

Camera traps for evaluating ungulate densities and interspecific  
interactions in the Beaver Hills region of Alberta

by

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## ABSTRACT

Interspecific interactions and species-habitat interactions are primary drivers in shaping distributions of wildlife populations across variable landscapes. The aspen parkland is a highly productive and heterogenous ecosystem characterized by a mosaic of habitat types maintained by disturbance that supports diverse ungulate assemblages. Elk Island National Park (EINP) and Cooking Lake – Blackfoot Provincial Recreation Area (BPRA) are two fenced natural areas in the Beaver Hills region of central Alberta where aspen parkland is being conserved. These areas maintain high densities of native ungulates including elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*), with plains bison (*Bison bison bison*) and wood bison (*B. bison athabascaae*) also inhabiting EINP. My first objective was to use camera traps to estimate ungulate densities in EINP and BPRA, and to evaluate cameras as a viable alternative to aerial ungulate surveys (AUS). I applied the time-in-front-of-the-camera (TIFC) method and compared TIFC density estimates to AUS densities, identifying strengths and weaknesses for both approaches per species. We collected data from 43 cameras in EINP between December 2016 and October 2020, and 23 cameras in BPRA from April 2019 to August 2020. I estimated yearly densities in the north and south sections of EINP (2017-2019), and in BPRA (2019). Moose had the lowest discrepancy between approaches, bison TIFC density estimates were lower than AUS densities, and elk TIFC density estimates were higher the AUS densities. I was also able to provide deer TIFC density estimates in EINP and BPRA in the absence of aerial survey data. Overall, I found that the TIFC and AUS approaches were complementary, where the AUS performed better for species in open habitats, while TIFC performed better for surveying species in closed habitats. My second objective was to evaluate spatiotemporal overlap and interspecific interactions between bison and elk in EINP.

Bison and elk have overlapping habitat use and diet and are the primary focus of ungulate management in EINP. I examined distributions of both species in relation to season, landscape characteristics, anthropogenic features, and heterospecifics using generalized linear models (GLMs). I then examined seasonal daily activity patterns of bison and elk and calculated the degree of overlap. The spatial analysis revealed that bison counts were positively associated with higher proportions of open habitats across seasons and in areas farther from water in summer and fall but had no associations with distance to water in winter. Bison removal year was a significant predictor variable for bison counts in winter when the bison roundup takes place. Spatial modeling revealed that elk avoided areas with high linear feature density across seasons. During fall and winter, I observed higher elk counts associated with bison presence. Temporal activity patterns revealed that elk were crepuscular in all three seasons, but bison activity patterns varied with diurnal activity being more common in the summer, crepuscular activity in winter, and intermediate activity patterns in the fall. Coefficients of overlap between elk and bison were high in all three seasons with the greatest difference in daily activity patterns in summer and the highest overlap in winter when both species showed strong crepuscular activity. Despite the fenced perimeter in EINP resulting in high ungulate densities, limited dispersal, and low predation, our data show similar patterns of habitat use and interactions between bison and elk to those in other systems. Spatiotemporal partitioning between bison and elk does not appear necessary to coexist in the aspen parkland. Future research should focus on ungulate impacts to vegetation in relation to fluctuating ungulate densities and interspecific interactions. Continued monitoring and active management are necessary to protect the ecological integrity of these natural areas for years to come.

## **PREFACE**

This thesis is an original work by Jennifer M. Foca. Field data were collected by Jennifer Foca, Darcy Visscher, and the Friends of Elk Island Society between December 2016 and October 2020. This project was granted an exemption from ACUC review by the University of Alberta Ethics Office due to being Category A Animal Use (observation of live animals; REO Reference number: 2018.031aFoca). Data collection was permitted by Parks Canada (EI-2016-23336, EI-2019-31317, EI-2020-35818) and Alberta Tourism, Parks and Recreation (19-093, 20-017). Marcus Becker of the Alberta Biodiversity Monitoring Institute provided guidance and technical support for the TIFC approach in Chapter 2.

To date, no manuscripts have been submitted for publication, but Chapter 2 will include Darcy Visscher, Marcus Becker, and Mark Boyce as co-authors, and Chapter 3 will include Mark Boyce as a co-author.

*Dedicated to Kanga, Roo, and Mreowser*

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## Chapter 1 – General introduction

Elk Island National Park (EINP) is a fully fenced park located in central Alberta, Canada on Treaty 6 territory. EINP is representative of the Southern Boreal Plains and Plateaux Natural Region (Parks Canada 2010) and is located in the Beaver Hills region. EINP is one of few national parks in North America that features the aspen parkland ecosystem. Aspen parkland is a transitional zone, that occurs between the boreal forest to the north and the grasslands to the south (Bird 1961, Riley et al. 2007). This landscape in EINP is characterized by glacial moraine topography, with interspersed deciduous forests, grasslands, and wetlands. Native ungulate assemblages are an integral part of the aspen parkland ecosystem and play a role in maintaining heterogeneity (Hobbs 1996). Ungulates in EINP include elk (*Cervus elaphus*), plains bison (*Bison bison bison*), wood bison (*B. bison athabascae*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*).

Ungulate density is high in EINP (Parks Canada 2017). EINP is the only fully fenced national park in Canada, and the fence is necessary to contain ungulates in the park (specifically bison, elk, and moose) in order to prevent conflict with nearby farmers. Fencing is a useful tool to separate wildlife from conservation threats (Somers and Hayward 2012), but this barrier prevents high density ungulate populations from dispersing. Due to the fenced perimeter and the park's location within an agricultural matrix, EINP does not have many predators and predation does not substantially influence ungulate populations. The combination of the highly productive aspen parkland ecosystem, limited ungulate dispersal, and lack of predation has resulted in high ungulates densities within EINP. Parks Canada actively manages ungulate populations to prevent overgrazing and protect the ecological integrity of the park (Parks Canada 2017). Current ungulate management includes reducing the bison populations through translocations and culls,

alternating between the northern and southern portions of EINP each year. Previously elk could be translocated as well, however cervids are no longer translocated due to the risk of spreading chronic wasting disease (Parks Canada 2017). Wildlife managers need accurate population estimates to manage ungulates in this system.

Ungulates in EINP are typically surveyed each winter using aerial surveys, attempting total counts. One major challenge with aerial surveys is visibility bias (Caughley 1974, Caughley et al. 1976). Sightability for each species varies greatly from high sightability of bison due to their large body size and use of open habitats (Wolfe and Kimball 1989, Hess 2002, Terletzky and Koons 2016), in contrast with the low sightability of deer that can be difficult to see in forested landscapes. Camera traps were selected to provide better temporal coverage compared to the aerial ungulate survey, and to be able to detect all ungulate species, rather than only species that are highly visible by aerial survey. Camera traps are a tool increasingly used for wildlife monitoring, including for density estimation of unmarked species (Rowcliffe et al. 2008, Chandler and Royle 2013, Burton et al. 2015, Moeller et al. 2018, Nakashima et al. 2018, Warbington and Boyce 2020).

In 2016, Larry Roy and the Friends of Elk Island Society (FEIS) partnered with Parks Canada to design a camera trap survey for estimating ungulate densities in EINP. Camera trap deployment began in December 2016, with FEIS overseeing project management for 2017. FEIS partnered with the Boyce lab at the University of Alberta in 2018 to carry the project forward. In 2018 Darcy Visscher at the King's University collaborated and added an additional study area, Cooking Lake – Blackfoot Provincial Recreation Area (BPRA). BPRA is a provincial protected area immediately south of EINP, and the two natural areas share a border. BPRA is home to elk,

moose, white-tailed deer, and mule deer, but not bison. Seasonal cattle grazing is permitted in BPRA.

I used camera traps to monitor ungulates in EINP and BPRA from December 2016 to October 2020. For part one of this study (Chapter 2), I used camera trap data to estimate ungulate densities using the Time-in-front-of-the-camera (TIFC) approach. I also compared camera trap density estimates to densities calculated from the aerial ungulate survey, identifying strengths and weaknesses for camera trapping and aerial survey approaches and how they differed by species. My study provides the first comparison between aerial surveys and the TIFC model in a multispecies monitoring context. For the second part of this study (Chapter 3), I turned my attention to bison and elk spatiotemporal interactions in EINP. Elk and bison are the focus of park management efforts to reduce ungulate populations in EINP while maintaining minimum viable populations (Parks Canada 2010). Grasslands are used by both bison and elk and might be a limiting resource for these species in EINP (Cairns and Telfer 1980). Bison may displace elk (Holsworth 1960) causing spatial partitioning in seasons with high habitat selection overlap (Telfer and Cairns 1979). Conversely, high ungulates densities might impede partitioning (Van Beest et al. 2014). High spatial overlap has implications for concentrated negative effects to grasslands in EINP because both bison and elk select grasslands (Telfer and Cairns 1979, Cairns and Telfer 1980).

To determine bison and elk spatiotemporal patterns, I first evaluated whether bison and elk distributions were related to landscape characteristics, human use, heterospecifics (i.e., bison/elk), or a combination of these factors. Next, I compared bison and elk and daily activity patterns and degree of overlap. I completed the spatiotemporal analyses across three biologically

relevant seasons: summer, fall, and winter. I offer insights about ungulate densities and interspecific interactions within two fenced natural areas in the aspen parkland ecosystem.

## **Chapter 2 - Camera traps for density estimation: Applying the TIFC model to multiple closed populations of ungulates**

### **Introduction**

Estimating density or abundance of wild populations is a common goal of wildlife managers (Williams et al. 2002). Such information is needed to connect populations to ecological processes and create management plans that lead to desired ecological conditions. Many ungulate populations have been increasing across North America (Mahoney and Cobb 2010, Krausman and Bleich 2013), presenting a greater need for accurate and precise density estimates to inform wildlife management decisions. This is especially true in areas where barriers (i.e., fencing, roads, etc.) limit ungulate dispersal and where predator populations have declined. There also has been a rising need for monitoring approaches that can be applied to a broader range of species at the same time. Aerial surveys are commonly used to estimate ungulate density or abundance, however aerial approaches have limitations including visibility bias (Caughley 1974, Caughley et al. 1976). Camera traps are a tool increasingly used by wildlife managers with many promising applications for density estimation (Burton et al. 2015).

In Canada, aerial ungulate surveys (AUS) are the predominate method for estimating ungulate densities (Gasaway et al. 1986, Steinhorst and Samuel 1989, McIntosh et al. 2009, Boyce et al. 2012, Habib et al. 2012). Advantages of aerial surveys include excellent spatial coverage and a relatively low time commitment for surveying. Drawbacks include cost, which often results in poor temporal coverage, with aerial surveys providing only a snapshot in time. Aerial surveys are generally constrained to certain times of year, specific flying conditions, and often have requirements like minimum snow cover (Lynch and Shumaker 1995, Allen et al. 2008). In contrast, camera traps have excellent temporal coverage relative to the amount of field



effort required, because data are collected remotely throughout the year. Spatial coverage is more limited for camera traps than aerial surveys because researchers are generally limited by the number of camera trap units available to deploy. For aerial surveys, sightability can be a major issue and varies greatly based on species, group size, vegetation cover, animal behavior, and flying conditions (Samuel et al. 1987, Graham and Bell 1989, Anderson and Lindzey 1996). Aerial surveys have limited ability to collect information of sex ratios for some ungulate species, which can be used in ungulate population management (Bender 2006). Camera trap surveys have greater potential for collecting detailed demographic data (i.e., sex ratios, age class), and may be more appropriate for collecting data on species in closed cover areas. Lastly, aerial surveys are considered much more dangerous for researchers than camera trap surveys (Sasse 2003). Overall, camera traps have potential for estimating densities for a broader range of species and time frames.

Most studies on density estimation using camera traps have focused on techniques for ‘marked’ populations (Burton et al. 2015), such as for species where individuals have uniquely identifiable coat patterns. Camera trap density methods for marked populations include conventional capture-recapture (CR; Karanth and Nichols 1998) and spatial capture-recapture (SCR; Efford 2004, Borchers and Efford 2008, Royle et al. 2014). Approaches that estimate population densities for unmarked species have greatly expanded camera trap applicability. Some camera trap developments for estimating density of unmarked populations include the Random Encounter Model (REM; Rowcliffe et al. 2008), spatial count models (SCM; Chandler and Royle 2013), space-to-event model (STE; Moeller et al. 2018), the Random Encounter and Staying Time model (REST; Nakashima et al. 2018), and the Time-in-Front-of-the-Camera (TIFC) model (Huggard 2018, Warbington and Boyce 2020). The TIFC model builds on the

REM and REST approaches and estimates the species density across camera sites using the cumulative animal staying time in the camera trap field-of-view, as well as the area and time frame sampled. The TIFC approach has no data requirements for animal movement rates, average group size, home range size, or effective trapping area (Foster and Harmsen 2012, Nakashima et al. 2018, Warbington and Boyce 2020), making it an attractive and accessible approach for researchers and wildlife managers.

