

Coyotes, cattle, and native prey in southwest Saskatchewan

By

Shayla Jackson

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Department of Biology

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University of Winnipeg

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Abstract

Native grasslands are home to a disproportionate share of species at risk, and typically consist of a mosaic of ranchland and protected parkland. Livestock carcasses can attract coyotes and potentially subsidize the coyote population or increase depredation, which is a concern to ranchers in southwest Saskatchewan. A subsidized predator population may increase pressure on native prey species through apparent competition. In this thesis, I investigated the relationship between coyotes, cattle and native prey. In the second chapter, I used molecular methods to test how commonly coyotes consumed cattle and species at risk, and how geographic factors affected the presence of cattle versus deer in coyote diet. Deer and cattle were the most common food items. Scat containing cattle was typically found closer to a boneyard and the bison enclosure, whereas scat containing deer was typically further from a boneyard and the bison enclosure. Different individual coyotes may be consuming cattle versus deer and coyotes consuming cattle may show different travel behaviour than coyotes consuming native prey. However, I found no evidence that coyotes pose a direct threat to species at risk during the winter. In the third chapter, I observed coyotes during summer to test whether coyotes obtained direct and/or indirect benefits from cattle pastures, and how cows responded to the presence of coyotes. Coyotes hunted native prey and specifically ground squirrels more commonly than cattle, showing that they obtained indirect benefits from the use of cattle pastures. Cows responded to coyotes defensively, and although observations of coyotes approaching individual calves, rushing cow-calf herds, or harassing females for afterbirth were uncommon, these observations, combined with the coyotes' scavenging from cattle carcasses, indicate that coyotes also benefit directly by consuming cattle or cattle by-products. Further work identifying individual coyotes would help

to determine what proportion of the population is being subsidized by cattle and factors that might predispose individual coyotes to depredation.

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Table of Contents

Abstract.....	ii
Acknowledgements	iv
Table of contents	vi
List of tables.....	viii
List of figures.....	ix
Chapter 1: General introduction.....	1
References.....	6
Chapter 2: Venison or beef? Geographic variation in coyote diet.....	11
Abstract.....	11
Introduction.....	12
Methods.....	16
Results.....	24
Discussion.....	38
References.....	46
Chapter 3: Coyotes, cattle and Richardson’s ground squirrels.....	60
Abstract.....	60
Introduction.....	61

Methods	65
Results	72
Discussion.....	81
References.....	88
Chapter 4: General conclusion	98
References	102
Appendix A: Rancher materials.....	106
Appendix B: Map of vantage points for Chapter 3	110
Appendix C: Glossary and ethogram for Chapter 3.....	111

List of Tables

Table 2.1. Percentage of scats containing common food items and rank for mammalian food items detected in scats identified to the <i>Canis</i> genus with at least one other identification from Dec. 2021 to Mar. 2022.....	27
Table 2.2. Model selection results for <i>a priori</i> models considering the role of distance to boneyards, distance to prairie dog colonies, and distance to the bison enclosure in explaining the presence of cattle in coyote scat at Grasslands National Park and surrounding ranchland.....	31
Table 2.3. Parameter estimates for the two top-ranked logistic regression models for the relationship between distance to boneyards and distance to the bison enclosure on the likelihood of cattle being present in coyote scat at Grasslands National Park and surrounding ranchland...	32
Table 2.4. Model selection results for <i>a priori</i> models considering the role of distance to boneyards, distance to prairie dog colonies, and distance to the bison enclosure in explaining the presence of deer in coyote scat at Grasslands National Park and surrounding ranchland.....	36
Table 2.5. Parameter estimates for the two top-ranked logistic regression models for the relationship between distance to boneyards and distance to the bison enclosure on the likelihood of deer being present in coyote scat at Grasslands National Park and surrounding ranchland....	37
Table C1. Glossary.....	111
Table C2. Ethogram of coyote activities and hunting behaviour.....	112

List of Figures

Figure 2.1. Map of study site depicting the West Block boundary, native grasses, tilled areas and built areas.....	18
Figure 2.2. Base map used for scat collection during winter 2021-22, depicting the bison enclosure, scat collection route, West Block boundary, prairie dogtowns and homesteads.....	21
Figure 2.3. Map of scats identified to the <i>Canis</i> genus with cattle, $N = 37$ scats, or deer, $N = 97$ scats, during winter 2021-22.....	26
Figure 2.4. Map of scats identified to the <i>Canis</i> genus with vole, $N = 19$ scats, moose, $N = 14$ scats, or Richardson’s ground squirrel, $N = 9$ scats, during winter 2021-22.....	26
Figure 2.5. The distance of scat from a) boneyards and b) the bison enclosure based on the presence of cattle in scat, $N = 202$ scats.....	29
Figure 2.6. The probability of scat containing cattle based on the distance they were collected from a) boneyards and b) the bison enclosure.....	30
Figure 2.7. The probability of scat containing cattle based on the distance they were collected from a boneyard at different proximities to the bison enclosure, $Q1 = 25^{\text{th}}$ percentile, MD = median, $Q3 = 75^{\text{th}}$ percentile.....	30
Figure 2.8. The distance of scat from a) boneyards and b) the bison enclosure based on the presence of deer in scat, $N = 202$ scats.....	34
Figure 2.9. The probability of scat containing deer based on the distance they were collected from a) boneyards and b) the bison enclosure.....	35

Figure 3.1. Map of study site depicting the West Block boundary, native grasses, tilled areas and built areas.....67

Figure 3.2. The percentage of time in which focal coyotes participated in different activities...73

Figure 3.3. The percentage of focal observations in which hunting or eating of different species occurred, $N = 34$ focal observations in which hunting or eating occurred.....76

Figure 3.4. The percentage of time that coyotes a) hunted ground squirrels and b) were observed at different distances from cattle at different times of day relative to sunrise and sunset.....77

Figure 3.5. The percentage of focal observations of coyotes with ground squirrel interactions depending on the coyote’s distance from cattle.....78

Figure 3.6. The percentage of focal observations in which at least one cow or calf chased coyotes between May 29 to August 6, 2022.....80

Chapter 1: General Introduction

Conservative estimates of species extinction rates are 100 times greater than expected without human influence (Ceballos et al., 2015). Rapid growth of the human population has led to alarming rates of habitat loss for many species (Hoekstra et al., 2005; Gallant et al., 2007). Habitat loss is projected to be the greatest driver of biodiversity loss for terrestrial ecosystems (Sala et al., 2000), and may cause nearly 2000 species to become at risk of extinction in the next 50 years (Powers & Jetz, 2019). Worldwide, humans have taken over nearly a quarter of the earth's land area (Hoekstra et al., 2005), destroying about half of the area once covered by tropical forests (Wright, 2005).

North American grasslands: Mediterranean and grassland ecosystems are most at risk of biodiversity loss (Sala et al., 2000); facing habitat loss at a rate far greater than habitat protection (Hoekstra et al., 2005). Conservation policies favouring fire suppression can allow woody encroachment into native grasslands at the detriment of biodiversity (Grau et al., 2015). Behling et al. (2007) and Bond (2016) emphasize the importance of recognizing that not all grasslands are the result of deforestation. At one point, grasslands covered almost half the earth's surface (Anderson, 2006). In North America, more than 50% of temperate grasslands and savannas have been converted to other land uses (Hoekstra et al., 2005). Grasslands once stretched across most of central North America (Pieper, 2005), but most of these grasslands have since been plowed (Selby & Santry, 1996).

Native grazers including bison (*Bison bison*), pronghorn (*Antilocapra americana*) and elk (*Cervus canadensis*) have largely been removed from grasslands in favour of cattle (*Bos taurus*; Atkinson, 2009). Remaining native grasslands have a disproportionate share of species at risk

(Atkinson, 2009). Most grassland bird species are declining (Peterjohn & Sauer, 1999), largely due to habitat loss (Hill et al., 2014). Conserving remaining grasslands will be key to the protection of grassland birds (Hill et al., 2014), and to the many other species at risk that occupy the grasslands, such as the swift fox (*Vulpes velox*) and black-tailed prairie dog (*Cynomys ludovicianus*), many of which require active management to regain stability (Martin et al., 2018).

The role of ranchers in conservation: Often, important conservation efforts go unappreciated. Across North America, millions of dollars each year are generated from hunting revenue that supports multiple conservation activities, including habitat protection and restoration (Heffelginer et al., 2013). Yet, many people are unaware of the important role hunters play in conservation (Duda et al., 1998), and may express concerns about the presence of hunters in wildlife habitat (Heffelginer et al., 2013). Declines in waterfowl hunters have cost millions of dollars in lost revenue and thousands of hectares of protected wetland (Vrtiska et al., 2013).

Similar trends exist in the grasslands. Since many remaining native grasslands are used for livestock ranching (Atkinson, 2009), the role ranchers play in grassland stewardship is crucial. While the United States protects species at risk on both public and private lands (Olive, 2015), Canada relies on monetary incentive programs that encourage landowners and managers to participate in habitat conservation for species at risk. In southwest Saskatchewan, these programs have been well-received by local ranchers who feel they benefit from the programs (Reiter et al., 2021). Yet, as in the case of hunters, the important role ranchers play in grassland conservation is often overlooked by the public.

Some have suggested ranching could be detrimental to the conservation of grassland birds through livestock crushing the nests, but Bleho et al. (2014) has shown nest-crushing to be

a rare occurrence. Different grassland songbirds benefit from different stocking rates, so multiple rates across a region could benefit grassland birds (Sliwinski & Koper, 2015). Burrowing mammals such as ground squirrels (*Spermophilus* spp.) and badgers (*Taxidea taxus*), and native vegetation communities (Hayes & Holl, 2003), can also benefit from differing stocking rates across a region, emphasizing the value ranching can offer to native grasslands. Education programs sharing such information with the public could further progress habitat conservation incentive programs (Reiter et al., 2021) and contribute toward gaining ranchers the respect they deserve as conservation leaders.

Coyotes as mesopredators: Large predators including wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) have been extirpated from Canadian grasslands (Atkinson, 2009), enabling coyotes (*Canis latrans*) to become the top predator in a likely case of mesopredator release. Across North America, reductions in large predators have led to the rapid expansion of mesopredator populations, including coyotes, foxes (*Vulpes* spp.) and skunks (*Spilogale* spp., *Mephitis* spp.). Mesopredators have the potential to have greater impacts on prey species, including species at risk, than larger predators due to versatile diets that enable mesopredator populations to reach high densities (Prugh et al., 2009; Ripple et al., 2013). Berger and Conner (2008) showed that pronghorn neonate survival was greater in areas with wolves as compared to areas without wolves because wolves suppressed coyote populations. Mesopredators also tend to have less fear of human-occupied areas than larger predators, increasing their chances of direct negative interactions with humans (Prugh et al., 2009).

Anthropogenic subsidies: Additional food sources made available to predators through human activity, whether intentional or not, can be detrimental to alternative prey sources through

apparent competition. This occurs when a predator population is supported by a common prey species which results in increased predation on an alternative prey species (Holt, 1977). Petroelje et al. (2019) showed that wolves with access to cattle boneyards (where livestock carcasses are disposed of) experienced behavioural and diet differences compared to wolves without access to boneyards; consuming more cattle and travelling less. In regions where native prey options include species at risk, livestock subsidies could endanger their survival, especially if predators highly dependent on subsidies lose them due to human intervention and are forced to exploit alternative food sources (Van Duyne et al., 2009).

Objective and hypotheses: I conducted my research in the greater Grasslands National Park ecosystem in southwest Saskatchewan, where native grasslands are spread through a mosaic of parkland and ranchland (Atkinson, 2009). Previous work in this region has shown that some coyotes gain nearly half of their consumed estimated mammalian prey biomass from cattle during the winter and nearly a third of their consumed estimated mammalian prey biomass from cattle during the rest of the year (Lingle et al., 2022), but whether this behaviour persists over ten years after this study was conducted remains unclear. I used molecular methods to identify both consumed prey and predator identities with greater accuracy than morphological identification (Morin et al., 2011; Gosselin et al., 2017). Observational studies of coyotes near livestock are uncommon (Connolly et al., 1976) and none have been conducted in this region, but insight into the behaviour of coyotes near cattle could be important to determining risk factors of depredation. The objective of my thesis was to determine how the presence of cattle on the landscape influences the diet and behaviour of coyotes in a grassland ecosystem. In the second chapter, I assessed coyote diet from scat samples collected throughout the region. I tested whether geographic factors influenced the presence of cattle or native prey in scat and how

commonly species at risk were consumed. In the third chapter, I aimed to determine the benefits coyotes gained from cattle pastures and how cows responded to the presence of coyotes by conducting observations of coyotes on cattle pastures. Understanding the relationship between coyotes and cattle can help to determine the impact coyotes may have on species at risk in the greater Grasslands National Park ecosystem and may contribute to our understanding of the factors leading to livestock depredation.

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Chapter 2: Venison or beef? Geographic variation in coyote diet

Abstract

Native grasslands are home to a disproportionate share of species at risk, and typically consist of a mosaic of ranchland and protected parkland. Livestock carrion can subsidize grassland populations of mesopredators like coyotes, which may increase predation on native prey species. I aimed to examine the contribution of cattle, native prey, and species at risk to the coyote's winter diet at a grassland study site in southwest Saskatchewan. I tested the hypothesis that geographic factors affect the coyote's consumption of livestock versus native prey, but in opposing ways. I used molecular methods to assess the diet of coyotes during winter and ArcGIS to measure the distance of each scat to cattle boneyards, the bison enclosure, and the nearest prairie dog colony. Coyote scat contained mostly deer (48% of scats) and cattle (18%). Scat containing cattle was typically closer to a boneyard and the bison enclosure but was less likely to be found within the bison enclosure, whereas scat containing deer was typically further from a boneyard and the bison enclosure. The spatial distribution of cattle and deer scats suggested cattle consumption may influence the travel behaviours of coyotes and that different coyotes may be consuming cattle versus deer; however, this scat distribution may also have occurred if individual coyotes consumed both cattle and deer, but at different times and locations. If many coyotes consume cattle regularly through the winter, it is likely the population is being sustained to the detriment of native prey species, including species at risk.

Introduction

Grasslands once covered almost half of the earth's surface (Anderson, 2006), and stretched across most of central North America during the 15th century (Pieper, 2005). Most Canadian grasslands have now been plowed (Selby & Santry, 1996) and native grazers such as bison (*Bison bison*), pronghorn (*Antilocapra americana*) and elk (*Cervus canadensis*) have largely been removed in favour of cattle (*Bos taurus*; Atkinson, 2009). Remaining native grasslands are home to a disproportionate share of species at risk, including the black-tailed prairie dog (*Cynomys ludovicianus*), which in Canada, is only found within Grasslands National Park (Wobeser et al., 2009), greater sage grouse (*Centrocercus urophasianus*) and swift fox (*Vulpes velox*). Many of the species at risk in southwestern Saskatchewan require management to regain stability (Atkinson, 2009; Martin et al., 2018).

Larger predators have also been removed from Canadian grasslands (Atkinson, 2009) in favour of smaller predators, such as coyotes (*Canis latrans*), which are now considered the top predator in Grasslands National Park and surrounding areas through a likely case of mesopredator release (Prugh et al., 2009; Ripple et al., 2013). Compared to wolves (*Canis lupus*), coyotes can have greater effects on populations of small mammals (Ripple et al., 2013) and ungulates such as pronghorn. Berger and Conner (2008) showed that the survival of pronghorn neonates was greater in areas where wolves were present. Since most neonate deaths were due to coyote predation, suppression of coyote populations by wolves was of benefit to pronghorn. However, the presence of coyotes could be protective to other species at risk. Mezquida et al. (2006) argued that coyotes support sage grouse populations through suppression of fox, badger (*Taxidea taxus*), and raven populations (*Corvus corax*).

Given that many remaining native grasslands are used for livestock ranching (Atkinson, 2009), ranchers play a crucial role in grassland stewardship. While the United States protects species at risk on both public and private lands (Olive, 2015), Canada relies on monetary incentive programs that encourage landowners and managers to participate in habitat conservation for species at risk. In southwest Saskatchewan, these programs have been well-received by local ranchers who feel they benefit from the programs (Reiter et al., 2021).

Many ranchers tend to respond negatively to coyotes on their ranchland (Fitch, 1948). Coyotes may be drawn to ranchland by native prey such as wild ungulates, which are commonly found near cattle (Yoakum, 1975; Cooper et al., 2008), and Richardson's ground squirrels (*Urocitellus richardsonii*), which are more common in areas where cattle grazing is intense (Bylo et al., 2014). Coyotes can also be attracted to ranchland by anthropogenic subsidies, such as cattle carcasses. Kamler et al. (2004) showed that cattle carcasses can attract large numbers of coyotes from over 20 km away. Such anthropogenic subsidies can sustain predator populations beyond their natural numbers (Newsome et al., 2014).

Greater numbers of coyotes could be detrimental to alternative prey, including both native prey and livestock, through apparent competition (Werner et al., 2016), which occurs when the population of a primary prey species sustains or increases a population of predators, thereby increasing predation on other prey species (Holt, 1977). Apparent competition, and specifically livestock subsidies, can be detrimental to populations of species at risk that share predators with alternative prey species, especially if predators highly dependent on subsidies lose them due to human intervention and are forced to exploit alternative food sources (Van Duyne et al., 2009; DeCesare et al., 2010). In addition to species at risk that may become prey to coyotes,

increased coyote numbers could be detrimental to other predators in Grasslands National Park, like the threatened swift fox (Parks Canada, 2018), through direct competition for prey items (Kamler et al., 2003; Kamler et al., 2007). Increased numbers of coyotes might also increase the amount of nuisance behaviour by coyotes on ranchland (Goodale et al., 2015).

