	2000.30	80.97	0.00
	Step 2: Identify top model with density covariates					
2	D~tenure λ_0~traptype + bk σ ~traptype	10	-956.16	1934.79	0.00	0.99
4	D~tertiary rd λ_0~traptype + bk σ ~traptype	9	-961.90	1943.79	9.00	0.01
1	D~fire λ_0~traptype + bk σ ~traptype	9	-963.16	1946.31	11.52	0.00
8	D~rddens λ_0~traptype + bk σ ~traptype	9	-963.26	1946.51	11.72	0.00
6	D~water λ_0~traptype + bk σ ~traptype	9	-963.49	1946.99	12.19	0.00
3	D~hunt λ_0~traptype + bk σ ~traptype	9	-963.90	1947.80	13.00	0.00

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[1] K = number of model parameters
[2] LL = log likelihood
[3] AICc = Akaike information criterion corrected for small sample sizes
[4] ΔAICc = difference in AICc value from top-performing model
[5] w_i = model weight
[6] GB = grizzly bear detection in previous occasion
[7] T = linear time trend

7	D~ndvi λ_0~traptype + bk σ ~traptype	9	-964.04	1948.08	13.28	0.00
5	D~canopy λ_0~traptype + bk σ ~traptype	9	-964.04	1948.09	13.29	0.00

Table A 8. RSF models comparing presence data versus all rub object for male black bears in southwestern Alberta, ranked by AIC values. We compared use/availability data from non-invasive genetic data collected in 2013 and 2014.

Model Number	Model	df[1]	LL[2]	AIC[3]	ΔAIC[4]	w_i[5]
2	fire + ndvi + shrub + tenure	6	-783.48	1579.02	0.00	0.51
15	fire + ndvi + shrub + tenure + GB IOU	7	-783.30	1580.69	1.68	0.22
1	water + tertiary rd + canopy + tenure	6	-784.84	1581.74	2.73	0.13
8	elevation + primary rd + deciduous + tenure	6	-785.34	1582.74	3.72	0.08
9	elevation^2 + primary rd + shrub + tenure	6	-786.07	1584.21	5.19	0.04
6	elevation + primary rd + house + canopy	5	-787.73	1585.50	6.49	0.02
11	fire + primary rd + deciduous + house	5	-788.58	1587.20	8.19	0.01
12	fire + primary rd + agriculture + house	5	-790.04	1590.12	11.11	0.00
3	TRI + primary rd + house + canopy	5	-791.11	1592.26	13.25	0.00
13	primary rd * agriculture + house	5	-793.47	1596.99	17.97	0.00
5	water + fire + canopy + tertiary rd	5	-794.14	1598.33	19.32	0.00
10	fire + tertiary rd + shrub + house	5	-795.90	1601.84	22.82	0.00
7	ndvi^2 + primary/secondary rd + house + canopy^2	5	-795.95	1601.94	22.93	0.00
Null	~1	1	-800.42	1602.85	23.83	0.00
4	TRI + primary/secondary rd + house + canopy^2	5	-796.98	1604.02	25.00	0.00
14	tertiary rd * agriculture + water	5	-798.98	1608.01	29.00	0.00

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[1] df = degrees of freedom

[2] LL = log likelihood

[3] AIC = Akaike information criterion

[4] ΔAIC = difference in AIC value from top-performing model

[5] w_i = model weight

Table A 9. RSF models comparing presence data versus all rub object for female black bears in southwestern Alberta, ranked by AIC values. We compared use/availability data from non-invasive genetic data collected in 2013 and 2014.

Model Number	Model	df[1]	LL[2]	AIC[3]	ΔAIC[4]	w_i[5]
15	fire + ndvi + shrub + tenure + GB IOU	7	-671.74	1357.58	0.00	0.84
1	water + tertiary rd + canopy + tenure	6	-675.07	1362.20	4.62	0.08
8	elevation + primary rd + deciduous + tenure	6	-675.79	1363.64	6.06	0.04
2	fire + ndvi + shrub + tenure	6	-676.34	1364.74	7.16	0.02
9	elevation^2 + primary rd + shrub + tenure	6	-677.12	1366.31	8.72	0.01
12	fire + primary rd + agriculture + house	5	-681.25	1372.56	14.97	0.00
3	TRI + primary rd + house + canopy	5	-682.30	1374.65	17.07	0.00
13	primary rd * agriculture + house	5	-683.04	1376.12	18.54	0.00
11	fire + primary rd + deciduous + house	5	-683.75	1377.55	19.96	0.00
6	elevation + primary rd + house + canopy	5	-684.52	1379.09	21.51	0.00
4	TRI + primary/secondary rd + house + canopy^2	5	-686.24	1382.52	24.94	0.00
10	fire + tertiary rd + shrub + house	5	-686.36	1382.77	25.18	0.00
14	tertiary rd * agriculture + water	5	-687.84	1385.72	28.14	0.00
5	water + fire + canopy + tertiary rd	5	-688.58	1387.20	29.62	0.00
7	ndvi^2 + primary/secondary rd + house + canopy^2	5	-689.60	1389.24	31.66	0.00
Null	~1	1	-697.66	1397.32	39.73	0.00

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[1] df = degrees of freedom

[2] LL = log likelihood

[3] AIC = Akaike information criterion

[4] ΔAIC = difference in AIC value from top-performing model

[5] w_i = model weight