We compared population density estimates from camera traps and aerial surveys for multiple closed populations of ungulates in two fully fenced natural areas. The objectives of this study were to (i) estimate ungulate densities using the TIFC approach (Huggard 2018, Warbington and Boyce 2020), (ii) compare TIFC density estimates to aerial survey densities, and (iii) identify strengths and weaknesses for each approach. This study took place in Elk Island National Park (EINP) and Cooking Lake - Blackfoot Provincial Recreation Area (BPRA), two fully fenced natural areas located in the Beaver Hills region in Alberta, Canada, with a total of five unmarked ungulate species: elk (*Cervus elaphus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and bison (*Bison bison*), with bison only being present in EINP. This allowed us to apply the TIFC method to multiple closed populations of ungulates across multiple years (2017-2019 for EINP, 2019 for BPRA). Aerial surveys have been conducted in EINP each winter using a total count approach, and during 2019-2020 we extended the survey to BPRA as well. We were able to calculate TIFC density estimates for all 5 ungulate species, but there are no reliable aerial counts for white-tailed deer and mule deer due to sightability issues. We therefore selected bison, elk, and moose as our three focal species to compare the TIFC estimates to aerial survey densities. In this study, we provide the

first comparison between aerial surveys and the TIFC model in a multispecies monitoring context, thereby allowing us to evaluate the efficacies of each.

## **Materials and Methods**

### *Study areas*

Elk Island National Park (EINP) and Cooking Lake – Blackfoot Provincial Recreation Area (BPRA) are adjacent protected areas located in the Beaver Hills region of central Alberta, Canada on Treaty 6 territory. These natural areas are representative of the Southern Boreal Plains and Plateaux Natural Region (Parks Canada 2010), which is characterized by glacial moraine topography with a mix of deciduous forests, lakes, wetlands, and grasslands. Forested areas in these natural areas are largely deciduous, dominated by trembling aspen (*Populus tremuloides*), with occasional clusters of conifers.

The Yellowhead Hwy, AB 16 transects EINP, dividing it into separate northern and southern areas (EINP-N and EINP-S respectively; Figure 2.1). BPRA shares its northern border with EINP-S. Each of these three areas are enclosed by a 2.2 m high fence which restricts wildlife movement in and out of each area. We therefore considered these areas as three independent study areas: EINP-N (134 km<sup>2</sup>), EINP-S (60 km<sup>2</sup>), and BPRA (97 km<sup>2</sup>). Vegetation cover is similar in all three study areas, however in BPRA approximately 50% of the landscape has been converted to grazing pastures. BPRA is a multiuse area with seasonal cattle grazing, Indigenous and licenced hunting, maintained gas wells, and a variety of opportunities for non-motorized recreation exist. Recreation opportunities are more limited in EINP, with hiking and biking being the most common types of recreation. Human use and human trail density are higher in EINP-N and BPRA compared to EINP-S.

Elk, moose, mule deer, and white-tailed deer are present in all three study areas. Plains bison (*Bison bison bison*) are only present in EINP-N, while wood bison (*B. bison athabasca*) are only present in EINP-S (this allows populations to remain genetically distinct for conservation purposes). Predation and dispersal are limited in all three sites due to the fenced perimeters. Predators include transient black bears, resident coyotes, and the occasional wolf; none of which are thought to have a limiting effect on ungulate populations. Active ungulate management in EINP is necessary to prevent populations from becoming overabundant (Parks Canada 2017). Current ungulate management includes bison removals (i.e., translocations, culls), alternating between EINP-N and EINP-S in winter each year. Elk translocations are no longer allowed due to the risk of spreading chronic wasting disease (Parks Canada 2017). Unlike BPRA, EINP does not allow hunting as part of its ungulate management. Other distinguishing characteristics between ungulate populations in the three study areas include very low moose numbers in EINP-N compared to other study areas due to mortality caused by liver flukes and winter ticks (Samuel 2004, 2007, Shury et al. 2019).

#### *Aerial densities*

Aerial ungulate surveys are conducted in EINP annually attempting total counts on a series of east-west transects at 0.5-km intervals. The surveys were conducted in the winter each year, typically during November-January depending on weather conditions (snow cover, cloud cover, etc.). We extended the survey to BPRA in winter 2019, corresponding to the BPRA camera trap survey period. Ungulates are counted separately for each study area (EINP-N, EINP-S, BPRA). We calculated aerial densities for each focal species (bison, elk, moose), study area, and year by dividing the corresponding total count by the study area's landcover in km<sup>2</sup>. Study area landcover was calculated using 30x30m resolution supervised Landsat 2015 raster. We excluded

open water from the total area ( $\text{km}^2$ ) of each study area by subtracting cells/pixels with open water. Bison, elk, and moose aerial densities were compared with TIFC estimates from the same study year. In this study, we consider a study year to be the time period beginning on April 16<sup>th</sup> until the following April 15<sup>th</sup> (i.e., Study year 2017 includes April 16, 2017 – April 15, 2018).

### *Camera Trapping*

We deployed camera traps (Reconyx Hyperfire: H500, P800, P900) on a  $2 \times 2 \text{ km}^2$  systematic grid across all three sites with 31 cameras in EINP-N, 12 cameras in EINP-S, and 23 cameras in BPRA (Figure 2.1). In places where a point on the grid fell within a lake or grassland, the camera was moved to the nearest tree. Each camera was attached to a tree 1m off the ground, facing northward to prevent glare. Camera traps were placed facing areas where ungulate detection would be possible, such as game trails or open areas. Cameras on game trails were placed approximately 4m away from the game trail with an unobstructed view of the game trail. In EINP-N and EINP-S, cameras that would have been placed on or near human-use trails were moved off trail by 100m for privacy concerns. Cameras deployed in BPRA were not placed to avoid human-use trails. To maximize the chance of capturing fast-moving individuals, cameras were set to take three rapidfire photos with up to two frames per second following each motion trigger. Cameras were serviced twice per year at minimum. We cleared vegetation within the field of view every time cameras were serviced.

For this study, we used camera trap data collected in EINP-N and EINP-S from April 2017 to April 2020, and we used camera trap data collected in BPRA from April 2019 to April 2020. The number of active cameras varied during each study year used for density estimation due to equipment removals and/or failures (Table 2.1).

Photos were stored in the Alberta Biodiversity Monitoring Institute (ABMI) database and image tagging system, WildTrax (WildTrax 2019), including metadata for each photo such as camera name, location, date, and temperature. Each photo was tagged with information for species name, age class, sex, and number of individuals following ABMI tagging protocols.

*Time in front of the camera (TIFC) model*

We calculated densities for each species at each camera station for each survey-year. To estimate density  $\hat{D}$  (animals/km<sup>2</sup>) using camera traps, we applied an adaptation of the Nakashima et al. (2018) method, the TIFC model (Huggard 2018, Warbington and Boyce 2020):

$$\hat{D} = \frac{\sum(N \cdot T_F)}{A_F \cdot T_O}$$

where  $N$  is the number of animals observed,  $T_F$  is the time spent in the field-of-view,  $A_F$  is the area in the field of view, and  $T_O$  is the camera operating time. In Warbington and Boyce (2020), a variation of this equation was used where  $M$  represents the cumulative staying time ( $\sum(N \cdot T_F)$ ),  $s$  is the area sampled ( $A_F$ ), and  $H$  is the camera operating time ( $T_O$ ). Unlike the REST approach, the TIFC approach does not require parameterization of encounter rates and staying times and instead uses the cumulative staying time for any member or a given species during the monitoring period (Warbington and Boyce 2020).

We defined independent events using an interval of 120 seconds between photo sequences. Staying time ( $N \cdot T_F$ ) was calculated per event by taking the average number of animals per photo in the event ( $N$ ) multiplied by the event duration ( $T_F$ ). Because our data consisted of discrete, time-stamped images, we modified the time spent in the field of view in two ways. First, we accounted for time spent in the field of view before the first photo and after the last photo by adding on a species-specific average time between photos to each event. Second, we

adjusted the time spent in the field of view based on the time intervals between photos in each event. For gaps less than 20 seconds we assumed the animal stayed in the field of view, for gaps greater than 120 seconds we assume the animal left (and the next detection would be a new independent event), and for gaps between 20-120 seconds, we applied species-specific models for the probability of leaving (Becker 2021). There was not a species-specific leaving-time model for bison, so for bison we used a model that applies for ‘Most ungulates’. Staying time for each species was then summed for all events per camera location, per survey period.

For camera operating time ( $T_O$ ) we used the number of camera trapping days sampled that season and study year. Area in the field of view ( $A_F$ ) was calculated using the following equation:

$$A_F (m^2) = \frac{(\pi * EDD^2 * angle)}{360}$$

where  $EDD$  is the effective detection distance (m). Effective detection distances were estimated for each species, each habitat type, and each season (Becker 2021). We assumed the *angle* to be 42° for all cameras (Reconyx 2017).

TIFC model assumptions include (1) representative sampling of microhabitats, (2) that animal movement is not altered by camera trap presence, and (3) there is perfect detection within 5m of the camera (Huggard 2018, Warbington and Boyce 2020).

### *Calculating density*

The TIFC equation is used to estimate the density of a species at each camera location for a given time period. We defined two seasons: summer (April 16–October 15) and winter (October 16-April 15). The time frame for the winter season was modified for bison in the study areas and years when bison handling took place (Table 2.1, Appendix 2.1). We used the TIFC method to calculate ungulate densities at each camera station for the summer and winter. We then

calculated the density for the study year by averaging the two seasons. Cameras with fewer than 20 days per season were excluded from the analysis. We then applied species and habitat specific correction factors to elk, moose, mule deer, and white-tailed deer estimates to account for the fact that their staying time is inflated by time spent investigating cameras, a violation of assumption 2 for which we attempted to adjust using correction factors estimated by Becker (2021). Lastly, we calculated densities per species, per study area, and per study year by averaging the density estimates at all cameras from the corresponding study area and time frame. We calculated 90% confidence intervals using a Monte Carlo simulation of both presence/absence and the abundance given presence. We compared TIFC densities to aerial densities using Wilcoxon signed-rank tests.

## **Results**

### *Aerial densities*

We calculated land area for each of the three study areas: 128.5 km<sup>2</sup> in EINP north, 55.5 km<sup>2</sup> in EINP-south, and 91.2 km<sup>2</sup> in BPRA. We used the counts from the winter aerial surveys divided by land area (km<sup>2</sup>) of the respective study area to calculate aerial densities for bison, elk, and moose (Figure 2.2, Table 2.2). There were problems with the aerial survey in EINP-S in 2017, namely that the survey could not be completed in the usual timeframe (Dec/Jan) and the survey was split and completed during two different time periods. Due to these sampling issues, we omitted the aerial total counts from the EINP-S 2017 survey and did not calculate aerial densities for this study area and time period. There are no estimates of precision associated with aerial survey total counts.



### *Camera trapping*

In total, this study included 43,102 camera trapping days (Table 2.1). The minimum number of camera trapping days for any study area and survey period was 2981. We summarized the total number of capture events for each species for each study area and year (Table 2.1). The minimum number of capture events for any study area and year were 224 for bison, 681 for elk, 65 for moose, 23 for mule deer, and 595 for white-tailed deer.

### *TIFC Density Estimates*

We calculated TIFC density estimates and 90% confidence intervals for bison, elk, moose, mule deer, and white-tailed deer for each study area and year (Figure 2.2, Table 2.2).

Bison TIFC estimates ranged from 1.82 to 6.19 bison per km<sup>2</sup> in EINP-N and from 2.54 to 8.07 bison per km<sup>2</sup> in EINP-S (Table 2.2, Figure 2.2). For study areas and years with both a camera density and aerial density for comparison, bison TIFC estimates were lower than aerial densities in 3 out of 5 occasions (Figure 2.3), and there was no significant difference between TIFC and aerial densities ( $W=3$ ,  $p=0.31$ ). Using these 5 occasions, bison TIFC density estimates were only 0.19 times lower than bison aerial densities with an average difference of 1.55 bison per km<sup>2</sup>.

TIFC estimates for elk ranged from 3.55 to 8.71 elk per km<sup>2</sup> across all study areas and years, with 90% confidence intervals overlapping for all estimates (Table 2.2, Figure 2.2) indicating that elk density was similar across the three study areas. For study areas with multiple years (EINP-N and EINP-S), elk density estimates were consistent across years (Figure 2.2). For study areas and years with corresponding camera and aerial densities, we found that elk TIFC density estimates were higher than aerial densities in all 6 occasions (Figure 2.3), and elk TIFC and aerial densities were significantly different ( $W=21$ ,  $p=0.03$ ). Using these 6 occasions, elk

TIFC estimates were 1.16 times higher than aerial densities with an average difference of 2.99 elk per km<sup>2</sup>.

In EINP-N, moose TIFC estimates were the lowest of the three study areas with estimates ranging from 0.06 to 0.11 moose per km<sup>2</sup> (Table 2.2). BPRA had an intermediate TIFC estimate at 1.36 moose per km<sup>2</sup>. EINP-S had the highest moose TIFC estimates ranging from 3.61 to 5.46 moose per km<sup>2</sup>. For study areas with multiple years (EINP-N and EINP-S), moose density estimates were consistent across years (Figure 2.2). For study areas and years with corresponding camera and aerial densities, we found that moose TIFC density estimates aligned well with aerial densities in all 6 occasions (Figure 2.3), and there was no significant difference between moose TIFC and aerial densities ( $W=11$ ,  $p=1.00$ ). Moose TIFC estimates were higher than moose aerial densities in EINP-S, but moose TIFC estimates were lower than moose aerial densities in EINP-N and BPRA. On average, moose TIFC estimates were higher than moose aerial densities by 0.29 moose per km<sup>2</sup> due to the higher TIFC values in EINP-S, the study area with the highest moose density. We found that proportional difference for moose was misleading because of the near zero density estimates for moose in EINP-N. Moose TIFC density estimates in EINP-N were only lower than moose aerial densities by 0.09 moose per km<sup>2</sup> on average but due to the low densities they had the highest proportional difference.