In Grasslands National Park, as elsewhere, ungulates are more common in the winter diet of coyotes while smaller prey items in the diet are more common in the summer (Crimmins et al., 2012; Lingle et al., 2022). However, even in the summer ungulates make up about half of the estimated mammalian prey biomass for coyotes, with about a third of the estimated mammalian prey biomass for coyotes in some areas consisting of cattle (Lingle et al., 2022), which some local ranchers suspect is obtained primarily as carrion. Coyote scats containing prairie dog remains were usually within half a kilometre of a prairie dog colony, while those containing cattle were distributed throughout the park, but far from prairie dog colonies (Lingle et al., 2022). The authors concluded this difference in location based on content could be due to different groups of coyotes specializing on different food sources within and around the park. Alternatively, coyotes could be accessing both food sources but at different times. If many coyotes are accessing cattle carcasses from nearby ranchlands, the coyote population could be sustained to the detriment of species at risk that could become prey items.

Non-invasive genetic sampling can expand knowledge on ecosystems by providing more accurate and detailed information on the predator of origin as well as consumed prey through collected scat samples (Monterroso et al., 2019). Compared to traditional identification of scat using morphological characteristics (Lingle et al., 2022), identification of predators through amplified mitochondrial DNA provides greater certainty. Morin et al. (2011) found this to be

especially true of coyote scats, which were only correctly identified in the field about half the time. However, Prugh and Ritland (2005) found estimated certainty levels for predator identification in the field corresponded well to molecular identification of coyote scats. Mitochondrial DNA can also provide a clearer picture of consumed prey within coyote scats when proper fecal sampling protocols are followed (Gosselin et al., 2017).

Molecular identification of prey can also have greater taxonomic resolution of prey remains and inclusion of prey remains that may not otherwise be identified, such as prey that was fully digested and therefore left no indigestible remnants for traditional identification (Deagle et al., 2009). This is particularly relevant to avian prey species, which are commonly underrepresented in scat, especially when mammalian remains are also present (Pires et al., 2011). Consequently, the role of avian species in a predator's diet can easily be misconstrued (Pires et al., 2011; Leighton et al., 2020). One study found a 4.5× greater proportion of avian prey in predator diet when using molecular rather than traditional methods (Oja et al., 2017). As a result, molecular markers, such as regions of the mitochondrial COI gene, are often used to identify the consumed prey of predators (Shedden et al., 2020; Quéméré et al., 2021). Within Grasslands National Park, many of the species at risk are avians (Martin et al., 2018), so a clearer picture of coyote diet will help to determine the impact of cattle subsidies on coyote diet and the potential risk coyotes may pose to populations of species at risk.

I tested the following hypotheses about coyote diet during the winter. First, I tested the hypothesis that geographic factors (boneyards, prairie dog colonies and an enclosure for bison) affect the consumption of livestock versus native prey. I predicted that scat containing cattle would be closer to cattle boneyards, but further from prairie dog colonies and the bison enclosure

because these two features are primarily inside the portion of Grasslands National Park where cattle do not occur. If particular individuals are relying on cattle vs. native prey, I would expect those individuals to remain closer to boneyards where cattle carrion is available and therefore, I would expect to find a greater number of scats containing cattle near boneyards. I predicted that scat containing deer would be further from cattle boneyards but closer to prairie dog colonies and the bison enclosure. Additionally, I tested the hypothesis that species at risk are present in the winter diet of coyotes. I predicted that species at risk would form a small but regular part of the winter diet of coyotes, indicating the potential of a subsidized coyote population to harm the recovery of species at risk.

Methods

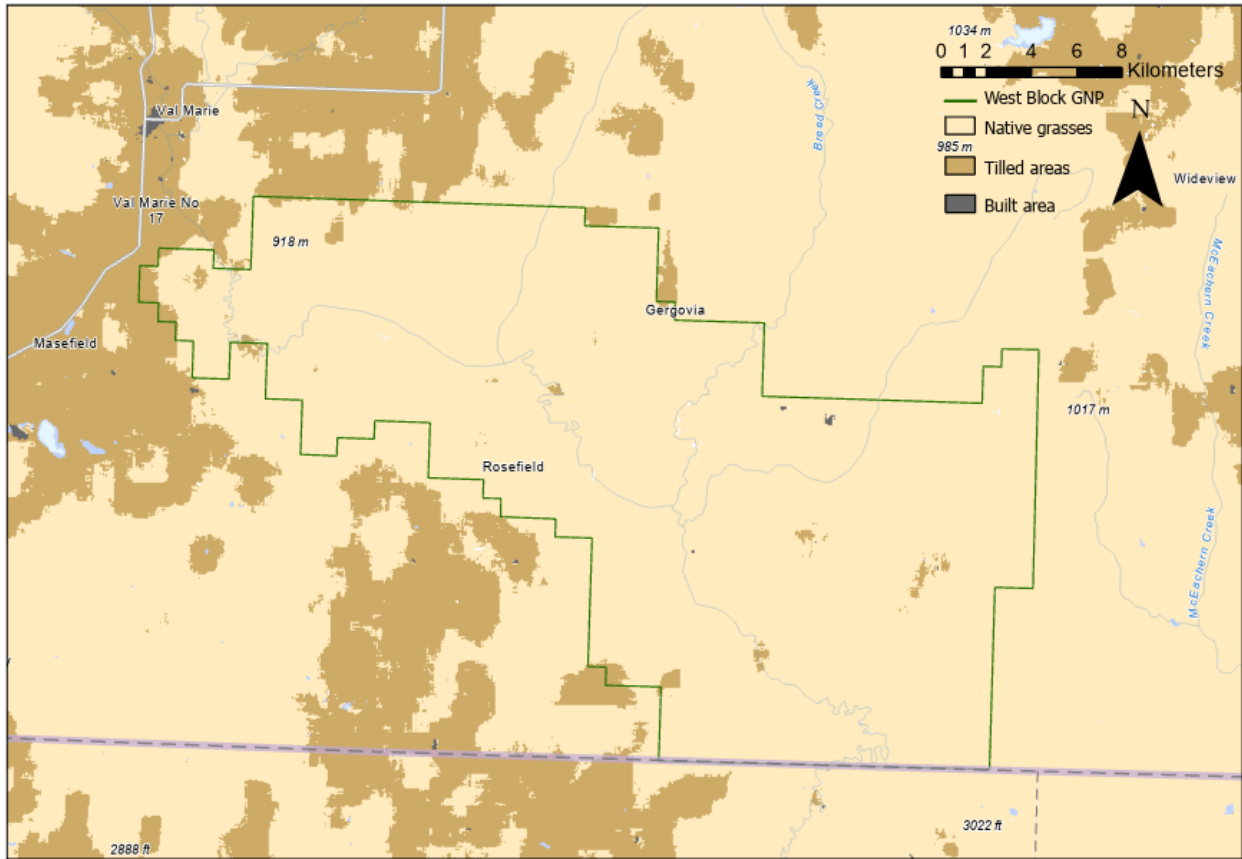
Study site: I conducted this research in the Greater Grasslands National Park (GNP) Ecosystem; including the West Block of GNP (~525km²), and cattle ranchlands adjacent to the West Block that extended approximately 27.5 km to the north. The West Block of GNP has a bison enclosure of about 181.69 km². Prairie dog colonies cover about 12.7 km² of the West Block, with a few additional colonies outside the park.

Terrain and climate: The Greater GNP Ecosystem mostly consists of native mixed grass prairie (Parks Canada Agency, 2018), but also contains tilled land (Figure 2.1). The terrain features “rolling hills, rugged coulees, and steep ravines” (Parks Canada Agency, 2018). During winter 2021 to 2022, the average temperature was -15.3°C in December (Min. = -38.9°C, Max. = 13.4°C), -10.3°C in January (Min. = -39.9°C, Max. = 6.3°C), -8.4°C in February (Min. = -35.7°C, Max. = 9.2°C) and -2.4°C in March (Min. = -31.5°C, Max. = 20.2°C). The approximate

average amount of snow on the ground was 4.56 cm in December, 9.32 cm in January, 4.40 cm in February and 7.64 cm in March (Government of Canada, 2023).

Native species: The Greater GNP Ecosystem contains critical habitat to many species at risk including the sage-grouse (*Centrocercus urophasianus*), black-tailed prairie dog (*Cynomys ludovicianus*) and swift fox (*Vulpes velox*; Parks Canada Agency, 2016; Parks Canada Agency, 2021). Mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) also occupy the park and surrounding area and are commonly consumed by coyotes, which are the dominant predator in the area (Lingle et al., 2022). Data on the abundance and geographic distribution of deer were not available. Moose (*Alces alces*) and pronghorn (*Antilocapra americana*) are also present. During the winter, hibernators such as Richardson's ground squirrels (*Uroditellus richardsonii*; Michener, 1992) and prairie dogs (Gummer, 2005; Kusch et al., 2021), and migrating avian species (Bent, 1907; Wedgewood, 1982) become largely unavailable to coyotes (Lingle et al., 2022). Although sage-grouse show some migratory behaviour, some individuals move as little as ~20 km to their winter range (Tack et al., 2012) so may still be available to coyotes in the study site through the winter.

Cattle practices: Most cattle are moved close to homesteads around December because ranchers feed cattle during the winter, then moved to grazing land further from homesteads in April or May, typically after calves have been born. Homesteads typically have boneyards nearby, where cattle carcasses are disposed of during the winter. Cows that die on grazing lands further from homesteads are typically left where they fall. During the winter, a research assistant monitored a boneyard in the study site. The boneyard had meat available each time it was checked throughout January and February 2022, and coyotes were regularly spotted at the boneyard.



Created by: Shayla Jackson

Date: Dec. 8th, 2023

Coordinate System: NAD 1983 UTM Zone 13N

Source: Field Data, Winter 2021-2022 & Karra et al. (2021)

Esri, NASA, NGA, USGS, Esri Canada, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, NRCAN, Parks Canada, Impact Observatory, Microsoft, and Esri.

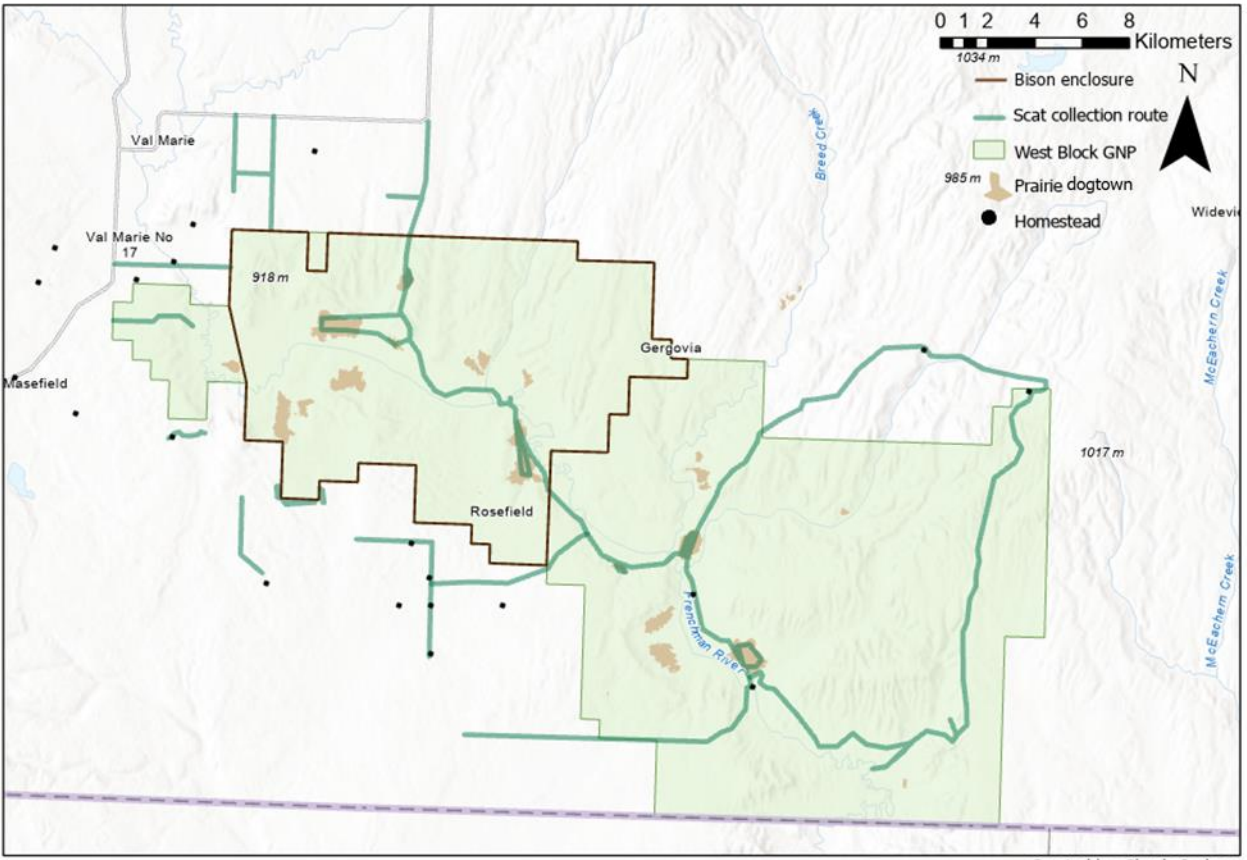
Figure 2.1. Map of study site depicting the West Block boundary, native grasses, tilled areas and built areas.

Collaboration with ranchers: I contacted several local ranchers by phone to seek permission to collect scat on private lands. I met with interested individuals during which they signed Landowner Access Authorization forms and answered questions (Appendix A) related to their seasonal cattle practices and experiences with coyotes. I used information gained from these meetings to develop a defined route from which I collected scat. I also used this information to create mapping layers on ArcGIS (ArcGIS 9.3, Redlands, CA) depicting the locations of cattle boneyards (not shown on maps).

Scat collection, storage, and transportation: With the help of a research assistant, I collected 890 predator scats along a pre-determined route from mid-December 2021 to mid-March 2022. The route included trails and roads inside and outside the park, prairie dog colonies and cattle carcass boneyards (Figure 2.2). The route was completed every 5-10 days during the collection period to increase the likelihood of collecting fresh scats (<5 days), except for between December and January, when scat was collected on December 19th and not again until January 7th. Research adhered to the Canadian Council on Animal Care (CCAC) Guidelines (University of Winnipeg Animal Care Committee AEW001).

I collected scats in medium Ziploc freezer bags. I removed as much air as possible from the bag before sealing it, then put it into another Ziploc bag that contained an identification card. I recorded the location of the scat on a Global Positioning System (GPS) unit using Universal Transverse Mercator (UTM) map coordinates. I copied this information onto the identification card for each scat, along with the date and time. At the end of each collection day, scats were moved into a -20°C freezer.

Frozen scats were shipped from the study site to the University of Winnipeg in boxes with dried ice. Upon arrival, research technicians at the university transferred the scats from the boxes into freezers at the university. Each scat spent a minimum of 1 week inside a -80°C freezer prior to analysis. *Echinococcus* spp. eggs can be disinfected in 2 days at this temperature (Krauss et al., 2003). Disinfected scats either continued to be stored at this temperature or were transferred to -20°C freezers.



Created by: Shayla Jackson
 Date: Sept. 24th, 2023
 Coordinate System: NAD 1983 UTM Zone 13N
 Source: Field Data, Winter 2021-2022
 Esri, NASA, NGA, USGS, Esri Canada, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, NRCan, Parks Canada

Figure 2.2. Base map used for scat collection during winter 2021-22, depicting the bison enclosure, scat collection route, West Block boundary, prairie dogtowns and homesteads.

Data analysis:

Final scat sampling: Of 890 collected scats, 564 were selected for molecular analysis. This number was selected based on time and cost constraints that prevented the analysis of all samples. To select these 564 samples, I removed scats recorded with incorrect UTM coordinates located outside the study site and scats that had been commented on as old (estimated >30 days). Of the remaining samples, all scats from December (27 scats) and March (102 scats) were included in the final dataset, as were scats that were <10 days old from January and February. The remaining samples were selected randomly from scats collected in January and February.

Molecular analysis: Post-collection, I prepared 12 mL homogenized subsamples from each scat with the help of a research assistant and sent these to the Canadian Centre for DNA Barcoding (CCDB) to determine the predator of origin and consumed vertebrate prey for each scat by sequencing 185 bp of the 3' end of the COI-5P barcode region of the COI gene (González et al., 2020; CCDB report, 2023). The CCDB extracted DNA from the homogenized subsamples and twice amplified DNA with the COI primer pair C_BloodmealF1_t1/ModMamRev_t1. The forward primer cocktail contained the primers BloodmealF1_t1 (TGTA AACGACGGCCAGTACCACWATTATTAAYATAAARCCMC) and BloodmealF2_t1 (TGTA AACGACGGCCAGTACTACAGCAATTAACATAAAACCMC), while the reverse primer cocktail contained the primers VR1d_t1 (CAGGAAACAGCTATGACTAGACTTCTGGGTGGCCRAARAAYCA), VR1_t1 (CAGGAAACAGCTATGACTAGACTTCTGGGTGGCCAAAGAATCA), and VR1i_t1 (CAGGAAACAGCTATGACTAGACTTCTGGGTGICCIAAIAAICA). Six 96-sample plates including 564 DNA samples as well as an extraction control and a PCR control for each plate

(CCDB correspondence) were sequenced on an Ion Torrent S5 next-generation sequencer (CCDB report, 2023). Sequence reads were filtered for size and quality and returned to me.

