Spatial predation risk for elk (*Cervus elaphus*) in a multi-predator community on the Rocky

Mountain East Slopes, Alberta

by

Kara Marisa MacAulay

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Abstract

There is evidence that prey can perceive the risk of predation, and may alter habitat selection, increase vigilance, alter social grouping, and reduce migratory behaviour in response. Previous approaches that quantify predation risk have focused on measuring the different phases of predation such as predator space use or predator kill sites; data which can be costly to accumulate and often results in low sample sizes. We used a non-invasive alternative using predator scats to assess summer predation risk to different migratory herds segments of the partially migratory elk (*Cervus elaphus*) herd in Ya Ha Tinda, Alberta, Canada. Elk predation risk was estimated by combining the summer distribution of bears, wolves, coyotes and cougars (*Ursus arctos*/*U. americanus*, *Canis lupus, C. latrans* and *Puma concolor*, n = 476) predicted from scat-based resource selection functions and presence of elk in the scat. Scat contents were analysed using macroscopic and DNA analysis methods to detect the presence of elk in scats. Multivariate analysis revealed high overlap in scat contents across predators with bear scats containing more vegetation and coyote scats containing more small mammals. Elk occurred more frequently in wolf and bear scats found where resident elk summered near the Ya Ha Tinda and elk occurrence was associated with areas with high herbaceous forage biomass and amount of open habitat. Elk occurred more frequently in cougar scats found on the range of the eastern migrants, where forest edge density was high. Overall, elk who migrated westward into Banff National Park were exposed to lower wolf, cougar and bear predation risk than resident elk and eastern migrants.

Preface

This thesis is an original work by Kara M. MacAulay. Field data were collected during a PhD project (J. Berg and E. Merrill, 2013-2019), a MSc project (E. Spilker and E. Merrill, 2014-2017), and during this MSc project (K. MacAulay and E. Merrill, 2016-2019). Field methods were in accordance with the Canadian Council on Animal Care Guidelines and approved by the University of Alberta Biosciences Animal Care and Use Committee (Protocol # AUP00000624).

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Acknowledgements

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CHAPTER 1 — Perspectives on predation on elk (*Cervus elaphus*) at Ya Ha Tinda, Alberta

Partial migrations are common among large herbivore species and are believed to be driven by a desire to access high quality forage (Berger 2004) and to reduce predation during summer months (Fryxell and Sinclair 1988). Declines in migratory behaviour in the last century have been observed throughout ungulate populations in North America, attributed often to differential hunting pressure (Smith and Robbins 1994) and habitat fragmentation along migration routes caused by human land-use (Berger 2004, Sawyer et al. 2005). The Ya Ha Tinda elk herd (*Cervus elaphus*), once one of Canada's largest migratory elk herd, has experienced a 70% population decline since the mid 1990s with shifts in the number elk following different migratory strategies (Berg et al. 2016, Hebblewhite et al. 2018). Historically, nearly the entire elk herd migrated from their winter range, a rough fescue (*Festuca campestris*) mountain grassland, into Banff National Park in the summer, a distance of about 25–50 km (Morgantini and Hudson 1989). While there have always been resident elk who summer on the winter range, the migrant-to-resident ratio has steeply declined from 12:1 in 1987 to 3:1 in 2004 (Hebblewhite et al. 2006), and the ratio is currently approaching 1:1 (Berg et al. 2016). Since 2011, we have observed a shift in migratory behaviour where nearly a quarter of the elk herd (n ~ 111; Killeen et al. 2015) are migrating east of their winter range to lands dominated by resource extraction from oil, gas, and forestry (Berg et al. 2016). Half of the herd (n ~185), does not migrate, and the last quarter (n ~ 111) migrates west of Ya Ha Tinda, into either the Red Deer River, Clearwater River, Panther River or Dormer River drainages (Killeen et al. 2015).

Reasons for the decline in elk and shift in migratory strategies have been the subject of numerous studies since the 2000s. Hebblewhite et al. (2006) took a retrospective approach to examine several long-term changes elk including harvest and translocations, and habitat

24 management including prescribed burns, winter range enhancement, and wolf (*Canis lupus*)

25 recovery, and their effect on the migrant-to-resident ratio from 1972-2005. The authors found

26 that prescribed burns, the number of horses (as an elk competitor), and elk harvest could not

27 explain an increase in migrants. The differences between migrant and resident ranges with

28 respect to winter range enhancements (*i.e.* elk accessing hay fed to Parks Canada-owned horses),

29 elk translocations, and wolf recolonization all predicted an increase in migrant populations and

30 may be the reason for changes in migratory behaviours.

31   Intensive telemetry studies by Hebblewhite and Merrill (2009) found that by migrating to

32 high elevation areas in Banff National Park, elk were exposed to lower wolf predation risk and

33 higher quality forage, resulting in higher pregnancy rates and heavier calves compared to

34 residents. By not migrating in summer, residents were exposed to lower forage quality but

35 higher biomass and reduced exposure to wolf predation risk. This occurred because elk used

36 areas of high human activity that wolves avoided during the day but not at night (Hebblewhite

37 and Merrill 2007, Hebblewhite et al. 2008). Hebblewhite and Merrill (2011) concluded that the

38 two migratory strategies resulted in equal demographic fitness overall, which allowed elk to

39 maintain partial migration by balancing forage-predation trade-offs. Robinson et al. (2010)

40 found migrant and resident elk were not spatially segregated on their winter range but behaved

41 differently in their response to humans. Resident elk were less vigilant in response to humans

42 because they were habituated to human activity, and as a result, they were better able to

43 coordinate vigilance and feeding (*i.e.* multitasking) except in areas with high wolf risk (Robinson

44 and Merrill 2013). In contrast, migrant elk had higher overall vigilance because they responded

45 to the presence of humans and wolf predation risk (Robinson and Merrill 2013). These

46   differences were likely to have foraging consequences only when elk were encounter-limited in

47   feeding such as during periods of deep snow (Robinson and Merrill 2012).

48   Predation risk from wolves on the Ya Ha Tinda elk herd has been the focus of these past

49   studies since wolf recolonization in the mid-1980s. Wolves were extirpated from the Rocky

50   Mountains during the 1900s through bounties and wide-spread trapping and poisoning but

51   recolonized the area and were considered established by the mid 1980s (Paquet et al. 1996).

52   Morgantini (1988) recorded very little wolf predation on the Ya Ha Tinda elk herd in the late

53   1970s. The lack of predation on elk by grizzly bears (*Ursus arctos*) and black bears (*U.*

54   *americanus*) at this time was also attributed to low densities of bears and high use of open

55   habitats by elk as an anti-predator strategy (Morgantini 1988). However, Knopff et al. (2014)

56   reported that cougars (*Puma concolor*) have been expanding their ranges in northern and eastern

57   Alberta since the 1990s, and there is evidence of a grizzly bear population increase (4% per year)

58   since 2007 in southern Alberta (Morehouse and Boyce 2016). Additionally, grizzly bear densities

59   have been documented to be 2.4 times higher within Banff National Park (12.4 $\pm$ 1.5

60   individuals/1000 km^2; Whittington and Sawaya 2015, Whittington et al. 2018) than on provincial

61   land (5.25 individuals/1000 km^2; Government of Alberta 2016). Data from adult and calf elk kill

62   sites at the Ya Ha Tinda collected from 2002 to 2016 where the cause of death was known,

63   indicates that bears are responsible for 25% of adult and 74% of calf kills, and cougars for 8-9%

64   of adult kills and calf kills (Martin et al. 2017). This has led to a broader appreciation of

65   predators other than wolves that may be contributing to the changes in elk migratory strategies.

66   Due to the costs of multi-predator telemetry studies, Spilker (2018) initiated a scat-based

67   study to spatially quantify the distributions of four large predators over the study area. He used

68   scat-detection dogs to sample predator scats from wolves, bears, cougars and coyotes (*Canis*

*latran*s) in 2014-2015 along sampling transects allocated within 57 5x5 km grid cells. These areas were sampled alongside remote cameras designed to measure carnivore occupancy (Steenweg et al. 2016). He tested the detection abilities of the 2 dog-handler teams in blind trails under typical field conditions and both teams detected > 94% of the scats in the trial. He compared landscape characteristics at scat locations to random locations along the transect within a cell to develop resource selection functions (RSF; Lele et al. 2013) for each predator and found correspondence to predictions from earlier RSFs of wolves (Hebblewhite and Merrill 2007) and grizzly bears (Nielsen et al. 2002) based on telemetry. Overall, ursids and canids selected for low-use, non-motorized linear features, while cougars did not show a similar avoidance of human activity, instead selecting for areas with low conifer cover and high proportion of edge habitat (Spilker 2018). Risk from bears and wolves was highest in Banff National Park, while cougar risk was highest in the eastern portion of the study area, suggesting the differential risk from predators may be contributing to the shifts in elk migration.

In this thesis, we expanded on Spilker's (2018) work by quantifying the contents of scats from these same four predators to determine whether there is differential predation risk to the three migrant segments of the Ya Ha Tinda elk herd based on what predators are eating. Using a univariate approach, we compared the frequency of occurrence and mean proportion of prey items in scats within predators; we then assessed the overlap in prey items in scats among predators using a multivariate approach. Next, we addressed the broad scale and habitat specific factors that influence the probability of elk presence in scats, and predicted elk presence in scats across the study area. Finally, we combined maps of scat-based resource selection functions (*i.e.* predator space use) and predator scat contents (n = 476) to map predator-specific predation for the Ya Ha Tinda elk herd during summer.

CHAPTER 2 — Spatial predation risk for elk (*Cervus elaphus*) in a multi-predator community

INTRODUCTION

Large predators play an important role in the trophic structure of ecosystems, and this awareness has led to a greater emphasis on their conservation and management (Estes et al. 2011). Predation can shape prey communities, and ecologists have long been interested in factors influencing predator-prey interactions in order to understand potential community-level impacts (Hairston et al. 1960, Schmitz et al. 2000). Not only can prey be affected directly via predation, there is also evidence prey can perceive the risk of predation and alter their behaviour in response (Laundré et al. 2001, Tolon et al. 2009). Indirect prey responses to predation risk can alter encounter rates and attack success given an encounter (Lima and Dill 1990), which may come at a cost to prey fitness (Ruxton and Lima 1997, Creel et al. 2007). For example, large herbivores may respond to predation risk by altering habitat selection and foraging patterns, increasing vigilance and grouping behaviour and changing migratory patterns (Fortin et al. 2004, Hebblewhite et al. 2006, Christianson and Creel 2010, Lesmerises et al. 2017). As a result, herbivore prey are often faced with making trade-offs in pursuing foraging opportunities while avoiding areas of high predation risk (Creel et al. 2005, Sih 2005, Hebblewhite and Merrill 2009, Visccher and Merrill 2017).

Large predators are expected to select habitats where prey are abundant to reduce search times and where prey are vulnerable to increase attack success (Sih 2005). McPhee et al. (2012) reported wolves (*Canis lupus*) in Alberta hunted in areas with high ungulate prey abundance but killed prey most frequently in areas near forest edges, where they inferred prey were more

detectable and therefore vulnerable. In Yellowstone National Park, wolf kill sites compared to random locations were disproportionately located along hard habitat edges or abrupt changes in vegetation cover, which Bergman et al. (2006) suggested these areas impeded elk movement, increasing vulnerability. Kill sites of cougars (*Puma concolor*), a stalk and ambush predator, also occurred in structurally complex habitats, such as steep slopes, dense hiding cover, and areas near habitat edge (Kunkel et al. 1999; Atwood et al. 2007; Elbroch et al. 2013). Prey may be easier to catch if these features allow cougars to hide while stalking (Hopcraft et al. 2005). At the same time, if predators avoid specific areas this can create prey refuges across heterogeneous landscapes (Schmidt and Kuijper 2015). Deer and elk (*Cervus elaphus*) have been observed escaping predation by moving into deep water, which slows the movement of wolves (Mech et al. 2015); however, shallow water also hinders their escape and may increase their vulnerability (Kauffman et al. 2007). There is also accumulating evidence that human activity mediates refuges for ungulate prey because predators like wolves and grizzly bears (*Ursus arctos*) avoid humans (Gibeau et al. 2002, Hebblewhite et al. 2005b, Musiani et al. 2010). Berger (2007) reported that female moose (*Alces alces*) in Grand Teton National Park calved near roads with high human use because grizzly bears avoided these areas. Shannon et al. (2014) found a reduction in vigilance and social grouping in elk and pronghorn (*Antilocapra americana*) near roads in Wyoming, which may also reflect that humans provide a refuge from predation in systems with major predation on ungulates.

Several approaches have been used to quantify the spatial risk to prey from a predator species. One of the most common approaches assumes predation risk is proportional to a predator's predicted space use because a predator has to be present and typically predator distribution is the most readily available data (Laundré et al. 2001, Theuerkauf and Rouys 2008,

138 Thaker et al. 2011). For example, Kristan and Boarman (2003) were among the first to use a

139 resource selection function (RSF) to quantify and map areas of high selection value by ravens

140 (*Corvus corax*) as risky areas to desert tortoises (*Gopherus agassizii*). Hebblewhite et al. (2005)

141 illustrated the use of RSFs to quantify risk to elk from wolves, refining the approach to include a

142 weighting factor for pack size (Hebblewhite and Merrill 2007). This approach for a single

143 species has been extended to multi-predator systems. Gustine et al. (2006) considered wolf and

144 grizzly bear RSFs independently as metrics of risk in their calf survival models whereas

145 Duquette et al. (2015) considered risk to white-tailed deer as the summation of the values of

146 individual resource selection probability functions (RSPF) for four predators. Alternatively,

147 intensity of use based on telemetry locations rather than selection has been used to indicate risk

148 to elk at the level of wolf packs in Alberta (Robinson et al. 2010) and to moose in Sweden

149 (Nicholson et al. 2014). Regardless of the approach, predator space use reflects primarily the risk

150 of encounters and does not correspond to attack success resulting in mortality (Lima and Dill

151 1990; Hebblewhite et al. 2005a).. To incorporate a successful encounter with the prey leading to

152 a kill, others have compared characteristics of prey kill sites to random points (Kauffman et al.

153 2007, McPhee et al. 2012). Kill sites are most commonly found by following predator tracks

154 (Knopff et al. 2010, Bojarska et al. 2017) or using clusters of GPS radio-collar locations, which

155 can be identified statistically and visited in the field (Anderson and Lindzey 2003, Webb et al.

156 2008, Knopff et al. 2009). A disadvantage to using kill site data is that results are often biased

157 towards large prey that can be readily detected in the field or by the extended time spent at a

158 cluster (Jedrzejewski et al. 2002, Webb et al. 2008, Bacon et al. 2011). A more economical

159 alternative for estimating spatial predation risk that also reflects mortality across a landscape is

160 analyzing the contents of predator scats. Prey contents can then be modelled as a function of

161   landscape features that may reflect prey presence and variables that are predicted to impact elk

162   vulnerability towards predators. The advantage of this approach is that it provides a relatively

163   cost-effective approach to collecting a large number of samples over a large spatial extent in a

164   relatively short period of time, especially when using scat-detection dogs (Wasser et al. 2004,

165   Spilker 2018). In addition to reflecting a kill, analyzing scats allows for detection of a full suite

166   of prey including small mammals and neonate ungulates.

167   In this chapter, we combined maps of scat-based resource selection functions and scat

168   contents (n = 476) from macroscopic and DNA analyses to map predator-specific predation that

169   reflects actual mortality. Using this approach, we assessed the evidence for broad-scale spatial

170   structure in multi-predator risk on the Ya Ha Tinda elk herd. The Ya Ha Tinda elk population is

171   a partially migratory elk herd that has declined by 70% over the past several decades.

172   Historically, over 90% of the population migrated ~50 km west from the Ya Ha Tinda winter

173   range into Banff National Park. The migrant to resident ratio has decreased in the last 2 decades

174   from 3:1 to 1:1 (Hebblewhite et al. 2006, Berg et al. 2016), and more elk are now migrating

175   eastward onto forest industrial lands, which is hypothesized to be driven by predation (Berg et al.

176   2016). In previous studies at the Ya Ha Tinda, it was shown that western migrant elk had higher

177   quality forage resulting in higher pregnancy rates and heavier calves compared to residents.