Mule deer TIFC density estimates were low across the three study areas, ranging from 0.08 to 0.62 mule deer per km<sup>2</sup> (Table 2.2), and estimates were generally consistent across years. White-tailed deer TIFC density estimates ranged from 1.37 to 1.56 deer per km<sup>2</sup> in EINP-N, with a similar density estimated in BPRA of 1.39 deer per km<sup>2</sup>. White-tailed deer TIFC estimates were higher in EINP-S, ranging from 4.20 to 5.63 deer per km<sup>2</sup>. In all study areas white-tailed

deer density estimates were higher than mule deer estimates, consistent with park staff observations.

## **Discussion**

Estimates of density and abundance are essential for wildlife management (Williams et al. 2002). Aerial surveys are the most commonly used tool for estimating ungulate abundance, with various methods being used in Alberta, Canada, including the total count method and the stratified random block or ‘Gasaway Method’ (Gasaway et al. 1986, Lynch and Shumaker 1992). While aerial surveys are commonly used, they are not without their downsides and are subject to visibility bias (Caughley 1974, Samuel et al. 1987). Camera traps are increasingly used for wildlife monitoring (Burton et al. 2015), and may be a viable alternative to aerial surveys. Several analytical approaches have been developed for estimating animal densities using camera traps, but the majority of camera trap density studies have used approaches that are only applicable to species with uniquely identifiable markings (Karanth and Nichols 1998, Efford 2004, Borchers and Efford 2008, Royle et al. 2014, Burton et al. 2015). Methods for density estimation of unmarked species (Rowcliffe et al. 2008, Chandler and Royle 2013, Moeller et al. 2018, Nakashima et al. 2018, Warbington and Boyce 2020), such as the TIFC method, will greatly increase camera trap applications for wildlife monitoring.

We applied the TIFC method to five species of ungulates in three enclosed study areas across multiple years. For the three species with aerial densities for comparison (bison, elk, and moose), we found the TIFC method yielded density estimates that were similar to aerial survey densities in most cases (Figure 2.2, Table 2.2), leading us to conclude that camera traps can be used to estimate ungulate densities that are realistic and appear to be consistent across years.

Similarly, the TIFC method produced comparable density estimates to spatial mark-recapture methods for sitatunga in central Uganda (Warbington and Boyce 2020).

We compared TIFC density estimates with aerial densities and found the specific relationship between them differed by species. Moose had the lowest discrepancy between the two (Figure 2.3). TIFC estimates were higher than aerial densities by only 0.29 moose per km<sup>2</sup> on average, and there was no significant difference between moose TIFC and aerial densities. Aerial surveys in our three study areas are considered to be fairly reliable for moose given the high visibility of moose within the habitat types present (Gasaway et al. 1986, Bisset and Rempel 1991). Moose are highly visible in deciduous forests (83% seen), deciduous shrub (100% seen), and open habitats (100% seen) – the three habitat types that constitute over 95% of each of our study areas (Anderson and Lindzey 1996). Both aerial and TIFC densities were realistic given our knowledge of moose populations in each study area. We observed consistently low densities (<0.26 moose/km<sup>2</sup>) for both TIFC and aerial approaches each year in EINP-N. The moose population in EINP-N has been drastically reduced due to mortality from winter tick and liver fluke (Samuel 2004, 2007, Shury et al. 2019), resulting in relatively low moose densities compared to the other two study areas. In contrast, the moose population in EINP-S is extremely high and is cause for management concern. Using both TIFC and aerial approaches, we observed high moose densities (2.75-5.46 moose/km<sup>2</sup>) across years in EINP-S (Figure 2.2). We predicted that BPRA would have intermediate values for moose density relative to EINP-N and EINP-S since the fenced perimeter limits dispersal and can increase density, however Indigenous and licensed hunting are permitted in BPRA which reduces population numbers. As expected, we observed intermediate moose densities in BPRA, with TIFC density estimates and aerial densities that were similar (1.36 and 1.5 moose/km<sup>2</sup>, respectively). Moose estimates were

reasonably precise across all three study areas regardless of the sample size (Figure 2.2, Table 2.2).

Bison TIFC density estimates were 0.19 times lower than aerial densities with an average difference of 1.55 bison per km<sup>2</sup>, and there was no significant difference between TIFC and aerial densities. We consider the aerial densities for bison to be reliable due to the high visibility of bison, with multiple studies estimating bison sightability of 92-97% (Wolfe and Kimball 1989, Hess 2002, Terletzky and Koons 2016). Bison sightability is high due to their large body size, gregarious behaviour, and use of primarily open habitats like grasslands. Aerial counts for bison are probably close to the true population size in the park, and thus the TIFC bison estimates were lower than actual densities. We think this was primarily due to inadequate sampling of open habitats like grasslands because we were unable to deploy cameras in the middle of fields. Post-hoc, we calculated the proportion of habitat types sampled compared to the proportion of habitats present in EINP-N and EINP-S and found that grasslands and other open habitats were underrepresented in both study areas (Appendix 2.2), a violation of assumption 1 of the TIFC method. Systematic grids are a common arrangement used in camera trapping studies for density estimation, however stratification by habitat type and/or increasing sampling effort should be considered for camera trapping studies, especially when monitoring multiple species with different patterns of habitat use. Burton et al. (2015) found that of the 42 camera trap studies they reviewed on estimating density or abundance, only 28.6% incorporated information on focal species' ecology into the sampling design. Future studies using the TIFC approach should carefully consider habitat use by the focal species to ensure the camera trap study design is representative.

For species like bison that primarily use open habitats, this brings up a few additional challenges. Camera traps are typically attached to trees or fence posts, so if a potential camera location were to fall in the middle of a field, researchers would have to either move the deployment location to the nearest suitable tree or we would need to install a post. Both approaches may introduce bias. If cameras were moved to trees or other edge habitats, we might not adequately sample open areas. This can lead to an underestimate of species in open habitats, which would explain why our bison TIFC density estimates were lower than expected. If we instead install a post to deploy the camera in the open area, posts act as attractants for species like bison and cattle that rub on them. This would violate the TIFC assumption that animal movement is not affected by camera traps (Huggard 2018, Warbington and Boyce 2020), and can lead to inflated estimates of bison density. Despite these challenges to estimating bison density with camera traps and the TIFC approach, the method usually performed well. Future TIFC research could focus on developing sampling designs for open areas.

Elk estimates differed between the camera trap and aerial survey approaches with TIFC estimates that were 1.16 times higher than aerial densities with a difference of 2.99 elk per km<sup>2</sup> on average. Elk TIFC and aerial densities differed significantly. Aerial surveys in our study areas are less reliable for elk compared to bison and moose because of visibility bias (Caughley 1974, Allen et al. 2008). Samuel et al. (1987) found that elk visibility varies greatly based on group size and percent vegetation cover, with visibility as low as 22% for individual elk and visibility only reaching 100% for groups larger than 15. Elk in our fenced study areas do not form large herds during winter in the same way that migratory elk do in other systems; during winter we typically saw groups of less than 15 elk. Aerial surveys in our study area attempted total counts not corrected for sightability, and almost certainly underestimate elk densities. Therefore, it is

possible our TIFC estimates are a better estimate of elk population densities because camera traps are better able to survey elk of various group sizes and within closed habitats. That said, we saw the largest discrepancy between elk TIFC estimates and aerial densities in EINP-S where elk TIFC estimates had high variance across years. This is likely due to the low number of cameras in EINP-S combined with elk having a higher variation in detection probability and staying time due to variable group sizes. Accurate censuses of elk likely require a greater number of cameras compared to solitary species like moose in order to improve precision. Also, the grid in EINP-S might be overrepresenting areas used by elk (the opposite issue we observed for bison), which could be resolved by increasing the number of cameras, taking additional measures to ensure the sampling design is representative, or stratifying by habitat type.

We did not have an aerial estimate of mule deer and white-tailed deer densities in our three study areas, so we could not compare deer TIFC estimates with aerial densities. However, using the TIFC model we were able to provide the only population estimates of mule deer and white-tailed deer park managers have in both EINP and BPRA. These estimates were consistent across years for study areas with multiple study years.

Overall, the two sampling approaches were complementary. Aerial surveys in our study areas had excellent spatial coverage compared to the camera trap surveys. The number of camera traps available to researchers can limit the spatial coverage of camera trap surveys. Further, it can be difficult to know if the number of cameras deployed is adequate and representative of areas used by the species of interest. While the aerial surveys excel at spatial coverage, they provided poor temporal coverage, with only a once-per-year snapshot in winter for each of our study areas. In contrast, the camera trap surveys had excellent temporal coverage and collected data remotely year-round. The aerial densities were considered generally reliable for larger

ungulates (moose and bison) and species that use primarily open habitats (bison). It's likely that our bison densities calculated from aerial counts are more reliable than the bison TIFC density estimates due to issues with the camera trap grid underrepresenting grassland. In contrast, it is likely that the camera trap surveys performed better than the aerial surveys for ungulates in forested areas. Camera trapping also was the only method that we could use to estimate densities for white-tailed deer and mule deer in our study areas due to poor aerial visibility of deer. Regarding demographic data, both the timing of the winter aerial survey and sightability issues make it challenging to collect any detailed demographic data (i.e., sex ratios, age class distribution). Using camera traps, we were able to identify a larger number of species and collect detailed demographic information throughout the year. We can use this information to subset the data in a variety of ways prior to estimating density. Lastly, a major challenge of camera trapping is the extensive labour required. In addition to field work for deploying and maintaining camera traps, photo processing can take a tremendous amount of time. Advancements in species recognition or 'auto-tagging' software will greatly reduce the time commitment required for processing photos (Glover-Kapfer et al. 2019).

A major strength of the TIFC approach is that it is more accessible than some of the other methods due to applicability for unmarked species and fewer data requirements. The TIFC method can be used to estimate densities for a broad range of species and demographic subgroups without needing individual recognition, movement rates, home range size, or average group size. In this study, we were able to estimate TIFC densities for non-focal species such as white-tailed deer, mule deer, black bears, coyotes, and wild boar (Appendix 2.3). One limitation of the TIFC approach is it can be difficult to determine if the camera trap array is collecting an adequate, representative sample, especially for multispecies monitoring. This issue is present in



other methods for density estimation as well (Rowcliffe et al. 2008, Burton et al. 2015). To counter this issue, camera trap researchers should incorporate knowledge of species ecology into sampling design, rather than simply adopting a systematic grid or random sampling design. Future research on the TIFC approach should investigate the effect of sample size and different sampling designs on TIFC density estimates.

In our study, we have demonstrated that the TIFC model is a viable alternative to aerial surveys that produces realistic and consistent density estimates. When comparing TIFC and aerial densities for bison, elk, and moose, we found that these two approaches were complementary, where one excels at detecting species in open habitats, while the other excels at detecting species in closed habitats. Wildlife managers often are limited by resources and funding, creating a need for cost effective methods to monitor multiple species. We found that camera traps provided superior temporal coverage and collected data on a variety of species.

**Table 2.1** Number of cameras (*n*), camera trapping days (CT days), and detection events for bison, elk, moose, mule deer, and white-tailed deer (WTD) in each of three study areas in central Alberta, Canada from 2017-2019.

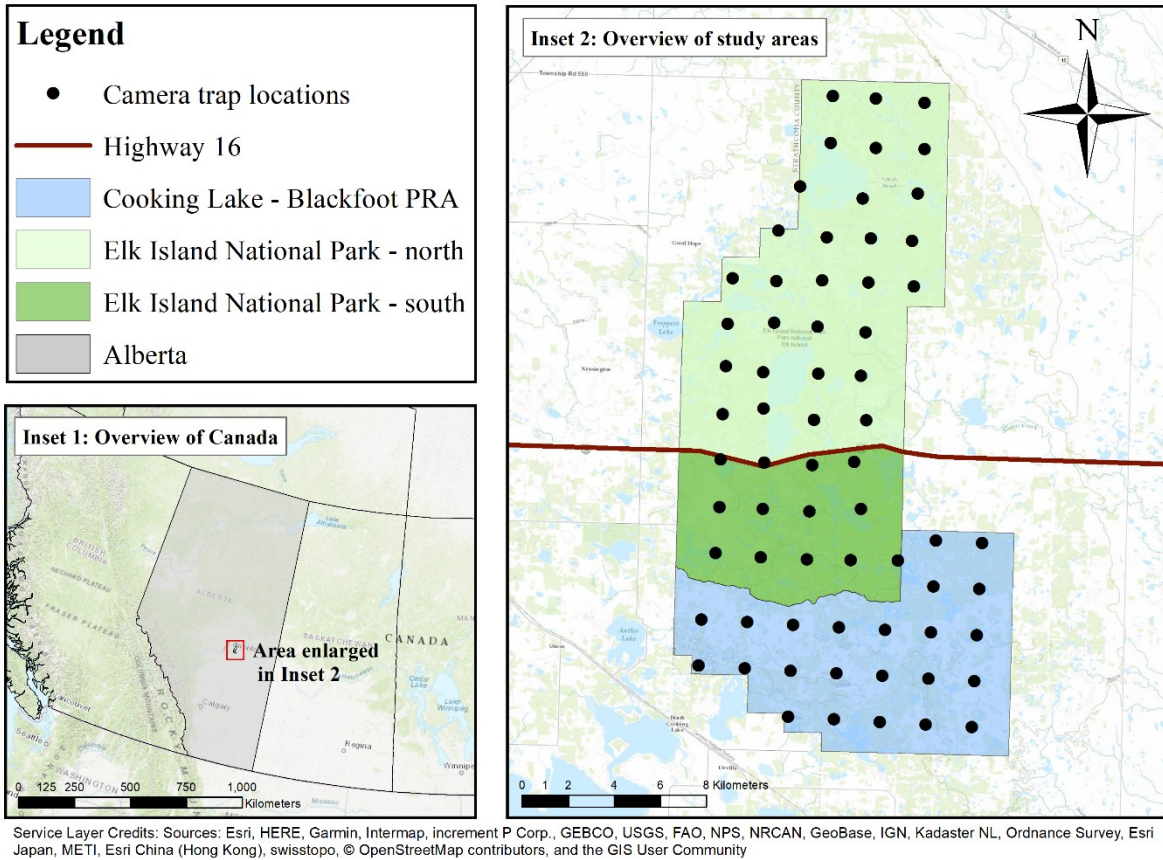
Study Area*	Study year	<i>n</i>	CT days	Number of detection events				
				Bison	Elk	Moose	Mule deer	WTD
EINP-N	2017	15	6096	776	1196	65	70	595
	2018	30	9245	551	2292	79	51	732
	2019	29	10824	1419	3064	81	68	983
EINP-S	2017	12	3747	618	879	634	76	1030
	2018	10	2981	224	681	479	31	732
	2019	10	3788	236	1160	547	23	1041
BPRA	2019	22	6421	-	989	535	180	783
Total:			43102	3824	10261	2420	499	5896

\* EINP-N = Elk Island National Park north, EINP-S = Elk Island National Park south, BPRA = Cooking Lake - Blackfoot Provincial Recreation Area

**Table 2.2** Sample size ( $n$ ), time-in-front-of-camera (TIFC) density estimates, TIFC 90% confidence intervals, and aerial densities for bison, elk, moose, mule deer, and white-tailed deer in three study areas in Alberta, Canada from 2017 – 2019.