I blasted reference OTU sequences received from the CCDB report at NCBI (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to identify the probable predator of origin and vertebrate prey the predator consumed for each scat: both the predator and prey were identified to the genus level. For identifications to be included in the final dataset, the processed sample had to have yielded at least 100 reads with at least 95% identity across at least 100 bp, as recommended by the CCDB (CCDB report, 2023). Five hundred and twenty-one of 564 scats sent for molecular analysis met these quality control measures. Four hundred ninety-five (95%) of the quality-controlled scats returned a *Canis* identification, 202 (41%) of which also contained at least one other identification, which were assumed to be eaten. Ninety-one percent of these scats contained only one food item, 9% two items, and 0.5% (1 scat) contained three food items. Although the short length of the molecular markers limited molecular identifications to the genus level, in some cases the geographic range of animals enabled me to determine species.

Geographic Information Systems Analysis: I developed mapping layers in ArcGIS (ArcGIS 9.3, Redlands, CA) providing information on the location of cattle carcasses (not shown on maps), and the location of each predator scat. I obtained base map data from Parks Canada including the location of prairie dogtowns, park boundaries and the bison enclosure as of 2021. I used these layers to measure the distance of each scat to potential food sources (boneyard, prairie dog colony) or the bison enclosure, from which cattle are excluded. When calculating the distance of each scat to the nearest boneyard, I included confirmed boneyards I identified during interviews with ranchers, as well as homesteads, which commonly have boneyards nearby.

Statistical analysis: To test the hypothesis that geographic factors (boneyards, prairie dog colonies and the bison enclosure) affect the consumption of livestock versus native prey, I determined the frequency of occurrence of each prey item in scat, defined as the percentage of scat containing each prey item. I used a Pearson's correlation to examine whether predictors were correlated. I used logistic regressions and information theory (Burnham et al. 2011) to compare a priori models examining whether the distance of scat to the nearest boneyard, prairie dog colony, bison enclosure, or a model including both the distance to the nearest boneyard and the distance to the bison enclosure predicted the presence of cattle or deer remains (the most common food items) in *Canis* scat. I identified the model producing the lowest Akaike information criterion, adjusted for sample size (AICc), as the most predictive of the presence of cattle or deer in the scat, choosing the simpler of two models if it fell within 2 AICc units of a more complex model (Arnold 2010; Burnham et al. 2011; Mundry 2011). I used odds ratios and logistic regression curves for predictors in the highest ranked models to determine the strength and direction of effects. Additionally, I used chi-square tests of independence to determine whether scat containing cattle or deer was more common inside or outside the bison enclosure. Statistical analyses were conducted in R (R Core Team, 2022).

Results

Overview of scats in southwest Saskatchewan: Deer was the most commonly detected prey genus, and occurred in 48% of scats, followed by cattle, at 18% (Figure 2.3, Table 2.1). Other mammalian groups that comprised 4% to 9% of scats included voles, moose, sciurids, leporids, and pocket gophers (Figure 2.4). Avian DNA was present in 5% of scats and was distributed across multiple genera (Table 2.1).

Five (3%) quality-controlled scats identified to the *Canis* genus with at least one other identification contained a species at risk. This included two scats identified as badger (*Taxidea*) that had consumed prairie dog (*Cynomys*); two (1%) *Canis* scats that consumed prairie dog, and one scat containing longspur (*Calcarius*), which did not return a predator identification.

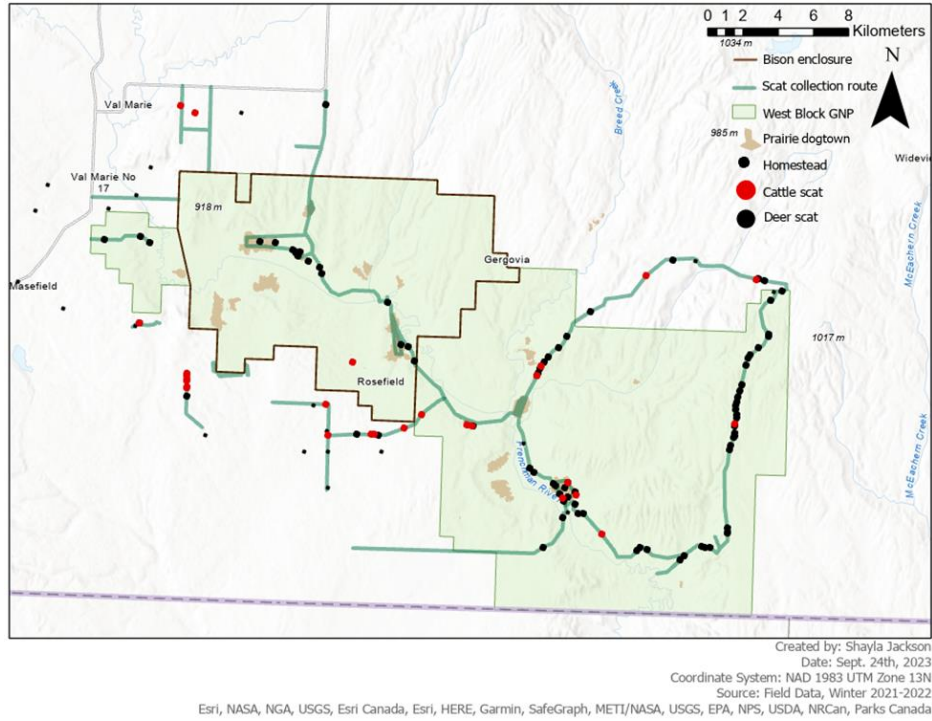


Figure 2.3. Map of scats identified to the *Canis* genus with cattle, $N = 37$ scats, or deer, $N = 97$ scats, during winter 2021-22.

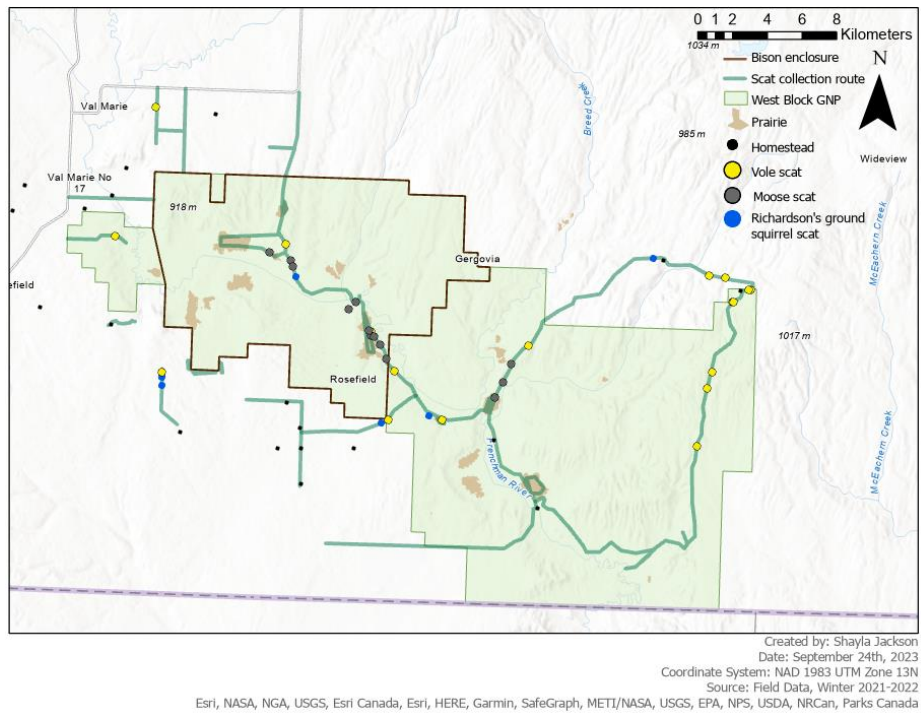


Figure 2.4. Map of scats identified to the *Canis* genus with vole, $N = 19$ scats, moose, $N = 14$ scats, or Richardson's ground squirrel, $N = 9$ scats, during winter 2021-22.

Table 2.1. Percentage of scats containing common food items and rank (1 to 4) for mammalian food items detected in quality-controlled scats identified to the *Canis* genus with at least one other identification ($N = 202$ scats; 222 prey detections) from Dec. 2021 to Mar. 2022. Percentages do not sum to 100 because some scats contained more than one food item.

Food item	Percent	Rank
Cattle	18	2
Wild ungulates	57	1
White-tailed & mule deer	(48)	
Moose	(7)	
Pronghorn	(2)	
Sciurids	6	4
Black-tailed prairie dog	(1)	
Richardson ground squirrel	(5)	
Leporid	5	
Vole	9	3
Pocket gopher	4	
Avian	5	

Avian prey items included sharp-tailed grouse (*Tympanuchus phasianellus*), grey partridge (*Perdix perdix*), ring-necked pheasant (*Phasianus colchicus*), black-billed magpie (*Pica hudsonia*), snow bunting (*Plectrophenax nivalis*), great horned or snowy owl (*Bubo*) and rock dove (*Columba livia*). Leporid included white-tailed jackrabbit or snowshoe hare (*Lepus*) and Nuttall's cottontail (*Sylvilagus nuttallii*). Vole included meadow vole (*Microtus pennsylvanicus*). Species for some genera were identified based on known distributions of members of each genus.

Spatial distribution of *Canis* scats containing cattle: Scat containing cattle was more likely to be closer to a boneyard and to the bison enclosure than scat without cattle remains (Figure 2.5, Figure 2.6, Figure 2.7, Table 2.2, Table 2.3). Scat containing cattle was typically 1.9 km from a boneyard and 2.8 km from the bison enclosure (Figure 2.5). Scat that did not contain cattle was typically 4.5 km from a boneyard and 4.9 km from the bison enclosure. These two predictor variables were not correlated ($r(200) = 0.09$, $p = .206$, $N = 202$ scats).

The best model (lowest AICc and highest weight) explaining the location of cattle scat included the distance to a boneyard, the distance to bison enclosure, and the interaction between these terms (Table 2.2; Table 2.3). The interaction between distance to boneyard and distance to the bison enclosure indicated that scat near boneyards was more likely to contain cattle when it was also near the bison enclosure (Figure 2.7). However, even though scat was more likely to contain cattle when closer to the bison enclosure, scat collected from inside the bison enclosure itself was less likely to contain cattle than scat collected outside the bison enclosure (1 of 34 vs. 36 of 168; $\chi^2(1) = 5.28$, $p = .022$, $N = 202$ scats).

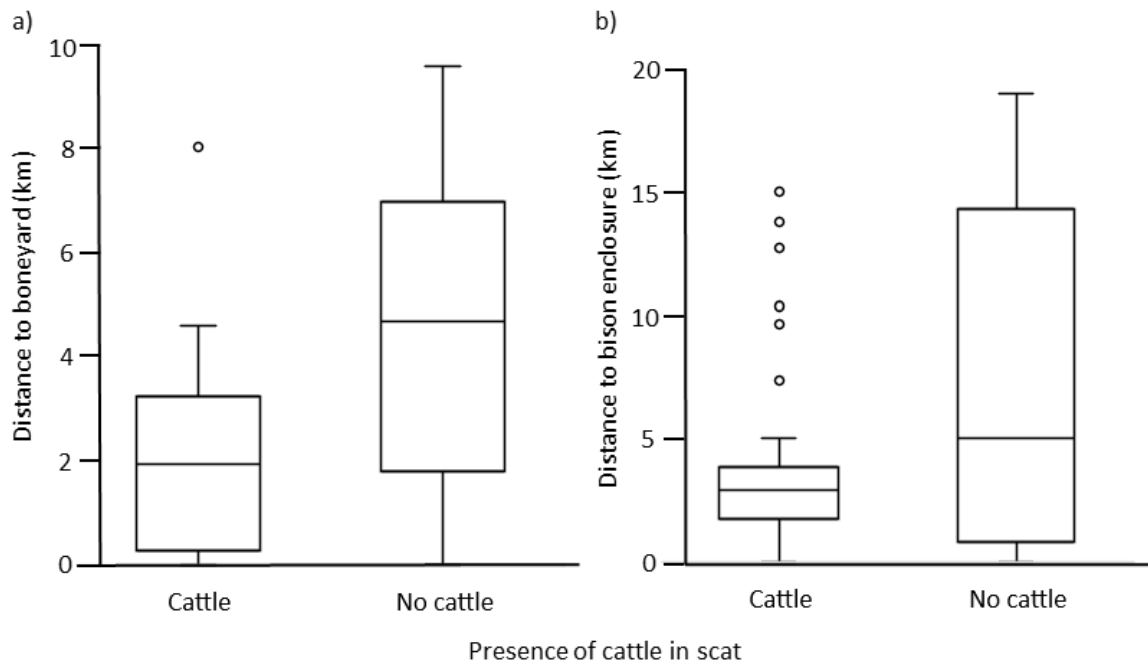


Figure 2.5. The distance of scat from a) boneyards and b) the bison enclosure based on the presence of cattle in scat, $N = 202$ scats. Lines depict the 25th percentile, median line and 75th percentile. Whiskers indicate the minimum and maximum values, excluding outliers.

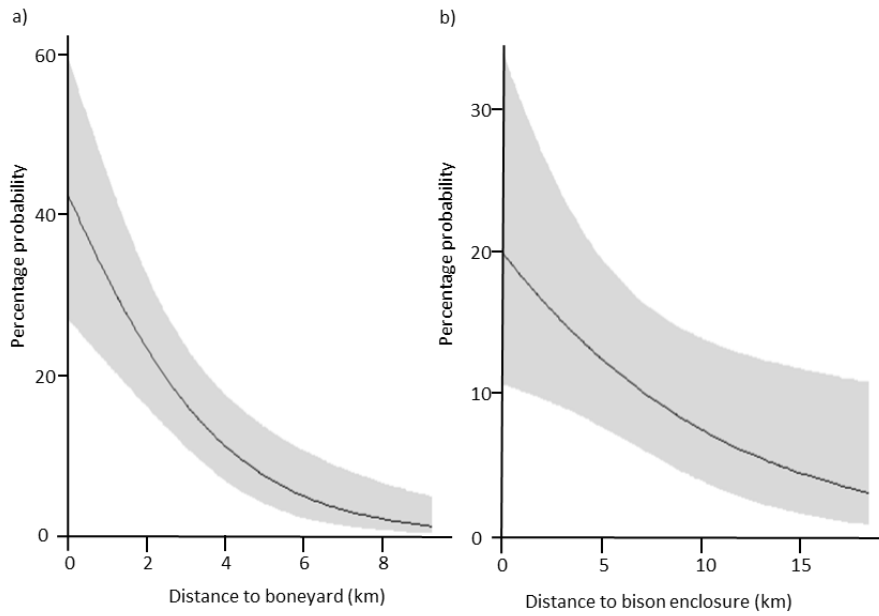


Figure 2.6. The probability of scat containing cattle based on the distance they were collected from a) boneyards and b) the bison enclosure. Shaded areas indicate 95% confidence interval.

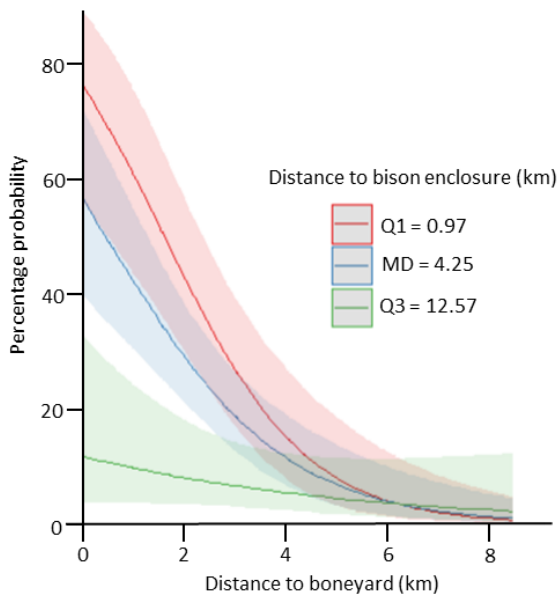


Figure 2.7. The probability of scat containing cattle based on the distance they were collected from a boneyard at different proximities to the bison enclosure, Q1 = 25th percentile, MD = median, Q3 = 75th percentile. Shaded areas indicate 95% confidence interval.

Table 2.2. Model selection results for *a priori* models considering the role of distance to boneyards (Boneyard), distance to prairie dog colonies (Dogtown), and distance to the bison enclosure (Bison enclosure) in explaining the presence of **cattle** in coyote scat ($N = 202$) at Grasslands National Park and surrounding ranchland. For each model, I present the AICc, Δ AICc, and model weight (w). The highest ranked models, as assessed by producing the lowest AICc with the fewest parameters, are highlighted in bold. The intercept is included as a parameter in all models.