178   Resident elk that did not migrate from the Ya Ha Tinda in summer were able to minimize

179   exposure to predation risk by exploiting a human-caused predation refuge as wolves avoided

180   human activity (Hebblewhite and Merrill 2011). Despite these differences, adult elk between the

181   different migratory strategies had similar and declining population growth rates (Hebblewhite et

182   al. 2018). Recent data on calf mortality from 2013-2016 show that the eastern elk had higher calf

183   survival and calf:cow ratios compared to residents and western migrants (Berg 2019) consistent

184   with an increase in number of elk migrating east to summer (Killeen et al. 2015).

185   Previous predation studies that examined elk exposure to predation risk at Ya Ha Tinda

186   focused on wolves and used abundance-weighted RSFs to quantify predation risk (Hebblewhite

187   and Merrill 2009). Recent research updated predation risk layers using locations of scats from

188   four major predators (wolves, coyotes, bears and cougars) to derive resource selection functions

189   as indicators of species-specific predation risk across a large portion of the elk summer range

190   (Spilker 2018). Here, we extended this work by using contents of scats to assess three questions.

191   First, we evaluated which predator was most likely to kill elk based on major prey items in the

192   scats. We used data from macroscopically analysed scats (n = 226) that identified the full suite of

193   prey in the scats (Cuicci et al. 1996, Bacon et al. 2011, Shores et al. 2015). In a univariate

194   approach, we compared the mean proportion and frequency of occurrence of different prey items

195   in scats between predators. Then, we assessed the overlap in prey items in scats among predators

196   using a multivariate statistical approach. Second, we addressed what environmental factors might

197   influence probability of elk being present in a predator scat. We analysed a larger sample (n =

198   476) of scats to detect the presence of elk DNA in the scat. We used a generalized linear

199   modelling (GLM) approach by predator species to assess hypotheses about the effects of habitat,

200   spatial location, and potential presence of other predators on occurrence of elk in the scat. Third,

201   we used the landscape factors we found influencing individual species from the GLM in a

202   canonical correspondence analysis (CCA) to determine where in environmental space scats of all

203   predators with a high proportion of elk fell compared to other ungulate prey.

204   Our focus was on the summer period to address elk predation risk in a multi-predator

205   system when migratory elk were on allopatric ranges. Overall, we expected wolf scats to have

the highest proportion of elk because wolves are known to be the largest source of mortality of tagged elk at Ya Ha Tinda (38% of known death causes; n=88). We also expected wolf scats to show the least spatial structure in scat composition because they prefer elk (Krawchuk 2014; Newsome et al. 2016) and as a coursing predator they have broad movements (Kunkel et al. 1999). We also expected elk would be found in wolf scats in steep and rugged terrain and areas with closed canopies where elk were reported to be more vulnerable (Kauffman et al. 2007, McPhee et al. 2012). Because bears are omnivores and consume large amounts of vegetation during the summer (Mattson et al. 1991, McLellan and Hovey 1995), we expected bear scats to have the least amount of ungulates overall, except for neonate elk because bears are efficient predators on neonates during a brief window in calving season (Barber-Meyer et al. 2008, Griffin et al. 2011, Berg et al. 2016). We expected elk to increase in bear scats in areas with high forage quality like recent burns or cutblocks (Sachro et al. 2005, Visscher and Merrill 2009) because elk and bears both select for high forage quality during early summer (Berg, in progress, Bastille-Rousseau et al. 2011). We expected elk contents in scats of cougars to be low because all but large-bodied males select smaller-bodied ungulates like deer (Kortello et al. 2007, Elbroch et al. 2013, Soria-Díaz et al. 2017). Cougars seem to hunt prey primarily along forested edges (Atwood et al. 2007, Elbroch et al. 2013), so we expected elk to be more abundant in cougar scats found near forest edges. Finally, we expected elk contents in scats of coyotes to be low because of their reliance on small mammals (Arjo et al. 2002) and because they are subordinate to wolves and cougars and rarely will gain access to a live elk kill (Berger and Gese 2007, Elbroch and Kusler 2018).

STUDY AREA

The 1425-km^2 study area is located along the eastern slopes of the Rocky Mountains in southern Alberta, approximately 60 km north of the Banff townsite (Figure 2.1). The area has short summers, with snow falling in spring and early fall (May-September). Summers from 2013-2016 were mild with an average daily temperature of 8˚C (ranging from -14˚C to 30˚C), and an average seasonal precipitation of 403 mm (Government of Alberta 2017). From October to April during the study period, temperature averaged -4˚C (ranging from -36˚C to 22˚C) and precipitation averaged 210 mm (Government of Alberta 2017).

The area has a strong east-west elevation gradient ranging from 1,343 m on the eastern edge to 3,018 m in the western portion. Vegetation cover is dominated by conifer forests (43%) comprised of Englemann spruce (*Picea engelmanii*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*). Grasslands, interspersed with herbaceous plants and shrubs comprised of *Salix* and *Betula* spp., cover 13% of the study area and aspen (*Populus tremuloides*) covers 2%. Burns since 1999 cover ~15% of the study area with the 2001 Dogrib burn being the largest (~11,000 ha). The remaining 1% of cover is water, with the Red Deer River as the dominant water body. High elevation (> 2,100 m) rocky areas cover 26% of the study area.

Approximately 34% of the study area is located within Banff National Park, 62% on provincial Crown land, and the remaining 4% is the Ya Ha Tinda Ranch. The Ya Ha Tinda Ranch is a Parks Canada working horse ranch and the winter range of the Ya Ha Tinda elk herd. The ranch itself is federally managed but wildlife management in the area falls within provincial jurisdiction. Resource extraction including timber harvest, oil and gas extraction, cattle grazing,

249 and human recreational activity including off-highway vehicles (OHV) on cut lines which follow

250 an east (high) to west gradient (low). Linear features density ranges from 2.32 km/km^2 in the

251 eastern portion of the study area to 0.28 km/km^2 in Banff National Park (AltaLIS, accessed

252 2017). While motorized activity is allowed on provincial Crown land, trail use in Banff National

253 Park is limited to hikers and horseback riders. The Ya Ha Tinda ranch prohibits OHV use but has

254 a dense network of trails (2.72 km/km^2) used by hikers and horseback riders (AltaLIS, accessed

255 2017).

256   The carnivore community is comprised of wolves, grizzly bears, black bears, cougars,

257 coyotes, and lynx (*Lynx canadensis*). Wolves were extirpated from Banff National Park in the

258 early 1900s (Gunson 1992), but have naturally recolonized since the mid-1980s. Wolves on

259 provincial lands were reduced by bounty and poisoning programs until the 1960s, but are now

260 relatively stable despite being trapped and hunted on provincial lands (Hebblewhite 2006).

261 Grizzly bears have been considered a threatened species under *Alberta's Wildlife Act* since 2010,

262 and densities on provincial lands from 2002-2014 were estimated at 4.79 to 5.25 bears per 1000

263 km^2 (Alberta Environment and Parks 2016). Densities within Banff National Park are ~2.4 times

264 higher (12.4 ± 1.5 individuals/1000 km^2; Whittington and Sawaya 2015; Whittington et al.

265 2018). Black bear densities were last estimated across Alberta in 1993, and reported as an

266 average of 49 bears per 1000 km^2 across the 5 wildlife management units (WMU) that

267 encompass the study area (Alberta Environment and Parks 2016*b*). Cougar density is estimated

268 to be approximately 30 cougars per 1000 km^2, in the eastern portion of the study area, and 15

269 cougars/1000 km^2 in the western portion (Alberta Environment and Sustainable Resource

270 Development 2012), and they have been expanding their range east over the last 2 decades

271 (Knopff et al. 2014b).

272   The ungulate community consists of elk, white-tailed deer, mule deer (*Odocoileus*

273   *hemionus*), moose, bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*)

274   and feral horses (*Equus caballus*). Deer numbers appeared to have increased in the last two

275   decades whereas elk numbers have declined from a high of 2000 individuals in the 1990s to a

276   current estimate of ~400 individuals (Berg et al. 2016). Feral horses are present year-round,

277   primarily in the eastern portion of the study area. Cattle (*Bos taurus*) are found in provincial

278   grazing leases east of Ya Ha Tinda in the summer and fall. Plains bison (*Bison bison bison*) were

279   reintroduced into Banff National Park in 2017, after the field collection of predator scats for this

280   study was completed.

281   Hunting is prohibited within Banff National Park boundaries, in the Ya Ha Tinda fenced

282   pastures, and along the Ya Ha Tinda wildlife sanctuary, a 365 m buffer on either side of Ya Ha

283   Tinda Ranch road from the Red Deer River Provincial Recreation Area to the Ya Ha Tinda

284   ranch. Antlered elk hunting is allowed in WMU 316, 318, 416, 417, 418, and 420 (east of Banff

285   National Park), while antlerless special licenses are permitted only in WMU 318. White-tailed

286   deer and bighorn sheep are hunted through a general open season, whereas moose and mule deer

287   are part of a special license draw (Government of Alberta 2017). Ungulate hunting season opens

288   in September, with archery season opening before rifle season. Indigenous peoples can hunt any

289   time of year with no tag restrictions. All carnivores except grizzly bears can be hunted in the 5

290   WMUs of the study area. Wolves and coyotes are hunted approximately 9 months of the year,

291   while black bears have two hunting seasons each year in April-May and September-October

292   (Government of Alberta 2017). Cougars can be hunted with the use of hounds and licenses are

293   available through a quota system.

METHODS

Scat Collection

294

295

296   We collected scats using trained scat-detection dogs from 15 May to 30 September in

297   2013, 1 July to 30 September in 2014-2015 and 31 July to 30 August 2016 to collect scats along

298   ~1,500 km of transects within 57 5x5 km^2 cells (Figure 2.1). The cells were placed

299   systematically across the area as part of a remote camera sampling grid designed to study

300   carnivore occupancy (Steenweg et al. 2016). Only 48 of the 57 cells were sampled in 2013 and

301   2014. Transect lengths ranged from 2 km to 26 km per cell with a median of 11.5 km and were

302   selected to sample vegetation communities in proportion to their availability in each cell (Spilker

303   2018). Approximately one-third of the transects were on human use trails, one-third on animal

304   trails, and the remaining transects were off trail. Sampling was not conducted during heavy rain,

305   strong winds (>30 km/hr), or when snow cover was >3 cm as these conditions affect detection by

306   the dogs. Scats (14%) were also collected opportunistically within the same area. When a scat

307   was located, the species, GPS location, and age post-defecation were recorded. Age of the scat

308   was ranked following Wasser et al. (2004) and very old scats were not included in the analysis as

309   they were assumed to be deposited before the study period. Scats were stored at -20°C until

310   analysis, autoclaved at 121°C for 60 minutes to kill biohazardous material, and washed through a

311   0.8 mm sieve with room temperature water to remove any debris.

312   We swabbed the mucous layer of ~20% of fresh scats in the field for a DNA sample and

313   DNA analysis was performed by Wildlife Genetics International (Nelson, BC, Canada) to

314   confirm accuracy of our field identification. Species identification was initially based on

315   published scat measurements and physical appearance (Thompson 1952, Weaver and Fritts 1979,

316   Elbroch 2003; Appendix 2.1), but guidelines for canids were modified as DNA results indicated

317   field identification accuracy in 2014-2015 was < 75% (Spilker 2018). We regressed the diameter

318   of coyote and fox scats confirmed by DNA analysis and found a 1.8 cm diameter discriminated

319   coyote from fox scats >75% of the time (see Spilker 2018 for details). We combined scats from

320   grizzly and black bears due to our low accuracy at discriminating between species in the field

321   (grizzly bear accuracy = 65.1%, black bear accuracy = 0%, see Spilker 2018).

322   *Scat Analysis*

323   Scats were analysed through two methods: (1) macroscopic scat analysis and (2) DNA of

324   hairs sampled from scats. Though macroscopic scat analysis can detect several species within

325   one scat it is time demanding, therefore we analysed a subset of the total scats spatially covering

326   the study area (n=226). We also analysed 492 scats using DNA analysis, which is time effective

327   but indicates only the primary species present. We analysed 65 scats by both approaches to

328   assess the detection of elk by DNA when it was dominant in the macroscopic scat analyses.

329   Because we were unsure of the best threshold value, we derived a Receiver Operator's

330   Characteristic curve and evaluated the area under the curve (AUC). We combined non-ungulate

331   animal prey items from both scat analysis methods into one "small mammal" category including

332   mammals from families *Cricetidae, Castoridae, Dipodidae, Erethizontidae*, *Leporidae,*

333   *Sciuridae* and *Soricidae*.

334   *Macroscopic Analysis of Scats*. A subset of scats (n=226) were analysed macroscopically, where

335   hair, bones, teeth and vegetation were identified contents to family or species level. We excluded

336   scats from the same species collected <100 m apart to ensure independent feeding events. We

337   further identified ungulate hair to either neonate (< 5 months) or juvenile and adult ($\geq$ 5 months).

338   We were unable to discriminate between juvenile hair and adult hair after the first moult

339   (~September) as they are microscopically indistinguishable (Kennedy and Carbyn 1981; Cuicci

340 et al. 1996). We selected hair by dividing the dried scat into 10 equal sections and removed two

341 random hairs per section for a total of 20 hairs. Hairs were wet mounted with 5% ethanol on a

342 glass slide and we used a compound light microscope to view medulla patterns. Cuticle scale

343 pattern imprints were made by pressing the hair into clear nail polish. The medulla pattern and

344 width, cuticle scale pattern, scale margin distance, length and colour of hair were recorded.

345 Dichotomous keys (Moore et al. 1974; Kennedy and Carbyn 1981; Jones et al. 2009), and

346 reference images (Adjornan and Kolenosky 1969) were used to identify species. Three observers

347 identifying hairs were trained and subject to "blind trials" on known hairs where they obtained a

348 > 80% (24/30) correct classification rate prior to hair analysis. Vegetation in scats was quantified

349 using a 3x3 cm grid, where the number of grid cells covered by each scat content category (hair,

350 bones and vegetation) was recorded (Cuicci et al. 1996). We reported animal scat contents for

351 each predator analysed with macroscopic hair analysis as the mean proportion of hairs across

352 scats. The difference between prey item proportions within a predator species were tested with a

353 Mann-Whitney U Test, with $\alpha = 0.05$. Differences in prey item proportions among predator

354 species were tested using Kruskal-Wallis test, with $\alpha = 0.05$, and a post-hoc pairwise Wilcoxon

355 Rank Sum test to determine *P*-values for each combination of predators with a Bonferroni

356 correction for multiple testing.

357 *DNA Analysis of Scats.* DNA analysis was performed by Wildlife Genetics International. Scat

358 samples (n=492) were prepared at the University of Alberta, under protocols recommended by

359 Wildlife Genetics International. Hairs randomly selected from scats (n~40) were soaked in a

360 3μL:100mL Sunlight soap solution for 24 hours. Hairs were then rinsed with hot water to remove

361 any remaining dirt and placed in a coin envelope and left 24 hours to dry. Polymerase chain

362 reaction (PCR) was used to amplify DNA of the prey species though only 70% of samples

363   (n=344) successfully amplified and produced reliable results. Hair samples were digested using a

364   mixture of QIAGEN ATL lysis buffer, proteinase K, and dithiolthreitol (DTT) and DNA was

365   extracted from hair shafts using QIAGEN's DNeasy Tissue kits (QIAGEN Inc., Valencia, CA).

366   Species identification was confirmed via a partial sequence analysis of a hypervariable region of

367   the mitochondrial 16S rRNA gene. Due to sequence competition during the PCR phase, this

368   analysis can only confidently report the most dominant prey species in the scat (*i.e.* the

369   proportion of DNA). For example, if there were 30 elk hairs and 10 squirrel hairs in a sample, it

370   is most likely the elk will dominate the PCR competition phase and amplify. Mixed samples

371   (samples where there was no "dominant" species, or approximately equal amounts of DNA from

372   each species), were re-run with ungulate-specific primers, and the probability of species

373   composition was determined.

374   We reported scat contents for each predator analysed by DNA analysis as the frequency

375   of occurrence within scats. The difference between frequency of occurrence in prey items within

376   and among predator species were tested across groups using a proportions z-test and between

377   groups using pairwise comparisons with a Bonferroni correction for multiple testing. To test the

378   differences in frequency of occurrence of prey in predator scats across space, we delineated the

379   study area into three strata corresponding to the summer ranges of the Ya Ha Tinda elk herd.

380   Stratification was based on visual inspection of telemetry locations of 66 collared female elk in

381   2013 – 2016 (Appendix 2.2) and included: west and south of Ya Ha Tinda, the Ya Ha Tinda

382   (YHT) ranch, and east on industrial forestry lands (Figure 2.1).