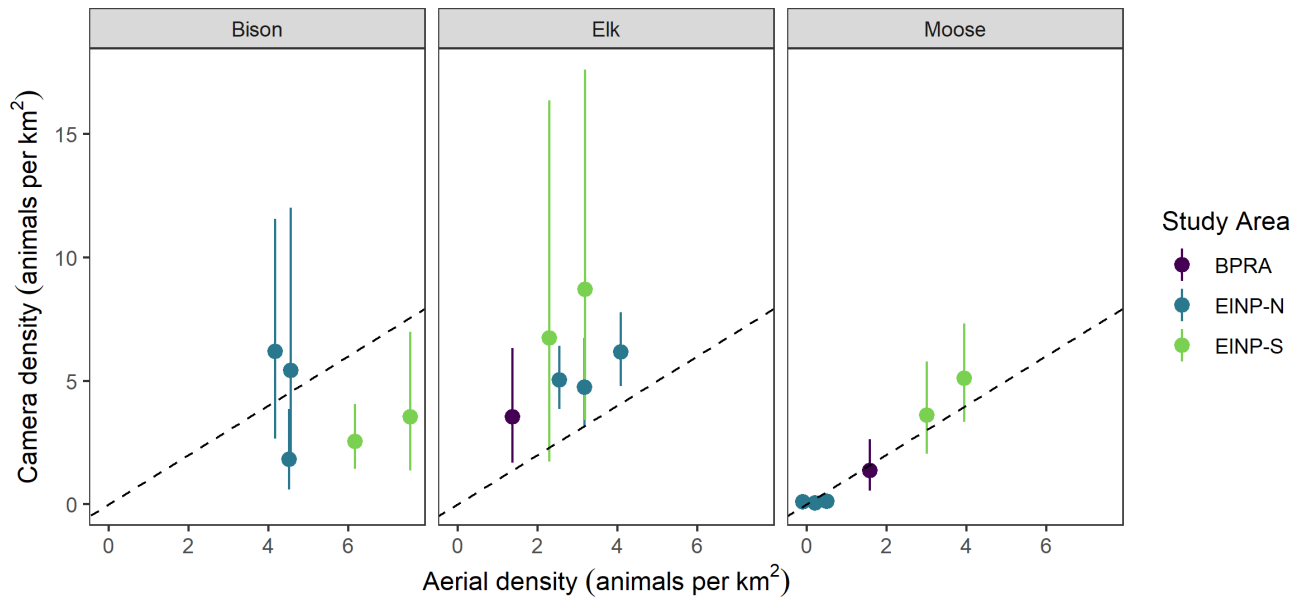
Species	Study Area*	Year	$n$	Density per km <sup>2</sup>			
				TIFC estimate	TIFC 90% CI	Aerial density	
Bison ( <i>Bison bison</i> )	EINP-N	2017	15	5.41	1.73-12.01	4.17	
		2018	25	1.82	0.61-3.86	4.87	
		2019	29	6.19	2.66-11.56	4.13	
	EINP-S	2017	10	8.07	2.85-17.10	-	
		2018	10	2.54	1.44-4.06	6.48	
		2019	10	3.53	1.38-6.97	7.56	
Elk ( <i>Cervus elaphus</i> )	EINP-N	2017	15	4.75	3.16-6.73	3.26	
		2018	30	5.03	3.88-6.39	2.56	
		2019	29	6.17	4.79-7.79	4.05	
	EINP-S	2017	12	7.87	3.90-13.58	-	
		2018	10	6.73	1.69-16.45	2.65	
		2019	10	8.71	3.38-17.39	3.22	
	BPRA	2019	22	3.55	1.68-6.35	1.27	
	Moose ( <i>Alces alces</i> )	EINP-N	2017	15	0.11	0.06-0.20	0.25
			2018	30	0.06	0.03-0.09	0.16
2019			29	0.10	0.05-0.18	0.13	
EINP-S		2017	12	5.46	3.32-8.33	-	
		2018	10	5.09	3.37-7.30	3.8	
		2019	10	3.61	2.07-5.75	2.75	
BPRA		2019	22	1.36	0.56-2.61	1.5	
Mule deer ( <i>Odocoileus hemionus</i> )		EINP-N	2017	15	0.25	0.06-0.60	-
			2018	30	0.08	0.03-0.15	-
	2019		29	0.10	0.04-0.18	-	
	EINP-S	2017	12	0.62	0.10-1.73	-	
		2018	10	0.15	0.04-0.34	-	
		2019	10	0.22	0.05-0.57	-	
	BPRA	2019	22	0.38	0.19-0.67	-	
	White-tailed deer ( <i>O. virginianus</i> )	EINP-N	2017	15	1.38	1.00-1.84	-
			2018	30	1.37	0.97-1.87	-
2019			29	1.56	1.14-2.07	-	
EINP-S		2017	12	5.63	4.54-6.86	-	
		2018	10	4.20	3.21-5.36	-	
		2019	10	5.30	3.88-7.01	-	
BPRA		2019	22	1.39	0.90-2.00	-	

\* EINP-N = Elk Island National Park north, EINP-S = Elk Island National Park south, BPRA = Cooking Lake - Blackfoot Provincial Recreation Area



**Figure 2.1** Camera trap survey across three study areas in central Alberta, Canada. Cameras were deployed on a  $2 \times 2 \text{ km}^2$  systematic grid, shown in black. The three adjacent study areas include Elk Island National Park-north (EINP-N;  $134 \text{ km}^2$ ), Elk Island National Park-south (EINP-S;  $60 \text{ km}^2$ ), and Cooking Lake - Blackfoot Provincial Recreation Area (BPRA;  $97 \text{ km}^2$ ). EINP-N and EINP-S are separated by Highway 16, shown in red. Each of the three study areas is enclosed by a 2.2m high fence, restricting ungulate movement between areas.





**Figure 2.3** Time-in-front-of-the-camera (TIFC) density estimates compared to aerial densities for bison, elk, and moose in three study areas in Alberta, Canada: Elk Island National Park-North (EINP-N), Elk Island National Park-South (EINP-S), and Cooking Lake - Blackfoot Provincial Recreation Area (BPRa). Error bars represent 90% confidence intervals for the TIFC density estimates. The dashed line represents the 1:1 relationship between aerial densities and camera densities (animals per km<sup>2</sup>).

## **Chapter 3 - Bison and elk spatiotemporal interactions in Elk Island National Park**

### **Introduction**

Interspecific interactions and species-habitat interactions are primary drivers in shaping distributions of wildlife populations across variable landscapes (Danielson 1991, Dunning et al. 1992). The availability and configuration of resources as well as assemblages of species present influence habitat selection and the types of interactions that occur (Sinclair and Norton-Griffiths 1982, Sinclair 1985, Wydeven and Dahlgren 1985, Murray and Illius 2000, Arsenault and Owen-Smith 2002, Van Beest et al. 2014). Many factors influence interspecific interactions, including the species assemblage in question, population densities, predation, and the composition and structure of available vegetation types (Danielson 1991, Dunning et al. 1992, Turner 2005, Van Beest et al. 2014). Ecosystems that are more heterogenous are able to support higher species diversity and densities (Dunning et al. 1992).

The aspen parkland is a highly heterogenous ecosystem characterized by a patchy mosaic of habitat types capable of supporting diverse ungulate assemblages (Bird 1961, Riley et al. 2007). The aspen parkland ecosystem is an ecotone that occurs between boreal forest and prairie ecosystems, with interspersed deciduous forests, grasslands, and wetlands (Riley et al. 2007). The diversity of vegetation types is maintained by climate conditions and various types of natural disturbances, including the impacts of ungulate grazing and foraging. During wet years, aspen and wetlands can overtake grasslands, whereas grasslands prevail under drought conditions, fire, and heavy grazing (Bird 1961, Riley et al. 2007). Native ungulates are an integral part of the aspen parkland ecosystem and play a role in maintaining heterogeneity (Hobbs 1996) by inhibiting aspen growth and maintaining grasslands (Campbell et al. 1994, Bork et al. 1997, Riley et al. 2007). In Canada, aspen parkland is one of the most highly exploited ecosystems, as

much has been cleared and converted to agricultural lands due to its rich soils, leaving less than 34% of natural cover remaining (Young et al. 2006, Riley et al. 2007, Ferrer-Paris et al. 2019). Other threats to this ecosystem include fire suppression and decreased grazing by wild herbivores.

Elk Island National Park (EINP) is a fully fenced park in central Alberta and is one of few areas in Canada where aspen parkland is being conserved with a diverse assemblage of native ungulates. The park maintains high densities of native ungulates including elk (*Cervus elaphus*), plains bison (*Bison bison bison*), wood bison (*B. bison athabascae*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*O. hemionus*). Because of intensive agriculture in the aspen parkland, the perimeter of EINP is fenced, containing all native ungulates within the park to prevent conflicts with farmers. While fencing can be a useful tool to separate wildlife from conservation threats and reduce agricultural losses, fencing also can introduce challenges for wildlife managers (Van Aarde et al. 1999, Somers and Hayward 2012). For example, due to the fenced perimeter and the partial isolation of the park within an agricultural matrix, EINP does not have many predators and predation does not substantially influence ungulate populations. The limited dispersal of ungulates, minimal predation, and highly productive aspen parkland ecosystem all contribute to high ungulate densities in EINP (Blyth 1995, Kuzyk et al. 2009, Parks Canada 2017). In the past, ungulate management goals in EINP included maximizing wildlife viewing opportunities with a focus on recreation (Blyth and Hudson 1992, Kuzyk et al. 2009), but since 1999 a reduction strategy for bison and elk was implemented and current management places greater focus on managing for ecological integrity (Parks Canada 2010, 2017). The fenced perimeter of the park is semipermeable to deer, and as a result population growth rates in EINP reflect regional demographic changes (Blyth 1995). Thus,



deer have not been a primary focus of ungulate management. Similarly, moose populations appear to be limited by density-dependent mechanisms including parasites such as liver fluke and winter tick (Blyth 1995, Samuel 2004, 2007, Shury et al. 2019). Bison and elk have been the focus of management actions by the Park (i.e., culls, translocations), to prevent hyperabundance (McShea et al. 1997, Bradford and Hobbs 2008, Parks Canada 2017). Currently, Parks Canada has placed emphasis on grassland health and aims to increase the proportion of grassland in EINP (Parks Canada 2010). Grasslands are used by both bison and elk and might be a limiting resource for these species in EINP (Cairns and Telfer 1980).

Many studies in EINP have investigated effects of ungulate grazing (Bork et al. 1997, Best et al. 2003, Best and Bork 2003, Hood and Bayley 2008) and attempts have been made to estimate ungulate carrying capacities (Blyth 1995, Kuzyk et al. 2009). Kuzyk et al. (2009) used a forage allocation to estimate economic carrying capacities. Bison usually are dominant over elk (Holsworth 1960) and can displace elk, resulting in spatial segregation between bison and elk and less available area for elk use (Arsenault and Owen-Smith 2002). In a scenario where elk are displaced by bison and have less access to grasslands, elk have the flexibility to use a variety of food sources (Cook 2002). Conversely high spatial overlap has implications for concentrated negative effects to rangelands in EINP because both bison and elk select for grasslands (Telfer and Cairns 1979, Cairns and Telfer 1980).

