University of Alberta

Trophic cascades: Linking ungulates to shrub-dependent birds and butterflies

by

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This work is dedicated to my dad, Gordie Teichman, and to all the wild creatures and places.

ABSTRACT

Top predators are known to regulate freshwater, marine, and terrestrial ecosystems. However, few studies have demonstrated trophic cascades in productive and biologically diverse terrestrial ecosystems. Elk Island National Park and surrounding protected areas have a wide range in the intensity of use by ungulates (IUU) (2.3 to 53.4 units/km^2) due to the functional loss of top predators, management for high ungulate numbers and variable hunting pressure. To evaluate whether high IUU results in a trophic cascade, I examined vegetation characteristics and the abundance of shrub-dependent yellow warblers (*Dendroica petechia*) and Canadian tiger swallowtails (*Papilio canadensis*). Areas with high IUU resulted in loss of horizontal shrub cover that resulted in reductions of yellow warblers. Abundance of Canadian tiger swallowtail was related to reductions in larval host plant density, particularly chokecherry (*Prunus virginiana*). This study provides evidence of a species-level trophic cascade, initiated by a combined effect of the loss of top predators and management for high ungulate densities.

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CHAPTER 1

GENERAL INTRODUCTION

An ecosystem is composed of multiple organisms and abiotic factors that are inextricably linked into a community. The multitude of predator-prey interactions within a community are often described using food web theory. Trophic cascades occur in food webs when changes in the size of populations of a species at one trophic level negatively affect populations at lower trophic levels (Polis 1999).

During European settlement, cougars were reduced or eradicated in eastern North America (McCullough 1997) and wolves eradicated south of the North American boreal forests (Boitani 1995, Paquet & Carbyn 2003). Loss of top-level carnivores has led to an increase and often an overabundance of ungulates in some areas. Aldo Leopold (Leopold *et al*. 1947) first noticed these ungulate irruptions and potential negative impacts on ecosystems in areas where predators no longer persisted. Since then, extensive research has attempted to understand the intricacies of predator-prey interactions and their effects on food webs to help make informed management decisions for the conservation of ecosystems.

Some of the most vivid examples of tropic cascades have been demonstrated in aquatic systems (Paine 1966, Estes & Duggins 1995; Carpenter *et al*. 2001). A classic example is the sea otter (*Enhydra lutris*), sea urchin (*Strongylocentrotus* spp.) and kelp (*Laminaria* spp.) food web in Alaska (Estes & Duggins 1995). Removal of predatory sea otters increased sea urchins (prey), thus resulting in large scale losses of kelp. The loss of kelp forests resulted in drastic reductions in ecosystem functioning by limiting fish and invertebrate habitat.

Although most terrestrial trophic cascades have been shown in food webs involving invertebrate top predators (Schmitz 2000), cascades had been demonstrated involving large mammalian predators (Hebblewhite *et al.* 2005; Ripple & Beschta 2006). For instance, increases in human activity in Zion National Park have reduced cougar abundance resulting in locally high populations of deer (Ripple *et al*. 2001). This has led to increases in browsing by ungulates and subsequent failure of recruitment in riparian cottonwood trees. Loss of cottonwood trees has resulted in fewer flowering plants, amphibians, lizards and butterflies (Ripple *et al.* 2001). Yellowstone National Park also provides an excellent example of the consequences of overgrazing and browsing on vegetation where overabundant ungulate populations following wolf eradication resulted in failure to recruit cottonwood trees (Beschta 2003).

Like Yellowstone, the Beaver Hills region in east-central Alberta, Canada lost its wolves due to human eradication. Loss of wolves combined with a policy to maximize ungulate densities provides an ideal setting for studying the effects of ungulates on lower tropic levels. Ungulate densities are further influenced in the area by humans through either hunting in provincial recreational areas or management strategies in the national park aimed at maintaining high ungulate numbers.

In this thesis, I examine whether trophic cascades occur in a mixed-wood boreal ecosystem of east-central Alberta by examining how the intensity of use of elk (*Cervus canadensis*), moose (*Alces alces*), plains bison (*Bison bison bison*), wood bison (*Bison bison*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) affect its vegetation and two shrub-dependent species: yellow warbler (*Dendroica petechia*) and Canadian tiger swallowtail (*Papilio canadensis*). I also examine the relationship between broad-scale vegetation patterns and intensity of ungulate use (IUU), as well as browsing pressure in relation to ungulate species.

In chapter 2, I test *a priori* candidate models (GLM) for moose, deer, elk and bison to assess whether location and/or broad-scale vegetation patterns influence IUU. I quantify vegetation patterns in categories of grassland, shrub and forest zones by measuring distance along transects of each vegetation type. I use linear regression to relate browse level to individual ungulate species (IUU).

In Chapter 3, I quantify IUU using pellet group counts and the relative abundance of yellow warblers using call playbacks and Canadian tiger swallowtail using Pollard walks. Vegetation characteristics, including shrub density, horizontal shrub cover and canopy cover, were also measured at each site. Initially, I aimed to examine a community-level trophic cascades by quantifying the shrub-nesting bird community including, but not limited to, yellow warbler, warbling vireo (*Vireo gilvus*), common yellowthroat (*Geothlypis trichas*), alder flycatcher (*Empidonax alnorum*), chipping sparrow (*Spizella passerina*), and song sparrows (*Melospiza melodia*). Furthermore, I planned to quantify the butterfly community that is dependent on shrubs that are relevant to my study system during their larval stages. However, due to logistical constraints and rarity of some focal species I was limited to examining a species-level trophic cascade where I focused on two relatively common species: yellow warblers and Canadian tiger swallowtails.

Yellow warblers were selected to test the indirect effects of high IUU because they are commonly found along riparian zones and nest site selection is driven by horizontal shrub understory patterns in areas with large shrub stands (Stauffer & Best 1980; Knopf & Sedgwick 1992). Both of these factors are influenced by ungulates. Canadian tiger swallowtails, on the other hand, were chosen based on their larval host plant requirements, willow (*Salix* spp.), aspen (*Populus* tremuloides), and cherry (*Prunus* spp.), all of which are found within the study system and are extensively browsed. Furthermore, both yellow warblers and Canadian tiger swallowtails were easily identifiable making field sampling by technicians feasible. I used Structural Equation Modeling to assess the direct and indirect effects of ungulates on shrubs and shrub-dependent bird and butterfly species. In Chapter 4, I summarize the main findings of this study.

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CHAPTER 2

HABITAT USE BY UNGULATES IN THE COOKING LAKE MORAINE

ABSTRACT

Managers of national parks have the challenge of preserving the integrity of natural areas. Overabundant ungulates can threaten ecosystem structure and function through excessive browsing. The objectives of this study were to: (1) identify vegetation patterns that relate best to local measures of intensity of ungulate use (IUU) and (2) assess the relationship between measured browse pressure and the intensity of habitat use by moose, deer, elk and bison. I used Generalized Linear Models to test hypotheses related to factors explaining the distribution of ungulates. Linear regressions were used to assess relationships between browse impact and IUU. IUU was estimated at 23.1units/km^2 in Elk Island National Park and half that use (11.6 units/km^2) in the surrounding provincial and recreational protected areas. In Elk Island, bison and elk use was highest in the south unit and burned areas of the park while moose and deer use were marginally higher outside of Elk Island. Bison use was highest in areas dominated by grasslands, while moose and elk use were highest in areas dominated by shrub and forest habitat, respectively. Total IUU was positive, but weakly related to measures of browse with elk being the only species significantly related to browsing pressure. Interspecific competition between bison and elk may account for high elk use of forested areas, thereby increasing their winter browsing pressure on vegetation.

INTRODUCTION

Managers of national parks have the challenge of preserving the integrity of natural systems. In the 1970s Parks Canada adopted an ‘ecological ethic’ for management of parks whereby plans to maintain ecosystems in an ‘unaltered’ state was prioritized (Blyth & Hudson 1987). This approach requires knowledge of baseline or reference conditions from which to establish management targets. In many cases, reliable historical data are unavailable making it difficult to discern human impact on the integrity of ecosystems.

The Beaver Hills of east-central Alberta represents a forested ‘island’ of habitats (mixed-wood boreal forest) located within the transition zone from prairie to boreal forest (Moss 1932). Prior to European settlement, it is claimed that the region flourished with bison, elk, deer and moose (Blyth & Hudson 1987). Also present were top predators including wolf, grizzly bear, cougar and aboriginals. The role of natural fires or of prescribed fires set by aboriginals is controversial because of the lack of documented historical fires (Bork *et al.* 1997). Fire may have maintained predominantly open grasslands with pockets of aspen and spruce, which supported large ungulate populations (Blyth & Hudson 1987). On the other hand, the region may have originally been dominated by forests prior to a large fire in 1895 (Parks Canada, unpublished report, 1977).