383   *Modelling elk presence in scats*

384   We addressed what environmental factors within a buffer around where the scat was

385   collected influenced the relative probability of elk being present in bear, cougar, coyote and wolf

386   scats using a generalized linear modelling approach. We used the presence of elk in a scat based

387   on data combined from the macroscopic and DNA scat analysis methods to increase the sample

388   size (n = 476) but not duplicating scats analysed by both scat analysis methods. For scats

389   analysed by both methods (n = 65), we used results from the macroscopic analysis. Rather than

390   comparing scats with elk to scats where elk was not detected, we compared scats containing elk

391   (1) to locations of a larger set of scats from the same predator species collected across the study

392   area as part of a companion study but not analysed for prey contents (Spilker 2018). This design

393   is similar to a use-availability design that predicts a relative probability of elk being present in

394   the predator scat given the set of landscapes factors where a scat was collected. The ratio of

395   scats containing elk (1) to random scats (0) varied among predator species from ~1:10 in bear (n

396   scats with elk present to random scats: 24:257) to 1:5 in wolf (75:363), 18:100 (42:226) in

397   coyote, and ~1:2 in cougar (16:27). We took this approach because we could not confirm an

398   absence of elk in either method of scat analysis (i.e., for elk presence-absence design). This

399   approach assumed that non-detection of elk in scats was random.

400   We used a model selection approach based on Akaike's Information Criterion corrected

401   for small sample size (AIC$_c$) to evaluate models. We used a conservative cut-off of ΔAIC$_c$ = 4 to

402   determine the model with the most support. In the event of competing top models (i.e. ΔAIC$_c$ <

403   4), we followed the principle of parsimony and removed variables where confidence intervals

404   overlapped zero.

405   To map spatial predation risk (PR$_{ij}$), we multiplied the relative probability of a predator-

406   specific scat being present (RSF$_{ij}$; Appendix 2.3) at location j by the relative probability of elk

407   being in scat (P_i) at location j as:

408 $$PR_{ij} = RSF_{ij} * P_i \qquad\qquad\qquad \text{Eq. 1}$$

409 where i refers to the species of the scat (bear, cougar, coyote or wolf) and j refers to a specific 30

410 x 30-m pixel. We used predator-specific, scat-based resource selection functions (RSF_i)

411 developed by Spilker (2018) for the same study area from 2014-2015 (Appendix 2.3) and used

412 the top spatial risk model from each predator species developed here to predict the relative

413 probability (P_i) of a scat containing elk.

414 *Landscape Covariates.* Environmental factors included land cover, terrain, anthropogenic

415 disturbances, forage indices, and metrics of elk resource use within a buffer and expressed as

416 either a percent or mean value within the buffer (Table 2.1) using the *raster* package in program

417 R (v. 3.5.1, Hijmans and van Etten 2012). Buffer sizes were species-specific and were

418 determined by information in the literature on the mean gut passage time and movement per day

419 for each predator species to best relate the scat location to the location of the kill site (Appendix

420 2.4). Before modelling, we tested for collinearity among variables where pairs of variables with r

421 > |0.6| were not included in the same model (Appendix 2.5). Landcover was derived from TM

422 Landsat imagery where 16 cover types were collapsed into 6 vegetation types including conifer,

423 deciduous-mixed, forest regenerated vegetation, herbaceous, shrub, and burned vegetation as

424 defined in Hebblewhite (2006). Burns included wild and prescribed fires ≤ 14 years old and were

425 mapped from the Banff Fire and Alberta Environment and Sustainable Resource Development

426 (ESRD) fire database. Cutblocks ≤ 20 years since harvest were mapped from Alberta

427 Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory. We used a landcover

428 mask that excluded closed vegetation and rock/ice to measure peak season vegetation greenness

429 based on Normalized Difference Vegetation Index (NDVI) that was derived from MODIS

430   imagery (27-28 July 2013-2016). We then weighted the yearly layers based on the number of

431   scats collected each year for each predator. Total new growth (g/m^2) of peak (1 August)

432   herbaceous biomass and of herbaceous plus shrub biomass was derived based on ground

433   sampling (Hebblewhite 2006, see Appendix 2.6.1). Topographic variables (elevation, slope, and

434   terrain ruggedness) were derived from a digital elevation model (DEM).   Anthropogenic

435   variables (*i.e.* roads, trails and cut lines) as well as perennial rivers and streams were measured as

436   linear density (km/km^2) within the buffer and the nearest linear distance (km) of a scat to water

437   or an anthropogenic feature using the Near tool in ArcMap (v. 10.3.1 Environmental Systems

438   Research Institute, Redlands, CA). Linear features were characterized based on their level and

439   type of motorized activity. Roads included paved and gravel roads built for resource extraction,

440   public traffic and for connecting campgrounds and campsites. Cut lines developed for forestry

441   access were also used by OHVs. Lastly, trails were restricted to non-motorized activity, used by

442   either hikers or horseback riders.

443   The effect of selection of other predators on scat contents of a predator was measured

444   with resource selection functions derived from scat locations of bears, cougars, coyotes and

445   wolves (Spilker 2018). To test the effect of high cumulative predator resource selection on elk

446   presence in scats, we used scat-based resource selection functions (RSF) developed by Spilker

447   (2018) for each of the four predators. We summed the 4 resource selection values (standardized

448   between 0 and 1) for each pixel as a metric for cumulative predation resource selection.

449   To indicate elk intensity of use across the study area as a model input, we developed an

450   elk resource utilization function (RUF, Marzluff et al. 2004) at the scale of a 30 x 30-m pixel

451   (Appendix 2.6). First, we created a population-level utilization distribution (UD) based on 6-hour

452   GPS relocations of 66 adult female elk ($\bar{x}$ = 359 relocations/individual) from 1 May to 30

453 September, using a 100% fixed kernel home range in Geospatial Modelling Environment (GME

454 version 0.7.4, http://www.spatialecology.com, accessed 10 Sept 2018). The UD bandwidth or

455 search radius was based on the plug-in method (Gitzen et al. 2006). Next, we used a GLM to

456 relate log-transformed UD values to environmental covariates hypothesized to affect elk

457 selection. We used the *ruf* package in program R (v. 2.13, Marzluff et al. 2004) to obtain RUF

458 coefficients. We ranked models using Akaike's Information Criterion (AIC), calculated from the

459 Matérn maximum log-likelihood estimate, with a cut-off of $\Delta AIC = 4$ to estimate the top model

460 (Burnham et al. 2011). To validate the RUF model, we compared the mean of predicted RUF

461 values at 1000 random elk telemetry points (*i.e.* a metric of use), to the mean RUF value at 1000

462 random points within the telemetry extent with a t-test. If the mean RUF values significantly

463 differed ($\alpha = 0.05$) between the use:random points, we would conclude support for our model.

464   Variable inputs in the RUF included herbaceous and total (herbaceous and shrub) forage

465 biomass, herbaceous land cover (Hebblewhite et al. 2008), distance to nearest forest edge,

466 burned vegetation (Hebblewhite 2006), wolf predation risk (Hebblewhite and Merrill 2007) and

467 grizzly bear predation risk (Nielsen et al. 2002). We used a wolf RSF as a metric for summer

468 wolf predation risk. The RSF was derived from locations of 14 VHF and 15 GPS collared wolves

469 (Hebblewhite and Merrill 2007), where land cover was updated to reflect changes (Smolko et al.

470 in prep.). RSF values were weighted by kill rate/pack/day (Thurber et al. 1994) to create a yearly

471 metric of pack level risk to elk. Similarly, grizzly bear predation risk was derived from an RSF

472 of 9 adult bears (Nielsen et al. 2002) and weighted by a probability density function of bears to

473 account for the difference in grizzly bear density inside Banff National Park compared to

474 provincial land, and again updated to reflect yearly changes in the landscape (Smolko et al. in

475 prep., see Appendix 2.6.1)

476   *Multivariate Analyses*

477   *Non-metric multidimensional scaling*. To explore overlap in predator scat contents, we used the

478   presence (0/1) of prey in a scat from the macroscopic scat analysis (n = 226) in a non-metric

479   multidimensional scaling (NMDS) ordination. NMDS ordination orders scats along axes derived

480   from variation in prey species composition using a distance matrix (Jongham et al. 1995;

481   McGarigal et al. 2000). Scats that have similar contents to each other will fall closer along

482   NMDS axes than scats that have dissimilar contents. We used Bray-Curtis distance to build the

483   distance matrix, which is predicted to perform better than Euclidean distance with respect to

484   community level datasets that have a high number of zero abundances (Legendre and Gallagher

485   2001). We excluded species that occurred < 5% across all scats as rare species can have

486   disproportionate effects on the ordination outcome (McCune 1996; Hedman et al. 2000;

487   Legendre and Gallagher 2001). Because we had a high amount of "unknown ungulate" identified

488   hairs (due to the inherent poor quality of scat hairs which affects our ability to confidently

489   conclude the species of hair), we combined all ungulates together, separated by age-class

490   (neonate or adult), resulting in four prey categories (adult ungulate, neonate ungulate, small

491   mammals, and vegetation). Because vegetation was only recovered in bear scats, we also

492   compared scats excluding vegetation as a prey item (n = 143) in the above framework to explore

493   the overlap among predator species with scat contents that occur across all predators.

494   *Canonical correspondence analysis*. To determine how the variation in contents of scats of

495   different species fell along environmental gradients, we used canonical correspondence analysis

496   (CCA) ordination. To keep the scale of analysis consistent across predators, we extracted

497   environmental covariates to a buffer corresponding to the smallest movement/gut passage buffer

498   of the predators, which is bear (7.07 km^2; Appendix 2.4). We constrained the proportion of prey

499   items measured from macroscopic scat analysis against environmental gradients based on

500   landscape variables found to influence the relative probability of elk in scats (P_i; Eq. 1) from the

501   GLMs for each predator species. We limited this analysis to elk and deer, separated by age-class

502   (n=96). The significance of each constraining variable was determined through permutation tests.

503   All multivariate analyses were performed in R 3.5.3 using the *vegan* package (Oksanen et al.

504   2018).

505   **RESULTS**

506   *DNA detection of elk in scats*

507   We analysed 65 scats whose contents were determined by both DNA analysis and

508   macroscopic scat analysis techniques. We found 88% were correctly classified as elk present in

509   DNA-analysed scats at a proportion level of $\geq$ 5%. The AUC was 0.77 (Appendix 2.7).

510   *Scat contents*

511   We summarized scat contents for the combined dataset (results from both macroscopic

512   scat analysis and DNA analysis methods) a univariate approach by species approach. Vegetation

513   was consistently higher in bear scats across both methods of analysis compared to other

514   predators where little to no vegetation was found in the other species' scats (Tables 2.2 - 2.3).

515   Bear scats consistently had the lowest ungulate occurrences relative to other predators and deer

516   and elk occurrences were lower than other predators (all pairwise P < 0.001; Table 2.2). Small

517   mammals were found in the scats of all species but were higher in coyote scats than the other

518   predators, although small mammal contents only significantly higher than wolf scats ($P < 0.001$),

519   not bear and cougar scats (all pairwise $P > 0.05$; Tables 2.2 - 2.3). Of the ungulate prey found in

520   scats, bighorn sheep, moose, mountain goat and domestic cow were infrequent (< 5% of scats)

521   except for cougars, where moose and bighorn sheep occurred relatively more frequently (Table

522   2.2). In contrast, deer and elk were commonly found in all predator scats. Elk occurrence in

523   coyote, wolf, and cougar scats was similar (all pairwise $P \geq 0.27$). Deer occurrence in wolf and

524   cougar scats were similar ($P \geq 0.23$), and deer occurrence in coyote scat was higher (all pairwise

525   $P \leq 0.03$) than in other predators (Table 2.2).

526   We compared the scat contents across predators from the macroscopic scat analysis data

527   in a univariate approach and multivariate approach in order to compare the amount of neonate

528   hairs to adult hairs in scats. Neonate deer and elk were proportionally higher than adult hairs in

529   wolf (Mann-Whitney U = 645, $P < 0.001$), coyote (Mann-Whitney U = 721, $P < 0.001$), and bear

530   (Mann-Whitney U = 3999, $P < 0.001$), but not in cougar scats (Mann-Whitney U = 144, df=1, P

531   > 0.95). Although substantive unknown ungulate material was found in the scats, the patterns

532   described here would be altered only if there is a systematic bias in prey identification.

533   In the NMDS, we found overlap in scat contents as in the univariate analysis. High

534   vegetation content in bear scats resulted in reduced overlap with other predators in the NMDS,

535   with bear scats clustering at low values along the first NMDS axis (NMDS1, Figure 2.2). In

536   contrast, because cougar scats had higher adult elk and deer than neonate ungulate hairs in scats,

537   there was reduced overlap along NMDS1. Wolf and coyote scat composition had the highest

538   overlap in ordination space, but the higher presences of small mammals in coyote scats relative

539   to wolves reduced overlap along NMDS2 axis with coyote scats falling closer to the small

540   mammal centroid. After excluding scats containing only vegetation, we found a similar

541   separation in multivariate space among contents of predator scat, although bears overlap more

542   with the other predator scat contents (Figure 2.3). Bear scats are tightly clustered along the centre

543   of the second NMDS axis (NMDS2), indicating higher small mammal and neonate ungulate

544   occurrences relative to adult ungulates.

545   *Spatial structure in scat contents*. There were spatial differences in the occurrence of elk in bear

546   scats ($Z = 8.13$, df=2, $P = 0.02$), where elk occurred more frequently in bear scats found in the

547   Ya Ha Tinda stratum compared to scats found in the east ($P = 0.04$), but not the western stratum

548   ($P = 0.19$; Figure 2.4a). Vegetation occurred more frequently in bear scats collected west and

549   east of the Ya Ha Tinda but the difference was significant only between scats collected at the Ya

550   Ha Tinda and west of Ya Ha Tinda ($P = 0.003$). Elk were found more often in scats of cougars

551   east of Ya Ha Tinda, although the differences among strata were not significant likely due to the

552   small sample size of scats ($Z= 3.13$, df=2, $P = 0.21$, Figure 2.4b). Deer were more frequently

553   found in cougar scats collected at the Ya Ha Tinda, although the difference was significantly

554   higher only in comparison to deer occurring in western scats ($P = 0.03$). There was no spatial

555   difference in the occurrence of elk or deer in coyote scats across the study area ($Z_{elk} = 1.03$, df=2,

556    $P = 0.59$; $Z_{deer} = 0.241$, df=2, $P = 0.89$, Figure 2.4c). In contrast, there were differences in the

557   frequency of occurrence of elk in scats of wolves collected across strata ($Z= 11.1$, df=2, $P = $

558   0.03), but not deer ($Z= 2.17$, df=2, $P = 0.34$, Figure 2.4d). Wolf scat collected in the Ya Ha

559   Tinda portion of the study area more often contained elk than scats in the eastern ($P = 0.04$) and

560   the western ($P = 0.02$) portions of the study area (Figure 2.4d).

561   *Factors influencing spatial patterns of elk in predator scats.*

562   Herbaceous forage biomass and elk resource use (RUF) were highly correlated with each

563   other, as well as slope, elevation and ruggedness, thus we did not use them in the same models

564   (Appendix 2.5). Across all predator species, parsimonious models with environmental variables

565   were better supported than the null model for all species (Table 2.4). The best supported models

566   predicting elk presence in a bear scat at a location consistently included the positive effect of

567   herbaceous biomass and the negative effect of an open cover type (Table 2.4). Distance to cut

568 line, road density and rugged terrain were also in the top 4 competing models. We chose the

569 most parsimonious model with herbaceous biomass and open cover type as the top model (Table

570 2.5). Predictions from this model indicated risk of elk being in bear scat was higher in the eastern

571 portion of the study area especially at Ya Ha Tinda and near the confluence of the Red Deer

572 River and Panther River (Figure 2.5a). We found strongest support for predicting the relative

573 probability of elk presence in coyote scat related to a positive effect of herbaceous biomass and

574 distance to water, and a negative effect of road density (Table 2.4 - 2.5). Predictions of the

575 relative probability of risk of elk being in a coyote scat indicated elk at the Ya Ha Tinda ranch

576 and east of Ya Ha Tinda (Figure 2.5b). There were 5 models with equal support for predicting

577 the relative probability of elk being in a cougar scats, where single variable models had lower

578 AIC_c values (Table 2.4) compared to models consisting of ≥ 2 variables. We selected the model

579 with edge density as our top model based on parsimony, as it had a relatively high model weight,

580 and has the same explanatory power as distance to nearest trail ($\Delta AIC < 2$). Additionally,

581 forested edge habitats are commonly selected by cougars for hunting (Laundré and Hernández

582 2003; Elbroch et al. 2013, Table 2.4). This model predicts a higher probability of elk presence in

583 cougar scats in areas with high edge density (Table 2.5), especially in the eastern portion of the

584 study area (Figure 2.5c). Finally, we found equal support for 2 models predicting the relative

585 probability of elk being in a wolf scat based on the positive effect of herbaceous forage and

586 rugged terrain and the negative effect of proportion of deciduous forest present (Table 2.4).