In this study, we used camera traps to examine the spatiotemporal patterns and interactions between elk and bison in EINP. We evaluated spatiotemporal patterns and interspecific interactions in three different biologically determined seasons: summer, fall and winter. Our first objective was to determine the relationship between bison and elk distributions and landscape characteristics, anthropogenic features, heterospecifics (i.e., bison/elk). We hypothesized that

bison and elk would have high spatial overlap during seasons with high habitat selection overlap because high densities of ungulates competing for resources can impede partitioning and cause more even use available habitats (Van Beest et al. 2014). We predicted a positive association between bison and elk use during winter due to higher overlap in habitats used (Telfer and Cairns 1979), despite bison and elk consuming different types of forage in winter. We considered anthropogenic features in addition to landscape characteristics and heterospecifics because humans have the potential to influence ungulate space use and patterns of overlap (Webb et al. 2011a, Ciuti et al. 2012). Our second objective was to determine if bison and elk partition time by comparing their daily activity patterns. We predicted that bison and elk would have different daily activity patterns because bison are diurnal (McMillan et al. 2021) and elk are largely crepuscular (Green and Bear 1990, Boyce et al. 2010). We also predicted that elk and bison would have higher temporal overlap in winter due to shorter day lengths. This study allows us to gain unique insight into how diverse ungulate assemblages coexist in the aspen parkland ecosystem under conditions of high ungulate density and limited dispersal.

## **Materials and Methods**

### *Study area*

This study took place in Elk Island National Park (EINP), a fully fenced park located in the Beaver Hills region of central Alberta, Canada on Treaty 6 territory (Figure 3.1). EINP is transected by Highway 16, dividing the park into northern (EINP-N; 134 km<sup>2</sup>) and southern (EINP-S; 60 km<sup>2</sup>) areas of the park. EINP-N and EINP-S are surrounded by a 2.2m perimeter fence, restricting movement of large mammals in and out of the park. EINP is a representative of the Southern Boreal Plains and Plateaux Natural Region and features glacial moraine topography with a patchwork of lakes and wetlands scattered throughout aspen parkland. Trembling aspen

(*Populus tremuloides*) is the dominant tree species, and deciduous forests cover over 60% of the park with some pockets of dispersed conifers (*Picea mariana* and *P. glauca*). Much of the forest understory is covered in beaked hazel (*Corylus cornuta*), as well as other woody shrubs such as prickly rose (*Rosa acicularis*). Open water and vegetated wetlands make up 33% of the park (Hood and Bayley 2008). Many of the lakes and ponds are surrounded by rings of open habitat, including grasslands and shrubland. The grasslands in EINP include a wide variety of grasses and forbs. Shrublands include many of the same species found in forested area, and also include aspen and poplar regeneration (Cairns and Telfer 1980). Habitat assemblages are very similar in EINP-N and EINP-S, however human use differs. EINP-N has more infrastructure, more linear features (paved roads and hiking trails), and higher human visitation rates than EINP-S.

EINP hosts a high density of ungulates including bison, elk, moose, mule deer, and white-tailed deer. Plains bison (*Bison bison bison*) are present in EINP-N and wood bison (*B. bison athabascaae*) are present in EINP-S. Bison densities during this study were high with 4-5 bison/km<sup>2</sup> in EINP-N and 7 bison/km<sup>2</sup> in EINP-S based on aerial survey data (Chapter 2; Table 2.2). Currently, bison populations are actively managed to prevent hyperabundance (Parks Canada 2017). Plains bison and wood bison populations are reduced every other year, alternating between the two subspecies (Appendix 3.1). Bison reduction currently involves removing animals from the park and translocating them to other areas in collaboration with bison reintroduction efforts elsewhere. Elk density is high in EINP, with 3-4 elk/km<sup>2</sup> based on aerial survey data (Chapter 2; Table 2.2). While elk translocations have happened in the past, they are no longer allowed due to the risk of spreading chronic wasting disease (Parks Canada 2017) and elk have not been removed from the park during this study. Moose numbers in EINP-N are extremely low due to liver flukes and winter ticks (Samuel 2004, 2007, Shury et al. 2019), but

moose density is high in EINP-S (~3-4 moose/km<sup>2</sup>; Chapter 2). Deer have not been the focus of management efforts because the fenced perimeter is semipermeable to them, and deer are difficult to survey aerially. The fenced perimeter, lack of predators, and high ungulate densities are important considerations for evaluating interspecific interactions in EINP.

### *Camera Trapping*

Camera traps were deployed in EINP on a 2x2km<sup>2</sup> systematic grid with 31 cameras deployed in EINP-N and 12 cameras deployed in EINP-S (Figure 3.1). Camera trap data collection took place between December 2016 and October 2020. Camera models included Reconyx Hyperfire H500, P800, and P900. If the camera location fell within an open area, the location was moved to the nearest tree. Camera traps were affixed to trees 1m off the ground. They were placed facing game trails or other open areas with an unobstructed view so that ungulate detections would be possible and were placed facing northward to prevent glare. Camera locations near hiking trails were moved at least 100m away from the trail due to privacy concerns. Cameras were programmed to take pictures 24 hours a day with 3 rapidfire pictures (up to 2 frames per second) per motion trigger. We serviced cameras at least twice per year and cleared vegetation to maintain the open field of view. Images were stored and tagged in WildTrax (WildTrax 2019). We tagged photos by species, age, sex class, and number of animals per photo.

### *Analytical Approach*

To study bison and elk interspecific interactions, we analyzed camera trap data using both a spatial and temporal approach across three seasons: summer, fall, and winter. We defined summer as April 1 to August 31, which includes bison calving (begins in late April and peaks in May), elk calving (May/June), green up (occurs in May), calf rearing for both species, and the

bison rut (June-August). We defined fall as September 1 to November 30, which includes most of the elk rut (peak in September) and leaf fall for deciduous plants. Winter spans December 1 to March 31 of the following year and is characterized by sub-freezing temperatures and snow cover. We pooled data across years for both the spatial and temporal analyses. We pooled data for EINP-N and EINP-S because habitats are similar in both areas, elk and bison densities are similar, and because modeling the two areas separately would have reduced our sample size.

For the spatial analysis we used generalized linear models (GLMs) to examine the relationship between bison/elk counts and camera site characteristics, including variables for habitat, anthropogenic features, and site use by heterospecifics. This method allowed us to examine relationships among species and landscape covariates, but not causality. Spatial overlap, or lack thereof, is not sufficient to infer mechanisms, such as competition or facilitation (Arsenault and Owen-Smith 2002). For our temporal analysis we examined bison and elk daily activity patterns using circular kernel density functions to determine if they were partitioning time instead of space. For both analyses, we defined independent photo events based on a 120 second gap between photo sequences.

#### *Landscape covariates*

For the spatial analysis, we reviewed a suite of landscape covariates that may influence bison and elk distributions (Table 3.1). For landscape covariates, we included distance to water, proportion of open habitat, and forest edge density. We included distance to water because EINP is characterized by a glacial moraine landscape, which includes pockets of different habitats surrounding water bodies dispersed throughout aspen forest (Hood and Bayley 2009). We also included a squared term for distance to water in case intermediate distances to water are more heavily used. For proportion of open habitat we included grassland and shrubland, two habitats

known to be important to bison and elk in EINP (Telfer and Cairns 1979, Cairns and Telfer 1980, Cook 2002, COSEWIC 2013). We calculated the proportion of open habitats within a 90x90m window at each camera trap location. This window size was chosen because it most closely reflects the vegetation at the site in which the animals were sampled, as opposed to a larger buffer that might encompass habitat types not used by the animal. We included forest edge density ( $\text{m}/\text{km}^2$ ) within a 500m buffer of each camera trap location because bison and elk have been documented to use edge habitats in EINP (Telfer and Cairns 1979, Cairns and Telfer 1980) and elk are known to use edge areas between forest and unforested interfaces (Skovlin et al. 2002). Buffer size for forest edge density was determined using univariate GLMs and selecting the covariate with the lowest AICc (Burnham et al. 2011).

For anthropogenic features, we included a covariate for linear feature density ( $\text{m}/\text{km}^2$ ) within a 500m buffer of each camera trap location. Linear features included paved roads, the park perimeter road, and hiking trails, and buffer size was determined by ranking univariate models. Elk are known to avoid linear features and other human disturbances (Ferguson and Keith 1982, Webb et al. 2011a, 2011b, Prokopenko et al. 2017a, 2017b). We expect that bison and elk would respond differently to linear feature density because bison in EINP are seemingly more tolerant of human use on roads and trails than elk.

We determined whether to use counts or presence/absence data for heterospecifics in the elk and bison models using univariate GLMs and selected the best-ranked covariate. In the bison GLMs, we used elk counts from camera trap data as the heterospecific model parameter. In the elk GLMs, we used bison presence/absence from camera trap data as the model parameter. We also included a parameter for bison removal year (Table 3.1, Appendix 3.1) in some of the

candidate models. Bison removal year was only present in an elk candidate model in conjunction with the parameter for bison presence/absence.

We assessed collinearity using a Pearson's correlation matrix and had no highly correlated covariates ( $r > |0.6|$ ). All continuous variables were scaled and centered. See Table 3.1 for details on variable creation and data sources.

### *Spatial Analysis*

We used generalized linear models with a negative binomial distribution to investigate species counts relative to landscape variables, anthropogenic features, and heterospecifics. We created *a priori* candidate model sets for each target species with 14 candidate models for bison (Appendix 3.2 – Table 1) and 19 candidate models for elk (Appendix 3.2 – Table 2). Both sets of candidate models also included a null model, and we used the same candidate model sets for each season. Each model included an offset for log camera trap days to account for differences in the response variable related to sampling effort. We excluded cameras with less than 10 active camera days in a season. We visually examined response variable distributions for each season and removed outliers to improve model fit. To account for repeated measures at a camera site due to pooling data across years, we included a random intercept for camera ID. We ranked models for each species and season using Akaike's Information Criterion corrected for small sample sizes (AICc; Akaike 1974, Burnham et al. 2011). We selected the most parsimonious model using a  $\Delta$  AICc of 2. Top models with a  $\Delta$  AICc less than 2 were considered competitive, and we chose the model with the lowest number of parameters as the best model. We considered beta coefficients to be significant if the 95% confidence intervals did not overlap 0 (Burnham et al. 2011). We calculated the proportion of deviance explained to assess model fit.

### *Daily activity patterns*

To investigate bison and elk temporal overlap, we compared daily activity patterns for bison and elk in each season: summer (April-August), fall (September-November), and winter (December-March). Data were pooled across years and were pooled between EINP-N and EINP-S. For each season we converted time to radians and used the R package ‘overlap’ to fit kernel density functions with a von Mises distribution for circular data (Meredith and Ridout 2020). Next, we calculated the coefficient of overlap ( $\Delta = 0$  means no overlap,  $\Delta = 1$  means complete overlap) between bison and elk for each season. For calculating this coefficient in package ‘overlap’, we selected the estimator Dhat4, which is recommended when the number of detections for both species are greater than 50, and we estimated 95% confidence intervals using a bootstrap method with 10,000 bootstrap samples (Meredith and Ridout 2020).

## **Results**

### *Camera trapping*

Cameras were active for 43,076 camera trapping days across 43 sites. For summer, there were 19,764 camera trapping days, 5,790 elk detections and 3,064 bison detections. For fall there were 8,568 camera trapping days, 2,690 elk detections and 801 bison detections. In winter there were 14,744 camera trapping days, 2,407 elk detections and 1,094 bison detections. Elk were detected on all cameras in summer and winter, and 41 of 43 cameras in fall. Bison were detected on 35 out of 43 cameras in summer, 28 out of 43 cameras in fall, and 32 out of 43 cameras in winter.

### *Spatial Analysis*

For each season, we compared 14 candidate models and a null model for bison and 19 candidate models plus a null model for elk (Appendix 3.2). Due to high sampling and



measurement error, the proportion of deviance explained was low for each top model (0.01-0.04), however the contrast between top models and null models was substantial based on AICc.

In the bison GLMs, proportion of open habitat was a significant predictor in all top models across seasons and was positively associated with bison counts (Table 3.2, Figure 3.2, Appendix 3.3). In summer and fall, the linear variable for distance to water was a significant predictor covariate and positively associated with bison, meaning bison counts were higher farther from water. Bison removal year was a significant predictor in winter and was inversely associated with bison counts. Linear feature density was absent from all bison top models. Elk count was present in some of the competing top models but not the final bison models selected for each season based on the lowest number of parameters. For models with elk counts as a parameter, elk were positively correlated with bison counts.

For elk GLMs, linear feature density was a significant predictor covariate in all top models and was negatively associated with elk counts (Table 3.2, Figure 3.2, Appendix 3.3). Bison removal year was present in the fall top model, though the beta coefficient for bison removal year was not significant (Appendix 3.3) and the 95% confidence intervals overlapped 0. Bison presence/absence was a significant predictor variable in both fall and winter elk GLMs with bison presence positively associated with elk counts. The linear variable for distance to water was a significant predictor in the elk winter GLM, with distance to water being positively associated with elk counts (i.e., elk counts were higher farther from water).

#### *Daily activity patterns*

Bison and elk daily activity patterns overlapped substantially in all three seasons (Figure 3.3). Summer had the lowest coefficient of overlap ( $\Delta_4 = 0.74$  [0.73-0.76]), fall had an intermediate coefficient of overlap ( $\Delta_4 = 0.76$  [0.72-0.79]), and winter had the highest coefficient

of overlap ( $\Delta_4 = 0.81$  [0.78-0.84]). Elk activity patterns were clearly crepuscular across seasons. Bison were generally diurnal with higher peaks in activity near dawn and dusk, but as day length shortened in winter, the bison daily activity pattern mirrored that of elk with peaks near dawn and dusk and a decrease in activity midday (Figure 3.3).