Model	Predictors	k	AICc	Δ AICc	w
1. Null	Intercept	1	194.39	39.68	0.00
2. Boneyard	Boneyard	4	167.47	12.76	0.00
3. Dogtown	Dogtown	4	196.07	41.36	0.00
4. Bison enclosure	Bison enclosure	4	187.96	33.25	0.00
5A. Combined 1	Boneyard + Bison enclosure	5	157.32	2.60	0.21
	Boneyard + Bison enclosure				
5B. Combined 2	+ Boneyard*Bison enclosure	6	154.71	0.00	0.79

Table 2.3. Parameter estimates for the two top-ranked logistic regression models for the relationship between distance to boneyards (Boneyard) and distance to the bison enclosure (Bison enclosure) on the likelihood of **cattle** being present in coyote scat ($N = 202$) at Grasslands National Park and surrounding ranchland. I report adjusted unit odds ratios and 95% confidence ratios of finding cattle in scat for each kilometre distance from a boneyard or each kilometre distance from the bison enclosure. P -values for variables are based on Wald- χ^2 scores.

Model 5A: Boneyard and Bison enclosure

Variable	df	Wald- χ^2	P -value	¹ Odds ratio	Lower 95%CI	Upper 95%CI
Boneyard	1	21.86	<.001	0.60	0.49	0.75
Bison enclosure	1	9.80	.002	0.85	0.77	0.94

Model 5B: Boneyard, Bison enclosure and Boneyard*Bison enclosure

Variable	df	Wald- χ^2	P -value	¹ Odds ratio	Lower 95%CI	Upper 95%CI
Boneyard	1	16.77	<.001	0.50	0.37	0.68
Bison enclosure	1	7.53	.006	0.76	0.66	0.88
Boneyard*Bison enclosure	1	5.68	.017	1.04	1.01	1.08

¹Unit odds ratios <1.0 represent the increased likelihood of cattle in a scat being closer to a boneyard/the bison enclosure.

Spatial distribution of *Canis* scats containing deer: Scat containing deer was more likely to be further from a boneyard and from the bison enclosure than scat without deer remains (Figure 2.8, Figure 2.9, Table 2.4, Table 2.5). Scat containing deer was typically 5.1 km from a boneyard and 9.4 km from the bison enclosure (Figure 2.8). Scat that did not contain deer was typically 3.0 km from a boneyard and 2.7 km from the bison enclosure.

The best model (lowest AICc and highest weight) explaining the location of deer scat included the distance to a boneyard and the distance to the bison enclosure (Table 2.4; Table 2.5). However, even though scat was more likely to contain deer when further from the bison enclosure, scat collected from outside the bison enclosure was not more likely to contain deer than scat collected inside the bison enclosure itself (16 of 34 vs. 81 of 168; $\chi^2(1) < 0.01$, $p > .999$, $N = 202$ scats).

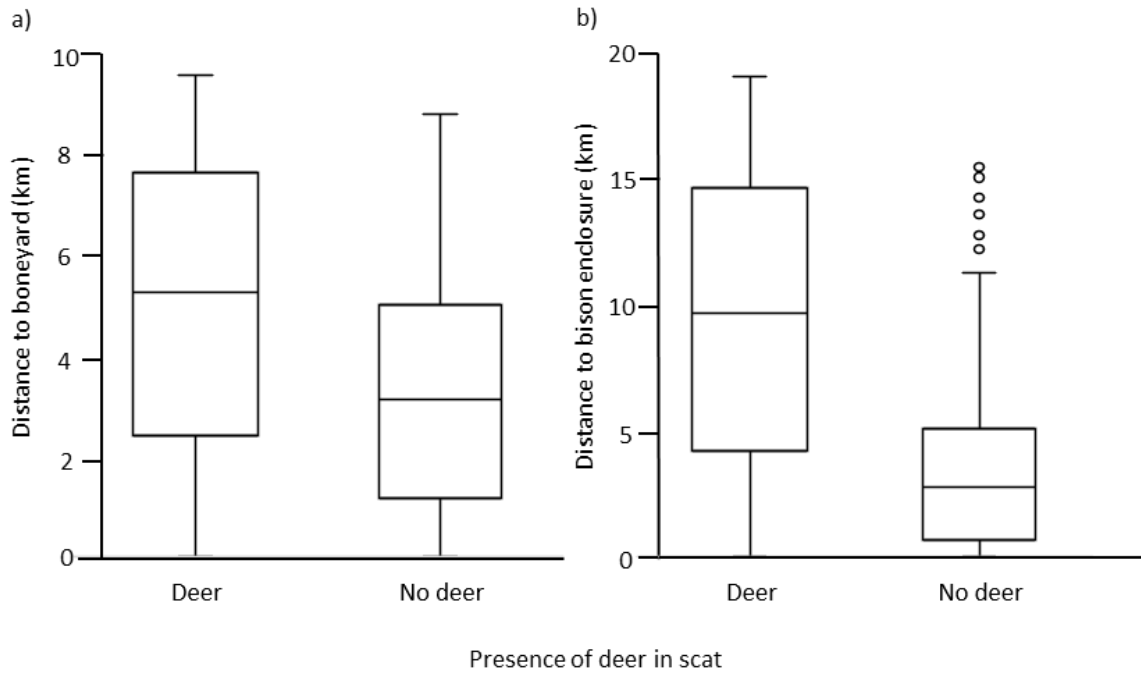


Figure 2.8. The distance of scat from a) boneyards and b) the bison enclosure based on the presence of deer in scat, $N = 202$ scats. Lines depict the 25th percentile, median line and 75th percentile. Whiskers indicate the minimum and maximum values, excluding outliers.

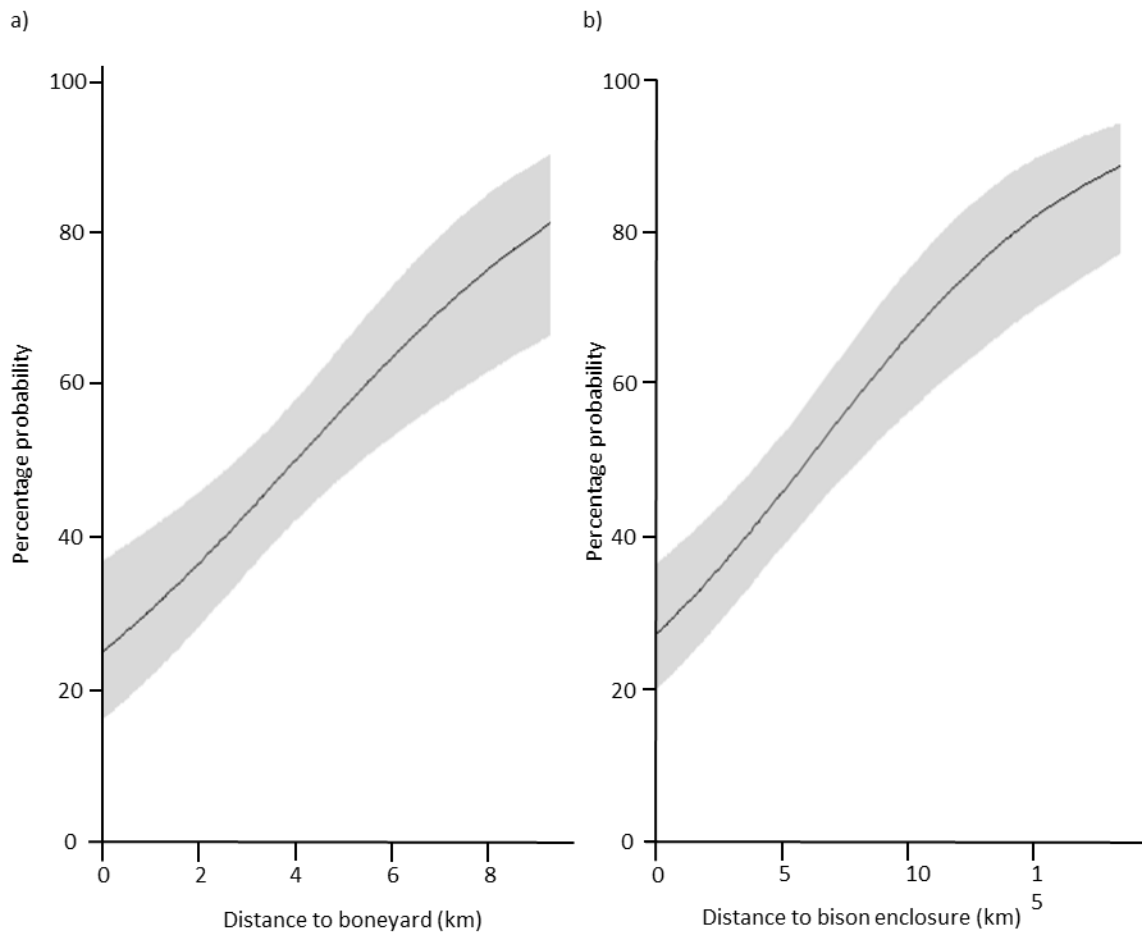


Figure 2.9. The probability of scat containing deer based on the distance they were collected from a) boneyards and b) the bison enclosure.

Table 2.4. Model selection results for *a priori* models considering the role of distance to boneyards (Boneyard), distance to prairie dog colonies (Dogtown), and distance to the bison enclosure (Bison enclosure) in explaining the presence of **deer** in coyote scat ($N = 202$) at Grasslands National Park and surrounding ranchland. For each model, I present the AICc, Δ AICc, and model weight (w). The highest ranked models, as assessed by producing the lowest AICc with the fewest parameters, are highlighted in bold. The intercept is included as a parameter in all models.

Model	Predictors	k	AICc	Δ AICc	w
1. Null	Intercept	1	281.73	51.77	0.00
2. Boneyard	Boneyard	4	264.13	34.16	0.00
3. Dogtown	Dogtown	4	283.77	53.81	0.00
4. Bison enclosure	Bison enclosure	4	248.84	18.87	0.00
5A. Combined 1	Boneyard + Bison enclosure	5	229.97	0.00	0.66
5B. Combined 2	Boneyard + Bison enclosure + Boneyard*Bison enclosure	6	231.29	1.32	0.34

Table 2.5. Parameter estimates for the two top-ranked logistic regression models for the relationship between distance to boneyards (Boneyard) and distance to the bison enclosure (Bison enclosure) on the likelihood of **deer** being present in coyote scat ($N = 202$) at Grasslands National Park and surrounding ranchland. I report adjusted unit odds ratios and 95% confidence ratios of finding cattle in scat for each kilometre distance from a boneyard or each kilometre distance from the bison enclosure. P -values for variables are based on Wald- χ^2 scores.

Model 5A: Boneyard and Bison enclosure

Variable	df	Wald- χ^2	P -value	¹ Odds ratio	Lower 95%CI	Upper 95%CI
Boneyard	1	18.01	<.001	1.33	1.16	1.51
Bison enclosure	1	27.57	<.001	1.19	1.12	1.28

Model 5B: Boneyard, Bison enclosure and Boneyard*Bison enclosure

Variable	df	Wald- χ^2	P -value	¹ Odds ratio	Lower 95%CI	Upper 95%CI
Boneyard	1	18.48	<.001	1.40	1.17	1.68
Bison enclosure	1	29.00	<.001	1.25	1.12	1.41
Boneyard*Bison enclosure	1	0.78	.781	0.99	0.97	1.01

¹Unit odds ratios >1.0 represent the increased likelihood of deer in a scat being further from a boneyard or the bison enclosure.

Discussion

Consistent with the tendency of coyotes to consume more large prey during the winter (Crimmins et al., 2012; Lingle et al., 2022), coyotes mostly consumed deer or cattle between December 2021 and March 2022. I obtained support for the hypothesis that geographic factors affect the consumption of livestock versus native prey, but in opposing ways. Both boneyards and the bison enclosure influenced the location of scats containing cattle and scats containing deer, with cattle scats located closer to boneyards and the bison enclosure and deer scats further away. I found little support for the hypothesis that species at risk would be present in the winter diet of coyotes. Only two *Canis* scats contained species at risk, although several *Canis* scats contained ground-nesting avian species. Within the Greater GNP Ecosystem, many species at risk are ground-nesting avians (Parks Canada Agency, 2016). No scats were identified as fox, which was surprising given red foxes (*Vulpes vulpes*) are common in the region and the endangered swift fox is also present (Parks Canada Agency, 2016).

Spatial distribution of scat containing cattle: Scat containing cattle was more commonly collected near boneyards, supporting my prediction. Kamler et al. (2004) recorded coyotes travelling greater distances to boneyards with greater amounts of carrion and staying near boneyards while large amounts of carrion remained. Wolves with access to boneyards use them frequently (Morehouse & Boyce, 2011; Petroelje et al., 2019) and travel less than wolves without access to boneyards (Petroelje et al., 2019). Morehouse and Boyce (2011) noted that cattle carrion consumption was greater in the winter, during which time cattle were kept on private rather than public lands. In the Greater GNP Ecosystem, most cattle are moved close to homesteads during the winter and moved to grazing land further from homesteads from spring to

fall, so the finding that scat containing cattle was commonly near boneyards could be restricted to, or more pronounced, during the winter.

If, like wolves (Petroelje et al., 2019), coyotes consuming cattle in the Greater GNP Ecosystem travel less than coyotes consuming native prey, then it is possible that individual coyotes in the region are specializing on cattle or native prey. Many coyotes consuming cattle could lead to a subsidized population (Ciucci et al., 2020), which could increase predation of native prey through apparent competition. This occurs when a predator population is supported by one species which leads to increased predation on another species (Holt, 1977), and can be a major threat to species at risk (DeCesare et al., 2010).

In contrast to my prediction, scat containing cattle was also more common near but outside the bison enclosure. This is likely an artifact of the high number of homesteads with confirmed and potential boneyards around the western and southwest borders of the park, where the bison enclosure is located, rather than an attraction of coyotes that have consumed cattle to the bison enclosure. An alternative explanation could be that coyotes move into the park where they are protected from human persecution after eating cattle, but this explanation is unlikely given that only one scat containing cattle was found inside the bison enclosure. If coyotes that consume cattle do travel into the park, it may be after the digestion and deposition of scat containing cattle.

Lingle et al. (2022) reported 8% of 284 coyote scats collected within the bison enclosure contained cattle during winters from 2007 – 2009, which is greater than the 3% of 34 reported here. Since reintroduction of 71 bison to Grasslands National Park in 2005, the herd has grown to 400-500 bison (Parks Canada Agency, 2022) and visitation to the park has more than doubled in

the last decade (Parks Canada, 2023a; Parks Canada, 2023b). It is possible this increased human activity has reduced coyote activity within the park or caused coyotes to shift their use of the park to less visited routes. Alternatively, greater vehicular traffic, and foot traffic of visitors and bison, may have led to a greater number of coyote scats being destroyed or removed from the trails, roads and prairie dog colonies inside the park where I collected scat.

The amount of time from ingestion to deposition of scat can vary based on factors such as diet composition (Burrows et al., 1982; Rolfe et al., 2002) and activity level (White et al., 2007), so although coyotes could potentially travel long distances between consumption of prey and deposition of scat, my results would suggest that any travel that occurs is not random. Wolves fed a diet of native prey including large ungulates deposited scats from 8 – 56 hours after feeding (Floyd et al., 1978), which is comparable to the reported digestion times of other canids (Burrows et al., 1982; Childs-Sandford & Angel, 2006) and so is likely also comparable to the digestion time of coyotes.

If this is the case, then scats containing cattle collected at boneyards could be indicative of coyotes remaining relatively close to boneyards hours after a cattle meal. A movement model using an estimated ingestion to deposition time of 2-50 hours to predict the capability of dingoes to disperse fungal spores indicated dingoes that had consumed small prey typically dispersed spores about 2 km. If coyotes follow similar behavioural patterns, then a long time to deposition may not indicate a long distance travelled. Given Petroelje et al.'s (2019) finding that wolves with access to boneyards occupy home ranges nearly half the size of and are less active than wolves without access to boneyards, it is likely that coyotes consuming cattle from boneyards during winter in this region do not regularly travel far into the park.

Spatial distribution of scat containing deer: In support of my prediction, scats containing deer were located further from boneyards. The average home range of resident coyotes is 10-15 km², but this number can vary considerably (Bowen, 1982; Gese et al., 1988; Kamler et al., 2004). For my study area, this means it is unlikely that I collected scat from the same coyote on opposite ends of the park, but there is certainly room for coyotes to access both cattle boneyards and deer based on scat locations within a 15 km² range. It is possible that different coyotes may be consuming cattle versus deer, or individuals could consume both cattle and deer regularly, but at different times and locations such that these two species do not co-occur in scats.

Scat containing deer tended to be located further from the bison enclosure, also contrary to my prediction. I expect this result is due to the especially high number of scats containing deer collected in the backcountry loop of Grasslands National Park, since scats containing deer were also common inside the bison enclosure. Nearly half of scats collected in the bison enclosure contained deer and most others contained moose. The backcountry loop of Grasslands National Park is more remote and consists largely of hills when compared with the bison enclosure and may provide coyotes with improved opportunities to hunt deer. Mule deer tend to occupy rougher terrain than white-tailed deer (Lingle, 2002; Brunjes et al., 2006), so scats containing deer collected in this area could also be indicative of the species hunted or coyote hunting success in this habitat.