587 Because the confidence limit of the beta coefficient for burns included zero, we selected the

588 competing model without this variable (Table 2.5). Predictions from this model indicated elk

589 were likely to be found in wolf scats across the study areas but in patches that reflect the strong

590 effect of high herbaceous forage biomass (Figure 2.5d).

591 *Predictive maps of predation risk.* We combined the expected distribution of predators and the

592 probability of elk being in a predator scat to map the spatial predation risk of elk from specific

593 predators (Figure 2.6; Eq 1). Elk were most at risk from wolves at the Ya Ha Tinda (Figure 2.6d)

594 and likely also coyotes (Figure 2.6b). Risk from bears was moderate around the Ya Ha Tinda and

595 high east and south of the Ya Ha Tinda and had a patchy distribution (Figure 2.6a). Risk from

596 cougars was wide-spread east of the Ya Ha Tinda (Figure 2.6c).

597 *Canonical Correspondence Analysis*

598 We used variables that best predicted elk occurrence in predator scats (Table 2.6) to

599 constrain elk and deer occurrences in a canonical correspondence analysis. The constraining

600 variables explained 8.7% of the total variation in predator scat contents. The first two canonical

601 axes accounted for 91.1% (CCA1 = 51.9%, CCA2 = 39.2%). Terrain ruggedness was negatively

602 correlated ($|r| \geq 0.6$) with CCA1, and positively correlated with CCA2. The other constraining

603 variables were not correlated with either canonical axis (Table 2.6). Whereas the centroids of

604 prey items fell close together around the centre of the CCA triplot (Figure 2.7), there were

605 general trends associated with prey items and constraining variables. Both adult elk and deer

606 were more common in predator scats along a gradient of increasing terrain ruggedness. Neonate

607 elk were more correlated with increasing edge density and open landcover, whereas neonate deer

608 were correlated with an increasing gradient of deciduous landcover. However, permutation tests

609 revealed that only terrain ruggedness produced a significant gradient (Table 2.6).

610 **DISCUSSION**

611 The ungulate prey most frequently found in scats were elk and deer; mountain goats,

612 bighorn sheep, and moose were not found to be major prey of the four large predators in the

613 study. Bear scats were high in vegetation and coyote scats were high in small mammals. We

614   found evidence that wolves and cougars relied on deer. Two previous wolf scat analysis studies

615   in this region found 16% of scats contained deer in 2004 (Merrill and Hebblewhite, unpublished

616   data) and 37% in 2011 (Knamiller 2011) compared to 55% found in this study. In contrast, elk

617   occurrence in wolf scats has decreased from 54% of scats in 2004 (Merrill and Hebblewhite,

618   unpublished data) to 38% in 2011 (Knamiller 2011) and 38% in this study. We do not anticipate

619   any biases when comparing these previous studies with our recent project as our methods of scat

620   analysis followed from these studies, where scat contents were reported as frequency of

621   occurrence of prey items. We submit these shifts in the diet of wolves reflect an increase in deer

622   abundance that wolves are now killing and a nearly 70% decline in elk abundance since the mid

623   1990s making for fewer elk that are available to be killed (Hebblewhite et al. 2018).

624   Contrary to our expectations, we found elk and deer to be equally represented in the scats

625   of cougars. Krawchuk (2014) used data from GPS kill sites of cougars and found that males, in

626   particular killed more elk than deer near Nordegg, Alberta, 90 km north of our study area.

627   Although we had limited samples of cougar scat (n = 33), elk was highest in scats of cougars

628   found east of the Ya Ha Tinda, which corresponds to an increasing number of Ya Ha Tinda elk

629   migrating to this area to summer (Killeen et al. 2015). There is evidence of coyotes killing

630   neonate deer (Cherry et al. 2016) and moose (Boisjoly et al. 2010); however, we hypothesize

631   occurrence of adult ungulates in scats are likely a result of scavenging by coyotes on wolf-killed

632   carrion. Arjo and Pletscher (1999) found little evidence of coyotes consuming ungulates before

633   wolves recolonized northwestern Montana, suggesting coyotes scavenge carrion killed by

634   dominant predators (Arjo et al. 2002). In our study area, Spilker (2018) found a positive

635   correlation between wolf and coyote RSF values, supporting our hypothesis.

In scats where we quantified the relative abundance of adult and neonate ungulate hairs, neonate hairs were most abundant, except in cougar scats. In bear scats, neonate hairs comprised 95% of the ungulate hairs found. These results mirror summer kills of Ya Ha Tinda elk from 2013-2016 where 97.5% of elk kills by bears (n = 40) were neonates (Martin et al. 2017). High predation from bears on elk calves is well documented in other areas across North America (Zager and Beecham 2006; Barber-Meyer et al. 2008; Griffin et al. 2011). Although bears are thought to be opportunistic predators (Zager and Beecham 2006; Bastille-Rousseau et al. 2011), the high proportion of neonates killed by bears indicates active searching for neonates during a window of time when they are available and vulnerable because calves are largely immobile (Gunther and Renkin 1990). We found high variation in the proportion of ungulates in bear scats, indicating active searching for neonates may come down to the individual personality of a bear (Jacoby et al. 1999; Bastille-Rousseau et al. 2011). Regardless, bears are likely to be effective predators that can impact elk recruitment. For example, a meta-analysis of elk populations across the western United States revealed the average reduction of recruitment was 5 calves:100 cows in a system containing only wolves, whereas a system with wolves and grizzly bears resulted in a reduction in recruitment of 12 calves:100 cows (Lukacs et al. 2018). Similarly, Griffin et al. (2011) reported systems with grizzly bears experienced higher neonate mortality, compared to systems without grizzly bears.

In contrast to bears, wolves are coursing predators who hunt in packs and their hunting style may not be as effective in finding neonate prey or they may encounter other small-bodied prey like deer. For example, based on marked calves at Ya Ha Tinda, Berg (2019) found bear predation was high within five days after parturition but dropped off after 20 days, whereas wolf and cougar predation was lower and constant across time. Nonetheless, based on combining

659   information from wolf kill sites and scat contents north of the study area, Knamiller (2011) found

660   wolves killed neonate prey proportionally more than adults in early summer then switched to

661   killing adults after approximately two months. We did not see an increase in neonate prey

662   compared to adults in scat contents of cougars. Again, this may be related to hunting style as

663   cougars are stalk and ambush predators and may not rely on prey vulnerability (*i.e.* poorer body

664   condition) to the extent that wolves do to successfully catch their prey (Kunkel et al. 1999).

665   We found evidence of broad-scale spatial patterns in prey occurrence in scats that may

666   imply consequences for the different migratory segments of the Ya Ha Tinda elk herd. If

667   occurrence in scats reflects total predation risk to elk, risk of predation by bears and wolves is

668   currently higher for resident elk in summer than migratory elk summering east and west of Ya

669   Ha Tinda (Figure 2.4). Contrary to this, elk density is highest in summer at the Ya Ha Tinda

670   ranch, where nearly 50% of the elk population remain for the season (Killeen et al. 2015). Based

671   on relocations from VHF and GPS collared female elk from 2002-2011, Hebblewhite et al.

672   (2018) found wolf predation is density independent at the population level across years and

673   concluded this mechanism will balance the ratio of residents to migrants. Indeed, we did not find

674   that our metric of elk abundance, based on utilization of collared elk, influenced the occurrence

675   of elk in wolf or cougar scats, even though and we sampled scats across a range of elk spatial

676   abundance. Instead, we found herbaceous forage biomass increased the probability of elk

677   presence in wolf scat whereas it decreased in areas with deciduous forests. It is possible forage

678   biomass is a better indicator of elk presence in summer (Skovlin et al. 2002, Boyce et al. 2003;

679   Mao et al. 2005, Smolko, in prep.), because our telemetry-based metric only reflects the use of a

680   portion of the elk herd (~23%). Whereas deciduous forests may provide obstruct visibility or

681   contain downed vegetation that can impede an elk's escape from a predator (Bergman et al.

682   2006; Eisenberg et al. 2015), elk in Yellowstone National Park have been observed to move into

683   closed canopied areas when wolves are near (Kauffman et al. 2007). In contrast, resident elk at

684   the Ya Ha Tinda avoid wolves during the day, exploiting a human-caused predation refuge

685   (Hebblewhite and Merrill 2007), although wolves move into these areas at night.

686   Predation risk to elk from cougars was determined to be higher in the eastern portion of

687   the study area; however, a small sample size increases the uncertainty of this trend. Forest edge

688   density increases west to east in the study area due to recent burns and clearcutting (Smolko, in

689   prep.) and Spilker (2018) found cougars selected for areas with high edge, consistent with other

690   studies (Holmes and Laundré 2006; Knopff et al. 2014a). This is attributed to their hunting

691   strategy where they use forest edge to stalk their prey (Laundré and Hernández 2003). A greater

692   number of cougar scats were found in surveys east of Ya Ha Tinda (Spilker 2018) therefore both

693   cougar distribution and habitat characteristics suggest elk may be more vulnerable to cougars in

694   this area. Predation risk from bears was patchy across the study area (Figure 2.6a) and

695   probability of elk presence in scats was most influenced by herbaceous biomass and the negative

696   extent of open areas (*e.g.* burns, regenerated vegetation, cutblocks and grasslands). Early in the

697   growing season, when bears actively predate on neonate ungulates, elk and bears may have high

698   spatial overlap because they are both selecting for high forage biomass (Berg, in prep.),

699   increasing predation risk to elk in these areas. Although Hebblewhite et al. (2005) speculated that

700   elk selection of open areas may be related to increased sightability and therefore vigilance

701   because elk were encountered and killed by wolves less often in open areas, risk in open areas

702   may be higher from bears. Similar to our results, Gunther and Renkin (1990) found evidence for

703   open habitats being risky to elk as they observed grizzly bears encountering elk in these areas,

704   charging repeatedly to separate calves from the group. Finally, predation risk from coyotes

mirrored that of wolves but was relatively low west of Ya Ha Tinda (Figure 2.6b). Elk presence

was influenced by distance to streams, where elk in scats increased further from streams.

Although distance to water was not an important variable in coyote habitat selection, wolves

selected areas near streams and rivers (Spilker 2018). Elk were less likely to be found in coyote

scats near rivers possibly because these are used as travel corridors for more dominant predators

like wolves (Webb and Merrill 2012).

Our study has shown that elk who migrate west into the high elevations of Banff National

Park are exposed to relatively low predation risk compared to elk that either remain on the Ya Ha

Tinda or migrate east/south of the Ya Ha Tinda. Hebblewhite and Merrill (2009) also reported

elk migrating to Banff National Park in the early 2000s were exposed to lower predation from

wolves than those remaining at Ya Ha Tinda based on wolf distribution models. Hebblewhite

and Merrill (2011) attributed the increasing number of resident elk at Ya Ha Tinda during the

early 2000s to the elk use of a refuge created by high human activity, despite relatively high wolf

risk. Furthermore, elk are concentrated at the Ya Ha Tinda in the summer and per capita risk may

be lower even if more elk are killed. Large group size of residents at Ya Ha Tinda can improve

the survival of collared elk (Hebblewhite and Merrill 2011; Figure 4).

Hebblewhite and Merrill (2011) also hypothesized elk were exposed to higher bear

predation risk in Banff National Park because bears killed more migrant elk than residents. This

is supported by estimates of summer bear densities in Banff National Park being greater than

those on provincial lands, where both studies used a DNA mark recapture approach (Boulanger

et al. 2005, Whittington and Sawaya 2015). However, our results do not support higher predation

risk from bears in Banff National Park. Scats of bears in this area were dominated by vegetation

whereas scats of bears from the Ya Ha Tinda more frequently contained elk. We have little

728   information on cause-specific mortality of marked elk calves in the Park to compared with our

729   scat analysis results because of difficulties accessing kill sites due to their remoteness. Mortality

730   rates of calves from cows that remain at low elevations on Ya Ha Tinda or migrate east of Ya Ha

731   Tinda (Berg 2019) support our findings. Elk calves suffer high mortality consistent with bear

732   predation risk in both these areas, whereas calves killed by wolves occurred more frequently at

733   the Ya Tinda than east of Ya Ha Tinda (Berg 2019). Wolves kill deer more frequently east of Ya

734   Ha Tinda, yet cougars may pose a relatively greater threat to elk, particularly calves, in these

735   areas (Berg 2019).

736   The Ya Tinda elk herd has declined by 70% over the past two decades and the ratio of

737   resident to migratory elk has dramatically changed. Hebblewhite et al. (2018) reported wolf

738   predation was the greatest source of elk mortality and has been density independent over time.

739   The authors also reported that elk mortality by bears has been density dependent. This is

740   consistent with our results where we found low predation risk from bears within the Park

741   following a decline of western migrants. Elk migrating east of Ya Ha Tinda onto industrial

742   forest lands currently exhibit higher cow:calf ratios than elk remaining at the Ya Ha Tinda in

743   summer (Martin et al. 2017), yet we found high risk from cougars, bears and to some extent

744   wolves. Our data suggest that higher predation risk by bears, wolves, and cougars in the eastern

745   portion of the study area may eventually reverse this new migration reflecting the loss of elk in

746   this area in the 1990s when cow elk harvest was stopped due to a decline in this segment of the

747   population (Hebblewhite et al. 2006a).

Table 2.1. Landscape covariates used in developing canonical correspondence analyses and spatial risk models from scats collected from four predator species on the eastern slopes of the Rocky Mountains of Alberta. The resolution of all variables unless otherwise stated is 30 x 30-m (900-m^2).

Variable	Code	Description	Units	Source of Data	Year of Data
Distance to water	distwater	Distance to nearest perennial stream, river or lake	km	AltaLIS	1996
Density of water	denswater	Linear density of perennial streams and rivers within a buffer[‡]	km/km^2	AltaLIS	1996
Vegetation NDVI	NDVI[*]	Normalized Differential Vegetation Index derived from the weighted average of 28 July (peak greenness) images from 2013-2016	-1 to 1	MODIS	2013-2016
Conifer forests	conif	Proportion of conifer forests in buffer[‡]	%	TM Landsat imagery	2009
Mixed & deciduous forests	mix	Proportion of deciduous-mixed forests within a buffered[‡] area	%	TM Landsat imagery	2009
Regenerated forest	regen	Proportion of regenerated vegetation within a buffered[‡] area	%	TM Landsat imagery	2009
Herbaceous	herb	Proportion of herbaceous vegetation within a buffered[‡] area	%	TM Landsat imagery	2009
Shrub	shrub	Proportion of shrub vegetation within a buffered[‡] area	%	TM Landsat imagery	2009
Burn	burn	Proportion of burned vegetation in buffered[‡] area from burns ≤ 14 years old	%	Banff Fire Database and ESRD Fire Database;	2009

Table 2.1 continued

Cutblocks	cutb	Proportion of cutblocks from ≤ 20 years old Within a buffered area	%	ABMI† - Human Footprint Inventory	2014
Elevation	elev	Mean elevation to nearest 30-m, within a buffered‡ area	m	Derived from AltaLIS, 20K Digital Elevation Model (DEM)	2009
Slope	slope	Mean degree slope within a buffered‡ area	0-90˚	Derived from AltaLIS, 20K Digital Elevation Model (DEM)	2009
Ruggedness	rugg	Mean SD of elevation of 8 neighbouring cells within a buffered‡ area standardized between 0 and 1	0-1	Derived from AltaLIS, 20K Digital Elevation Model (DEM)	2009
Road density	roaddens	Linear density of motorized paved or gravel roads within a buffered‡ area	km/km²	AltaLIS	2014
Distance to road	distroad	Distance to nearest motorized paved or gravel road	mm	AltaLis	2014
Trail density	trldens	Linear density of non-motorized human/horse trails within a buffered‡ area	km/km²	AltaLIS	2014
Distance to trail	disttrail	Distance to nearest non-motorized human/horse trail	km/km²	AltaLIS	2014
Cutlines	cutdens	Linear density of cutlines (used for OHV activity) within a buffered‡ area	km/km²	AltaLIS	2014
Distance to cutline	distcut	Distance to nearest cutline (used for OHV activity)	Km	AltaLIS	2014

Table 2.1 continued

Distance to nearest edge	distedge	Distance to nearest edge, where edge is 30-m buffer along conifer or mixed/deciduous forest	m	Derived from TM Landsat imagery from ABMI†	2014
Edge density	edgedens	Density of edge cover within a buffered‡ area, where edge is 30-m buffer along conifer or mixed/deciduous forest	%	Derived from TM Landsat imagery from ABMI†	2014
Elk habitat use	RUF	Mean resource utilization function value derived from 66 GPS collared elk within a buffered‡ area	0-1	n/a	2013-2016
Total forage biomass	totfg	Mean forage biomass of herbaceous and shrub vegetation (available to elk) within a buffered‡ area	g/m^2	Smolko et al. (in prep) Hebblewhite (2006)	2013-2016
Herbaceous biomass	herbfg	Average forage biomass of herbaceous vegetation (available to elk) within a buffered‡ area	g/m^2	Smolko et al. (in prep) Hebblewhite (2006)	2013-2016
Predator resource selection	bearRSF, cougarRSF, coyoteRSF, wolfRSF	Mean resource selection function value derived from scat locations of predators within a buffered‡ area	0-1	Spilker (2018)	2014-2015
Cumulative predator resource selection	cRSF	Mean value derived from sum of individual predator resource selection functions	0-1	Spilker (2018)	2014-2015

748 * Resolution size is 250 x 250-m

749 † Alberta Biodiversity Monitoring Institute

750 ‡ Buffers are species-specific and based on movement per day and gut passage time of each predator (bear = 7.07-km^2, cougar = 12.57-km^2,

751 coyote = 12.57-km^2 and wolf = 28.27-km^2).