After European settlement, much of the region was transformed to agriculture and infrastructure (Blyth & Hudson 1987) with excessive hunting reducing ungulate populations and the eradication of top predators such as wolves, cougars and grizzly bears. In 1906, Elk Island National Park was established at the north end of the Beaver Hills and managed to protect ungulates from poachers (a fence was installed) and to maintain forests through fire suppression. With successful fire suppression, vegetation converted to aspen forests with small grassland openings persisting. This limited forage for grazing ungulates. Because of the fenced perimeter and small size of Elk Island (196 km^2), overabundant ungulates have reduced vegetation biomass (Bishoff 1981) resulting in starvation of ungulates at times. As a result, park management reduced ungulate populations by slaughter or trapping (Blyth & Hudson 1987).

To increase forage and reduce forest encroachment of grassland openings, Elk Island began using prescribed fire in 1979 (Blyth & Hudson 1987). Since that time over 51 % of Elk Island has been burned at least once with prescribed fire (Hood & Bayley 2007) resulting in more forage for ungulates. Despite cyclical ungulate populations due to natural and managed processes, ungulate density in Elk Island is considered to be some of the highest in Canada (Blyth & Hudson 1987; Hood & Bayley 2008). Although many plant species have evolved with herbivory, browsing and grazing by multiple herbivores can disrupt plant communities (Hood & Bayley 2009). Furthermore, excessive browsing by any one species can negatively impact vegetation structure and composition by reducing plant cover and diversity (McLaren & Peterson 1994; Côté 2004).

Understanding how large mammalian herbivores interact with vegetation helps provide information for management of mixed-wood boreal ecosystems. The objectives of this study were therefore to: (1) estimate intensity of ungulate use (IUU) inside and outside Elk Island National Park; (2) determine whether location and/or vegetation patterns affect the distribution of ungulate species; and (3) examine relationships between browsing pressure and intensity of moose, deer, elk and bison use.

METHODS

Study area

The study area is located in the Beaver Hills Region of east-central Alberta, approximately 45 km east of Edmonton Alberta. This region includes Elk Island National Park, Cooking Lake-Blackfoot Provincial Recreation Area, Edgar T. Jones Natural Area and Miquelon Lake Provincial Park (Figure 2.1). I sampled within these parks in order to represent environments with different ungulate densities and hence browsing pressures. Elk Island National Park is a 196 km² fenced enclosure (ungulate-proof fence) that is divided into a north and south section by a major highway (Yellowhead Highway 16). There are no resident top predators in the park with ungulates considered to be at high densities relative to the surrounding areas. Ungulate species in Elk Island include elk (*Cervus canadensis*), moose (*Alces alces*), plains bison (*Bison bison bison*), wood bison (*Bison bison*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*).

Areas outside of Elk Island contain all ungulate species except bison, have not been managed with prescribed burning, nor have high fences that restrict ungulate movement. Cooking Lake-Blackfoot Provincial Recreation Area is a 98.8 km^2 public area consisting of designated areas for seasonal cattle grazing and hunting. Although forested, in the late 1950s thousands of hectares of upland deciduous forests were logged to increase cattle grazing. In 1987 a fence was built to limit grazing to 28.75 km^2 of pastures seeded with agricultural grasses. Areas with cattle grazing were not used in this study. The remaining study sites include Miquelon Lake Provincial Park (~13 km^2) and Edgar T Jones Natural Area (0.92 km^2).

Elk Island and surrounding sample sites are characterized by having knob and kettle topography with pockets of small water bodies within a matrix of aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) forests and sporadic patches of black and white spruce (*Picea mariana* and *P. glauca*, respectively). Shrub understory is mostly dominated by beaked hazelnut (*Corylus cornuta*) and other shrub species including saskatoon (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana)*, willow (*Salix* spp.), rose (*Rosa* spp.) pincherry (*Prunus pensylvanica*), red raspberry (*Rubus idaeus*), high-bush cranberry (*Viburnum edule*), red-osier dogwood (*Cornus stolonifera*), western snowberry (*Symphoricarpos occidentalis)*, currant (*Ribes* spp.), honeysuckle (*Lonicera* spp.) and buffaloberry (*Shepherdia canadensis*).

Site Selection

Shrub and forest communities with riparian-like characteristics were targeted for this study and identified from an Alberta land cover classification (Canada Forest Services 2007) for the Beaver Hills region. Each site was adjacent to a wetland and was characterized by having three distinct zonal vegetation communities: grassland, shrub and forests. Land cover classes were reclassified to edge and watercourses (Natural Resources Canada 2002) and overlaid with forested areas to identify riparian edges for sampling. Resulting edge polylines ≥300 m in length were buffered by 10 m to enable spatially referenced points in a GIS with no more than 1 location per 300 m length. Seventy random points were selected as sample locations.

Intensity of Ungulate Use

Pellet group transect surveys were used to index intensity of ungulate use (IUU). Using pigtail markers and GPS route planner, I marked pellet transects in September and October of 2010 and removed all pellets within 1 m of transects. In May 2011 pellet transects were revisited to count pellet groups by species in order to index intensity of winter ungulate use from pellet group counts. Winter intensity of use was used since browsing of shrubs occurs most during winter.

Pellet counts were carried out in 100 x 2 m belt transects perpendicular to the to the wetland, crossing grassland, shrub and forest habitats (Figure 2.2). Three transects 100 m apart were completed at each site for a total search area of 600 m^2 or 0.06 ha. Pellets were distinguished by species and classified as large (>5) or small (≤5) pellet groups (Hood & Bayley 2008). I noted the vegetation class where pellets were found (grassland, shrub or forest) and pooled pellets across vegetation types to obtain a per site sampling unit. Only large (>5) pellet groups were used for these analyses to prevent overestimation of animals defecating on the move. Although I used a density formula, pellet conversions should be considered IUU due to the small spatial scale being assessed:

$$\mathrm{IUU} = \frac{X}{A \times F \times \mathrm{t}}$$

where X is the number of pellet groups, A is the area of the plot, F is the defecation rate and t is the time of pellets to accumulate at a site (Skalski *et al*. 2005). Defecation rates vary due to diet, season, location, recording methodology and whether animals were free ranging or penned (see Appendix I). Because species-specific defecation rates were unknown for the Beaver Hills, I used the average defecation rates for each species (moose, deer, elk and bison) based on estimates from the published literature (see Appendix I). These included 15.9 pellet groups/day for moose, 18.3 pellet groups/day for deer, 14 pellet groups/day for elk and 9 plops/day for bison.

Ungulate browse

I estimated ungulate browsing using percent browse and “browse severity” indices similar to Hood & Bayley (2009). Using a point-centered quarter method, browse levels were assessed for the closest stems to the center point of each plot. Percent browse was estimated as the ratio of the number of browsed branches to total number of branches off the main stem and recorded in 1 of 5 categories including, 0% (0), 1-5% (1), 6-20% (2), 21-50% (3) and 51-100% (4). Browse severity, on the other hand, was estimated using qualitative visual assessments of individual shrubs based on the amount of leader and secondary growth, hedging and amount of dead wood. Browse severity was categorized into ‘none’ (0), low (1), medium (2) and high (3) classes. For example, a browsed branch with no dead wood and some healthy leader growth was considered ‘low’ browse severity while a branch with substantial secondary growth (hedging) and excessive deadwood was classified as ‘high’ browse severity. When there were differences of browse severity on the branches of an individual, the median value was recorded. For example, if 6 stems were browsed and the browse severity equated to 1, 2, 2, 2, 3, 3 then a median (2) browse severity was recorded.

Browse Impact Index (BI index) was estimated as the multiplicative of percent browse and browse severity (Hood & Bayley 2009). That is, if a shrub had a percent browse of 80% (4) with a medium browse severity (2) then the Browse Impact index would be 8. I used this index to quantify the impact of browsing on multiple shrub species and to determine the relationship between quantified ungulate densities (via pellet group counts) and browse impact.

Grassland, shrub and forest zones

At every site I measured the width of vegetation zones along each of the 3 meter pellet transects. Grassland habitats were characterized by having less than 50% emergent grasses closest to the water and less than 50% shrub in the uplands at the grassland-shrub interface. Shrub habitat was identified as having ≥50% shrub cover and fewer than five trees within a 5 m radius (78.5 m^2 plot). Forests were defined as ≥5 trees within a 5 m radius representing a stem density >636 trees per hectare. All species were considered shrubs if their DBH (diameter at breast height) was ≤5 cm. Total widths of each vegetation layer were averaged to estimate for each site the proportion of grassland, shrub and forests. For example, if the shrub widths were 30 m, 40 m and 20 m along each100 m pellet transect, I recorded the proportion of shrub layer as 0.30. Estimates of proportion of grassland, shrub and forest are based on sites bordering water bodies and do not estimate the total grassland, shrub and forest across the entire study area.