Neither scat containing cattle nor deer were affected by the location of prairie dog colonies. Lingle et al. (2022) likewise found no relationship between prairie dog colonies and scats containing deer. Those authors reported that scats containing cattle were likely to be further from a prairie dog colony, but this relationship only existed from spring to fall. This relationship

makes sense given that coyotes consumed prairie dogs regularly from spring to fall, but much less through the winter (Lingle et al., 2022) when prairie dogs in their northern range are hibernating (Gummer, 2005; Kusch et al., 2021). Scats containing prairie dog in the winter are likely to be old scats deposited in the fall, or scats collected in February or later, when prairie dogs began to emerge from hibernation (Kusch et al., 2021).

Presence of species at risk: Only two *Canis* scats contained prairie dog, weakly supporting my prediction that species at risk would be consumed by coyotes during the winter. This finding suggests that coyotes pose a minimal direct threat to species at risk during the winter. However, Lingle et al. (2022) found higher levels of prairie dog consumption from spring to fall. Additionally, in my results, avian prey was more common than prairie dog, and many of the avian species detected were ground-nesting birds. Coyotes are unlikely to show a high level of discrimination between avian species with similar characteristics and many of the species at risk in the Greater GNP Ecosystem are ground-nesting avian species (Parks Canada Agency, 2016). Many of these species migrate south during the winter (Bent, 1907; Wedgwood, 1982) and so could not be consumed during the winter. Unsurprisingly, Lingle et al. (2022) found a higher level of avian consumption from spring to fall than during the winter. It is likely that coyotes pose a greater threat to these species during the summer months, and this threat could be exacerbated by winter subsidies (Newsome et al., 2014).

Future work: In addition to year-round investigations that would provide further information on the impact of coyotes and carrion subsidies on species at risk, this work could be expanded by more detailed molecular work. In the present research, I was able to identify 95% of quality-controlled scats to the *Canis* genus but could not confirm the predator species that deposited each

scat. Most *Canis* scats collected were likely to have originated from coyotes, since no other wild predators in the *Canis* genus occupy the Greater Grasslands National Park (GNP) Ecosystem (Atkinson, 2009). Although pet dogs are commonly brought on trails inside the park and through cattle pastures by ranchers, this is likely to be less common in the winter and I aimed to collect fresh scats (<5 days) during collection. Sightings of coyotes at boneyards through the winter were common and many scats containing cattle were collected further from boneyards than pet dogs might be expected to wander from their homes, but molecular confirmation of predator species would provide greater certainty (Morin et al., 2011).

Prey species can also be identified more effectively with DNA metabarcoding (Gosselin et al., 2017), since prey items can be identified when no physical material remains for morphological identification (Deagle et al., 2009). Egeter et al. (2014) found molecular identification of frogs consumed as prey improved detection by 53% in predator scats as compared to morphological identification, and Casper et al. (2007) found the number of prey items detected in separate scat samples increased by 24% when using molecular methods. In my research, most scats contained only one food item. Given that molecular identification was unlikely to miss many food items and 75% of scats consisted of either wild ungulates or cattle, it may be that coyotes are less inclined to consume more than one food item when the initial food item yields a large meal, leading to these food items being deposited individually. Additional molecular identification involving further mtDNA testing and primer set design (Gosselin et al., 2017) could enable the distinction between certain prey species within the same genus, such as white-tailed deer and mule deer, which could provide further insight as to how coyotes make use of different habitats within the Greater GNP Ecosystem.

Moving one step further, individual predator identities can be determined with the use of microsatellites (Fedriani and Kohn, 2001) or single nucleotide polymorphism genotyping (Eriksson et al., 2020). This additional information can be used to estimate population size (Prugh et al., 2005), dietary differences between social groups (Prugh et al., 2008), and genetic diversity and gene flow between populations (Waits et al., 2000). Fedriani and Kohn (2001) suggest accounting for individual differences in diet is important to avoid biases in population-level estimates of diet. In my research, identification of individual coyotes would have enabled me to determine whether individual coyotes or social groups were specializing on certain food sources, namely native prey, or cattle. I would also have been able to determine an index of the distance individuals travelled based on the locations at which I had collected their scats.

However, genetic markers can vary between populations (Seddon et al., 2005; Karlsson et al., 2011), so those identified as diagnostic for individuals in one region may not be diagnostic in another region (Eriksson et al., 2020). Identifying new markers can be a time-consuming process (VonHoldt et al., 2011; Monzón, 2014; Eriksson et al., 2020) that can quickly accumulate labour and material costs (Monterroso et al., 2019). Additionally, scat, and especially carnivore scat, provides a low-quality source of DNA that is prone to degradation (Vynne et al., 2011; Ramón-Laca, et al., 2015; Kubasiewicz et al., 2016), which can make the identification of individual predators from scat difficult.

For more detailed movement data, telemetry could be used to track individuals across habitats to determine individual home ranges. GPS or radio collars could also provide information on social groups and interactions that could affect diet, such as group-specific diets (Prugh et al., 2008) or territory-specific resources. Within GNP, Lingle et al. (2022) found that

scat containing prairie dog was usually collected within half a kilometre of a prairie dog colony, whereas scat containing cattle was more distributed, but further from prairie dog colonies from spring to fall, when prairie dogs are active (Gummer, 2005; Kusch et al., 2021). One possible explanation for this spatial variation in scat contents is the territorial defence of prairie dog colonies by coyotes specializing on native prey. To link movement data from GPS or radio collars to individual diet with confidence, molecular identification of predator and prey species from scat, or identification of coyote prey at kill sites or by direct observation, would still be required. Spatial variation in scat contents could also result from the distribution of cattle compared to deer on the landscape, so future work could benefit from the use of distance sampling (Urbanek et al., 2012) to estimate the abundance of cattle, deer and coyotes in the region.

Consistent with previous research (Lingle et al., 2022), my results suggest that cattle continue to form a regular part of the diet of coyotes in the Greater GNP Ecosystem. Additionally, the proximity of scat containing cattle to boneyards, the distance of scat containing deer from boneyards, and previous work relating the presence of cattle in scat to prairie dog colonies (Lingle et al., 2022) suggests that some individuals may be specializing on different food sources in the region, although this cannot be confirmed without further research. Many coyotes consuming cattle regularly could lead to a subsidized population at the detriment to native prey, including species at risk (DeCesare et al., 2010; Ciucci et al., 2020). For ranchers, an increase in coyotes could lead to greater coyote presence near livestock and an increased risk of depredation (Blejwas et al., 2002), but removal of subsidies through offsite or contained storing of carcasses may help to reduce conflict (Beckmann & Berger, 2003) and decrease the coyote population (Brunk et al., 2021).

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Chapter 3: Coyotes, cattle and Richardson's ground squirrels

Abstract

Around the world, mesopredators have become more common as larger predators have been purposely removed or unable to thrive in human-dominated landscapes. The versatile diet and reduced fear of mesopredators toward humans increases their risk of conflict with humans, including the depredation of livestock. Conditions leading coyotes to use cattle pastures or that result in depredation are poorly understood. To better understand the relationship between coyotes, cattle pastures, and native prey, I hypothesized that coyotes obtain direct (e.g., killing or scavenging calves) and indirect (e.g., hunting native prey) benefits from cattle pastures. I further hypothesized that cows in this region respond defensively to the presence of coyotes; if not, it may reflect a relaxation of antipredator behaviour through domestication. I conducted observations of coyotes during the spring and summer in southwest Saskatchewan and recorded the coyote's activity, the prey species coyotes targeted, the distance between cattle and the coyote, and the response of cattle to encounters with coyotes. Coyotes devoted most of their hunting time to ground squirrels and were often within 100 and even 10 m of cattle when hunting ground squirrels. Coyotes scavenged from cattle carcasses, and I occasionally observed coyotes approach calves ($N=2$), rush a cow-calf herd ($N=2$), or obtain afterbirth from a female ($N=1$) but there were no attacks or kills. Cows often chased coyotes that encountered cow-calf herds. My data suggest that coyotes primarily use cattle pastures to obtain benefits in hunting native prey, although the periodic opportunity to scavenge cattle or kill a calf may contribute to use of these areas. Understanding the typical behaviour of coyotes when in the presence of cattle is the first step to understanding conditions that may lead to depredation.

Introduction

Depredation of livestock by large predators such as wolves (*Canis lupus*), real or imagined, has long factored into the view of such predators as “enemies in the West” (Jones, 2002), and livestock losses continue to cost producers thousands of dollars each year (Muhly & Musiani, 2009). In Canada, the largest cattle inventories are held in Alberta and Saskatchewan (Statistics Canada, 2022), the southern portions of which were once primarily native grasslands (Atkinson, 2009; Elofson, 2012). In these regions, native grazers such as bison (*Bison bison*), pronghorn (*Antilocapra americana*) and elk (*Cervus canadensis*) have largely been removed in favour of cattle (*Bos taurus*). Large predators such as wolves and grizzly bears (*Ursus arctos*) have mostly been extirpated (Atkinson, 2009), enabling coyotes (*Canis latrans*) to become the top predator in the ecosystem in a likely case of mesopredator release (Prugh et al., 2009; Ripple et al., 2013). Like other mesopredators, coyotes have a versatile diet (Prugh et al., 2009). Learned habituation from parents can make coyotes less risk-averse toward humans (Schell et al., 2018). These traits enable coyotes and other mesopredators to populate areas near humans, which can increase the risk of negative interactions with humans (Prugh et al., 2009). Indeed, coyotes have been considered a “menace” to livestock (Fitch, 1948), accounting for nearly 30% of average annual livestock monetary losses in Alberta and Saskatchewan (Canadian Cattlemen Staff, 2015).

However, coyotes have also been referred to as “nature’s clean-up crew” due to their propensity to scavenge (Bradford, 2019). Livestock carrion has the potential to subsidize predator populations (Ciucci et al., 2020), which can increase predation on native prey species (Holt, 1977), including species at risk, of which there are many in southwest Saskatchewan

(Martin et al., 2018). Wolves with access to cattle boneyards use them regularly (Morehouse & Boyce, 2011; Petroelje et al., 2019), attaining nearly a quarter of their diet from scavenged cattle (Petroelje et al., 2019). Wolves scavenging from boneyards travel less than wolves without access to boneyards, revealing the ability of cattle subsidies to influence both the diet and behaviour of predators (Petroelje et al., 2019). Ciucci et al. (2020) suggest that an abundance of livestock subsidies reduces the amount of native prey wolves hunt and that this is likely to impact their role as apex predators. Cattle carcass boneyards attract coyotes from over 20 km away (Kamler et al., 2004) and could increase the coyote's presence on ranchland, which may lead to an increase in nuisance behaviours (Goodale et al., 2015). Many ranchers respond to nuisance behaviours and depredation with lethal measures, but these can be ineffective as new coyotes often move into areas where others have been killed if food sources are still available (Blejwas et al., 2002).

Cattle characteristics can influence depredation. Most cattle depredation by coyotes is of neonatal calves in the spring (Boggess et al., 1978). Neonates might be especially vulnerable if calving complications leave adult cows in a weakened state (Gilliland, 1995). Depredation of cattle tends to decrease throughout the summer (Boggess et al., 1978), which may be due to the increasing ability of calves to evade capture (Green, 1994). Coyotes preferentially hunt in areas where the young of domestic or native ungulates are present (Paquet, 1992; Blejwas et al. 2002), but defensive behaviour of livestock can discourage coyote attacks (Connolly et al., 1976). Cows defending their calves from a perceived threat can be lethal (Turner & Lawrence, 2006), and the cooperative defence of calves by cows may be an important factor in the tolerance of some cattle producers toward predators (Allen & Fleming, 2004).

In some species, the process of domestication has been shown to reduce wariness toward predators (Johnsson & Abrahams, 1991), but Kluever et al. (2009) reported that domestic cattle maintain vigilance in response to predator cues at the cost of foraging. Behavioural traits in cattle are highly variable between individuals (Cafe et al., 2010; Adamczyk, 2011). Friedrich et al. (2015) suggest that behavioural traits may not be considered in breeding programs due to a trade-off between desirable production traits, such as milk yield, and deleterious side effects resulting in behavioural traits (Oltenacu & Broom, 2010) that may impair the animal's responses to natural predators. For instance, traits related to maternal care may increase the risk of injury to ranchers who must handle cows with calves (Turner & Lawrence, 2006). More recent genetic work suggests this perceived trade-off between production traits such as weight and milk yield and behavioural traits such as aggression may not be justified (Titterington et al., 2022). The heritability of traits varies by breed (Titterington et al., 2022), so it is possible that certain individuals (Flörcke et al., 2012), populations or breeds of cows may be less inclined to defend their calves than others. Additionally, some individuals may spend more time away from their calves to access resources (Mufford et al., 2019) such as feed or water, which could leave young calves vulnerable to depredation.

Coyotes typically hunt large prey items in groups (Gese et al., 1988; Lingle, 2000). Wild ungulates, which form a regular portion of coyote diet (Lingle et al., 2022), frequently overlap with cattle (Yoakum, 1975; Cooper et al., 2008). This can be especially true in grassland landscapes (Yoakum, 1975). Coyotes are more likely to travel alone or in pairs while individually hunting smaller prey items (Lingle, 2000), and often consume many small mammals on pastures alongside cattle without conflict (Fitch, 1948). In particular, Richardson's ground squirrels are commonly consumed by coyotes (Lingle et al., 2022) and are present in areas with a

high cattle-density (Bylo et al., 2014). Coyotes might experience greater hunting success of ground squirrels when near cattle if the presence of cattle reduces the ability of ground squirrels to see or hear approaching coyotes. If so, one might expect coyotes to be closer to cattle at times of day when ground squirrels are active.

Southwest Saskatchewan is a mosaic of parkland and ranchland, making ranchers a crucial part of grassland stewardship (Atkinson, 2009). Previous reports indicate that nearly half the diet of coyotes in some areas of southwest Saskatchewan consists of cattle (Lingle et al., 2022), which according to local knowledge is primarily obtained as carrion. However, reports of depredation in the region are not uncommon. Understanding how coyotes use cattle pastures and interact with cattle could play an important role in the tolerance ranchers have for coyotes and the prevention of depredation.

In this research, I tested three hypotheses about coyotes near cattle. First, I tested the hypothesis that coyotes frequently use cattle pastures due to direct benefits they obtain from the cattle (e.g., killing calves or scavenging cattle carcasses). I predicted that coyotes on cattle pastures hunt (test or attack) or kill calves, harass females to obtain by-products such as after birth, and scavenge from cattle carcasses. Next, I tested the hypothesis that coyotes benefit from cattle pastures, and from staying close to cattle, in ways other than accessing cattle as a food source. I predicted that coyotes on cattle pastures hunt native prey species more frequently than they hunt cattle and stay near (<100 m) cattle more often than they are further away from cattle. I further predicted that coyotes on cattle pastures are more likely to hunt specific prey species (e.g., ground squirrels), and to be more successful, when near (<100 m) cattle than when further away. Finally, I tested the hypothesis that cows in this region respond defensively to the presence

of coyotes. I predicted that cows would display defensive behaviour (bunch together or chase coyotes) when coyotes encountered herds of cattle, especially during the time when calves were more vulnerable to predation. If not, the lack of antipredator defences could reflect a relaxation in cow responses to predators through domestication.

Methods

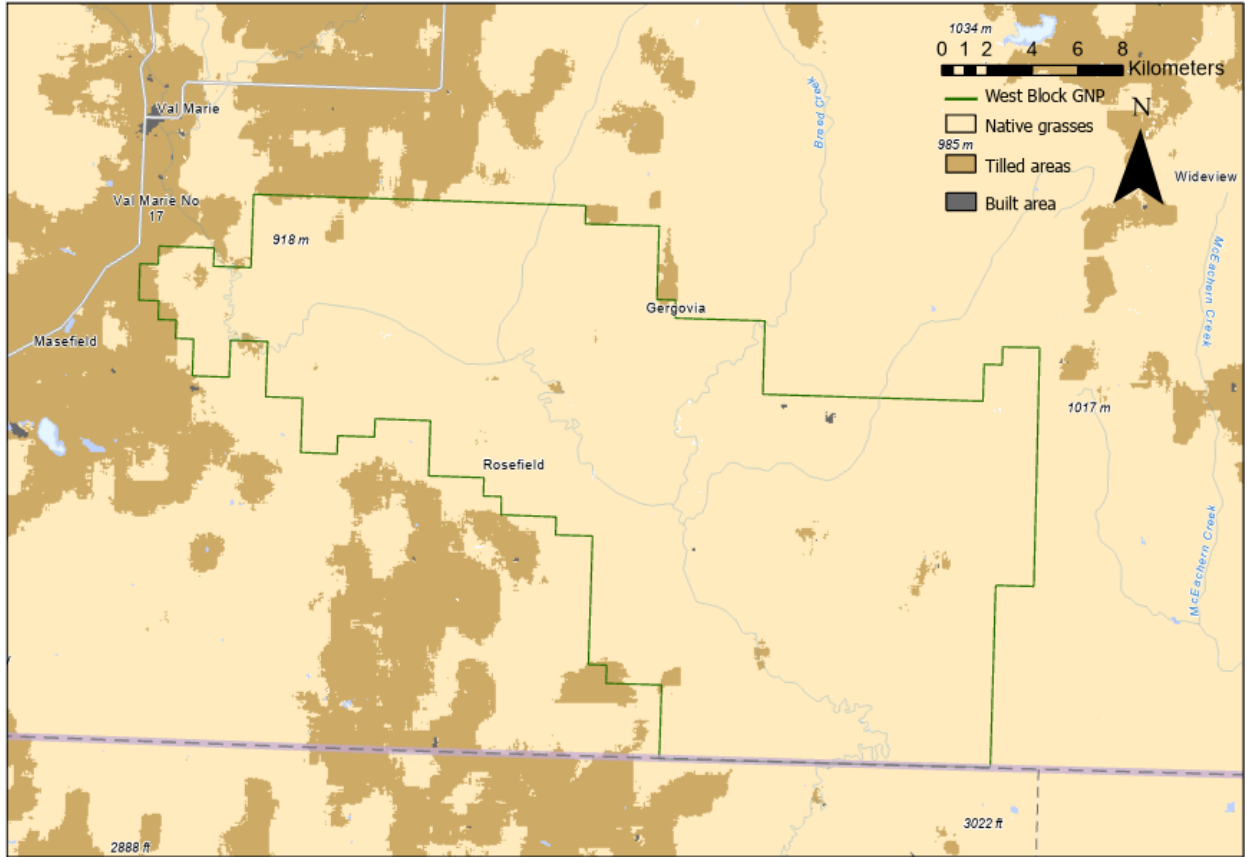
Study site: I conducted this research in the Greater Grasslands National Park (GNP) Ecosystem; including the West Block of GNP (~525km²), and cattle ranchlands adjacent to the West Block that extended approximately 27.5 km to the north. The West Block of GNP has a bison enclosure of about 181.69 km². Prairie dog colonies cover about 12.7 km² of the West Block, with a few additional colonies outside the park.