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Table 2.2. Combined frequency of occurrence of prey items found in scats of four predator species along the eastern slopes of the Rocky Mountains in Alberta analysed by either DNA (n=250) or macroscopic scat analysis n = (226).

	Elk	Deer	Moose	Mountain Goat	Bighorn Sheep	Unknown Ungulate	Small Mammal	Domestic Cow	Vegetation
Bear (n=130)	0.191	0.137	0.015	0.000	0.00	0.099	0.137	0.026	0.695
Cougar (n=33)	0.455	0.333	0.091	0.030	0.121	0.242	0.061	0.030	0.000
Coyote (n=114)	0.360	0.702	0.009	0.000	0.035	0.254	0.219	0.079	0.000
Wolf (n=199)	0.377	0.553	0.015	0.050	0.045	0.075	0.045	0.000	0.000

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Table 2.3. Mean proportion and standard error (SE) of prey items in scats of four predator species collected along the eastern slopes of the

Rocky Mountains in Alberta and analysed through macroscopic scat analysis.

		Prey Items								Ungulate Age Class	
		Elk	Deer	Moose	Bighorn Sheep	Unknown Ungulate	Small Mammal	Domestic Cow	Vegetation	Adult	Neonate
Bear (n=99)	Mean SE	0.028 ± 0.014	0.003 ± 0.003	0.004 ± 0.004	0.000 ± --	0.100 ± 0.027	0.140 ± 0.031	0.025 ± 0.013	0.604 ± 0.027	0.950 ± 0.020	0.050 ± 0.006
Cougar (n=17)	Mean SE	0.229 ± 0.058	0.079 ± 0.033	0.047 ± 0.033	0.018 ± 0.010	0.394 ± 0.077	0.103 ± 0.055	0.006 ± 0.006	0.000 ± --	0.500 ± 0.090	0.500 ± 0.100
Coyote (n=55)	Mean SE	0.186 ± 0.039	0.151 ± 0.035	0.001 ± 0.001	0.016 ± 0.011	0.189 ± 0.034	0.418 ± 0.058	0.039 ± 0.013	0.000 ± --	0.230 ± 0.040	0.770 ± 0.070
Wolf (n=55)	Mean SE	0.264 ± 0.050	0.100 ± 0.031	0.011 ± 0.009	0.016 ± 0.015	0.218 ± 0.039	0.227 ± 0.050	0.001 ± 0.001	0.000 ± --	0.180 ± 0.050	0.820 ± 0.060

Table 2.4. Summary of model selection results based on AIC for predicting elk presence in scats for four predators along the eastern slopes of the Rocky Mountains in Alberta. The top model for each predator is bolded.

Model variables*	k	AIC	ΔAIC	weight
<u>Bear</u>				
herbfg - open - distcut	4	151.54	0.00	0.47
herbfg - open	**3**	**152.99**	**1.45**	**0.23**
herbfg - open - rugg	4	153.97	2.44	0.14
herbfg - open - roaddens	4	155.02	3.49	0.08
RUF - open + rugg	4	157.03	5.50	0.03
-open - distcut	3	157.20	5.66	0.03
herbfg - distcut	3	157.44	5.90	0.02
herbfg	2	160.31	8.77	0.01
null	1	166.00	14.46	0.00
-open	2	167.07	15.53	0.00
<u>Coyote</u>				
herbfg + distwater - roaddens	**4**	**217.03**	**0.00**	**0.71**
herbfg + distwater	3	220.51	3.49	0.12
herbfg - roaddens	3	220.57	3.54	0.12
herbfg	2	222.30	5.27	0.05
distwater	2	231.61	14.58	0.00
distwater - roaddens	3	231.80	14.77	0.00
null	1	234.39	17.37	0.00
RUF	2	235.06	18.04	0.00
-roaddens	2	235.76	18.74	0.00
<u>Cougar</u>				
disttrail	2	33.39	0.00	0.30
edgedens	**2**	**33.67**	**0.28**	**0.26**
edgedens + disttrail	3	34.18	0.79	0.20
edgedens + herbfg	3	35.04	1.64	0.13
edgedens + disttrail - RUF	4	36.34	2.95	0.07
null	1	38.66	5.27	0.02
-RUF	2	40.75	7.36	0.01
<u>Wolf</u>				
herbfg + rugg - decid	**4**	**288.93**	**0.00**	**0.43**
herbfg + rugg - burn - decid	5	289.71	0.79	0.29
herbfg + rugg	3	305.06	16.13	0.00
herbfg - decid	3	317.68	28.75	0.00
-decid - rugg + RUF	4	370.69	81.76	0.00
-burn - decid - rugg + RUF		372.26	83.33	0.00
-deicd - rugg	3	385.86	96.93	0.00
-burn - decid - rugg	4	387.89	98.96	0.00
null	1	402.70	113.77	0.00

*Variable codes defined in Table 2.1

Table 2.5. Beta coefficients (β), lower and upper confidence intervals (CI) for the top model based on AIC$_c$ predicting elk presence in scat for four predators along the eastern slopes of the Rocky Mountains of Alberta.

Species	Variable	β	95% CI	
			Lower	Upper
Bear	Herbaceous forage biomass (herbfg)	0.06	0.03	0.10
	Open canopy (open)	-4.83	-8.58	-1.63
Cougar	Edge density (edgedens)	1.25	0.31	2.49
Coyote	Herbaceous forage biomass (herbfg)	0.050	0.030	0.070
	Distance to streams (distwater)	0.00032	0.00006	0.00058
	Road density (roaddens)	-0.88	-1.83	-0.13
Wolf	Herbaceous forage (herbfg)	0.21	0.16	0.27
	Terrain ruggedness (rugg)	0.85	0.53	1.19
	Deciduous cover (decid)	-36.29	-56.85	-18.25

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Table 2.6. Correlations of the constraining variables with the first two canonical axes of a canonical correspondence analysis of predator scat compositions along the eastern slopes of the Rocky Mountains in Alberta.

	CCA1	CCA2	*P*
decid	0.340	-0.039	0.628
rugg	-0.632	0.670	0.024
open	-0.254	-0.430	0.311
herbfg	0.248	-0.393	0.934
roaddens	0.439	0.272	0.285
distwater	-0.181	0.059	0.908
edgedens	-0.219	-0.172	0.113

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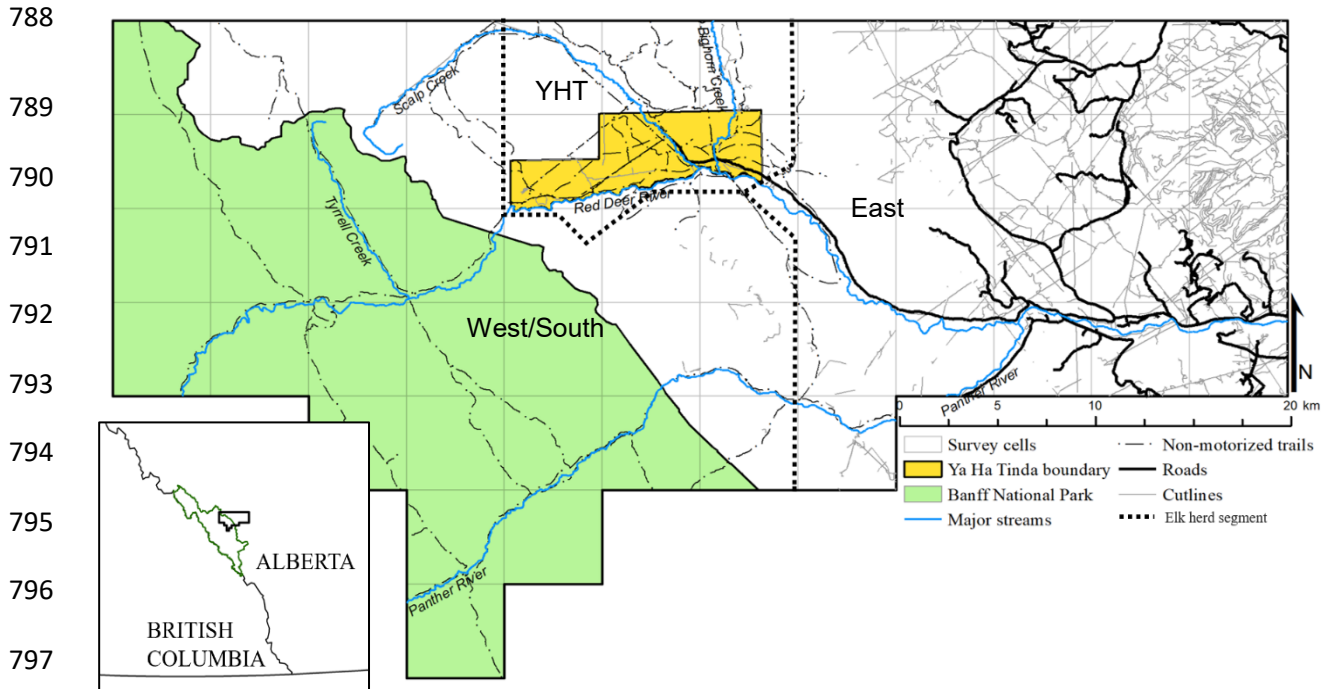
Figure 2.1. Location of study area, within the Red Deer River and Panther River drainages, encompassing the Ya Ha Tinda ranch (YHT) and the north-eastern corner of Banff National Park in Alberta, where predator scats were collected from 2013-2016. West/South, YHT and East refer to the spatial strata defined by the summer distribution of the elk herd.
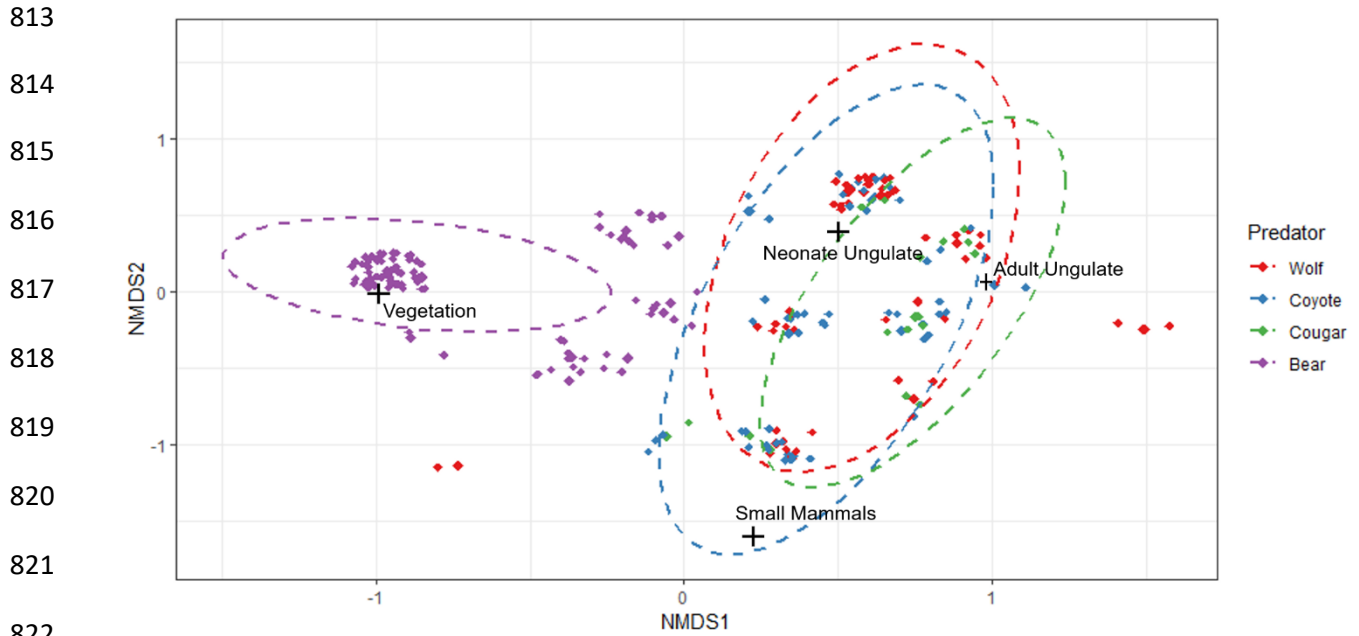
Figure 2.2. NMDS scores for presence of animal and vegetation scat contents based on macroscopically analysed data of individual predator scats from wolf (n=55), coyote (n=55), cougar (n=17) and bear (n=99). Points with the same NMDS score are shown as a point jitter. Ellipses around the centroid of each predator species represent the 95% multivariate t-distribution, and "+" refers to the centroid of prey item clusters.
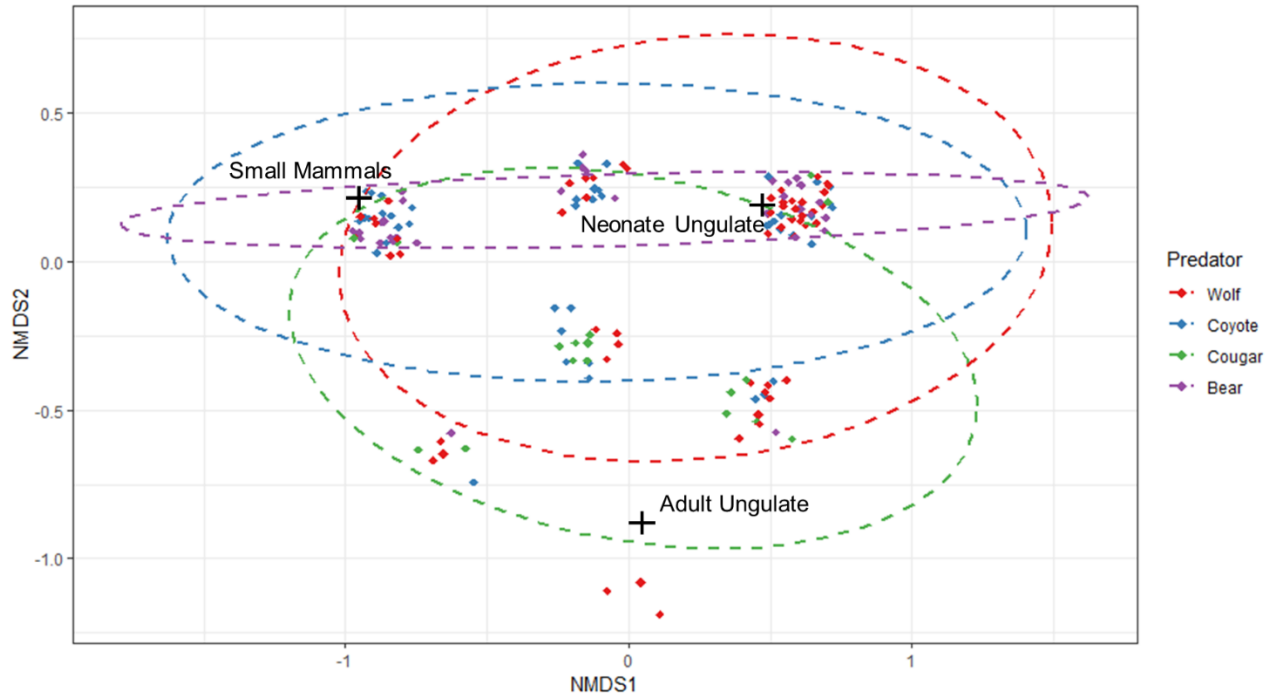
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Figure 2.3. NMDS scores for presence of animal prey contents based on macroscopically analysed data of individual predator scats from wolf (n=55), coyote (n=55), cougar (n=17) and bear (n=31). Points with the same NMDS score are shown as a point jitter. Ellipses around the centroid of each predator species represent the 95% multivariate t-distribution, and "+" refers to the centroid of prey item clusters.
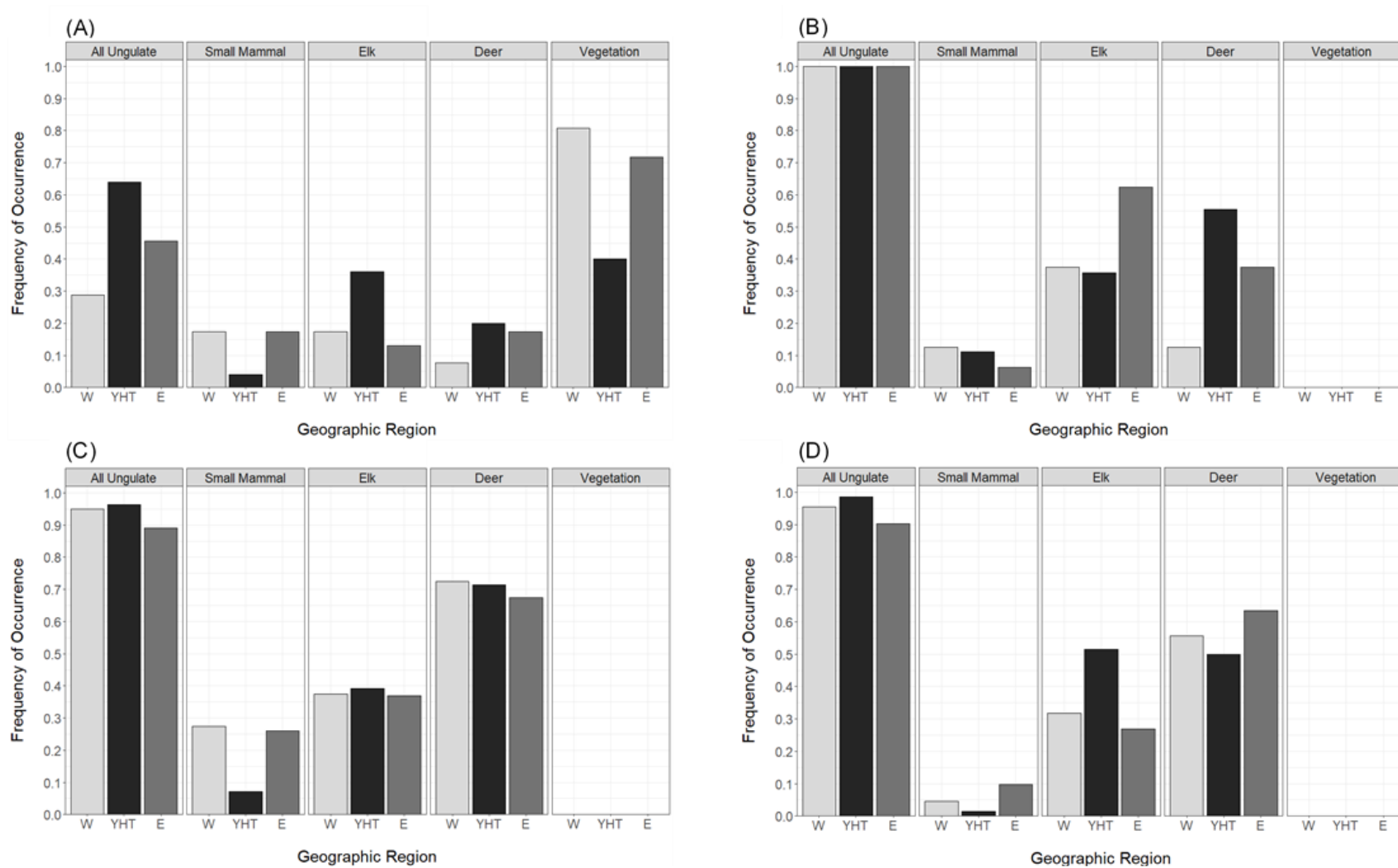
Figure 2.4. Frequency of occurrence of prey items in (A) bear, (B) cougar, (C) coyote and (D) wolf scats across a spatial strata within the study area covering 3 segments of the summer Ya Ha Tinda elk herd (W = west and south of YHT, YHT = Ya Ha Tinda, E = east of YHT, (Figure. 2.1). "All Ungulate" refers to all ungulate contents combined.