Statistical Approach

Predicting IUU using location and broad-scale vegetation

To assess what variables best predict local ungulate use, I tested *a priori* candidate models (GLMs) that described moose, deer, elk and bison use based on site conditions (see Appendix II for list of all models considered for each species and *a priori* model selection explanations). All variables were screened for correlations ($r > |0.7|$) and only variables when $r < |0.7|$ were used within the same model. If necessary, dependent variables in the models were log-transformed to normalize data. Independent variables included location (i.e. south Elk Island, north Elk Island, burned Elk Island and outside the park) and the amount of different vegetation types (i.e. proportion grassland, shrub and forest). I calculated Akaike's Information Criterion corrected for small sample sizes (AICc) for each model and used the difference from the null model (ΔAICc) and Akaike weights (w) to rank the models

Comparing browse impact and intensity of moose, deer, elk and bison use

I used linear regression to assess relationships between browse impact and intensity of use for each ungulate species. The dependent variable, browse impact, was examined for normality by histograms where it approximated a Gaussian distribution and thus used without transformation.

RESULTS

Areas outside of Elk Island National Park had lower total IUU compared to inside the park ($\beta = -1.82$, SE = 0.36, $P = <0.01$). Average IUU in Elk Island was 23.1 units per km^2, while areas outside of Elk Island were ~50% of that inside Elk Island at 11.6 units/km^2. Related to individual species, intensity of elk use was higher in Elk Island compared to outside the park ($\beta = 0.31$, SE = 0.13, $P = 0.02$), while moose and deer use were marginally higher outside Elk Island ($\beta = - 0.24$, SE = 0.13, $P = 0.07$; $\beta = - 0.27$, SE = 0.17, $P = 0.10$, respectively). IUU by species varied between areas inside EINP and outside the park (Table 2.1).

Within sample sites, grassland habitat was more abundant in burned areas within Elk Island compared to outside the park ($\beta = 0.12$, SE =0.05, p = 0.02). Even unburned areas in south Elk Island had, however, higher proportion of grassland when compared to outside the park ($\beta = 0.18$, SE = 0.05, $P < 0.01$). South Elk Island also had a higher proportion of shrub compared to both the northern and burned areas of the park ($\beta = 0.18$, SE = 0.05, $P < 0.01$; $\beta = 0.17$, SE = 0.06, $P < 0.01$, respectively). The proportion of grassland in north and south Elk Island did not differ from burned areas ($\beta = - 0.70$, SE = 0.07, $P = 0.31$; $\beta = 0.05$, SE = 0.07, $P = 0.44$, respectively).

Predicting ungulate distribution using location and vegetation patterns

Moose

Nine *a priori* models were tested to examine factors affecting intensity of moose use (Appendix II). The top ΔAICc models differed from the null model (Table 2.2).

The top ΔAICc-ranked moose model had 4 parameters, included variables of location only, an AICc weight of 0.21 and explained 10.7% of the deviance (Table 2.2). Moose were less abundant in the north (β = – 0.34, SE 0.15, *P* = 0.02) and within burned areas (β = – 0.42, SE = 0.17, *P* = 0.01) of Elk Island compared to outside the park (Table 2.3) with intensity of moose use being similar in south Elk Island and outside the park (β = 0.03, SE = 0.16, *P* = 0.87).

Deer

Of the nine *a priori* candidate models tested for deer (Appendix II), the most supported models did not differ significantly from the null model (Table 2.2). Therefore, intensity of deer use was similar among locations (inside vs. outside Elk Island) and different habitats sampled.

Elk

Fifteen *a priori* models were examined for intensity of elk use (Appendix II). The top ΔAICc models differed significantly from the null model and included covariates of location and vegetation (Table 2.2).

The top ΔAICc-ranked elk model had 5 parameters, an AICc weight of 0.41 and explained 24.7% of the deviance (Table 2.2). Elk were more abundant in forested areas (β = 1.59, SE = 0.32, *P* = <0.01) and in the southern (β = 0.86, SE = 0.18, *P* = <0.01) and burned areas (β = 0.37, SE = 0.12, *P* = 0.03) of Elk Island National Park than areas outside of the park (Table 2.3). There was no difference in intensity of elk use between north Elk Island and areas outside the park (β = 0.10, SE = 0.15, *P* = 0.52).

Bison

Nine *a priori* models were tested to explain patterns of bison use (Appendix II). The top ΔAICc models differed significantly from the null model and included covariates of location and vegetation (Table 2.2). Because bison are absent from areas outside of Elk Island, those sites were not considered in the model.

The top ΔAICc bison model had 5 parameters, an AICc weight of 0.36 and explained 30.8% of the deviance (Table 2.2). Bison were more abundant in areas with more grassland (β = 3.28, SE = 0.73, *P* = <0.01). Bison were also more abundant in the south (β = 0.86, SE = 0.18, *P* = <0.01) and in burned areas (β = 0.366, SE = 0.12, *P* = 0.03) of the park compared to north Elk Island (Table 2.3). Proportion shrub within a site was not related to intensity of bison use (β = 1.41, SE = 0.83, *P* = 0.88).

Relating browse impact and intensity of moose, deer, elk and bison use

Intensity of elk use and browse impact were positively, but weakly related ($r^{2} =$ 0.08, $P = 0.03$) (Figure 2.3). Moose, deer and bison use were not related to browse impact ($r^2 = 0.02$, $P = 0.24$; $r^2 = 0.00$, P = 0.86; $r^2 = 0.01$, $P = 0.37$, respectively). However, when intensity of moose, deer and elk use were pooled, there was a weak positive relationship with browse impact ($r^2 = 0.08$, P=0.03) and a stronger relationship when examining browse impact only in the shrub layer of each site ($r^2 = 0.13$, P= 0.01). Although generally grazers, bison do browse in Elk Island (Holsworth 1960; Hood & Bayley 2008; Teichman, *personal observation*). Therefore I pooled all ungulate species to assess the relationship of IUU on browsing pressure. At the site level there was a weak positive relationship between total IUU and browse impact (r^2 =0.05, $P = 0.09$) with a stronger relationship evident when examining browse impact within the shrub zone of each site ($r^2 = 0.10$, $P = 0.03$).

DISCUSSION

IUU in Elk Island National Park is high relative to areas outside of the park. Elk Island contains some of the highest year-round ungulate densities reported in Canada (Blyth & Hudson 1987; Hood & Bayley 2008). High IUU in the park is, in part, a result of bison and the ungulate-proof fence that surrounds the park which prevents dispersal and hunting mortality. Despite the historic ungulate culling program in Elk Island, park management promotes increased ungulate food supply and generally more open or early seral stage habitats through prescribed burning (Blyth & Hudson 1987).

Intensity of moose use was highest in south Elk Island and outside of the park and lowest in the north and burned areas within Elk Island (Table 2.1). Elk Island management includes prescribed burns to maintain grassland systems and to increase forage for ungulates (Blyth & Hudson 1987). Burn treatments can result in increased shrub density, particularly if burns are managed at a low intensity (Bork, Hudson & Bailey 1997). The lack of shrub forage for moose in the burned areas may be the result of high intensity burns which leads to shrub mortality, therefore limiting winter forage for ungulate browsers.

There was more grassland habitat in burned areas within Elk Island compared to outside the park which may, in part, contribute to reduced winter browse for moose. However, unburned areas in south Elk Island also have more grassland compared to areas outside the park possibly due to high bison use (27.6 units /km^2) preventing forest regeneration. This pattern is similar to that in Africa where large herds of wildebeest and elephants maintain open savannah and preclude the growth of trees (Dublin *et al*. 1990). The proportion of grassland in north and south Elk Island did not differ from the burned areas which further suggests that high herbivory by ungulates in the park, particularly by bison, are responsible for maintaining grasslands, irrespective of prescribed burning. Regardless, there are more moose in south Elk Island likely due to the high proportion of shrub compared to both the northern and burned areas of the park. However, this model explained only 10.7% of the deviance so moose distribution may be largely random or other variables likely influence moose habitat use. For example, moose mortalities have been high due to liver fluke in north Elk Island resulting in dramatic declines in moose populations (Ross Chapman, Parks Canada, *personal communication*). This might obscure observed patterns of IUU of certain vegetation.

For deer, the model selected a single estimate of intensity of deer use (null model) which suggests that broad-scale vegetation patterns do not influence deer habitat use or that deer are randomly distributed across the landscape. Indeed, the fence barrier of Elk Island does not prevent deer from moving inside to outside the park or vise versa (Blyth and Hudson 1987) which may explain the random distribution of deer across the study area.