Terrain and climate: The Greater GNP Ecosystem mostly consists of native mixed grass prairie (Parks Canada Agency, 2018), but also contains tilled land (Figure 2.1). The terrain features “rolling hills, rugged coulees, and steep ravines” (Parks Canada Agency, 2018). During the observations season in 2022, the average temperature was 9.9°C in May (Min. = -6.1°C, Max. = 26.8°C), 15.8°C in June (Min. = -2.0°C, Max. = 32.2°C), 20.6°C in July (Min. = 3.6°C, Max. = 39.2°C) and 20.9°C in August (Min. = 4.3°C, Max. = 38.1°C; Government of Canada, 2023).

Native species: The Greater GNP Ecosystem contains critical habitat to many species at risk including the sage-grouse (*Centrocercus urophasianus*), black-tailed prairie dog (*Cynomys ludovicianus*) and swift fox (*Vulpes velox*; Parks Canada Agency, 2016; Parks Canada Agency, 2021). Mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) also occupy the park and surrounding area and are commonly consumed by coyotes, which are the dominant predator in the area (Lingle et al., 2022). Data on the abundance and geographic

distribution of deer were not available. Moose (*Alces alces*) and pronghorn (*Antilocapra americana*) are also present.

Cattle practices: Most cattle are moved close to homesteads around December because ranchers feed cattle during the winter, then moved to grazing land further from homesteads in April or May, typically after calves have been born. Homesteads typically have boneyards nearby, where cattle carcasses are disposed of during the winter. Cows that die on grazing lands further from homesteads are typically left where they fall.



Created by: Shayla Jackson
Date: Dec. 8th, 2023

Coordinate System: NAD 1983 UTM Zone 13N

Source: Field Data, Winter 2021-2022 & Karra et al. (2021)

Esri, NASA, NGA, USGS, Esri Canada, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, NRCAN, Parks Canada, Impact Observatory, Microsoft, and Esri.

Figure 3.1. Map of study site depicting the West Block boundary, native grasses, tilled areas and built areas.

Collaboration with ranchers: I contacted several local ranchers by phone to seek permission to observe coyotes on private lands. I met with interested individuals during which they signed Landowner Access Authorization forms and answered several questions (Appendix A) related to their seasonal cattle practices and experiences with coyotes. I used information gained from these meetings to inform the selection of vantage points from which to observe coyotes (Appendix B).

Observations: From May-August 2022, a field assistant and I spent 158 hours sitting on hills that overlook cattle pastures to observe coyote interactions with cattle and native prey species. I conducted 62 observation periods that lasted an average of 154 ± 7 min (mean \pm SE). I conducted at least one focal observation of a coyote during fifty of these observation periods. Focal coyotes were in view during their observation for an average of 35 min (SE = 5 min). I used high-powered binoculars and spotting scopes to view animals 500-2500m away without disturbing them. I conducted two observation periods a day: one running from about an hour before sunrise until three to four hours after sunrise and one beginning three to four hours before sunset and lasting until sunset. Sunrise and sunset times were recorded for each day an observation period occurred (Maplogs, n.d.). If I did not see a coyote within two hours of beginning an observation period, I ended the observation period. Otherwise, I would end the observation period after four hours, one hour after the last sighting of a coyote, or if it became too dark to observe the animals.

I selected the first coyote seen during an observation period as the focal coyote. If more than one coyote was spotted in a group together, defined as a coyote that is within 100 m of at least one other coyote (see Appendix C, Table C1), then the coyote that appeared to be leading the group was chosen as the focal coyote. If the coyotes were not travelling in the same direction, then the coyote that appeared to be travelling to an area where they would continue to be in view

the longest was chosen as the focal coyote. If I lost sight of a coyote for over 30 minutes, I began a new focal observation on another coyote if one was visible. Observation periods contained one to five (1.18 ± 0.09) focal observations. To estimate distances between animals, I estimated the body length (from shoulders to base of tail) of visible animals (an adult cow at ~2 m, a deer at ~1 m, or a coyote at ~0.5 m), or the distance between nearby fenceposts (~2 m), and then counted how many animals or fenceposts could fit in the unknown distance.

During observations, I collected data on a focal individual coyote. At the start of each minute, I recorded the coyote's activity (See ethogram, Appendix C, Table C2) and group size. If the focal coyote was hunting/eating, I recorded the prey/food item if known and any escalation of hunting behaviour (e.g., to an approach, pursuit, capture) during each 1-minute interval (one-zero sampling). When cows were visible from the vantage point, the field assistant recorded the number of cows in each herd of cattle (cows with or without calves within the same fenced area with free access to one another; see Appendix C, Table C1), and whether calves were present. I recorded the number of times a cow or calf chased a coyote, defined as a direct movement without pause toward a coyote that is faster than a relaxed walk (see Appendix C, Table C1). A chase was considered separate from a previous chase occurring in the focal if the cow or calf stopped moving toward the coyote, even briefly. I also recorded the date, time, and vantage point for each observation period.

I was able to distinguish the individual focal coyote from other coyotes during an observation but was usually not able to distinguish individual coyotes across different days. To keep track of individual coyotes, I monitored the focal coyote continuously and the field assistant monitored other coyotes, including any coyotes in the same group as the focal coyote and

coyotes in other groups or alone. Some coyotes had physical markings that enabled us to distinguish them from other individuals. When coyotes were obscured from sight by topography, cows, etc., we monitored potential exit points where they could return to view. In some cases, topography enabled coyotes to remain hidden from our view or to exit the observation area without our knowledge. All observational work adhered to the Canadian Council on Animal Care (CCAC) Guidelines (University of Winnipeg Animal Care Committee AEW001).

Data Analysis:

Direct benefits of cattle: To test my first hypothesis that coyotes frequently use cattle pastures because they hunt and kill young calves or scavenge from carcasses, I first examined the activities (travel, rest, or hunt/eat) coyotes conducted on cattle pastures and then the prey species coyotes hunted, interacted with, or consumed. I used non-parametric tests because the data distributions did not meet assumptions of parametric tests. I used the Wilcoxon paired rank test to compare the time coyotes spent on travel, resting, or hunting/eating, including focal coyotes that had performed at least one of these three activities during the focal observation. For this analysis, I restricted focal observations to those lasting over 20 minutes in duration, so that coyotes had greater opportunity to engage in more than one activity. For each activity, I report the group size of focal coyotes. Since the group size could change during an observation, I calculated an average value using the maximum group size for each focal observation during each activity.

I used sign-tests to test whether coyotes were more likely to hunt ground squirrels (eating was excluded), hunt native ungulates (eating was excluded), interact with cattle (approach a calf, rush a herd, or harass a cow for afterbirth), or to scavenge cattle, including data for all focal

observations during which coyotes hunted prey or interacted with or scavenged cattle. I selected the sign-test and used presence/absence data instead of comparing amounts of time because coyotes never interacted with more than one prey species during a given focal observation. I report the frequency of specific coyote interactions with cattle, including coyotes approaching calves, rushing cattle, harassing cows for afterbirth, and the frequency of coyotes scavenging cattle carcasses. I was informed of the presence of cattle carcasses by ranchers, so the frequency of carcass use compared to other activities would likely be higher than would have been the case if I had viewed coyotes without *a priori* knowledge of cattle carcasses. I only observed coyotes scavenging cattle at locations identified by ranchers.

Indirect benefits of cattle: To test the hypothesis that coyotes benefit from cattle pastures, and from staying close to cattle, in ways other than accessing cattle as a food source, I compared the time of day when coyotes hunted ground squirrels to the time of day coyotes were near cattle. I used a general linear mixed model with a binomial response variable to determine the time of day when coyotes hunted ground squirrels. I used a sign-test to determine whether coyotes spent more time near (<100 m) or further (>100 m) from cattle when cattle were present in the field with coyotes. I did not have sufficient data prior to sunrise or post-sunset to conduct a similar analysis for that time period.

I used general linear mixed models with binomial response variables to determine whether the likelihood of coyotes hunting or pursuing ground squirrels was greater when within 100 m of cattle than when >100 m or when hunting on cattle pastures without cattle in view. The identity of the focal coyote was designated as a random factor to control for different coyotes

observed across different focal observations. However, some individuals may have been observed multiple times on different dates.

Response of cows and calves to coyotes: To test the hypothesis that cattle in this population employ defensive behaviour to protect calves, I examined the frequency of encounters with coyotes, defined as a coyote within 10 m of at least one cow or calf (see Appendix C, Table C1), that resulted in cows and/or calves displaying protective behaviour, defined either as bunching together or chasing coyotes. I used a logistic regression to test for a relationship between female and calf chases of coyotes and date, using data for individual focal observations that had encounters between coyotes and cow-calf herds. For females, I predicted that chases would be more likely to occur during the middle of the observation season, when more young calves were present. I therefore multiplied date by itself to create a quadratic term, also including date as a main effect in the model. For calf chases of coyotes, I used a simple logistic regression, with date entered only as a main effect, because I assumed calves would become better at self-defence as they grew. For both analyses, date was distinguished into five two-week periods. Further, I used a sign-test to determine whether cows were more likely to chase coyotes than calves. I used presence-absence data for individual focal observations that had encounters between coyotes and cow-calf herds. All data analysis was performed using R Statistical Software (R Core Team, 2022).

Results

Overview of activity: Coyotes differed in the time spent on different activities. Coyotes spent more time travelling than hunting/eating (Figure 3.2; Wilcoxon paired signed rank test: $V = 300$, $p = .008$, $r_{rb} = 0.59$ [95th CI = 0.23, 0.81], $N = 27$ focal coyotes) but did not spend more time

travelling than resting (Figure 3.2; Wilcoxon paired signed rank test: $V = 216$, $p = .524$, $r_{rb} = 0.14$ [95th CI = -0.29, 0.53], $N = 27$ focal coyotes) or resting as compared to hunting/eating (Figure 3.2; Wilcoxon paired signed rank test: $V = 223$, $p = .421$, $r_{rb} = 0.18$ [95th CI = -0.30, 0.59], $N = 27$ focal coyotes).



Figure 3.2. The percentage of time in which focal coyotes participated in different activities. All hunting and eating activities were combined when comparing the time spent hunting/eating with the time spent travelling or resting. Different letters (a, b) indicate significant differences between the time spent travelling, resting, or hunting/eating, $N = 27$ focal coyotes. Box lines depict the 25th percentile, median line and 75th percentile. Whiskers indicate the minimum and maximum values, excluding outliers.

Direct and indirect benefits of cattle: Coyotes were more likely to hunt ground squirrels than native ungulates, interact with cattle, or scavenge cattle (Figure 3.3; dependent-samples sign-test: native ungulates, $p < 0.005$, Cliff's delta = 0.46, $N = 28$ focal coyotes; interact with cattle, $p = .012$, Cliff's delta = 0.43, $N = 28$ focal; scavenge cattle, $p = .027$, Cliff's delta = 0.39, $N = 28$). The average maximum group size when travelling was 1.72 ($N = 54$ focal observations); 1.70 when resting ($N = 23$), 1.47 ($N = 15$); when hunting ground squirrels; and 2.20 ($N = 5$) when interacting with cattle.

Of 25 focal observations when coyotes were within 100 m of calves, a coyote approached an individual calf on two separate occasions (8%), coyotes rushed a cow-calf herd twice (8%) and harassed a cow for access to its afterbirth once (4%). Coyotes did not attack or capture an individual cow or calf during these observations but did obtain the afterbirth. Calves were present in 91% of the 32 observed cattle herds for which the presence or absence of calves was recorded. Coyotes did not initiate interactions with cattle in herds without calves. All instances of approaches, rushes, and harassment of cattle by coyotes were observed in June 2022, with no similar observations in July or August. Five focal observations included scavenging of one of two known cattle carcasses by coyotes. The high frequency of this behaviour would be biased by my decision to observe in areas where known carcasses occurred (see methods). There were no observations in which coyotes both ate from carcasses and approached calves or rushed herds of cattle.

Coyotes showed a non-significant tendency to hunt ground squirrels more often one to three hours after sunrise and before sunset than within one hour of sunrise or sunset (Figure 3.4a; GLMM with binomial response: $\beta \pm SE = 0.80 \pm 0.43$, Odds Ratio = 2.23 [95th CI of Odds Ratio

= 0.96, 5.15], Wald- $\chi^2 = 3.50$, $p = .062$, $N = 47$ focal coyotes). When conducting observations of areas where cattle were visible and the distance between the focal coyote and cattle was known, coyotes were more likely to be within 100 m of cattle than further away (>100 m) during both the morning and evening (Figure 3.4b; dependent-samples sign-test: $p = .005$, Cliff's delta = 0.52, $N = 30$ focal coyotes), in fact, coyotes were within 10 m of cattle for $40\% \pm 7\%$ (mean \pm SE) of the time they were within 100 m of cattle.

Coyotes hunted ground squirrels in 10 (40%) of 25 focal observations when near cattle (<100 m), pursuing squirrels in seven and capturing squirrels in three of these focal observations (Figure 3.5). The seven coyotes that pursued squirrels pursued 17 squirrels (mean = 2.4 pursuits/coyote) and captured four squirrels. In contrast, coyotes hunted ground squirrels in 1 (9%) of 11 focal observations when further away from cattle (>100 m) and made no pursuit. The difference in likelihood of a ground squirrel hunt occurring was not significant (Figure 3.5; GLMM with binomial response: $\beta \pm SE = -1.92 \pm 1.21$, OR = 0.15 [95th CI = 0.01, 1.56], Wald- $\chi^2 = 2.53$, $p = .112$, $N = 30$ focal coyotes). Coyotes made no pursuits or captures when further away from cattle (>100 m; Figure 3.5).

During observations of coyotes in pastures where cattle were not visible to the observers and presumably not in view to the focal coyotes, coyotes hunted ground squirrels in 21% of 19 focal observations, and pursued ground squirrels in 11% (Figure 3.5). These values did not differ from the likelihood of a hunt or a pursuit when coyotes were within 100 m of coyotes (GLMM with binomial response: hunt, $\beta \pm SE = -0.92 \pm 0.70$, OR = 0.40 [95th CI = 0.10, 1.56], Wald- $\chi^2 = 1.74$, $p = .188$, $N = 44$; pursuit, $\beta \pm SE = -1.20 \pm 0.87$, OR = 0.30 [95th CI = 0.06, 1.67], Wald- $\chi^2 = 1.89$, $p = .170$, $N = 44$).