(A) Bear

(B) Coyote

(C) Cougar

(D) Wolf

Ya Ha Tinda boundary

Major streams

High : 1

Low : 0

N

0   15   30   60 km
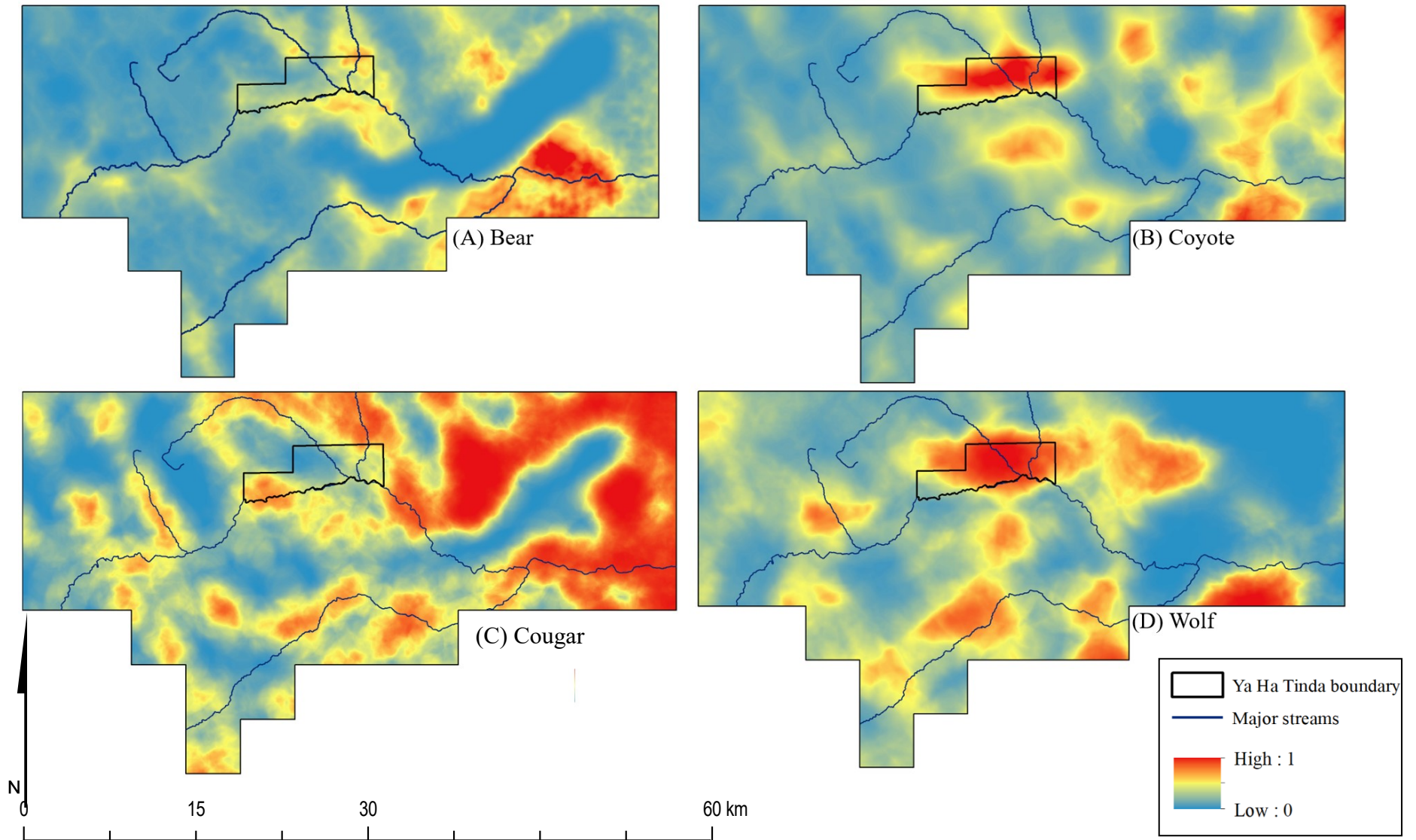
845   **Figure 2.5.** Maps of predicted elk presence in from both macroscopically and DNA analysed scats from four predators collected from the eastern slopes of the Rocky Mountains in Alberta. Predictions were based on a logistic regression comparing elk present in predator scats to locations of predator scats (Table 2.7).

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0   5   10   20   30   40   50   60 km
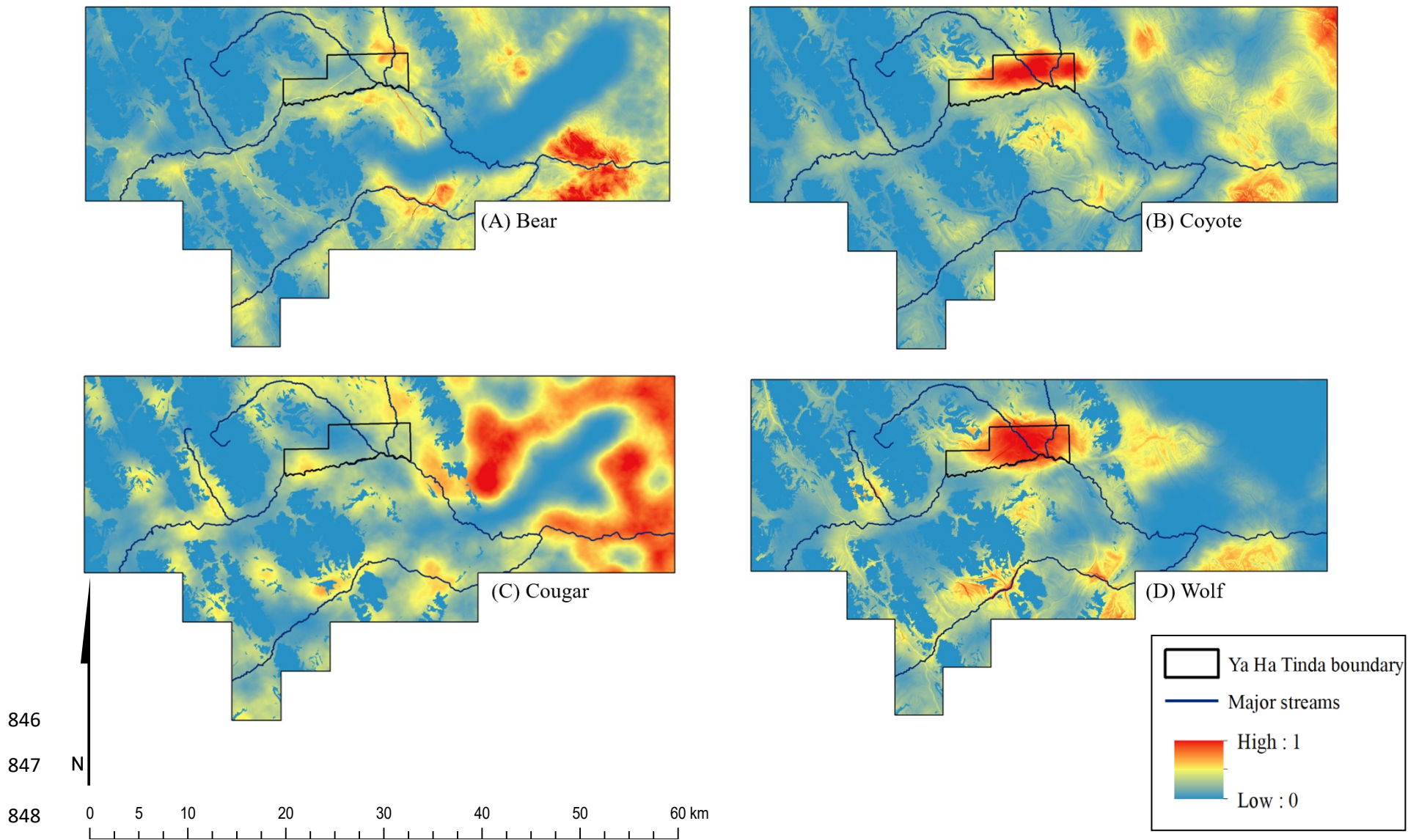
Figure 2.6. Maps of predicted predation risk for elk from 4 predators along the eastern slopes of the Rocky Mountains in Alberta based on Eq. 1 in text. Predation risk was calculated by the relative probability of a predator being present multiplied by an elk containing scat of that predator.
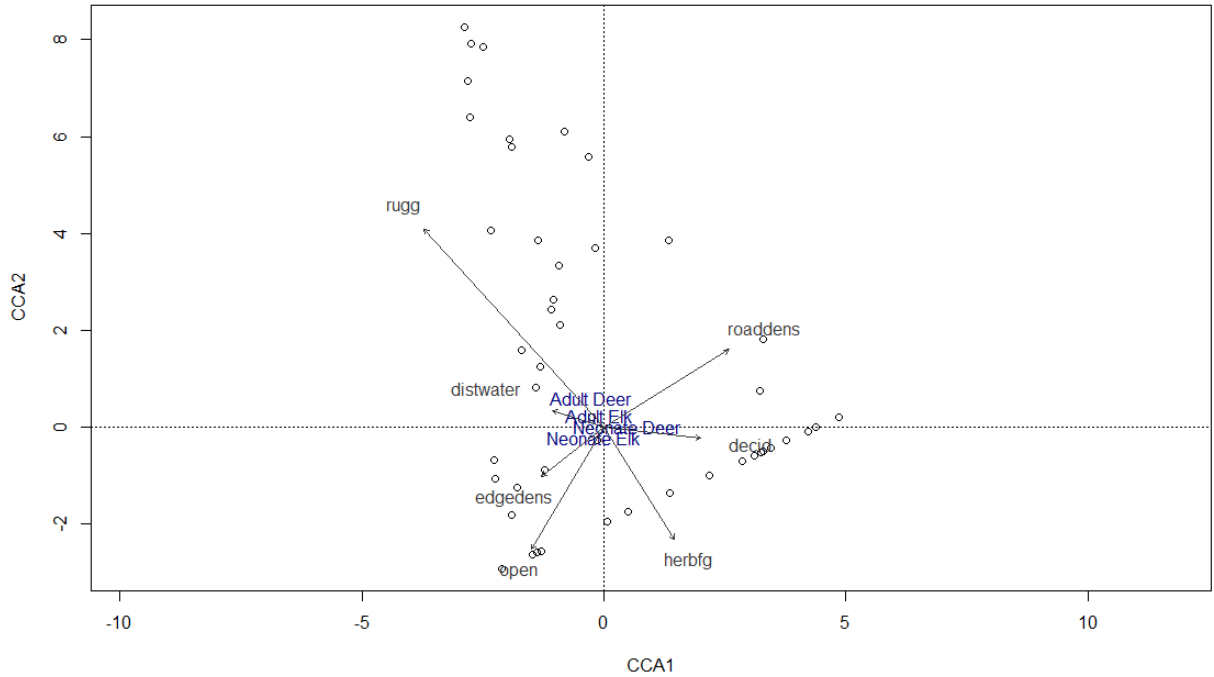
Figure 2.7. Canonical correspondence analysis plot relating elk and deer presence in scats of all predators along environmental characteristics predicted affecting scat composition of 4 predators. All predator scats containing elk or deer (bear (n=9), cougar (n=13), coyote (n=35) and wolf (n=39), were combined to create a community level ordination.