Elk and bison were both abundant in the south and burned areas of Elk Island when compared to other areas (north Elk Island and outside of Elk Island). As grassland increased so, too, did the intensity of bison use. Intensity of bison use was highest in both the south and burned areas and therefore bison may be creating more grassland habitat due to overgrazing (Dublin *et al*. 1990). Interestingly, elk were found mostly in the forested areas. Previous work in Elk Island showed that elk select habitats seasonally. For example, during the calving season cow elk and calves were rarely seen in open areas and were often encountered in forests (Holsworth 1960). Holsworth (1960) showed that during the winter elk preferred grassland meadows, thereby reducing their overall browse pressure. However, during Holworth's (1960) study, bison cows, yearlings and most other age classes were baited onto feedlots after the first snow fall. Elk Island no longer manages bison herds this way; bison are free roaming within the park boundaries year round (Blyth & Hudson 1987) with the exception of a biannual cull (Glynnis Hood, *personal communication*). Therefore, bison may be directly or indirectly outcompeting elk (Holsworth 1960; Stewart *et al.* 2002). When food resources are more limiting during the winter months, a behavioural shift of elk to forested habitat may occur. Indeed, within the park, intensity of elk use increased in forested areas (β = 1.12, SE = 0.40, P = <0.01) but there was no relationship between elk use and forest outside the park, where bison are absent (β = 0.84, SE = 0.55, P = 0.13).

Browse levels were correlated most to intensity of elk use. Although often considered a grazer, elk have been shown to browse in many systems (Baker *et al.* 1996; Beyer 2007, Ripple & Beschta 20001; Hebblewhite *et al.* 2005). In Elk Island, browse made up approximately 25% of the summer elk's diet and 30 % of the winter diet based on rumen content analyses (Holsworth 1960). Although not directly addressed in this study, it is likely that browse material would make up more of the elk's current diet due to the increased potential of year-round competition with bison.

Intensity of moose and deer use were considerably lower compared to elk and bison in all locations suggesting moose and deer may be less dense (Table 2.1). This may account for the lack of relationship between individual species use and browse pressure. Although bison are predominantly grazers, bison also browse on shrubs. Holsworth (1960) used rumen contents to show that browse made up approximately 10% of bison winter diet in Elk Island, a percentage estimated when bison herds were simultaneously fed hay during the winter. In my study there was no statistical significance between intensity of bison use and browse impact. However, Elk Island supports high intensity of bison use (Table 2.1) so the impact of bison on vegetation may nevertheless be biologically significant. When all ungulate species were pooled, there was a weak positive relationship with browse levels. The influence of browse on plant species occurs over a long period of time and is therefore dependent on ungulate distribution over multiple years or decades. Estimates of IUU were for the winter 2011 and may not have been reflective of general year-round browsing pressure or pressure in different years.

This study attempted to assess whether vegetation patterns in riparian areas could provide insight into the distribution of ungulates in Elk Island and surrounding areas. Because this study focused only on riparian zones, I did not consider other habitat that was available to ungulates in the study area. For example, the results show that there are no differences in amount of grassland near wetlands in the north, south and burned areas of the park. However, this assessment does not include distinct upland grassland pockets found throughout aspen stands that would provide forage for bison and elk, thereby affecting total IUU. Furthermore, Elk Island National Park has a long history of managing ungulates and therefore human intervention plays a major role in the density of ungulates observed in the park. Because of high ungulate density, culling and live trapping of elk has occurred throughout the past half century (Blyth & Hudson 1987). Historically bison have been managed through culling as well as live trapping for reintroduction purposes. In addition, over half of the park has been burned to increase forage quality and palatability for ungulates (Hood *et al.* 2007). The effect of fire on vegetation structure and composition is complex and depends on multiple factors including burn frequency, severity and intensity (Turner *et al*. 1994). The spatial distribution of burned and unburned areas may also influence succession on burned sites, resulting in various levels of forage quality. Future work should consider differences in the type of prescribed fire and should also quantify biological diversity and forage quality of graminoids and shrubs in burned areas and how these may influence habitat use by ungulates.

Elk Island National Park uses prescribed fire to maintain grasslands. Current management practices are largely devoted to a single, yet critical, ungulate species, bison. The intensity of use for both moose and deer were marginally higher outside of Elk Island which may be attributed to more forest and less grassland compared to inside the park. The results suggest that moose, elk and bison occupy or exploit different habitats within the same area. Bison abundance increases with grassland habitat, while elk increases with forest cover and moose with shrub cover. Because elk are primarily grazers, interspecific competition between bison and elk may be occurring (Holsworth 1960).

Because of a limited historical record of ecological conditions (range of reference conditions) in the Beaver Hills region, it is unclear whether the goal of maintaining ecosystem function and biodiversity is currently being met. Historically, it is suggested that bison grazed the area only during winter (Blyth & Hudson 1987). Therefore, managing bison at lower densities may provide more forage for other ungulate species that historically persisted in the region year-round.

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Table 2.1 Estimates of intensity of ungulate use (IUU) for north Elk Island National Park (NEINP), south Elk Island National Park (SEINP), burned areas in Elk Island National Park (BEINP) and outside Elk Island National Park (OEINP). Table includes mean use (units/km^2) and standard error for moose, deer, elk, bison and all ungulates pooled.

Location	**n**	**Moose**		**Deer**		**Elk**		**Bison**		**All Ungulates**	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
NEINP	16	0.3	0.11	1.8	0.43	7.0	1.07	4.5	1.71	13.5	1.73
SEINP	13	1.2	0.21	2.5	0.62	8.4	0.91	15.5	3.63	27.6	3.87
OEINP	30	1.2	0.28	2.8	0.52	5.3	0.54	-	-	9.3	0.77
BEINP	11	0.3	0.22	0.9	0.19	7.9	1.46	15.3	2.92	24.5	3.84

Table 2.2 Top ΔAICc Generalized Linear Models (GLM) describing intensity of use for moose, deer, elk, and bison. Model description, number of estimated parameters (K), model log-likelihood (LL), Akaike's Information Criterion (AIC), small sample size corrected AIC (AICc), AICc difference (ΔAICc), AIC weight (w) and % deviance explained are shown**.**

Model Description	**K**	**LL**	**AIC**	**AICc**	**ΔAICc**	**Exp(-1/2Ai)**	**w**	**% Dev. Expl.**
Moose								
null model	1	-50.17	102.30	102.4	3.8	0.15	0.03	0.0
location	4	-44.79	97.58	98.7	0.0	1.00	0.21	10.7
Elk								
null model	1	-59.55	121.10	121.2	19.8	0.00	0.00	0.0
prop_forest location	5	-44.87	99.74	101.4	0.0	1.00	0.41	24.7
Bison								
null model	1	-57.93	117.86	118.0	23.2	0.00	0.00	0.0
prop_grass prop_shrub location	5	-40.13	90.25	92.0	0.0	1.00	0.36	30.8

NEINP = North Elk Island National Park, SEINP = South Elk Island National Park, BEINP = Burned areas in Elk Island National Park. Note: Moose and Elk models compared to OEINP while bison model compared to NEINP

Table 2.3 Coefficients, standard errors, and P-values for the top rank ΔAICc Generalized Linear Models (GLMs) predicting IUU.

Variable	Coefficient	Standard Error	*P*-value
Moose			
SEINP	0.028	0.157	0.865
BEINP	- 0.418	0.167	0.012
NEINP	- 0.341	0.146	0.020
Elk			
prop forest	1.588	0.324	0.000
SEINP	0.859	0.178	0.000
BEINP	0.366	0.117	0.030
NEINP	0.096	0.148	0.518
Bison			
prop grass habitat	3.280	0.732	0.000
prop shrub habitat	1.410	0.826	0.880
SEINP	0.578	0.329	0.079
BEINP	1.035	0.281	0.000

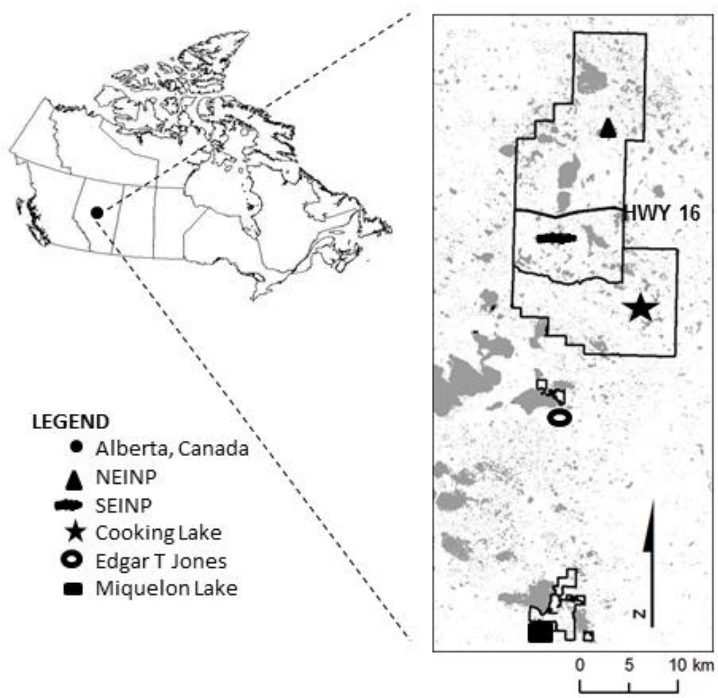

Figure 2.1 Location of study area in the Beaver Hills region of Alberta, Canada including Elk Island National Park, Cooking Lake-Blackfoot Provincial Recreation Area, Edgar T. Jones Natural Area and Miquelon Lake Provincial Park. Elk Island is divided by a major highway into a north and south section. Gray represents water bodies.