## **Discussion**

The aspen parkland ecosystem is able to support high ungulate densities that play a key role in maintaining the diversity of vegetation types (Bird 1961, Riley et al. 2007). In this study, we had the unique opportunity to examine intraguild dynamics in a fully fenced protected area within the aspen parkland ecosystem. We examined bison and elk spatiotemporal patterns and interactions across three seasons in EINP. Bison counts were primarily related to habitat characteristics, while elk counts were influenced by anthropogenic features and bison presence. As expected, we found high spatial and temporal overlap between bison and elk in EINP, likely due in part to high ungulates densities impeding spatial partitioning (Van Beest et al. 2014). Bison were present on 65-81% of camera traps across seasons whereas elk were present on almost every camera (95-100%). Additionally, we saw high overlap of daily activity patterns across seasons with increasing overlap in winter.

In all three seasons, we found that higher bison counts were associated with open habitats (Table 3.2, Figure 3.2). This was expected because bison are grazers, with diets consisting of >90% graminoids and are therefore reliant on grasslands (COSEWIC 2013, Kagima and Fairbanks 2013). We also found bison were positively associated with increasing Euclidean distance to water during summer and fall. This is likely due to bison use of larger, dry grasslands in the park, which occur farther from water bodies, rather than the rings of open habitats surrounding water bodies. However, distance to water was not present in the winter model for

bison counts. Because bison switch their diet to sedges in the winter when snow is deep, they are more likely to be found in sedge meadows near water bodies (Larter and Gates 1991). The use of sedge meadows by bison has been documented in EINP (Telfer and Cairns 1979, Cairns and Telfer 1980), and bison used both upland grasslands and sedge meadows during winter.

The binary variable for bison removal year was a significant predictor in the bison winter model. This was expected because bison handling and removal occurs in winter (Appendix 3.1). We observed a negative association between bison counts and bison removal year, meaning there were lower bison counts in EINP-N and EINP-S during their respective bison removal years. The parameter for linear feature density, which included paved roads, the park perimeter road, and hiking trails, was absent from all of the bison top models (Table 3.2). This aligns with our prediction that bison would not be negatively associated with linear features because they are more tolerant of human use. Bison also are known to use linear features such as roads and human-use trails throughout EINP based on tracks and park staff observations (Telfer and Cairns 1979), but we did not observe a positive association between bison and linear feature density either.

In contrast to the bison results, linear feature density was present in elk top models for all seasons with increased linear feature density being associated with lower elk counts (Table 3.2, Figure 3.2). This supports our prediction that elk are less tolerant of human use compared to bison. Other studies have documented similar elk responses to linear features (Webb et al. 2011a, 2011b, Prokopenko et al. 2017a, 2017b) and associated recreational activity (Ferguson and Keith 1982, Naylor et al. 2009). The parameter for bison removal year was present in the fall elk top model and was positively associated with higher elk counts, but it was not significant. The effect of bison presence on elk was significant for both fall and winter models, and elk counts were

positively associated with bison presence. This was expected because bison and elk select similar habitats during winter despite consuming different forage (Telfer and Cairns 1979, Cairns and Telfer 1980, Wydeven and Dahlgren 1985, Singer and Norland 1994). The linear variable for distance to water was present in the elk winter model, with higher elk counts associated with areas farther from water bodies. We suspect this was also due to elk shifting their diet in winter towards a higher proportion of graminoids and browse, because elk in EINP have been documented to heavily select upland grasslands and aspen woodlands during winter (Cairns and Telfer 1980). These findings indicate that grasslands are important habitats for not only bison, but also elk in EINP across seasons. This was also documented by Cairns and Telfer (1980), who found that upland grass is one of the least available habitat types in EINP, and is highly selected by both bison and elk, though in different seasons. They suggested maintenance of upland grass in EINP is important for supporting high ungulate densities. Interestingly, the proportion of open habitats was not represented in any of the elk top models, but this is likely because elk use a variety of habitat types in each season, apparently in proportion to their availability (Telfer and Cairns 1979). In winter when elk in EINP select upland grass and browse, they spend a majority of time in aspen forests (Telfer and Cairns 1979, Cairns and Telfer 1980). This highlights the importance of the mosaic of deciduous forests interspersed with grasslands that is characteristic of the aspen parkland ecosystem.

Bison and elk daily activity patterns overlapped substantially in all three seasons (Figure 3.3). In summer, we saw the greatest separation in activity patterns of the three seasons, with bison showing a clear diurnal pattern with slightly higher peaks at dawn and dusk compared to the crepuscular pattern of elk. Elk activity patterns were crepuscular in all three seasons. Bison are generally considered to be diurnal, though we observed a shift towards a more crepuscular

pattern in winter, and subsequently a higher coefficient of overlap. During winter, bison and elk activity patterns mirrored each other closely (Figure 3.3), with bison and elk sharing the same temporal peaks in activity.

Our observations appear to be consistent with bison and elk patterns of overlap in other studies. Spatial and temporal overlap are not synonymous with habitat overlap or diet overlap, two indices we were not able to evaluate in this study. However, we observed a significant positive association between elk counts and bison presence in the elk spatial model for winter, the season when bison and elk have the highest habitat overlap but low diet overlap (Telfer and Cairns 1979). This is consistent with ungulate habitat relationships in Wind Cave National Park where some heterospecifics had high spatial and habitat overlap, meaning that they overlapped spatially and selected for the same habitat types within their spatial overlap, but coexisted by eating different types of vegetation within the same areas (Wydeven and Dahlgren 1985). Similarly, studies of niche relationships in Yellowstone National Park determined that, although increasing bison and elk populations resulted in greater spatial overlap there was no evidence for competitive exclusion (Singer and Norland 1994); bison and elk increased in habitat overlap, but only moderately increased in dietary overlap. Although we did not examine habitat selection or diet, Telfer and Cairns (1979) showed that bison use more sedge (*Carex* spp.) and elk use more browse during winter when their habitat overlap is greatest, a pattern also found for bison and elk in Yellowstone (Singer and Norland 1994).

Overall, we found that bison and elk in EINP have both high spatial overlap and high temporal overlap in daily activity patterns. We did not find strong evidence for spatial or temporal partitioning, although we observed higher positive associations between bison and elk during winter when habitat overlap is highest, and saw more separation in daily activity patterns

during summer, the season when bison and elk have the highest diet overlap (Telfer and Cairns 1979, Cook 2002). We suspect there might be stronger evidence for spatial avoidance at finer temporal scales that we were unable to detect because of the broad seasonal time scale, and future research could incorporate monthly, weekly, or daily intervals. The seasonal patterns of spatial and temporal overlap between bison and elk demonstrated in this study paired with existing evidence of seasonal habitat selection and diet overlap (Telfer and Cairns 1979) illustrate the complexity of intraguild sympatry within EINP. Our observations indicate that spatial and temporal partitioning between bison and elk in EINP is not necessary for ungulates to coexist in the highly productive system with high ungulate densities (Chapter 2). However, as there is evidence of high spatiotemporal overlap of elk and bison combined with both species selecting for grasslands (Telfer and Cairns 1979, Cairns and Telfer 1980) that are limited in availability (Blyth 1995, Parks Canada 2010), there is potential to concentrate negative impacts in this habitat type. Park managers are currently working to address declining grassland health in EINP (Parks Canada 2010). Understanding the effects of interspecific interactions and anthropogenic influences on ungulate distributions will be necessary to understand the spatial variation in grassland health and ecosystem condition throughout the park.

**Table 3.1** Descriptions of covariates used in bison and elk generalized linear models.

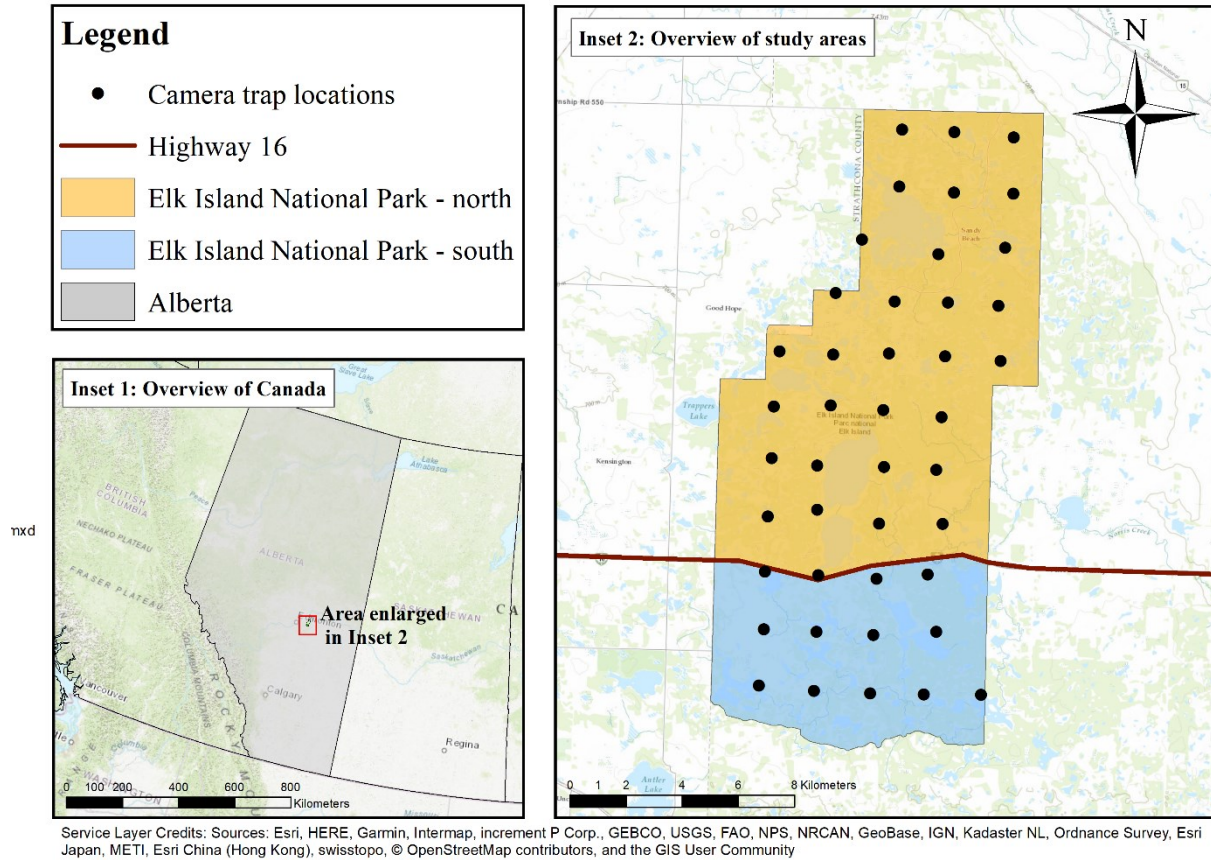
Covariate name	Code	Description	Data source
Bison presence/absence	bison	Binary variable for bison presence (1) or absence (0)	Camera trap data
Bison removal year	BRY	Binary variable for bison removal year (1) or non-bison removal year (0)	Information provided by Parks Canada; see appendix 3.1
Distance to water	DW	Euclidean distance to water (m)	Supervised 30x30m Landsat 2015 raster provided by Parks Canada; Euclidean distance raster created in ArcMap
Elk abundance	elk	Elk count	Camera trap data
Forest edge density	FED	Forest edge density (m/km <sup>2</sup> ) within a 500m buffer of camera locations	Supervised 30x30m Landsat 2015 raster provided by Parks Canada; edge density raster created in ArcMap
Linear feature density	LFD	Density (m/km <sup>2</sup> ) of anthropogenic linear features within a 500m buffer of camera locations; linear features included paved roads, the park perimeter road, and hiking trails	Linear feature shp files provided by Parks Canada; linear feature density raster created in ArcMap
Proportion open	open	The proportion of open habitat (shrubland and grassland) within a 90x90m window around camera trap locations	Supervised 30x30m Landsat 2015 provided by Parks Canada; proportion of open habitat raster created in R Studio

**Table 3.2** Model selection table of the top-ranked models and null models for bison and elk in summer, fall, and winter. Predictor variables, number of parameters ( $k$ ), Akaike's Information Criterion scores corrected for small sample sizes (AICc), and the difference in AICc ( $\Delta$  AICc) are displayed. Models with a  $\Delta$  AICc of less than 2.00 were considered competitive. Top models selected are shown in bold and shaded.