CHAPTER 3 — Conclusion

In this thesis, we used non-invasive sampling techniques to quantify predation risk from multiple predators to a declining, partially migratory herd of elk along the eastern slopes of the Rocky Mountains in Alberta. This herd is of particular interest due to its continued decline over the last few decades (Hebblewhite et al. 2018) and the shift in migratory behaviour onto lands dominated by resource extraction (Killeen et al. 2015). Predation is thought to be a driving force behind these changing dynamics, although past studies have only focused on wolf-elk interactions. To understand the broader predator community and how that affects risk to elk, (Spilker 2018) initiated a scat-based study to spatially quantify the distributions bears (*Ursus arctos*/*U. americanus*), wolves (*Canis lupus*), coyotes (*Canis latrans*) and cougars (*Puma concolor*). We extended this work by quantifying prey items in scats using standard macroscopic hair analysis to quantify the proportion of prey items, along with a DNA analysis technique designed to detect elk presence in scats. We focused on summer scats from predators to understand the differential predation risk across the major segments of the Ya Ha Tinda elk herd while occupying their allopatric ranges. We related the scat location to the approximate site the prey was killed by buffering the scat with a distance derived from the mean movement/day and gut passage time of each predator. We derived a map measuring relative predation risk to elk by relating the probability of a predator scat being in a given location by the probability of that scat containing elk. To our knowledge, this is the first study to use contents of predator scats to measure broad-scale risk to a prey population. Overall risk to elk from all predators was low in Banff National Park similar to Hebblewhite and Merrill (2009), where western migrant elk were exposed to lower predation risk from wolves than residents. Whereas eastern elk are currently experiencing higher survival and calf:cow ratios relative to their resident and western

896 counterparts, we predict that the relatively higher risk on this segment of the elk herd from

897 cougars and bears may eventually reverse these demographic benefits if more elk continue to

898 adopt this strategy.

899   Both methods we used to identify scat contents have uncertainty that must be addressed

900 when interpreting these results. In macroscopically analysed scats, 23% of the total hairs

901 analysed (n = 5,810) could not be identified to a specific ungulate species and were classified as

902 "unknown ungulate", therefore only 77% of hairs were given a species identification. Although

903 the DNA analysis method used can identify the hairs we classified as "unknown ungulate" to

904 species, 30% of the scats we analysed for DNA did not amplify, leaving us with results for 70%

905 of scats. While DNA analysis is more time efficient than macroscopic scat analysis, it gives less

906 information (*e.g.* age-class of hairs, more than one species per scat) than macroscopic scat

907 analysis. A combination of these methods quantifies neonate ungulate occurrence in scats, while

908 allowing us to understand how scat contents differ at a broad spatial scale, in a time-efficient

909 manner. Because our goal was to spatially predict only elk presence in scats, the implications for

910 uncertainty in hair identification are likely minor, as we assume that the non-detection of elk is

911 scats is random.

912   Whereas we propose this method is a non-invasive approach to sampling multiple

913 predator diets and thus risk to prey, there are issues with using scats as a proxy for predation risk.

914 The scale of analysis must be addressed when relating scat contents to predation risk for a prey

915 species. Prey kill sites located from radio-collared predators or prey allows for extraction of fine

916 scale habitat features once GPS collar error is accounted for. Our approach related the scat

917 location to the assumed kill site, using relatively large buffers to extract covariates (Appendix

918 2.4). Large buffer sizes may reduce the variation in covariate values among buffers near each

919   other, possibly resulting in weak signals in which covariates predict elk presence in scats. On the

920   other hand, large buffer sizes around scats far from each other may increase the variation in

921   covariates across buffers, due to the steep elevation and anthropogenic disturbance gradient

922   present in the study area from east to west. Despite this, we believe using buffers derived from

923   gut-passage time and movement per day of each predator is a valid approach because our study

924   focused on broad-scale patterns of predation risk. Investigating fine-scale spatial interactions or

925   temporal interactions between predator and prey may not be possible with this approach.

926   An approach to decrease buffer radii, while still relating the assumed kill site to the scat location,

927   may be to use the distance each predator moves around a kill as a function of the prey body size.

928   For example, a wolf would likely move less following an adult elk kill compared to a neonate elk

929   kill, resulting in a smaller buffer radius.

930   The predation risk maps we developed for each predator species (Figure 2.6) were

931   derived from the selection by predators and the probability of elk presence in scats for each

932   predator species. The maps predict spatial risk, assuming that the predator species killed the elk

933   within the buffered area (i.e., not scavenging). Assuming every predator scat is reflective of that

934   predator's kill is likely violated in the coyote risk model. Because of their small body size

935   relative to wolves, elk occurrences in coyote scats are more likely from scavenging off wolf-

936   killed carrion (Arjo et al. 2002). Additionally, we found a spatial mismatch in the probability of

937   coyote resource selection compared to the probability of finding elk in their scats, where

938   selection was widespread across the study area (Appendix 2.3), and elk in scats mirrored that of

939   wolves (Figure 2.6). Whereas bears have been observed displacing cougars from their kills in

940   Yellowstone National Park (Murphy et al. 1998), bear scat contents in our study system were

941   likely not reflective of scavenging because of the high amount of neonate occurrences compared

942 to adult. If bears were scavenging off cougar kills in this study system, we would expect to see

943 more adult ungulate occurrences in bear scats because adult ungulates were more common in

944 cougar scats relative to other predators (Table 2.3). Although interpreting the coyote risk maps

945 as predation risk from coyotes may be problematic, we suggest they are valid from the

946 perspective of overall risk to elk. Regardless of what predator killed that elk, it still was killed

947 near the scat location, and thus represents a risky area.

948   Using scat contents is a novel approach to assess elk predation risk, where we assumed

949 where elk occurs in predator scat is reflective of an elk kill (within a buffered area). A logical

950 next step would be to compare our predictions of risk to those derived from actual elk kill sites.

951 We propose a non-invasive metric, but validating this metric of risk with a more commonly used

952 metric would provide legitimacy for using this approach onward.

953 *Management Implications*

954   Large carnivores are considered to have high trophic importance, leading to a greater

955 emphasis on their management (Estes et al. 2011). In addition, their ungulate prey has high

956 economic and social importance and how these two species interact is of use to wildlife

957 managers when predicting long-term population trends and harvest quotas. Monitoring these

958 interactions can be costly, and non-invasive techniques like remote cameras, hair snares, and

959 scats are evolving to address these issues (Wasser et al. 2004; Mumma et al. 2015; Steenweg et

960 al. 2016). In addition to providing a non-invasive approach to understanding the Ya Ha Tinda elk

961 herd dynamics, we contributed information on elk predation risk within the bison reintroduction

962 zone in Banff National Park. Plains bison (*Bison bison bison*) were reintroduced to this area in

963 early 2017, and a subset of the collared migrant elk reside in this area during the summer. We

964   collected predator scats in this area from 2015-2016, to provide baseline data on elk predation

965   risk before the addition of a potential competitor to elk and new prey species for predators.

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CHAPTER 2 SUPPLEMENTARY MATERIAL

APPENDIX 2.1. Scat identification characteristics used to identify predator scats collected from 2013-2016 along the eastern slopes of the Rocky Mountains, Alberta. Adapted from Spilker (2018).

Predator Species	Diameter (cm)	Physical Characteristics	Scat contents	Citation
Black bear	3.2-7.0	Unsegmented, loose unformed pellets	Contains vegetation	Rezendes (1992); Elbroch (2003)
Grizzly bear	> 5			
Coyote	1.78 - 3.3	Segmented, tapered	Contains large bone fragments and hair	Thompson (1952); Weaver and Fritts (1979); Rezendes (1992); Elbroch (2003)
Wolf	1.4 - 4.8			
Cougar	2.5 - 3.8	Segmented, not tapered	Contains bone fragments and hair, fruit seeds may be present	Rezendes (1992; Elbroch 2003)

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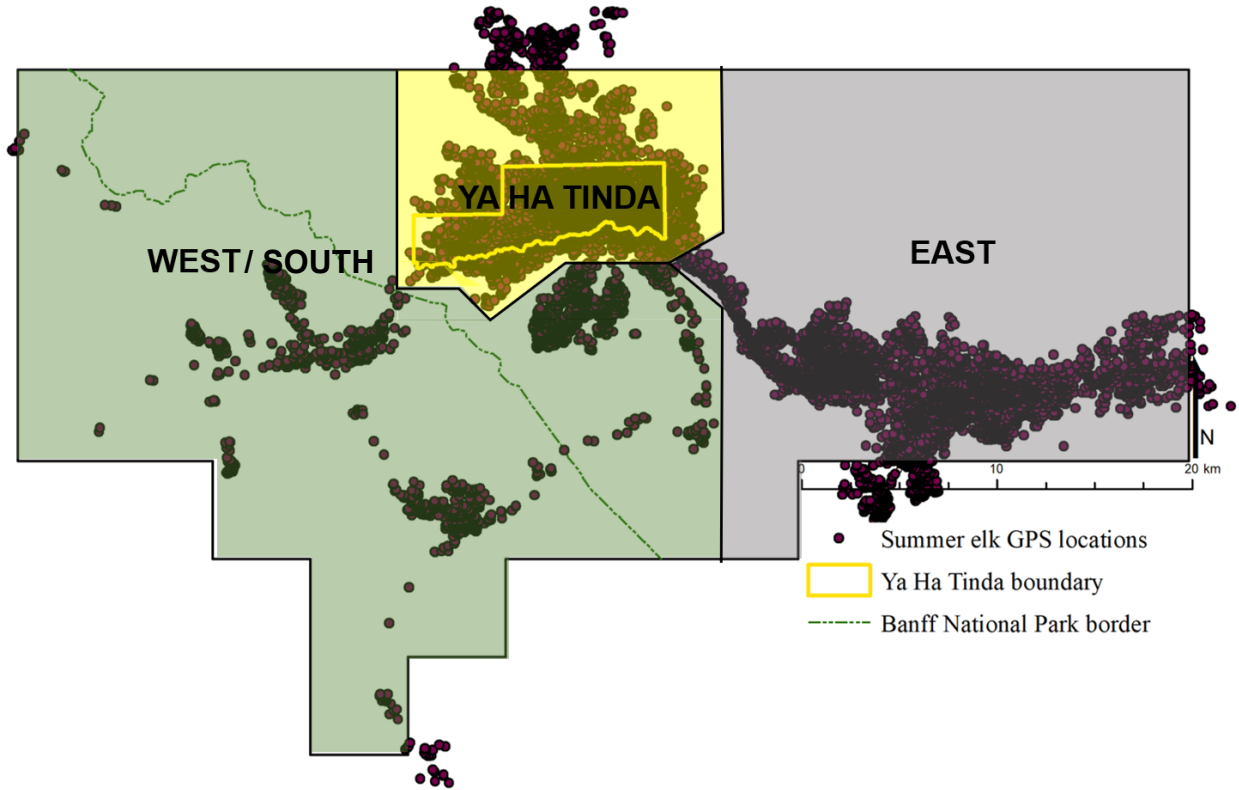
APPENDIX 2.2. Elk GPS relocations from 66 female elk from May – September 2013-2016 defining the 3 segments (west/south of Ya Ha Tinda , Ya Ha Tinda, and east) of the Ya Ha Tinda elk herd.
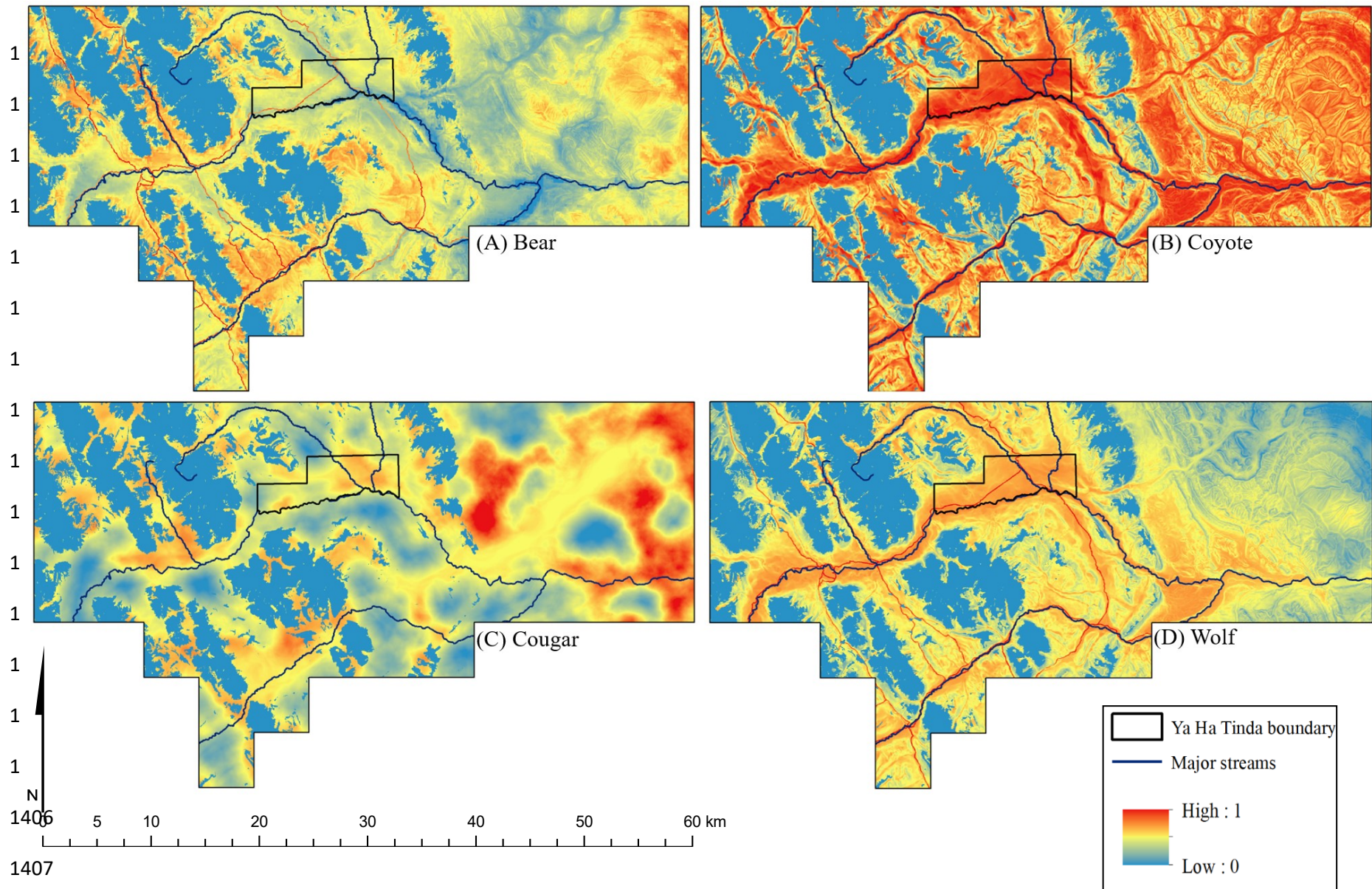
APPENDIX 2.3. Maps of resource selection (RSF_{ij}) based on scat locations for 4 predators along the eastern slopes of the Rocky Mountains in Alberta. Maps were adapted from Spilker (2018).

APPENDIX 2.4. Summary of movement rates and digestive retention times used to estimate the size of buffers used to quantify the

environmental variables around each scat of each predator species. Buffers were used in canonical correspondence analysis and spatial

risk analysis.

	Movement per day (km)	Citation	Digestive retention time (hours)	Citation	Minimum buffer size	Maximum buffer size	Buffer Radius for Analysis (km)
Grizzly bear	2.4 - 3.4	Craighead 1976; Gibeau et al. 2001	13.0 ± 2.3	Pritchard and Robbins 1990; Elfström et al. 2013	2.4 km/day*0. days = 1.3	3.4 km/day * 0.54 days = 1.8	
Black bear	1.0 - 1.7	Amstrup and Beecham 1976; Garshelis 1978; Garshelis et al. 1983	12.9 ± 3.0	Pritchard and Robbins 1990	1.0 km/day * 0.54 days = 0.54	1.7 km/day * 0.54 days = 0.900	1.5
Wolf	4.4 - 6.0	Jedrzejewski et al. 2002; Webb 2009	8 - 56	Floyd et al. 1978	4.4 km/day * 0.3 days = 1.3 6 km/day * 0.3 days = 1.8 km average = 1.5 km	4.4 km/day * 2.3 days = 10 km 6 km/day * 2.3 days = 13.8 km average = 12 km	3
Coyote	4 – 4.4 (straight line distance)	Bekoff 1977; Andelt and Gipson 1979	2-5 km (bead "retention" distance)*	Lunney et al. 2002	2 km	5 km	2

Appendix 2.4 continued

		Laundré 2005; Dickson and Beier 2007	0.4-4.2 km from kill site†	Beier et al. 1995			
Cougar	10.4 - 16.5				0.4 km	4.2 km	2

*Gut passage time for coyotes could not be found in the literature. We used a measure of "retention distance" calculated for foxes (*Vulpes Vulpes*) and dogs (*Canis lupus familiaris*) using non-poisoned baits containing bead markers and measuring the distance from marked scat to the bait site.