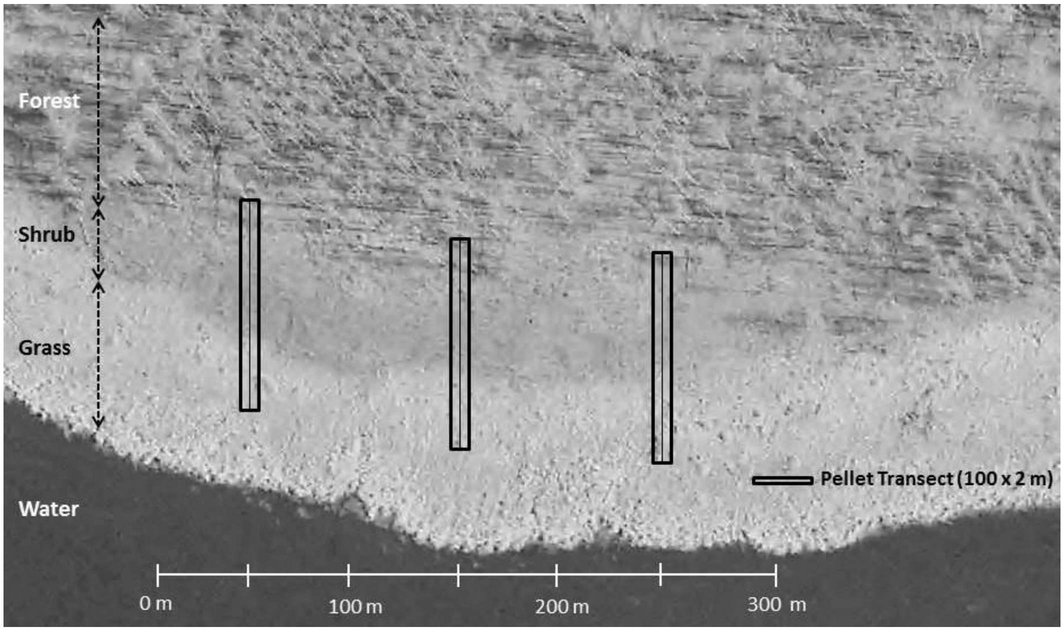

Figure 2.2 Ungulate pellets were quantified at 70 sites using three 100 × 2 m belt transects running perpendicular to the wetland and thus crossing grass, shrub and forest zones. Vegetation zones were quantified by measuring distance along pellet transects.

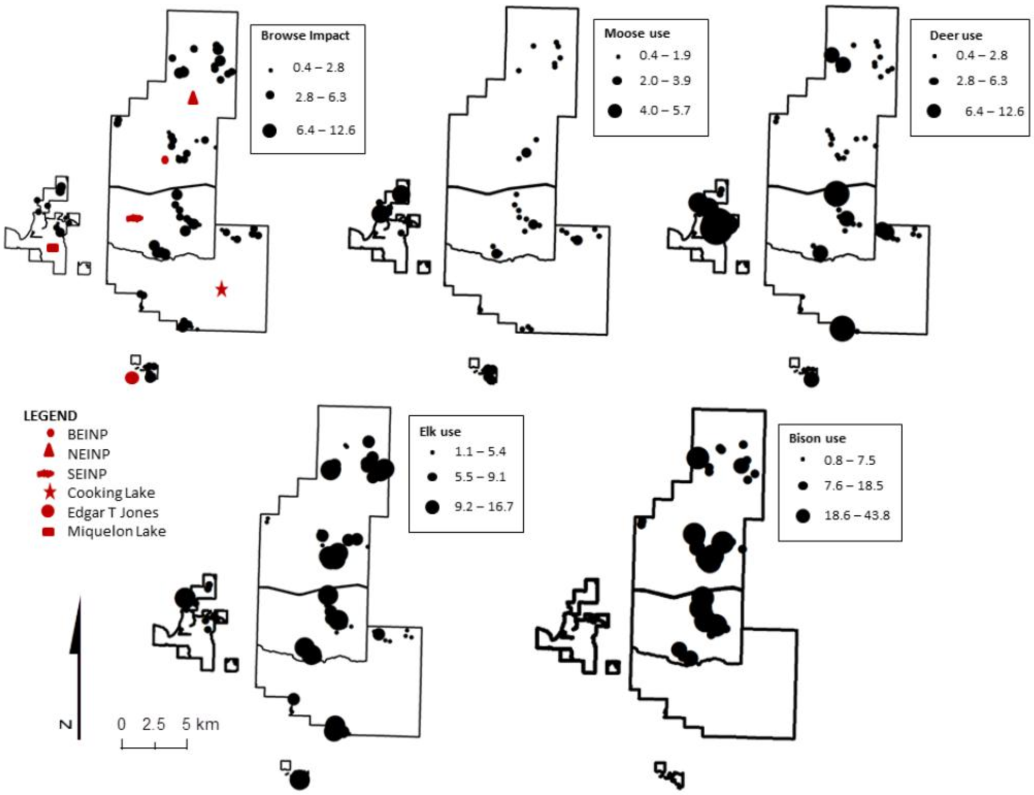

Figure 2.3 Comparing IUU (by species) and browse impact at 70 sites in and around Elk Island National Park. Note that Miquelon Lake Provincial Park is shown to be west of Elk Island for illustration purposes when in fact it is located ~100 km south of the park.

CHAPTER 3

TROPHIC CASCADES IN A MIXED BOREAL FOREST: OVERABUNDANT UNGULATES, VEGETATION AND SHRUB-DEPENDENT BIRD AND BUTTERFLY SPECIES

ABSTRACT

Few studies have demonstrated trophic cascades in productive and diverse terrestrial ecosystems relative to low biologically diverse systems. The Beaver Hills region in Alberta, Canada is a mixed boreal forest that contains a diverse gradient of intensity of ungulate use (IUU) due to the loss of top predators and management practices that strive to maintain high ungulate density. To examine the cascading effects of high IUU on vegetation and shrub-dependent bird and butterfly species, I quantified vegetation characteristics and abundance of yellow warbler (*Dendroica petechia*) and Canadian tiger swallowtail (*Papilio canadensis*) in and around Elk Island National Park. Using Structural Equation Models, I found that IUU was inversely related to horizontal shrub cover with shrub cover positively related to yellow warbler abundance. Moreover, chokecherry (*Prunus virginiana*) abundance was inversely related to browse impact and positively related to Canadian tiger swallowtail abundance. These results demonstrate a cascading effect of high IUU on yellow warblers through reductions in shrub cover and Canadian tiger swallowtail numbers through reductions in larval host plant density. The loss of top predators, in conjunction with managing for high ungulate densities, can result in negative indirect effects on shrub-dependent species even within productive and seemingly resilient ecosystems like Elk Island.

INTRODUCTION

Predators are known to regulate populations and communities in a ‘top-down’ manner across freshwater, marine and terrestrial ecosystems (Estes *et al.* 2011). Biologically diverse ecosystems are often associated with areas having functional populations of apex predators (Berger *et al*. 2001; Hebblewhite *et al*. 2005; Ripple & Beschta 2006; Sergio *et al*. 2006). However, a growing number of studies have shown no association between top predators and biodiversity suggesting loss of top level predators does not always alter ecosystem structure (Kerr 1997; Caro *et al*. 2004; Ozaki *et al*. 2006; Cabeza, Arponen & Teeffelen 2008). An important challenge in managing biodiversity is to understand the role of trophic interactions and the potential consequences to biodiversity caused by losing particular linkages.