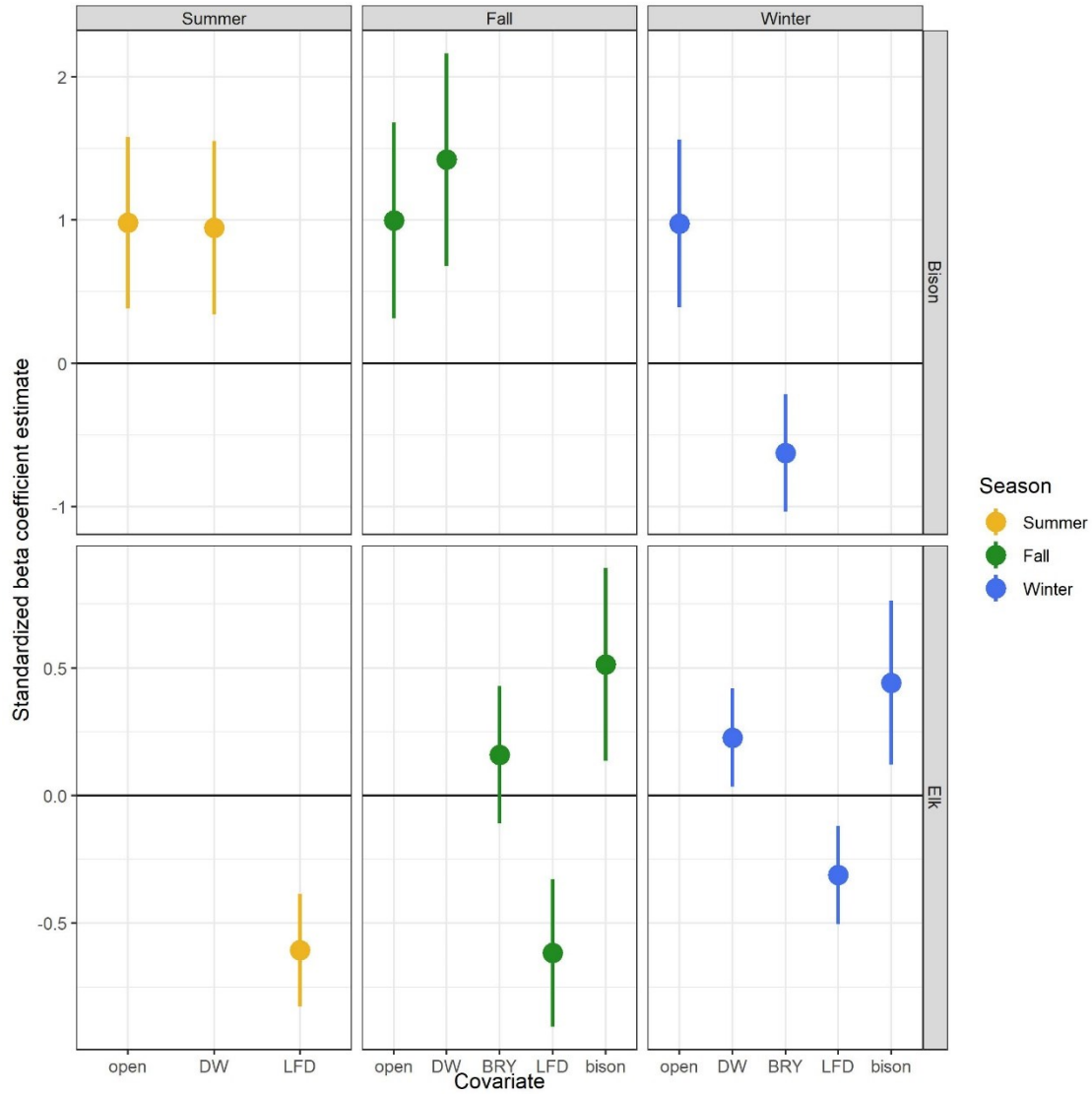
Species	Season	Model	Predictor variables*	$k$	AICc	$\Delta$ AIC
Bison	Summer	M11	open + DW + elk	6	1029.09	0
		<b>M6</b>	<b>open + DW</b>	<b>5</b>	<b>1031.04</b>	<b>1.95</b>
		M0	NULL	3	1043.70	14.61
	Fall	<b>M6</b>	<b>open + DW</b>	<b>5</b>	<b>511.75</b>	<b>0</b>
		M13	open + DW + DW <sup>2</sup>	6	513.12	1.37
		M0	NULL	3	528.30	16.55
	Winter	<b>M8</b>	<b>open + BRY</b>	<b>5</b>	<b>738.03</b>	<b>0</b>
		M12	open + BRY + elk	6	738.26	0.22
		M11	open + DW + elk	6	739.06	1.03
		M0	NULL	3	751.71	13.68
Elk	Summer	M7	LFD + FED	5	1396.46	0.00
		M5	LFD + DW	5	1397.65	1.18
		<b>M1</b>	<b>LFD</b>	<b>4</b>	<b>1398.15</b>	<b>1.68</b>
		M16	LFD + FED + bison	6	1398.24	1.78
		M0	NULL	3	1418.15	21.68
	Fall	<b>M9</b>	<b>LFD + bison + BRY</b>	<b>6</b>	<b>846.27</b>	<b>0</b>
		M0	NULL	3	874.26	27.98
	Winter	<b>M14</b>	<b>LFD + DW + bison</b>	<b>6</b>	<b>1201.06</b>	<b>0</b>
		M19	LFD + DW + DW <sup>2</sup> + bison	7	1202.12	1.05
M0		NULL	3	1216.86	15.80	

\*open = proportion open, DW= distance to water, elk = elk abundance, BRY = bison removal year, LFD = linear feature density, FED = forest edge density, bison = bison presence/absence

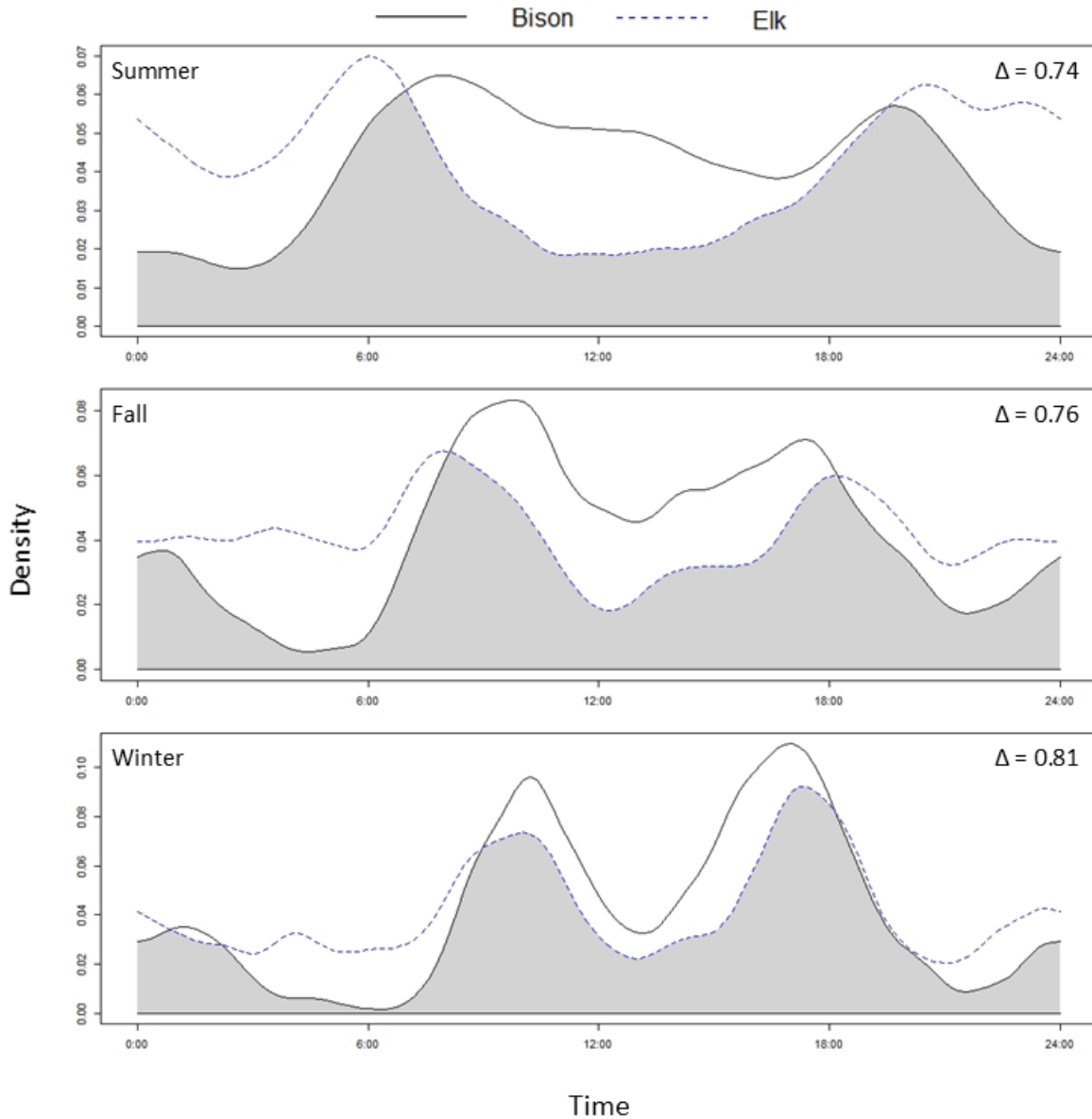




**Figure 3.1** Camera trap survey in Elk Island National Park, Alberta, Canada. Cameras were deployed on a  $2 \times 2 \text{ km}^2$  systematic grid, shown by black points. Elk Island National Park is bisected by Highway 16, shown by the red line. Both northern and southern portions of Elk Island National Park are surrounded by a 2.2m high perimeter fence, which restricts ungulate movement.



**Figure 3.2** Scaled beta coefficient estimates from the top-ranked models for bison and elk space use during three seasons: summer (April-August), fall (September-November), and winter (December-March). Camera trap data were collected from 2016-2020 in Elk Island National Park in Alberta, Canada. Error bars represent 95% confidence intervals.



**Figure 3.3** Activity patterns and coefficient of overlap of bison (*Bison bison*) and elk (*Cervus elaphus*) in summer (April-August), fall (September-November), and winter (December-March). Camera trap data were collected from 2016-2020 in Elk Island National Park in Alberta, Canada. The area of overlap is shaded in grey and  $\Delta$  is the coefficient of overlap.

## Chapter 4 – Conclusion

In this thesis, I estimated ungulate densities and examined bison and elk spatiotemporal patterns using camera traps in two natural areas in the Beaver Hills region of central Alberta, Canada. These natural areas are located within the aspen parkland ecotone, a highly productive transitional ecosystem found between boreal mixed wood forests and grasslands. This area is able to support high ungulate densities due to rich soils, diverse vegetation types, and the close proximity of interspersed habitat types (Bird 1961, Riley et al. 2007).

In Chapter 2 I applied the TIFC method (Huggard 2018, Warbington and Boyce 2020) for estimating animal densities using camera traps to all five species of ungulates. I estimated densities in EINP-N and EINP-S for three study years (2017-2019), and estimated densities in BPRA during 2019. Comparisons between TIFC density estimates and aerial densities varied by species. Moose had the lowest discrepancy between TIFC and aerial densities. Because aerial surveys in EINP and BPRA are reliable due to high visibility of moose within the habitat types present (Gasaway et al. 1986, Bisset and Rempel 1991), I concluded that the moose TIFC estimates are likewise reliable. Bison TIFC density estimates were lower than aerial densities, and I consider the aerial total counts for bison to be reliable due to the high visibility of bison (Wolfe and Kimball 1989, Hess 2002, Terletzky and Koons 2016). However, I concluded the TIFC method is likely underestimating bison numbers due to underrepresentation of grasslands in my study design. Sampling open habitats is challenging, especially where installing posts in open areas is not possible because bison and cattle will knock down posts. Elk TIFC density estimates were higher than aerial densities, but the aerial survey is missing elk due to issues with sightability (Caughley 1974, Samuel et al. 1987). While we could not compare white-tailed deer and mule deer TIFC density estimates with aerial densities because aerial surveys are ineffective

for deer, I was able to provide EINP and BPRA with TIFC density estimates for these species. These estimates were consistent across years for study areas with multiple study years.

Overall, I found that the TIFC approach using camera traps and the aerial survey approach were complementary, where aerial ungulate surveys performed better for species in open habitats, while cameras were able to detect species in closed habitats. I found the TIFC model is a viable alternative to aerial surveys, producing reasonable and consistent density estimates, but sampling designs need to be carefully evaluated prior to applying the method to ensure proportional representation of available habitats. Future work could focus on overcoming challenges associated with sampling open areas such as grasslands, either by quantifying the bias caused by moving camera traps to forest edges or by installing bison-proof posts in grasslands and evaluating the degree to which the posts serve as an attractant. Stratified designs could be considered as well with TIFC densities calculated per stratum and then combined. This approach may be necessary in cases where some strata have higher variation in species use.

In Chapter 3 I examined bison and elk spatiotemporal patterns and interactions across three seasons in EINP. For spatial modeling, I found that bison counts were primarily related to habitat characteristics and that higher bison counts were associated with a higher proportion of open habitats. Bison are primarily grazers and are reliant on grasslands year-round (COSEWIC 2013, Kagima and Fairbanks 2013). Bison counts were higher farther from water in summer and fall, which might be due to bison using larger grasslands in EINP farther from water bodies. In winter, bison use a combination of upland grass and sedge meadows (Telfer and Cairns 1979, Cairns and Telfer 1980), which explains why distance to water was not important in the winter model of bison distribution. Bison removal year was a significant variable in the winter bison model, which was expected because bison handling and removal occurs in winter (Appendix A).

Elk counts were higher farther away from linear features (paved roads, the park perimeter road, hiking trails) in all three seasons, indicating that elk avoid human use areas (Ferguson and Keith 1982, Webb et al. 2011a, 2011b, Prokopenko et al. 2017a, 2017b). The variable for bison removal year was in the top elk model for fall but had a weak effect, whereas we found that bison presence/absence was a significant predictor in fall and winter. Higher elk counts were associated with bison presence, likely due to shared habitat use during winter despite low diet overlap (Telfer and Cairns 1979).