† Gut passage time for cougars could not be found in literature. We used a measure of "retention distance" calculated for cougars where the authors reported an average distance of cougar scat from the last kill site.

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APPENDIX 2.5. Correlation matrix of continuous variables used in the spatial risk modelling for four predators from scats collected along the eastern slopes of the Rocky Mountains in Alberta. "0" refers to no correlation, "+" refers to a positive correlation (i.e. r > 0.6) and "—" refers to a negative correlation (i.e. r < -0.6).

	rugg	elev	slope	RUF	dist edge	dist trail	dist road	dist cut	dist water	cut dens	trail dens	road dens	edge dens	water dens	burn	cutb	closed	open	conif	decid	regen	herbac	shrub	ndvi	herbfg	totalfg
rugg	X	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
elev		X	+	—	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
slope			X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RUF				X	0	0	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+
distedge					X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
disttrail						X	0	0	0	+	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0
distroad							X	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
distcut								X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
distwater									X	+	0	0	0	—	0	0	0	0	0	0	0	0	0	0	0	0
cutdens										X	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0
traildens											X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
roaddens												X	0	0	0	0	0	0	0	0	0	0	0	0	0	0
edgedens													X	0	0	0	0	0	0	0	0	0	0	0	0	0
waterdens														X	0	0	0	0	0	0	0	0	0	0	0	0
burn															X	0	0	0	0	0	0	0	0	0	0	0
cutb																X	0	0	0	0	0	0	0	0	0	0
closed																	X	—	+	0	0	0	0	0	0	0
open																		X	—	0	0	0	0	0	0	0
conifer																			X	0	0	0	0	0	0	0
decid																				X	0	0	0	0	0	0
regen																					X	0	0	0	0	0
herbac																						X	0	0	0	0
shrub																							X	0	0	0
NDVI																								X	0	0
herbfg																									X	0
totalfg																										X

*Variable codes are defined in Table 2.1

APPENDIX 2.6. Description of methods and results from elk resource utilization function analysis

APPENDIX 2.6.1. Description of elk use, forage and predation covariates

Elk Use. To measure elk use of the study area, we created a population-level resource utilization function (RUF; Marzluff et al. 2004). We built a utilization distribution (UD) based on 6-hour GPS relocations of 66 adult female elk ($\bar{x}$ = 359 relocations per individual) from 1 May to 30 September, using a 100% fixed kernel home range in Geospatial Modelling Environment (GME version 0.7.4, http://www.spatialecology.com, accessed 10 Sept 2018), and calculated the bandwidth or search radius using plug-in, likelihood cross-validation and smoothed cross validation methods. After a visual assessment of the resulting UDs with the various bandwidth estimators, we determined the plug-in method best represented the land use of our elk population. Additionally, the plug-in estimator is ideal for large GPS datasets and in simulation models, had the lowest overall percent error for the overlap of estimated and true utilization distributions (Gitzen et al. 2006). Histograms indicated the UD was right-skewed, so we log transformed the UD to normalize the data. Next, we determined landscape characteristics at each UD pixel. Variable inputs in the RUF included herbaceous and total (herbaceous and shrub) forage biomass, herbaceous land cover (Hebblewhite et al. 2008), distance to nearest forest edge, burned vegetation (Hebblewhite 2006), wolf predation risk (Hebblewhite and Merrill 2007) and grizzly bear predation risk (Nielsen et al. 2002). Last, we related the resources at each pixel to the relative utilization value to calculate coefficients of resource use to then predict relative elk use across the study area. To account for spatial autocorrelation of pixel values inherent in a UD, we used a Matérn covariance function, which uses 2 parameters: (1) the range of spatial dependence (ρ) estimated from the bandwidth of the UD and (2) the smoothness of the UD

1444 surface (θ) (Marzluff et al. 2004). We calculated ρ by averaging the square root of the x and y

1445 variances estimated from the UD, and used the default 1.5 for the maximum likelihood

1446 smoothing estimate (Stonehouse et al. 2015). We used the *ruf* package in R 2.13 (Marzluff et al.

1447 2004) to obtain resource use coefficients. We ranked models using Akaike's Information

1448 Criterion (AIC), calculated from the Matérn maximum log-likelihood estimate, with a cut-off of

1449 ΔAIC = 4 to estimate the top model (Burnham et al. 2011).

1450 *Forage biomass.* We modelled herbaceous and total (shrub and herbaceous) biomass available to

1451 elk as a covariate in our elk resource utilization function and in spatial models predicting the

1452 presence of elk in predator scats. We estimated forage biomass (dry matter g/m^2) across the study

1453 area for each year from 2013-2016, accounting for annual precipitation and landcover changes

1454 affecting forage quality. Hebblewhite et al. (2008) derived annual estimates of peak herbaceous

1455 and shrub biomass (1-August) from a general linear model, predicting biomass as a function of

1456 land cover type, year, elevation, aspect and distance to continental divide based on field

1457 sampling of transects of 983 sites across the summer extent of the Ya Ha Tinda elk herd from

1458 2002-2004. Forage biomass was then estimated yearly from 2013-2016 to account for changes in

1459 forage availability caused by timber harvest (cutblocks) and fires that occurred in the study area.

1460 For cutblocks, forage availability was modelled based on Visscher and Merrill (2009), where

1461 they estiamted peak herbaceous and shrub biomass from sampling in 159 cutblocks from 1-20

1462 years post cut from 2001-2002 in areas north of the Ya Ha Tinda ranch. To estimate the forage

1463 availability for prescribed burns and wildfires, we followed methods of Hebblewhite et al. (2009)

1464 where they derived the relationship between time since burn and herbaceous and shrub biomass.

1465 Fire extents and date of origin were obtained from Banff National Park and Alberta Environment

1466 and Sustainable Resource Development's database. Hebblewhite et al. (2009) sampled biomass

1467   on 187 plots in 2002-2004 with 55 sites that were burned in 2003, and these sites were resampled

1468   in 2012. Separate quadratic relationships were developed for sites that were grassland pre-burned

1469   and sites that were shrub and forest pre-burn. For use in the RUF, we weighted the average of

1470   yearly RSFs from 2013-2016 by how many GPS points from elk were in each year.

1471   *Predation.* We modelled wolf and grizzly bear predation risk across the study area as a covariate

1472   in the elk resource utilization function. We considered wolf predation risk for elk proportional to

1473   a resource selection function (RSF) weighted by a probability density function (PDF) accounting

1474   for wolf pack size and kill rates. We used VHF collared wolves (n = 14) and GPS collared

1475   wolves (n = 16), part of 5 wolf packs that overlap the Ya Ha Tinda, to derive day- and night-time

1476   RSFs, where the wolves' locations were monitored from ground or air 0.5 to 1x per week

1477   (Hebblewhite and Merrill 2007). Covariates in the wolf RSF top model included: elevation (m),

1478   slope (%), aspect class (north, south or flat), landcover type, distance to edge (km), and distance

1479   to linear features (km) as a metric for human activity. Wolf RSFs were created yearly,

1480   accounting for landcover changes (burns, cutblocks, distance to edge), and within each year

1481   separate day and night RSFs were estimated. For use in the RUF, we averaged day and night

1482   RSFs (as we have equal GPS points from elk in the during day-time and night-time hours), and

1483   weighted the average of yearly RSFs from 2013-2016 by the number of GPS points from elk in

1484   each year.

1485   We considered predation risk for elk from grizzly bears rather than black bears, as bear

1486   predation on elk at Ya Ha Tinda is largely due to grizzly bears (Berg, unpubl. data). Nielsen et al.

1487   (2002) created an RSF for the study area from 9 GPS collared grizzly bears (6 females, 3 males).

1488   Variables in the bear RSF top model included: forest canopy cover, tree species composition,

1489   compound topographic index, distance to forest edge from regenerating forests, non-vegetated

1490   habitats, upland herb and upland treed sites, distance to stream and landcover type. Three RSFs

1491   per summer were created based on bear season: 1 May - 15 June: hypophagia, 16 June – 31 July:

1492   early hyperphagia, and 1 August – 15 October: late hyperphagia. We averaged each bear season

1493   to create a yearly RSF, then weighted the average of yearly RSFs from 2013-2016 by the number

1494   of GPS points from elk that were in each year. We weighted the grizzly bear RSF by estimates of

1495   grizzly bear numbers rather than telemetry data as telemetry data were not available. We

1496   weighted the final RSF by a probability density function (PDF) to account for spatial differences

1497   in reported densities of grizzly bears inside of Banff National Park (12.4 ± 1.5 individuals/1000

1498 km^2; Whittington and Sawaya 2015, Whittington et al. 2018) and outside the Park on Provincial

1499   lands (5.25 individuals/1000 km^2; Alberta Grizzly Bear Recovery Plan 2016). We smoothed the

1500   PDF population density values along the BNP border using a 12.9 km moving window, the size

1501   corresponding to the average kernel home range for local female grizzly bears ($520 \ km^2 \approx 12.9$-

1502   km radius; Nielsen et al. 2002).

1503   **APPENDIX 2.6.2** Resource utilization function results

1504   We built a resource utilization function (RUF) model to determine the habitat and

1505   predation variables that affect elk use across the study area. The top model (defined as ΔAIC >

1506   4) included all habitat and predation variables, where herbaceous biomass performed better as a

1507   metric for forage biomass than total (shrub + herbaceous; Appendix 2.5.3-2.5.4). Overall, elk

1508   used areas with high herbaceous forage biomass, burned areas, further from edge habitat, and in

1509   areas of high wolf and low grizzly bear selection. The mean RUF value at 1000 telemetry points

1510   was significantly higher than the mean RUF value at 1000 random points (t = 1.96, df = 1998, *P*

1511   < 0.001), indicating support for the elk resource utilization model.

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APPENDIX 2.6.3 Summary of model selection results based on AIC for resource utilization functions (RUF) that predict elk utilization based on habitat and predation variables. The top model (bolded) was used to create the resource utilization function for the study area along the eastern slopes of the Rocky Mountains in Alberta.

Model Variables*	k	AIC	ΔAIC	weight
herbfg + burn + wolf - gb - edge	**6**	**9565.66**	**0.00**	**1.00**
totalfg + burn + wolf - gb - edge	6	9780.10	214.44	0.00
wolf – gb	3	9789.52	223.86	0.00
herbfg + burn - gb - edge	5	9830.78	265.12	0.00
herbfg + burn – edge	4	9977.18	411.52	0.00
null model	2	10020.31	454.65	0.00
herbfg + burn + wolf - edge	5	10075.38	509.72	0.00

*Variable codes defined in Table 2.1

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APPENDIX 2.6.4 Beta coefficients (β), lower and upper confidence intervals (CI) for top resource utilization function (RUF) based on AIC predicting elk resource use across the study area along the eastern slopes of the Rocky Mountains in Alberta.

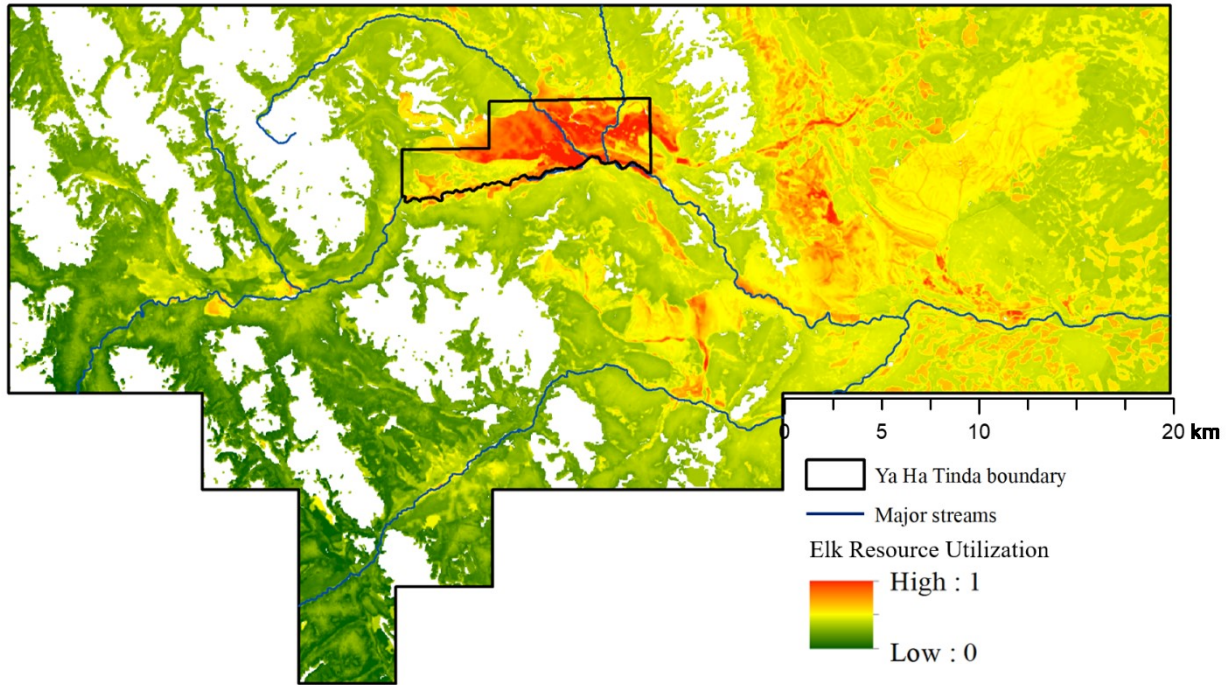| Model Variable	β	95% CI	
		Lower	Upper
Herbaceous forage biomass	0.022	0.019	0.024
Burns	0.95	0.72	1.18
Wolf predation risk	0.74	0.67	0.82
Grizzly bear predation risk	-0.17	-0.18	-0.16
Distance to edge	-0.0012	-0.0015	-0.0009

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APPENDIX 2.6.5. Elk resource utilization function based on GPS relocations from 66 female elk and habitat and predation risk variables predicting resource use (Appendix 2.6).
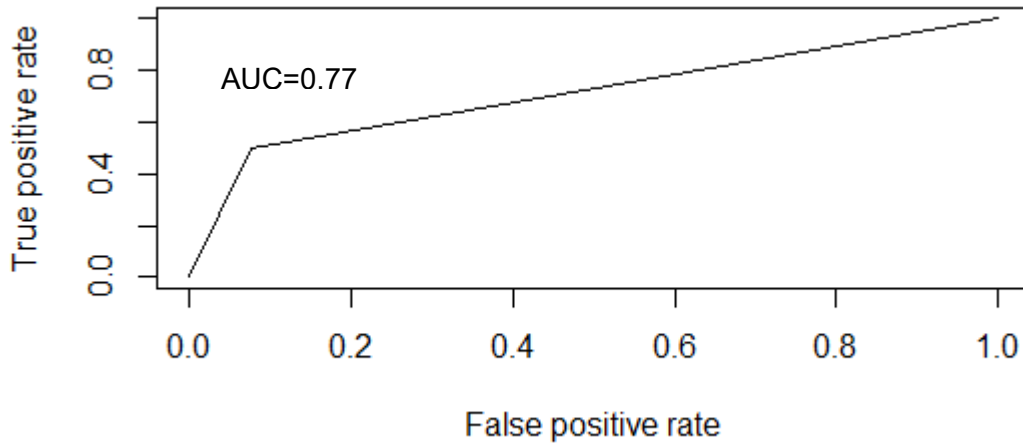
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APPENDIX 2.7. Receiver Operator Characteristic Curve assessing the two methods (macroscopic and DNA) used to detect elk presence in predator scats collected along the eastern slopes of the Rocky Mountains in Alberta. True positive rate refers to the macroscopic analysis results and false positive rate refers to the DNA analysis results.