Trophic cascades occur when changes in the size of one population in the web results in changes in populations at lower levels of the food web (Polis 1999). Studies have shown that multiple factors influence the strength and occurrence of trophic cascades. If resources are highly edible or are dominated by few species it is more likely that a trophic cascade will occur (Strong 1992; Polis 1999). Self-regulation of guilds through intraguild predation (Polis and Holt 1992) or territoriality (Sullivan & Sullivan 1982) or the regulation across trophic levels through omnivory (Fagan 1997), may limit the extent of cascades. Food web complexity and species diversity also play a role in the regulation of populations across trophic levels and thus whether a trophic cascade will occur (Pace *et al.* 1999).

The interaction strength between trophic levels influences ecosystem stability. Many weak interactions may limit the destabilizing effect of strong consumer-resource interactions (McCann 2000). For simple ecosystems with low diversity, such as the tidal pools examined by Paine (1966), the removal of a top predator in a 3-tiered food chain (i.e. sea star; *Pisaster ochraceus*) resulted in the erosion of species diversity. How a cascade manifests however, can depend on the number of trophic levels in a food chain.

Although the classic trophic cascade is based on a 3-tiered system consisting of predators, herbivores and plants (Hairston *et al*. 1966), top down forces can manifest themselves through 4 levels in the food chain (Power 1990; Gastreich 1999; Carpenter *et al*. 2001). Carpenter *et al*. (2001) demonstrated that largemouth bass, an apex predator, reduced zooplanktivorous fishes which subsequently lead to an increase in zooplankton and a decrease in phytoplankton. Thus top predators can indirectly reduce the abundance and production of primary producers or, more commonly, reduce herbivory thus increasing primary production (Estes *et* al. 2011).

Trophic cascades have been regularly reported in aquatic systems (Carpenter & Kithell 1988, Strong 1992; Estes & Duggins 1995; Polis 1999). In terrestrial ecosystems predators generally have less direct effect on plant biomass. Trophic cascades, therefore, may be less common in terrestrial than aquatic systems (Shurin *et al.* 2002). However, most trophic cascades in terrestrial ecosystems have been reported from small scale experiments involving invertebrate predators including spiders, beetles and ants (Pace *et al*. 1999; Schmitz, Hamback & Beckerman 2000; Persson 2005). Mensurative studies assessing trophic cascades based on large mammals are fewer due to logistical constraints and difficulties associated with experimentally manipulating large carnivore populations (Ripple & Beschta 2006). However, those studies done involving large top predators in terrestrial ecosystems have often shown that loss of top-down regulation by the removal or reduction of predators can result in increased herbivory which affects ecosystem structure and stability (McLaren & Peterson 1994; Ripple *et al*. 2001; Terborgh *et al*. 2001; Sergio *et al*. 2008). Mammalian carnivores can increase plant biomass indirectly by reducing herbivorous prey populations which is referred to as a density-dependent cascade or by altering herbivore behaviour which is referred to as a trait-mediated cascade (Terborgh *et al*. 2001).

A density-dependent cascade in Zion National Park was associated with a reduction in cougar abundance which indirectly limited cottonwood recruitment due to increased deer herbivory along riparian edges (Ripple *et al*. 2006). Loss of cottonwood trees resulted in fewer flowering plants, amphibians, lizards and butterflies. In some instances, it is difficult to discern the mechanism of a trophic cascade (Trussell, Ewanchuk & Bertness, 2002; Kauffmann, Brodie & Jules 2010). A study that examined the effects of green crabs as predators of herbivorous snails and their effects on the algae food web (Lubchenco 1978; Trussell, Ewanchuk, & Bertness 2002) showed that what was initially assumed to be a density dependent response of herbivores was, in fact, a trait-mediated response to perceived predatory threat. Similarly, a behaviourally-mediated mechanism was demonstrated in Yellowstone National Park following the reintroduction of wolves where aspen recruitment increased due, in part, to elk becoming increasingly vigilant – a ‘landscape of fear’ response (Ripple & Larsen 2000; Fortin *et al*. 2005). More recent work for the same wolf-elk-aspen cascade showed, however, no differences in aspen recruitment in areas with low versus high predation risk, which suggests a lack of a behaviourally-mediated trophic cascade (Kauffmann, Brodie & Jules 2010).

Research on trophic cascades involving herbivores has mostly focused on cascades through direct predator–prey interactions (McLaren and Peterson 1994, Berger *et al*. 2001; Terborgh *el al*. 2001). I investigated the potential indirect effects of high ungulate density, mediated by both the historic loss of wolves, cougars and grizzly bears and recent management strategies geared towards maintaining high ungulate density. The study area includes Elk Island National Park, an area delineated by an ungulate-proof fence and considered to have some of the highest ungulate densities in Canada (Blyth & Hudson 1987;

Hood & Bayley 2008). The study system is characterized by being resilient due to the fact that dominant woody species have vegetative reproductive strategies that facilitate rapid recovery from disturbance (Bork, Hudson & Bailey 1997; White, Olmsted & Kay 1998). The objective of this study was to test a density-dependent, species-level trophic cascade for a forested ecosystem in east-central Alberta that is characterized as being resilient by evaluating the direct impacts of intensity of ungulate use (IUU) on vegetation and the indirect effects of IUU on shrub-dependent bird and butterfly species. Moderate browsing pressure may benefit shrub-nesting birds by creating nest sites (Erin Bayne, *personal* communication) or butterfly larval performance through increasing plant carbon and nitrogen content (Scriber 1991). However, due to the historic and current high ungulate densities within the study system, I predicted that, despite having evolved an ability to recover rapidly from disturbance, high IUU and/or browse impact should result in structural and compositional changes in vegetation that would limit nest-sites for yellow warblers and larval host plants for Canadian tiger swallowtails and thus reduce their abundance.

METHODS

Study area

The study was conducted in the Beaver Hills region, approximately 45 km east of Edmonton, Alberta. This region includes Elk Island National Park, Cooking Lake-Blackfoot Provincial Recreation Area, Edgar T. Jones Natural Area and

Miquelon Lake Provincial Park (Figure 3.1). I sampled within these parks to represent a broad gradient in IUU and thus browsing pressures (Figure 3.2). Elk Island National Park is a 196 km² reserve that was fenced immediately after its establishment in 1906. There are no resident apex predators in the park and ungulates occur at high densities. Ungulate species include elk (*Cervus canadensis*), moose (*Alces alces*), plains bison (*Bison bison bison*), wood bison (*Bison bison*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*). All other reserves in the Beaver Hills lack apex predators and contain these same ungulate species with the exception of bison that occur only in Elk Island National Park. Elk Island actively manages ungulate habitat through the use of prescribed fires and so to avoid confounding effects associated with post-fire responses in vegetation due to different successional states, number of burns and intensity of burn, the burned areas with the park were not included in this analysis. Of the areas outside of Elk Island, Cooking Lake-Blackfoot Provincial Recreation Area is another large (98.8 km^2) reserve that supports ungulate hunting and, in designated areas, is used for seasonal livestock grazing. In the late 1950s parts of the upland deciduous forests in the Cooking Lake-Blackfoot reserve were logged to enhance livestock grazing. In 1987 a fence was built to limit grazing to a 28.75 km^2 area of pastures that were seeded with agricultural species. These areas were not used in this study. Miquelon Lake Provincial Park (~13 km^2) and Edgar T Jones Natural Area (0.92 km^2) are designated protected areas and were also sampled for this study to represent different ungulate densities.

All study sites are characterized as a mosaic of wetlands surrounded by aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) forests with sporadic patches of black and white spruce (*Picea mariana* and *P. glauca*, respectively). Shrub understory is dominated by beaked hazelnut (*Corylus cornuta*) with other shrub species including saskatoon (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), willow (*Salix* spp.), rose (*Rosa* spp.) pin cherry (*Prunus pensylvanica*), red raspberry (*Rubus idaeus*), bush cranberry (*Viburnum* spp.), red-osier dogwood (*Cornus stolonifera*), western snowberry (*Symphoricarpos occidentalis),* currant (*Ribes* spp*.),* honeysuckle (*Lonicera* spp.) and buffaloberry (*Shepherdia canadensis*).

Site selection

Shrub and forest communities with riparian-like characteristics were identified from an Alberta land cover classification (Canada Forest Services 2007). Each site was adjacent to a wetland and was characterized by having three distinct vegetation communities: grassland, shrub and forest. Land cover was classified as edges and watercourses (Natural Resources Canada 2002) and was overlain with forested areas to define riparian edges for sampling. Resulting edge polylines ≥300 m in length were buffered by 10 m and random spatially referenced points in GIS created (1 per 300 m) to identify sample locations. Fifty nine locations were randomly selected and used as sampling locations.