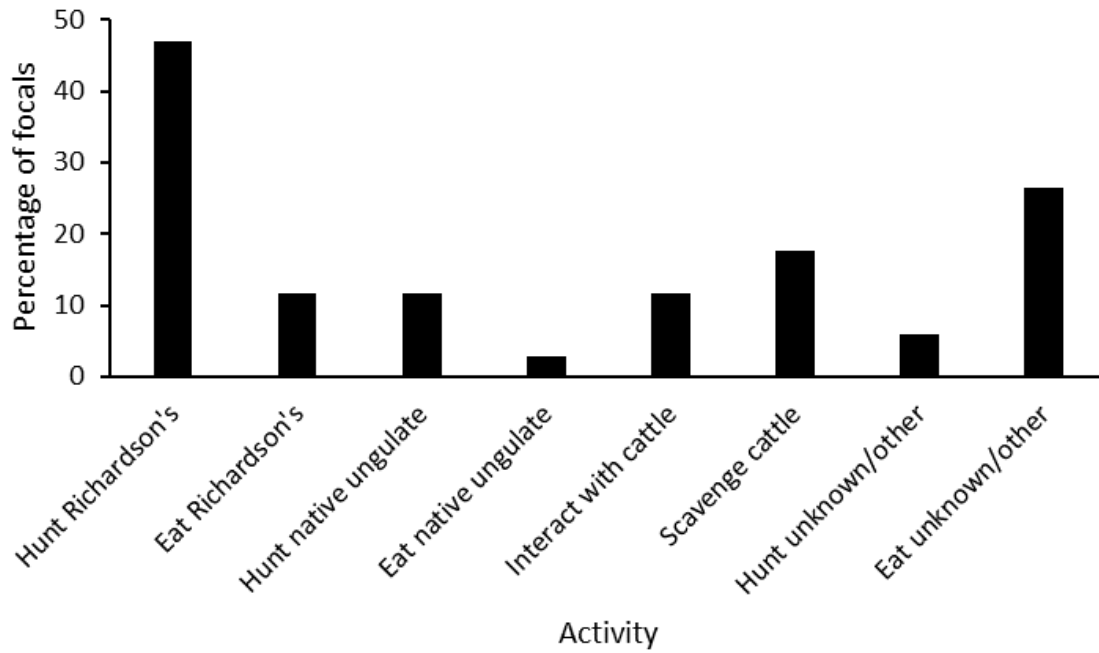


Figure 3.3. The percentage of focal observations in which hunting or eating of different species occurred, $N = 34$ focal observations in which hunting or eating occurred.

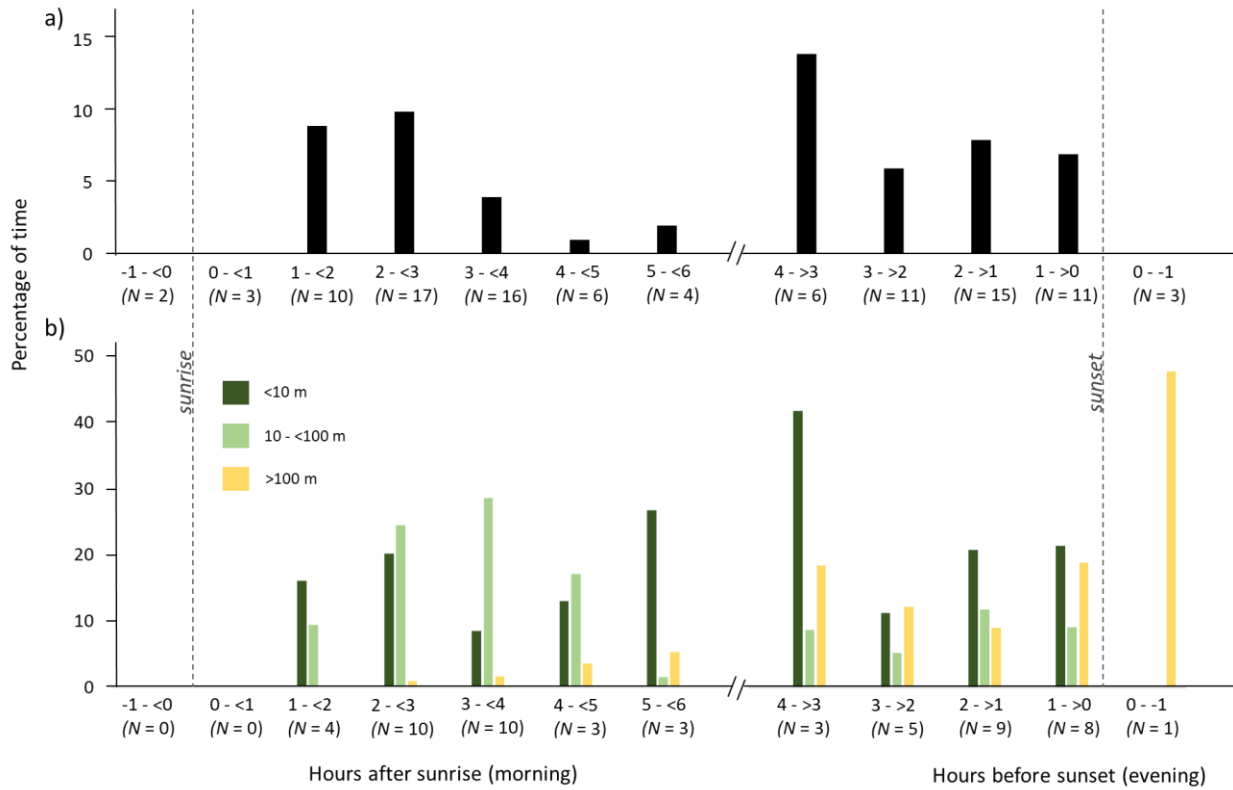


Figure 3.4. The percentage of time that coyotes a) hunted ground squirrels and b) were observed at different distances from cattle at different times of day relative to sunrise and sunset. The gap in the day corresponds to ~5.5 h in May, ~6 h in June, ~5.75 h in July and ~4.5 h in August. Panel a): $N = 58$ focal coyotes; panel b) $N = 30$ focal coyotes.

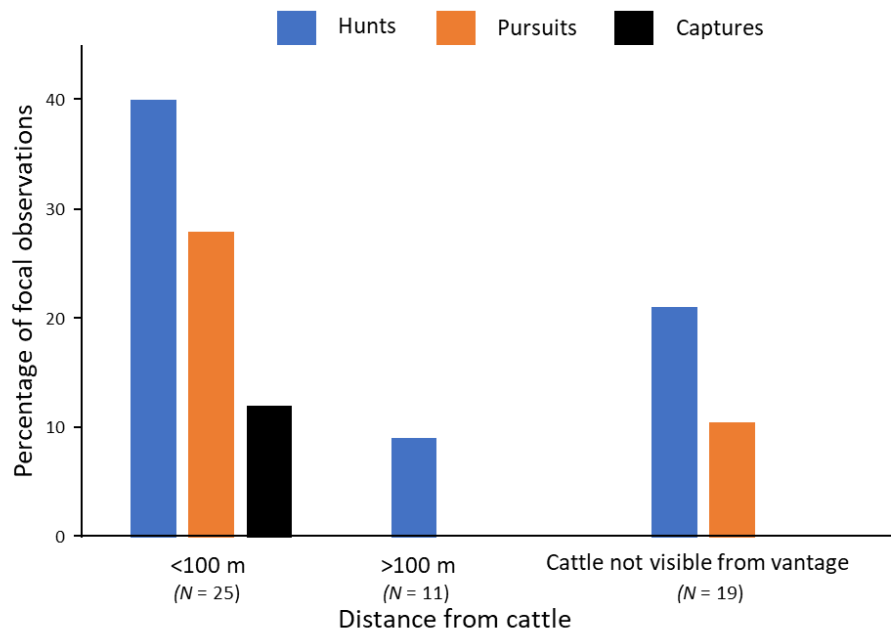


Figure 3.5. The percentage of focal observations of coyotes with ground squirrel interactions (hunt, pursuit, capture) depending on the coyote's distance from cattle.

Response of cows and calves to coyotes: Cows and/or calves chased coyotes in 9 (43%) of 21 focal observations when coyotes were within 10 m of cattle, resulting in 29 separate chases over the 21 focal observations, including the two cases when coyotes approached a calf. In one of these 21 focal observations, a cow-calf herd bunched together after coyotes harassed a cow and calf for access to the cow's afterbirth. Cows appeared to be more likely to chase coyotes from June 26 to July 9 (Figure 3.6), but I did not detect a curvilinear relationship between cow chases of coyotes and the date ($\beta \pm \text{SEM} = -0.66 \pm 0.46$; Wald- $\chi^2 = 2.10$, $p = .148$, $N = 21$ focal observations). The failure to detect a relationship may be due to a lack of statistical power from the small sample for certain time periods (Figure 3.6). I likewise did not detect a relationship between date and the likelihood of calves chasing coyotes ($\beta \pm \text{SEM} = 0.45 \pm 0.40$; Wald- $\chi^2 = 1.28$, $p = .260$, $N = 21$ focal observations). Cows did not chase coyotes more commonly than calves (Figure 3.6; dependent-samples sign-test: $p = 1.0$, Cliff's delta = -0.05, $N = 21$ focal observations).

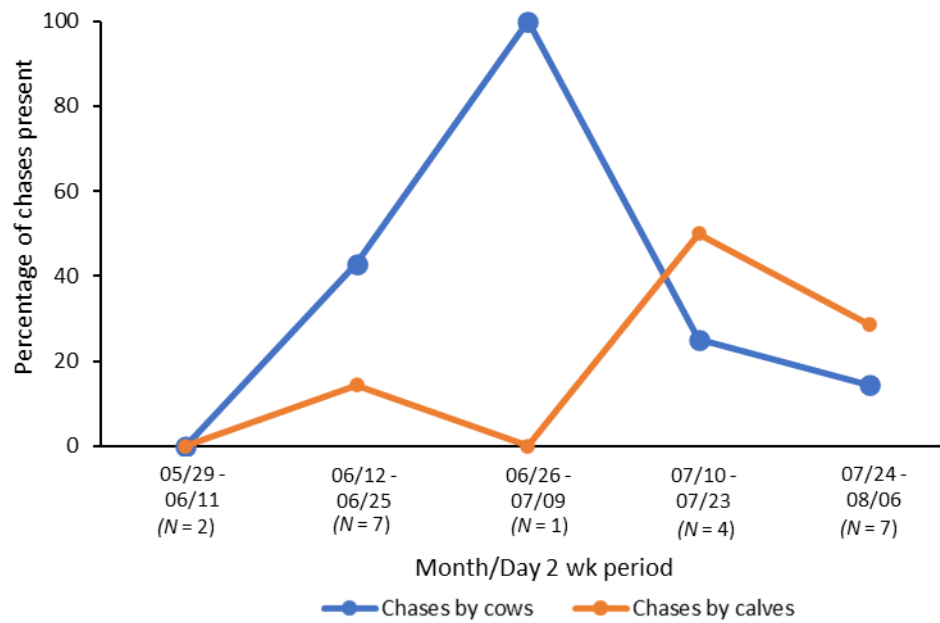


Figure 3.6. The percentage of focal observations in which at least one cow or calf chased coyotes between May 29 to August 6, 2022. Data are distinguished into two-weekly periods. $N = 21$ focal observations in which coyotes were within 10 m of cattle.

Discussion

Coyotes spent considerable time on cattle pastures and close to cattle between May and August 2022. Of the time they spent hunting or eating, most of this was devoted to hunting native prey and specifically ground squirrels. On a few occasions, coyotes approached a calf, rushed a cow-calf herd, or scavenged from cattle carcasses.

I found partial support for hypothesis 1, that coyotes frequently use cattle pastures due to direct benefits they obtain from the cattle. Coyotes rarely appeared to gain direct benefits from cattle and may instead travel to cattle pastures for access to native prey. I found support for hypothesis 2, that coyotes benefit from cattle pastures, and from staying close to cattle, in ways other than accessing cattle as a food source. Coyotes spent more time near cattle than further away and hunted native prey, especially ground squirrels, more commonly than cattle. I found support for hypothesis 3, that cows would respond defensively to the presence of coyotes. Cows frequently chased coyotes. Here, I review the findings for the predictions of each of these hypotheses and compare my findings to previous records of coyote behaviour in other regions. I suggest future work directed at longer-term data that accounts for habitat and season.

Direct benefits of cattle: Consistent with findings elsewhere, the few direct interactions coyotes initiated with cattle (i.e., coyotes approaching an individual calf; rushing a cow-calf herd) that I observed occurred in the spring, were in herds where calves were present, and coincided with the calving season (Boggess et al., 1978). Cows were able to interrupt both approaches of calves by coyotes, as might be expected from the ferocity with which cows defend their calves from human handlers (Turner & Lawrence, 2006). Cows did not successfully prevent the single scavenging of afterbirth I observed, despite chasing the coyotes. The sample of herds without calves did not

enable me to compare the likelihood of a coyote approaching a herd with calves to a herd without calves. These findings support the predictions that coyotes use cattle pastures to obtain direct benefits by hunting calves or harassing cows for by-products. However, given the infrequency of these events, it did not appear that coyotes were travelling to cattle pastures because of the direct benefits of live cattle or their by-products as a food source. Coyotes may instead travel to cattle pastures to access native prey (see indirect benefits of cattle). Alternatively, coyotes could maintain proximity to cattle to monitor for vulnerable individuals and hunt ground squirrels while present.

Coyotes also scavenged cattle carcasses, which could be an important intermittent resource for coyotes on cattle pastures. Previous work has shown that coyotes will travel long distances to scavenge cattle (Kamler et al., 2004). The two cattle carcasses I observed were well-attended by coyotes. Adult cow mortality is largely due to calving and weather-related problems (APHIS 2010), suggesting a seasonal pulse of carcasses may be available during the spring. The possibility of carcasses being available during calving may be another factor attracting coyotes to cattle pastures. Scavenging of cattle carcasses by coyotes is probably more common in the winter, when carcasses are kept at boneyards near homesteads and other food sources, such as seasonally available prairie dogs, ground squirrels and insects, become scarce (Lingle et al., 2022). Carcasses may also be available during winter if cows are unable to access enough forage to maintain their body temperatures and die of exposure (Whiting et al., 2012). If many coyotes rely on cattle carcasses as a source of food through the winter or year-round, then it is possible that the coyote population in this region is being subsidized by cattle carcasses (Ciucci et al., 2020; see future work below).

Indirect benefits of cattle: Coyotes hunted native prey more commonly than cattle, supporting the indirect benefits hypothesis that coyotes benefit from cattle pastures in ways other than accessing cattle as a food source, and specifically supporting the prediction that coyotes hunt native prey species more frequently than they hunt cattle. Coyotes have been known to hunt small mammals frequently near cattle elsewhere (Fitch, 1948) and Richardson's ground squirrels may provide some benefit to grazing cattle by improving forage quality (Newediuk et al., 2015). Cattle grazing shortens grass height, and Richardson's ground squirrels are well known for being more common in areas with shorter vegetation (Proulx et al., 2012). In the upland habitats of Grasslands National Park, Richardson's ground squirrels are more common where cattle grazing is intense (Bylo et al., 2014). These data suggest that the effects of grazing cattle may provide benefits to small mammals and to their predators.

I found mixed support for the predictions that coyotes obtain indirect benefits from associating with cattle, and not just from occupying cattle pastures when cattle may or may not be present. Coyotes did spend more time near cattle (<100 m) than further away throughout the day, and much of this time was spent within 10 m of cattle, as predicted if they benefit by associating with cattle. Coyotes hunted ground squirrels more commonly than other species, so it is possible that this association with cattle corresponded to the time of day when coyotes hunt ground squirrels, which tends to begin about one hour after sunrise and cease after squirrels enter their burrow around sunset (Clark, 1970). However, I did not detect a statistical difference in the frequency of hunts or in hunting success on ground squirrels when closer to cattle than when cattle were in the area but further away. Further, coyotes on cattle pastures that had no cattle during the observation had a similar frequency of hunts and rate of hunting success to coyotes

that were close to (<100 m) cattle. Whether the coyote's association with cattle, and not simply cattle pastures, is related to opportunities to hunt ground squirrels requires further investigation.

Response of cows and calves to coyotes: I found support for my prediction that cows would display defensive behaviour when coyotes encountered herds of cattle. Cows and calves responded defensively to coyotes in 43% of focal observations in which encounters occurred, including during the two cases in which coyotes directly approached a calf. One of these responses included cattle bunching together when coyotes rushed a cow-calf herd, a behaviour that deters coyotes from further pursuit of native ungulates (Lingle, 2001). Cows appeared to be more likely to respond defensively during a two-week period between late-June and mid-July, suggesting that they may adjust their responses to temporal variation in the perceived risk of predation on their calves, but I was unable to find a statistical difference in the frequency of defensive behaviour compared to date. This may have been due to a small sample size for certain time periods. The sample of coyotes approaching calves or rushing herds did not enable me to test whether the antipredator behaviour of cows reduced coyote success, so future work would be needed to test the effectiveness of these defences. The sample likewise did not allow me to investigate whether coyotes were more likely to harass cows or make hunting attempts on calves when the coyote group was larger, though previous reports indicate that resident coyotes, which are more likely to form packs, are responsible for most depredation events (Sacks et al., 1999; Blejwas et al. 2002) and larger prey items are usually hunted in groups (Gese et al., 1988; Lingle, 2000). Notably, more than one coyote (groups of two and five) made the two rushes of cow-calf herds, which were likely an attempt to flush or separate calves from the herd, whereas coyotes that appeared to be on their own made the direct approaches of individual calves. One possible

explanation for this is that hunting attempts were made by groups of coyotes while individual coyotes opportunistically investigated individual calves.

Future work: My observations of coyote behaviour on cattle pastures shed light on factors that may influence depredation and future work could help further clarify coyote-cow interactions. First, more conclusively identifying individuals would help to identify factors leading to depredation. Previous work has suggested that sexually mature adults with territories, as opposed to younger transient coyotes (Windberg & Knowlton, 1988), are responsible for most depredation events (Sacks et al., 1999; Blejwas et al. 2002). The deployment of GPS or radio collars would enable the identification of individuals, enable more continuous tracking of these individuals across habitats and potentially provide information on other individuals with which coyotes spend their time, including during the night and early-morning hours. These data would provide information on differences in the behaviour of coyotes that may affect their interactions with cattle and enable one to assess whether coyotes are specifically travelling to cattle pastures at times of day when ground squirrels are available to coyotes.