I observed overlap of daily activity patterns in all three seasons with increasing overlap in winter. Elk were highly crepuscular in all three seasons, whereas bison were diurnal with minor activity peaks at dawn and dusk compared to midday in summer. In winter though, bison daily activity patterns closely mirrored elk activity patterns. Bison daily activity patterns in fall were intermediate to their summer and winter patterns. I did not find strong evidence for temporal partitioning, although I saw more separation in daily activity patterns during summer, the season when bison and elk have the highest diet overlap but low habitat selection overlap (Telfer and Cairns 1979, Cook 2002). For both the spatial and temporal analyses, scale is important to consider. I examined data at the seasonal scale, and I might have seen partitioning at finer spatiotemporal scales. Future research could take advantage of time stamped images using a time to event approach, which would allow for fine scale evaluation of bison and elk temporal interactions. Additionally, spatial and temporal overlap are not synonymous with overlapping habitat selection or diet (Telfer and Cairns 1979). A study in Wind Cave National Park demonstrated that some species had high spatial overlap and similar habitat selection, but partitioned food sources within the same habitat type (Wydeven and Dahlgren 1985). Further, a study in Yellowstone National Park found that even as bison and elk populations increased and

spatial overlap increased, only moderate changes in niche overlap were observed (Singer and Norland 1994). Despite unique interventions seen in EINP including the fenced perimeter, limited dispersal, and low predation, our data show similar patterns of habitat use and interactions between bison and elk to those in other systems (Singer and Norland 1994, White et al. 2013). Spatial and temporal partitioning between bison and elk do not appear to be necessary for ungulates to coexist in the aspen parkland.

Future research on ungulate interactions in EINP should incorporate information on bison and elk interactions at finer spatiotemporal scales. At present, EINP wildlife managers have equipped several plains bison and several wood bison with GPS collars, and have plans to collar elk. GPS collar data can be used to evaluate habitat selection and space use in EINP at finer scales than is possible using camera traps. Additionally, future research should focus on distinguishing between the different types of grasslands ungulates use throughout the year and effects of fluctuating ungulate densities. Cairns and Telfer (1980) found that elk and bison in EINP both selected upland grass relative to availability and that maintaining upland grasslands might be essential for maintaining high densities of ungulates in EINP. Grassland health is currently a major focus for resource managers in EINP, and high ungulate herbivory is known to have lasting effects on vegetation communities (Bork et al. 1997, Best et al. 2003, Bradford and Hobbs 2008, Teichman et al. 2013). Continued active management and adaptive management (Nichols and Williams 2006) will be necessary to protect the ecological integrity of the park for years to come.

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## Appendix 2.1 – Accounting for bison removal year in the TIFC analysis

Bison handling takes place in Elk Island National Park each year, alternating between the plains bison in the north side of the park and the wood bison in the south. Bison handling typically takes place in January or February. During this time, hundreds of bison are temporarily housed within a handling facility in the park and data on animal health are collected. Park managers decide how many bison will be permanently removed from the park based on the aerial ungulate survey, and the rest of the bison are later released back onto the landscape. Bison in the handling facilities are not sampled by camera traps, so during bison handling the bison density on the landscape is effectively and dramatically reduced, and then drastically increased when bison are rereleased. For estimating bison density using the TIFC model, we completely excluded the period of winter during and after bison handling. Instead, we use the time period prior to bison handling (October 16 – December 31) to calculate winter bison density. For the years and study areas where bison handling was not done in a study area, we used the full time period for winter (October 16 – April 15).

**Appendix 2.1 - Table 1** Schedule for bison handling conducted annually in Elk Island National Park (EINP). Park staff alternate between handling plains bison in EINP north and wood bison in EINP south each year.

Study year	Study area with bison handling
2017-2018	EINP – south
2018-2019	EINP – north
2019-2020	EINP – south

## Appendix 2.2 – Proportion of habitat types in EINP

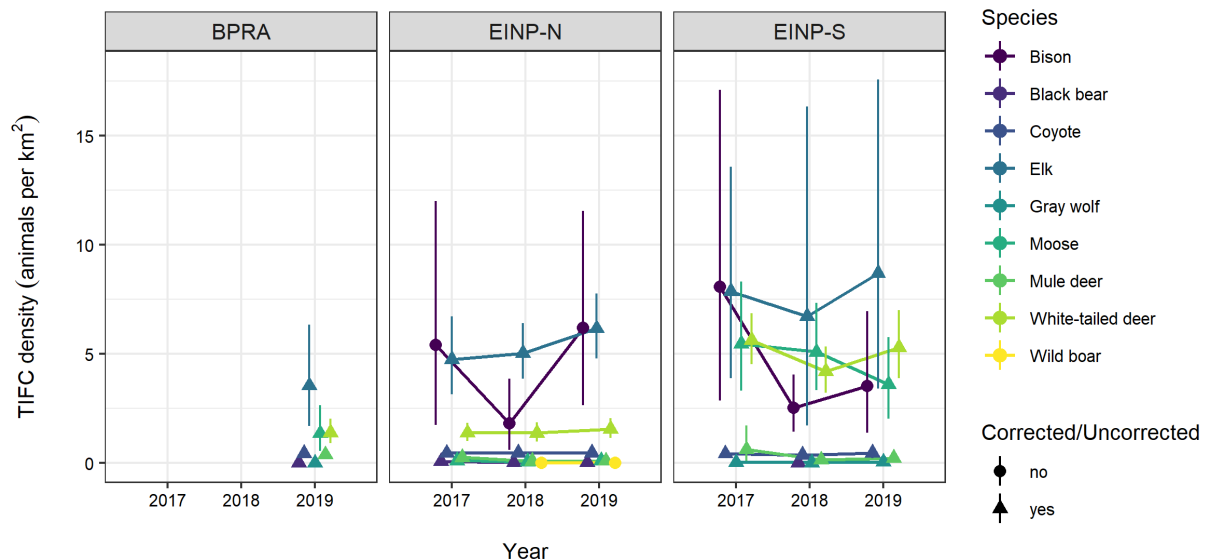
We found that bison TIFC estimates were lower than we expected, which we believe may be due to the camera trap grid underrepresenting grasslands. Post-hoc, we calculated the proportion of habitat types sampled via camera traps and compared them to the proportion of habitats present in EINP-N and EINP-S (the two study areas with bison). We found that grasslands and other open habitats were underrepresented in both study areas. The proportion of habitat types sampled by camera traps was calculated using the complete grid in each study area (n=31 in EINP-N; n=12 in EINP-S). Habitat type sampled by a camera trap was determined by extracting data from a 30x30m pixel Landsat raster with the following habitat types: Aspen dominated, spruce dominated, shrubland, grassland, wetland. We then used camera images to verify or reclassify the sampled habitat type. Proportion of each habitat type present was calculated from the same 30x30m Landsat raster.

**Appendix 2.2 - Table 1** The proportion of habitat types present versus the proportion of habitat types sampled via camera trapping grid in two study areas: Elk Island National Park-north (n=31; area=134km<sup>2</sup>) and Elk Island National Park-south (n=12; area=60km<sup>2</sup>). Camera traps were deployed in both study areas on a 2x2km<sup>2</sup> grid with cameras that would have fallen in an open area being moved to the nearest edge.

Study Area	Habitat type	Proportion present	Proportion sampled
Elk Island National Park-north	Aspen dominated	0.66	0.90
	Shrubland	0.19	0.03
	Grassland	0.07	0.03
	Wetland	0.05	0.00
	Spruce dominated	0.04	0.03
Elk Island National Park-south	Aspen dominated	0.58	1.00
	Shrubland	0.31	0.00
	Grassland	0.05	0.00
	Wetland	0.05	0.00
	Spruce dominated	0.01	0.00

## Appendix 2.3 – TIFC estimates of additional species in EINP and BPRA

The TIFC method can be used to estimate densities using camera trap data without the need for individual recognition, movement rates, home range size, or average group size. Since this method does not require additional data sources for each species, it can be applied in a multispecies monitoring framework. We were able to estimate TIFC densities for our three focal species (bison, elk, and moose) as well as several non-focal species: white-tailed deer, mule deer, black bears, coyotes, and wild boar. We adjusted the staying time for gaps using the species specific models for the probability of leaving when available, but there were not species specific models for bison and wild boar. We applied the model for ‘most ungulates’ to bison, and we did not apply a model to wild boar. We applied correction factors provided in Becker (2021) when available, but there were no correction factors available for bison and wild boar. TIFC densities were calculated as described in the methods for most species, where summer and winter were averaged to produce an estimate for the study year. Black bears were the one exception, and black bear TIFC estimates were calculated using only the summer season (Apr 16 – Oct 15) and excluding winter from the sampling period. Black bears are not detected during hibernation, so including winter in the camera operating time would bias TIFC estimates low.



**Appendix 2.3 - Figure 1** Time-in-front-of-camera (TIFC) density estimates for nine mammal species in three study areas: Cooking Lake - Blackfoot Provincial Recreation Area (BPRA), Elk Island National Park north (EINP-N) and south (EINP-S). Camera trap data were collected from 2017-2019 in EINP-N and EINP-S, and 2019 in BPRA. We applied correction factors for time spent investigating cameras when available.

### Appendix 3.1 – Bison removal year as a variable in the GLM spatial analysis

A bison round-up occurs in Elk Island National Park each year, alternating between the north and south sides of the park. Bison handling takes place during winter, typically during January or February, during which time bison are attracted to and held at the handling facility. Based on current population numbers, some bison are removed from the park (i.e., translocated), and the rest of the bison are later released back onto the landscape. We classified each season of each year with the binary covariate for bison removal year (BRY), with 1 indicating a bison removal year, and 0 indicating a non-removal year. Elk Island National Park north and south were classified separately because bison removal alternates between the two parks. The winter during which bison removal occurs, as well as the subsequent summer and fall, were assigned a 1 for bison removal year.

**Appendix 3.1 - Table 1** Bison removal year by site, management year, and season. Bison removal occurs each year in winter, alternating between Elk Island National Park north (EINP north) and south (EINP south). A management year starts April 1 and ends the following March 31. Each management year was divided into three seasons: summer (April-August), fall (September-November), and winter (December-March).

Site	Management Year	Season	Bison Removal Year
EINP north	2016	winter	1
EINP north	2017	summer	1
EINP north	2017	fall	1
EINP north	2017	winter	0
EINP north	2018	summer	0
EINP north	2018	fall	0
EINP north	2018	winter	1
EINP north	2019	summer	1
EINP north	2019	fall	1
EINP north	2019	winter	0
EINP north	2020	summer	0
EINP south	2016	winter	0
EINP south	2017	summer	0
EINP south	2017	fall	0
EINP south	2017	winter	1
EINP south	2018	summer	1
EINP south	2018	fall	1
EINP south	2018	winter	0
EINP south	2019	summer	0
EINP south	2019	fall	0
EINP south	2019	winter	1
EINP south	2020	summer	1

### Appendix 3.2 – Candidate model sets

**Appendix 3.2 – Table 1** Candidate model set to evaluate bison space use in Elk Island National Park. Each model includes an offset for the log number of camera trap days, and a random effect of camera trap location. All continuous covariates were scaled and centered.

Model Name	Variables*
Model 0	Null
Model 1	open
Model 2	LFD
Model 3	BRY
Model 4	open + FED
Model 5	open + LFD
Model 6	open + DW
Model 7	open + elk
Model 8	open + BRY
Model 9	open + FED + elk
Model 10	open + LFD + elk
Model 11	open + DW + elk
Model 12	open + BRY + elk
Model 13	open + DW + DW <sup>2</sup>
Model 14	open + DW + DW <sup>2</sup> + elk

\*open = proportion open, LFD = linear feature density, BRY = bison removal year, FED = forest edge density, DW = distance to water, elk = elk abundance

**Appendix 3.2 - Table 2** Candidate model set to evaluate elk space use in Elk Island National Park. Each model includes an offset for the log number of camera trap days, and a random effect of camera trap location. All continuous covariates were scaled and centered.

Model Name	Variables*
Model 0	Null
Model 1	LFD
Model 2	FED
Model 3	open
Model 4	bison
Model 5	LFD + DW
Model 6	LFD + open
Model 7	LFD + FED
Model 8	LFD + bison
Model 9	LFD + bison + BRY
Model 10	open + DW
Model 11	open + FED
Model 12	open + bison
Model 13	open + bison + BRY
Model 14	LFD + DW + bison
Model 15	LFD + open + bison
Model 16	LFD + FED + bison
Model 17	LFD + DW + DW <sup>2</sup>
Model 18	open + DW + DW <sup>2</sup>
Model 19	LFD + DW + DW <sup>2</sup> + bison

\* LFD = linear feature density, FED = forest edge density, open = proportion open, bison = bison presence/absence, DW= distance to water, BRY = bison removal year



### Appendix 3.3 – Beta coefficients from top models

**Appendix 3.3 - Table 1** Parameter estimates from best bison and elk spatial models for summer, fall, and winter in Elk Island National Park. All beta estimates were significant, except for bison removal year in the fall elk model (95% confidence interval overlapped 0).

Species	Season	Variable	$\beta$	SE
Bison	Summer	Proportion open	0.982	0.305
		Distance to water	0.945	0.308
	Fall	Proportion open	0.998	0.348
		Distance to water	1.422	0.379
	Winter	Proportion open	0.976	0.299
		Bison removal year	-0.626	0.209
Elk	Summer	Linear feature density	-0.606	0.113
		Linear feature density	-0.617	0.148
	Fall	Bison	0.514	0.193
		Bison removal year	0.16	0.137
	Winter	Linear feature density	-0.312	0.098
		Distance to water	0.227	0.098
		Bison	0.442	0.164