Abundance of butterflies

I assessed the relative abundance of Canadian tiger swallowtail using Pollard Walk surveys (Pollard & Yates 1993; Royer, Austen & Newton 1998). Pollard transects were 300 m long and ran parallel to wetlands along the shrub-grass interface (Figure 3.3). Focal butterfly species were chosen based on larval host plants, population status in Alberta (common or rare) and habitat preferences. Pollard Walks were conducted in 2011 during peak flight times and suitable temperature and wind conditions (Pollard &Yates 1993) with the observer recording focal butterfly species seen within 5 m of the transect and in front of and above the observer. Butterflies that could not be easily distinguished in flight were captured using a sweep net for further identification in hand and then immediately released (Royer *et al*. 1998). If butterflies escaped capture, an in-flight description was recorded. Focal species include Canadian tiger swallowtail, gray comma (*Polygonia progne*), giant sulfur (*Colias gigantea*) and fritillary species. Fritillary species included *Boloria bellona* (meadow fritillary), *Boloria selene* (silver-bordered frittillary), *Boloria eunomia* (bog fritillary), *Speyeria atlantis* (Atlantis fritillary), *Speyeria mormonia* (Mormon fritillary), *Speyeria aphrodite* (Aphrodite fritillary), and *Speyeria hesperis* (northwestern fritillary). Gray comma (*Polygonia progne*) and giant sulfur (*Colias gigantea*) were too uncommon to assess further. Due to difficulty in differentiating between fritillary species in flight, I pooled all fritillaries. However, this was problematic due to variations in peak flight times. Fritillary species were therefore not considered further. Canadian tiger swallowtails were the only species used and relative abundances were estimated from surveys conducted between June and July 1 of 2011.

Abundance of yellow warblers

In May and June of 2011 the relative abundance of yellow warblers were estimated at 59 sites using call playbacks. Call playbacks were located at the center of each 300 m transect and within the middle of the shrub community (i.e., the ecotone between the forest and open wetland communities) (Figure 3.3). Call playbacks were conducted by playing a one minute call followed by one minute of silence during which time the observer recorded any yellow warblers visible or audible. Call playbacks occurred between half an hour before sun-rise and 10 am provided that weather conditions were favourable – no precipitation and <2 on the Beaufort Wind Scale (Alberta Biodiversity Monitoring Institute 2007). All counts were made by two observers with both observers recording playback observations at 30 sites prior to independent observations. To eliminate double counting of yellow warblers, any bird believed to be previously detected was not recorded.

***Intensity of Ungulate Use* (IUU)**

I used pellet group surveys along transects to index intensity of ungulate use (IUU) (Figure 3.3). In September to October 2010, using pigtail markers and GPS route planner, pellet transects were marked and run to remove all pellets within 1 m of transects. In May 2011 pellet transects were revisited to index intensity of winter ungulate use from pellet group counts.

Pellet counts were carried out in 100 x 2 m belt transects perpendicular to the 300 m butterfly transects running parallel to the wetland (Figure 3.3). Three transects 100 m apart were completed at each site for a total search area of 600 m^2 or 0.06 ha. Pellets were distinguished by species and classified as large (>5) or small (≤5) pellet groups (Hood & Bayley 2008). I noted the vegetation class where pellets were found (grass, shrub or forest) and pooled pellets across vegetation types to obtain a per site sampling unit. Only large (>5) pellet groups were used for these analyses to prevent overestimation of animals defecating on the move. Although I used the following density formula, pellet conversions should be considered IUU due to the small spatial scale being assessed:

$$\text{IUU} = \frac{X}{A \times F \times \mathrm{t}}$$

where X is the number of pellet groups, A is the area of the plot, F is the defecation rate and t is the time of pellets to accumulate at a site (Skalski *et al*. 2005). Defecation rates vary due to diet, season, location, recording methodology and whether animals were free ranging or penned (Appendix I). Because species-specific defecation rates were unknown for my study system, I used the average defecation rates for each species (moose, deer, elk and bison) based on estimates from the published literature (Appendix I). These included 15.9 pellet groups/day for moose, 18.3 pellet groups/day for deer, 14 pellet groups/day for elk and 9 plops/day for bison (Appendix I).

Increased browsing reduces availability of herbaceous forage due to snow accumulation and to the energetic costs associated with foraging in snow (Parker, Robbins, & Hanley 1984; Fancy & White 1985). All ungulate species, including bison, have been shown to browse (Holsworth 1960), particularly during the winter months. Therefore, once IUU was calculated for each species, I summed use across all species to acquire a total IUU estimate for each site. For the entire study area, I estimated an average IUU by species. I also compared IUU by partitioning data into North Elk Island National Park (NEINP), South Elk Island National Park (SEINP) and outside Elk Island National Park (OEINP). North and south Elk Island are fenced areas that were expected to have higher IUU than outside Elk Island.

Vegetation surveys

In 2010 and 2011, vegetation surveys were conducted at 100 m increments along the established 300 m butterfly transects at each site. Plots were located in the middle of the shrub zone and at a 15 meter distance into the forest, for a maximum of three shrub plots and three forest plots per site (Figure 3.3). Shrubs were considered to be any species with a DBH < 5.

Because all statistical modeling was performed at the scale of a site (i.e. maximum 6 plots per site) shrub variables were first quantified at the plot level and then averaged the plots to estimate a single site value.

Shrub density

A variation of the point-centered quarter method was used to estimate shrub and tree densities (Y. Feng, University of Alberta, unpublished). I restricted the plot radius to 3 m because it was impractical to do a limitless search for each species. As a result some plots had fewer than 4 observed distances for each of the focal species. I accounted for quadrants absent of a species by using the equation:

$$\hat{\lambda}_q = \frac{\pi}{4}\left(\frac{a_{q1}^2 + .. + a_{qk}^2 + (4-k)r^2}{k}\right),$$

where *a* is the distance from the center point to the closest individual shrub, *k* is the number of quadrants with a plant and *r* is the search radius (3 m). This equation calculates an area per plant, from which I estimate plants per unit area. The closest stem to the center point was used to estimate total shrub density, particularly focusing on densities for target plants of willow, aspen and chokecherry.

Ungulate browse

I estimated ungulate browse using percent browse and browse severity indices similar to Hood & Bayley (2009). Chokecherry, willow and aspen were all examined because these are known to be host plants for Canadian tiger swallowtail. Browse levels were assessed for the closest stems to the center point of a plot for each selected shrub species. Percent browse was estimated as the ratio of the number of browsed branches to total number of branches from the main stem and recorded as 1 of 5 ordinal browse categories representing, 0% (0), 1-5% (1), 6-20% (2), 20-50% (3) and 51-100% (4). Browse severity, on the other hand, was estimated using qualitative visual assessments of individual shrubs based on the amount of leader and secondary growth, hedging and amount of dead wood. Browse severity was categorized into 'none' (0), low (1), medium (2) and high (3) classes. For example, a browsed branch with no dead wood and some healthy leader growth was considered 'low' browse severity while a branch with substantial secondary growth (hedging) and excessive deadwood was classified as 'high' browse severity. When there were differences of browse severity on the branches of an individual, the median value was recorded. For example, if 6 stems were browsed and the browse severity equated to 1, 2, 2, 2, 3, 3 then a median (2) browse severity was recorded.

A Browse Impact Index (BI index) was estimated as the multiplicative of the percent browse and browse severity (Hood & Bayley 2009). That is, if a shrub had a percent browse of 80% (4) with a medium browse severity (2) then the

Browse Impact index would be 8. This index was used to quantify the impact of browsing on butterfly larval host plant species.

Horizontal cover

At each plot, the percent horizontal shrub cover was estimated using a modified Robel pole (Robel *et al*. 1970) or checkerboard at 0.5 m increments up to 2 meters. Standing at a 5 m distance from the checkerboard, the observer recorded horizontal cover in the four cardinal directions and the average cover at each height class. I then averaged horizontal cover across plots and height classes to estimate site-level horizontal cover at 0.5 m, 1 m, 1.5 m and 2 m heights. To estimate total site-level horizontal cover (i.e. all height classes combined), the percent cover of all height classes were averaged.

Canopy cover

To estimate canopy cover for each site, a single observer used a spherical densiometer (Lemmon 1956) with obstructed shrubs moved to the side of the observer in order to observe canopy (tree) cover. Canopy cover was averaged across plots to estimate a single site-level canopy cover.