Habitat type influences the impact of cattle grazing on Richardson's ground squirrel populations (Bylo et al., 2014), and so it is likely that habitat influences how coyotes interact with ground squirrels and cattle as well. Given my findings that coyotes benefit from cattle pastures in ways other than accessing cattle as a food source, I would expect coyotes to spend more time on cattle pastures than expected from their availability as compared to other land types but was unable to test this prediction. Likewise, I did not have enough data to test whether coyotes were in proximity to cattle prior to sunrise or after sunset, when ground squirrels would be underground (Clark, 1970). Expanding this research to a larger sample size, other land types

and accounting for habitat type in analyses would further clarify how coyotes use available land types. This could be accomplished with telemetry or further observation and could help to determine whether coyote hunting success improves when on cattle pastures overall, which could be due to high densities of ground squirrels or behavioural effects of coyotes near cattle, such as using cattle as a blind to prevent detection by ground squirrels.

Although I observed scavenging of cattle carcasses in the spring, and cattle is common in coyote diet from fall to spring (Lingle et al., 2022), coyotes are most likely to rely on carrion in the winter (Bekoff & Wells, 1980). Investigation of winter coyote-cattle interactions is necessary to determine whether the coyote population in this region is subsidized through the winter by cattle carcasses, a season when native prey species are generally more limited (Lingle et al., 2022). A subsidized coyote population could be detrimental to alternative prey, including species at risk, through apparent competition, which occurs when a predator population is supported by a common prey species and leads to increased predation on alternative prey species (Holt, 1977). Apparent competition can be a major contributor to declining populations of species at risk that share predators with alternative prey species (DeCesare et al., 2010). In the greater Grasslands National Park ecosystem, a subsidized coyote population could jeopardize the recovery of species at risk (Lingle et al., 2022), despite considerable efforts to improve their habitat (Parks Canada Agency, 2021).

Increased numbers of coyotes might also increase the amount of depredation or other nuisance behaviour by coyotes on rangeland (Goodale et al., 2015). If this population is being subsidized, removal of subsidies, through means such as offsite or contained storing of livestock carcasses, could reduce the risk of human-coyote conflict (Beckmann & Berger, 2003) and

decrease the coyote population (Brunk et al., 2021), so consultations with local ranchers regarding carcass management strategies such as offsite or contained storing of livestock carcasses may be advisable. Such management actions may become more important over the years, for larger predators such as cougars, grizzly bears, and wolves, are returning to Canada's grasslands (Government of Canada, 2015). Although many ranchers tolerate coyotes because they "clean-up" cattle carcasses, most ranchers are far less accepting of larger predators. Steps taken to minimize the availability of anthropogenic food sources will likely benefit ranchers' livelihood, while also benefitting wildlife.

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Chapter 4: General conclusion

Conservation problems are often complex and involve many parties. Ranchers have strived to protect livestock from predators for hundreds of years with a variety of strategies, mostly lethal, enacted both individually and federally (deCalesta, 1976). When wolves were reintroduced to Yellowstone National Park in 1995, they became the central talking point of much larger underlying issues related to social power, landowner rights and environmental uses (Wilson, 1997). Decades later, conflict remains between hunters and wolf advocates, primarily when park-living wolves are legally killed outside the park (Smith et al., 2016).

Similarly complex interests exist elsewhere. Coyotes are frequently perceived as posing a threat to humans, pets and livestock leading to little tolerance for their presence (Goodale et al., 2015). Coyotes on ranchland seeking livestock (Boggess et al., 1978), carrion from boneyards (Kamler et al., 2004) or native prey (Fitch, 1948) are often met with gunshots, but such lethal measures can fail to remove the threat of depredation if new coyotes move into the area (Blejwas et al., 2002). Successful removal of many coyotes could risk cascading effects for native prey species (Mezquida et al., 2006) in ecosystems where coyotes are the top predator (Prugh et al., 2009). Conversely, coyotes allowed to scavenge from boneyards could lead to a subsidized population, which might increase nuisance behaviour on ranchland (Goodale et al., 2015) and further endanger species at risk through apparent competition (Holt, 1977; DeCesare et al., 2010).

In my thesis, I examined the impact of cattle presence on the diet and behaviour of coyotes in the Greater Grasslands National Park (GNP) Ecosystem in southwest Saskatchewan. In the second chapter, I used scat samples collected on trails, roads, prairie dog colonies and

cattle carcass boneyards to determine the diet of coyotes. I predicted that scat containing cattle would be closer to cattle boneyards but further from prairie dog colonies and the bison enclosure, whereas scat containing deer would be further from cattle boneyards but closer to prairie dog colonies and the bison enclosure.

I found that although prairie dog colonies did not affect the locations of scat, scat containing cattle was closer to both cattle boneyards and the bison enclosure, whereas scat containing deer was further from cattle boneyards and the bison enclosure. These results may indicate that different coyotes are consuming primarily cattle or deer. If many coyotes are consuming cattle from boneyards throughout the winter or year-round and staying relatively close to cattle boneyards, many of which are located near the bison enclosure, the coyote population could be subsidized at the detriment of native prey species, including species at risk (Holt, 1977; DeCesare et al., 2010).

Additionally, I predicted species at risk would form a small but regular part of coyote diet. I found no evidence to support this prediction, but it is possible that coyotes pose a greater threat to species at risk in other months, when prairie dogs are above ground (Gummer, 2005; Kusch et al., 2021) and a greater number of ground-nesting birds, which were commonly identified in scat, occupy the grasslands. Many of the migratory ground-nesting birds that do not occupy the grasslands through the winter are categorized as at-risk (Bent, 1907; Wedgewood, 1982; Parks Canada Agency, 2016).

In the third chapter, I evaluated reasons why coyotes spend time on cattle pastures and near cattle, and how cattle responded to coyotes. I conducted observations in which I recorded coyote activity, the presence of cattle, and the response of cattle to coyotes. I predicted that

coyotes on cattle pastures would receive direct benefits from hunting calves and scavenging cattle carrion and by-products such as afterbirth, and indirect benefits from hunting native prey, namely ground squirrels, near cattle. I also predicted that cows would respond defensively to the presence of coyotes.

Scavenging of carrion was common on the two carcasses I observed, suggesting direct benefits are gained by coyotes from boneyards, consistent with other research on coyotes and wolves (Kamler et al., 2004; Morehouse & Boyce, 2011; Petroelje et al., 2019). Although coyotes infrequently approached calves or harassed cows for afterbirth, they did spend more time near cattle than further away and frequently hunted native prey, particularly ground squirrels, on cattle pasture, suggesting coyotes gain indirect benefits from cattle. However, I did not find a difference in the number of hunts or hunting success on ground squirrels when near cattle compared to further away, so whether these benefits are related to cattle pastures or specifically to cattle requires further investigation. Both cows and calves frequently chased coyotes they encountered, but the effectiveness of these defences in preventing or interrupting depredation attempts requires further investigation.

Taken together, the results of my thesis show that cattle pastures are an important resource for coyotes in grassland habitats through the winter, spring and summer. Depredation of calves in the region is uncommon but does occur based on reports from local ranchers. Consistent with other research (Boggess et al., 1978), the few direct interactions I observed coyotes initiate with cattle occurred in the June, with no more observed during July or August. More typically, coyotes in proximity to cattle were hunting native prey or scavenging from boneyards. Results from the second chapter show that cattle consumption persists through the

winter, and previous findings attest that cattle consumption by coyotes in this region is common from fall to spring (Lingle et al., 2022).

My results, combined with previous work (Lingle et al. 2022) and rancher reports (Mandes, 2023), suggest that the coyote population in this region is being subsidized by cattle carrion, which may further endanger species at risk (Holt, 1977; DeCesare et al., 2010), despite efforts at their recovery (Parks Canada Agency, 2021). If increased numbers of coyotes survive the winter when native prey is limited (Lingle et al., 2022) because of anthropogenic subsidies, the risk of cattle depredation might also increase since a larger coyote population is likely to increase coyote presence on ranchland and near boneyards (Kamler et al., 2004). Removal of subsidies has been shown to reduce predator populations (Brunk et al., 2021), so consultations with local ranchers regarding carcass management strategies that would prevent access by coyotes and other wild predators (Morehouse & Boyce, 2011), such as offsite or contained storage, may be advisable. Given the encroaching ranges of larger predators into the grasslands (Government of Canada, 2015), preventative actions now could help to dissuade larger predators such as cougars, grizzly bears and wolves from approaching homesteads and boneyards regularly in search of subsidies, while also supporting the recovery of native grassland species.

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Appendix A: Rancher materials

Landowner Access Authorization

*adapted from South of the Divide: Access Authorization and Field Work Protocols, Appendix 1

Landowner Name(s): _____

Organization/Ranch: _____

Phone Number Home: _____ Cell: _____

Home Quarter RM: _____

Mailing Address: _____

Email Address: _____

Permission to Access the following Quarters +/-Conduct Field Work (caveats noted below):

I, _____, give Shayla Jackson and a designated research assistant permission to access and conduct field work in the following areas:

Quarters :

Permit:

QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):
QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):
QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):
QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):
QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):
QTR____ SEC ____ TWP____ RGE____ MER____	Y	Y-Caveat or	N (Reason):

I, _____ give permission to Shayla Jackson and a designated research assistant to conduct the following activities during fieldwork:

Scat collection will occur about once per week from approximately December to February, and again from approximately April to October.

Periodically drive on private roads inside the property to collect predator scat: _____

Periodically walk on private trails inside the property to collect predator scat: _____

Walk near a livestock carcass or carcass pit to periodically monitor consumption of carcass or to collect predator scat: _____

Observe and monitor coyotes near a carcass for a few hours at a time: _____

Observation periods will occur throughout April to October.

List specific guidelines or restrictions:

Landowner Signature: _____ Date: _____

Questions and notes for a verbal interview with ranchers

Before I ask any questions, I want to state that we (my supervisor or I) will never identify the source of information or an opinion unless we specifically asked you for permission to do that. We would not present maps with locations you tell us, unless we specifically asked and obtained permission.

Questions for rancher

1. Winter ranching

Where are your cattle located during winter (Dec-February)?

Can I outline that area on this map?

Does that include cows, calves, or both?

About how many cows does that include?

If a cow or calf dies, is the carcass moved to any specific location, such as a pit?

Do you keep track of the animals that die during winter? If so, is it possible for me to get that information, including the location of the carcass and whether the animal is a cow or a calf?

2. Timing:

When, approximately, are cattle (cows, calves, or both) moved to the winter range?

When are your calves born?

When (approximate month) are cattle moved to the summer range?

3. "Summer" (more like spring to fall)

Where do your cattle graze during summer?

Does that include cows, calves, or both?

Can I outline that area on this map?

If a cow or calf dies, is the carcass left on the range? If not, what is done with the carcass?

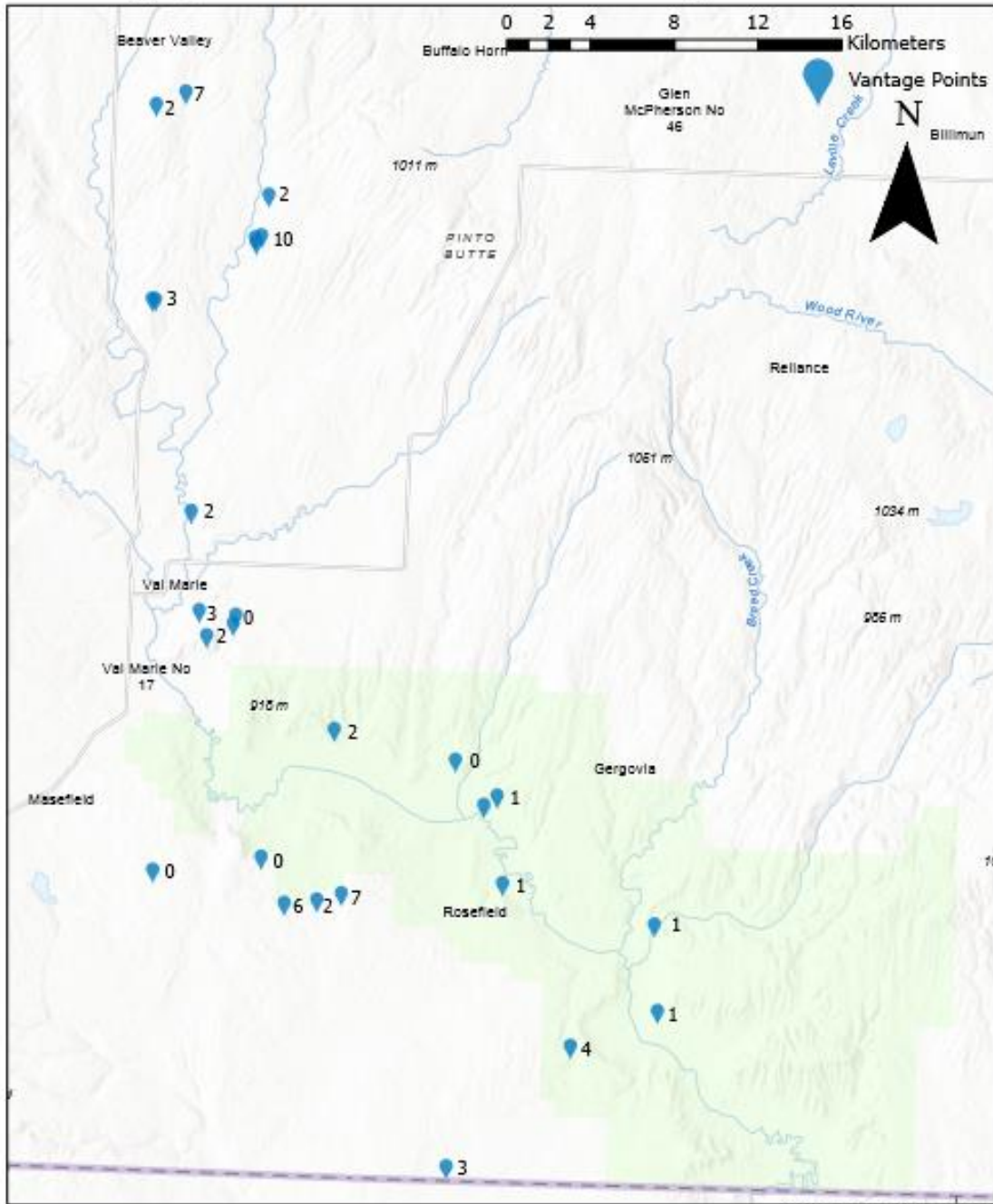
Does anyone keep track of the animals that die during summer? If so, is it possible for me to get that information, including the location of the carcass and whether the animal is a cow or a calf?

I will write down the responses to these questions and give you a copy by email later, just to make sure I recorded your answers accurately.

Note that we may want to make a map of carcass availability – will check back for permission before doing so.

Appendix B: Map of vantage points

Vantage points used for summer 2022 coyote observations



Created by: Shayla Jackson
Date: 14/03/23

Coordinate System: NAD 1983 UTM Zone 13N

Source: Field Data, Summer 2022

Esri, NASA, NGA, USGS, Esri Canada, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, EPA, NPS, USDA, NRCAN, Parks Canada

Map of vantage points used for coyote observations. The number of focal observations per location, rather than vantage point, is indicated. Vantage points with 0 focal observations indicate locations where observations were conducted but no focal coyotes were observed.

Appendix C: Glossary and ethogram

Table C1. Glossary

Term	Definition
Observation period	The period of time from arrival at a vantage point to departure from a vantage point.
Focal observation	The portion of the observation period that contains data on an individual focal coyote. An observation period may contain multiple focal observations, each with a distinct focal individual.
Coyote group	A coyote that has at least one other coyote within 100 m. Group size does not account for social interactions (e. g., aggressive vs. affiliative).
Herd of cattle	Cows with or without calves within the same fenced area with free access to one another.
Coyote-cattle encounter	A coyote within 10 m of at least one cow or calf.
Cow/calf chase	Direct movement without pause by at least one cow or calf toward a coyote that is faster than a relaxed walk. Cows tended to trot toward coyotes in a stiff motion, whereas calves tended to charge coyotes in a bouncier motion with both hindlegs moving together.

Table C2. Ethogram of coyote activities and hunting behaviour.

Activity	Definition
Resting	Stationary position sitting or lying down.
Locomotion (not hunting)	More than two steps walking or running in any direction. This category excludes travel that was determined to be part of a hunt (e.g., with behavioural indications that the coyotes were searching for or approaching small or large prey). Motion is relaxed as opposed to stiff.
Eating	Consuming or chewing food.
Hunting	Alert to prey in view. Must include motion toward a prey item during the behaviour but may also include a few seconds of stillness between steps, or a coyote standing, sitting, or lying down and waiting while alert to prey in view.
Approach	More than two steps walking toward a live prey item that is <10 m away; facing prey with ears forward.
Rush	A short burst of running toward a live prey item.
Pursuit	More than two steps running toward a live prey item that is fleeing; either the coyote or the prey can run first.
Capture	Aggressive physical contact with the prey that results in the death of the prey.
Other	Any behaviour not described in another cell.
Unknown	Behaviour could not be determined, possibly due to partial obstruction of view or distance.
Out of View	Not visible.