Grassland, shrub and forest zones

At each site the width of each vegetation zone was measured for each of the 3×100 meter pellet transects. Grassland habitats were characterized by having less than 50% emergent grasses closest to the water and less than 50% shrub in the uplands at the grass-shrub interface. Shrub habitat was identified as having ≥50% shrub cover and less than five trees within a 5 m radius (78.5 m^2). All species were considered trees if their DBH (diameter at breast height) was ≥5 cm. Forests were defined as areas having ≥5 trees within a 5 m radius representing a stem density >636 trees per hectare. A 5 m radius was used because broad vegetation patterns (i.e. grassland, shrub, and forest zones along water bodies) reflected discrete edges rather than gradual transitions to designated vegetation types. Total width of each vegetation layer was then used to estimate proportion grassland, shrub and forest for each site as the amount of each habitat varied among sites. It should be noted that estimates of proportion grassland, shrub and forest are based on sites bordering water bodies and thus are not representative of all areas in the study area.

Statistical approach

I used Structural Equation Models (SEMs) in STATA/SE-64 to examine direct and indirect relationships between ungulates, shrubs, butterflies and birds by using a path analysis framework. Prior to analysis, bivariate relationships were examined between dependent and independent variables using Generalized Linear Models (GLMs) in order to identify potentially nonlinear relationships (Grace 2006). Non-linear models included a squared term of the independent variable. Linear model fit was compared to nonlinear model fit by comparing AIC values. If the difference in AIC values that was < 2, I considered there to be no difference in model fit between a linear and non-linear model and thus used linear models.

Dependent variables that were non-normally distributed based on histograms were log-transformed with a constant (value of 1) to approximate a normal distribution. Structure of variables and relationships in the SEMs were based on theoretical causal relationships between variables and then altered according to the modification indices to improve the fit between the model and data. I tested combinations of vegetation and ungulate variables without altering the overall structure of the model and used variables that resulted in the best overall model fit. Modifications were only considered if they were ecologically relevant. A χ^2 test was used to determine the overall model fit because a non-significant result ($P > 0.05$) is a good indication of whether the data and model fit is adequate (Grace 2006).

Standardized path coefficients and P-values were used to assess significance of individual variables within the model. Due to the small sample sizes and the exploratory nature of the analyses, coefficients with $P < 0.1$ were considered significant.

Hypothesized cascade affecting yellow warblers

The hypothesized yellow warbler model included a direct path from IUU to horizontal shrub cover. In this case IUU was used as a surrogate for browsing intensity where it would be expected that increases in IUU would result in reduced horizontal shrub cover (Baker, Peinetti & Coughenour 2005). I hypothesized that the proportion of shrub habitat would be reduced by IUU because overgrazing along the grass-shrub interface may limit shrub seedling recruitment and establishment of young shrubs, thereby limiting the proportion of shrub zone (Dublin *et al*. 1990). Furthermore, overbrowsing of shrubs by moose and deer may limit shrub habitat by reducing shrub density (Prins & Van der Jeugd 1993). Bi-directional relationships between horizontal shrub cover and IUU and proportion of shrub habitat and IUU were not used because SEM cannot correlate endogenous and exogenous variables (program STATA/SE-64). Direct paths from both horizontal shrub cover and the proportion of shrub habitat to yellow warbler abundance were selected because yellow warblers prefer thick shrub understory in areas with high proportion of shrub habitat to reduce risk from predation and brood parasites (Knopf & Sedgwick 1992). A direct path from canopy cover to yellow warbler abundance was also selected due to yellow warblers preference for open or non-forested shrub habitat (Hanski, Fenske & Niemi 1996). I also included direct paths from horizontal shrub cover and proportion of shrub habitat to canopy cover because canopy cover limits precipitation and light to shrub understory (Anderson, Loucks & Swain 1969), thereby limiting plant growth.

Hypothesized cascade affecting Canadian tiger swallowtails

The hypothesized Canadian tiger swallowtail model had direct paths from IUU and browse impact of chokecherry, aspen and willow to their corresponding shrub density with the expectation that increased IUU and browsing pressure would limit shrub density (Bailey, Irving & Fitzgerald 1990; Singer & Renkin

1995). The effects of herbivory on shrubs can enhance plant quality, thereby increasing butterfly performance (Scriber 1991) or, alternatively, limit foliage for butterfly larva, limiting larval development (Ouellet, Boutin, & Heard 1994). Based on the expected heavy browsing pressure of Canadian tiger swallowtail's larval host plants, I hypothesized that chokecherry, aspen and willow (Layberry, Hall & Lafontaine 1998) density would be positively related to Canadian tiger swallowtail abundance. I hypothesized a positive direct relationship between Canadian tiger swallowtail abundance and proportion of shrub habitat because more shrub habitat should increase larval host plant density. A path from the proportion of grassland to Canadian tiger swallowtail abundance was included because avian predation rates of adult butterflies are expected to be higher in open grassland compared to areas with shrub and forest cover. Although a general response of flying butterflies to predation is to erratically shift flight patterns to unpredictable changes in direction (Marden & Chai 1991), I expected butterflies to have greater success of escaping avian insectivores in areas with more shrub or forest. I hypothesized that IUU and browse impact of Canadian tiger swallowtail's larval host plants would both affect each other so bi-directional paths were used for IUU and browse impact. Similarly, I expected grassland and shrub habitats to influence as well as be influenced by IUU. A bi-directional path was therefore used between IUU and grassland/shrub habitats.

RESULTS

Patterns of Intensity of Ungulate Use (IUU)

IUU varied substantially among sites with bison and elk having a larger presence than moose and deer (Figure 3.4a). Total IUU ranged from 2.3 to 53.4 units/km^2 with an average of 19.2 units/km^2. Overall, south Elk Island National Park had a higher IUU suggesting there were more ungulates than either north Elk Island National Park ($\beta = 0.64$, $P < 0.01$) or outside Elk Island National Park ($\beta = 0.90$, $P < 0.01$). North Elk Island National Park also had greater IUU than did outside Elk Island National Park ($\beta = 0.26$, $P = 0.07$) (Figure 3.4b). The intensity of bison use increased as the proportion of grassland increased ($\beta = 4.48$, $P < 0.01$), while the intensity of moose use increased with increased shrub habitat ($\beta = 1.02$, SE = 0.52, $P = 0.05$). Deer showed no preference for either grassland ($\beta = 0.04$, SE = 0.61, $P = 0.95$), shrub ($\beta = -0.77$, SE = 0.67, $P = 0.79$) or forest areas ($\beta = 0.78$, SE = 0.45, $P = 0.86$), while elk were found more often in areas with more forest ($\beta = 0.68$, SE = 0.36, $P = 0.06$).

Yellow warbler cascade

The hypothesized yellow warbler model required no modifications to improve model fit ($\chi^2_2 = 1.79$, $P = 0.41$) and was therefore accepted (Table 3.1; Figure 3.5a). Overall model fit was excellent ($r^2 = 0.52$). Based on this model structure, IUU was inversely related to horizontal cover ($\beta = -0.29$, $P = 0.01$) with a positive relationship between horizontal cover and abundance of yellow warblers ($\beta = 0.20$, $P = 0.09$) (Table 3.2). There was also a positive, direct effect between proportion of shrub habitat and abundance of yellow warblers ($\beta = 0.34$, $P = 0.02$), an inverse relationship between canopy cover and proportion of shrub habitat ($\beta = -0.63$, $P < 0.01$), and an inverse relationship between canopy cover and yellow warblers ($\beta = -0.28$, $P = 0.05$). Not all hypothesized relationships were supported (Table 3.2). There was a positive direct effect of canopy cover on horizontal cover ($\beta = 0.27$, $P = 0.02$) and no significant effect of the proportion of shrub habitat and IUU ($\beta = -0.04$, $P = 0.63$).

Canadian tiger swallowtail cascade

The hypothesized Canadian tiger swallowtail model had adequate fit ($\chi^2_{19} = 14.39$, $P = 0.76$) with no recommended modifications and was therefore accepted (Table 3.1; Figure 3.5b). Overall model fit was excellent ($r^2 = 0.64$). Of the larval host plants examined, only chokecherry density was negatively affected by browse impact ($\beta = -0.79$, $P < 0.01$) (Table 3.3). As chokecherry density increased, so too did Canadian tiger swallowtail abundance ($\beta = 0.26$, $P = 0.09$). There was an indirect negative effect of chokecherry browse impact on abundance of Canadian tiger swallowtail ($\beta = -0.21$, $P = 0.10$). IUU was positively related to both chokecherry ($\beta = 0.53$, $P < 0.01$) and aspen browse impact ($\beta = 0.71$, $P < 0.01$). The proportion of grassland was also positively related to IUU ($\beta = 0.05$, $P < 0.01$). All other hypothesized relationships were insignificant.

DISCUSSION

The yellow warbler cascade

The results of this study illustrate a cascading effect of areas of ungulate use on yellow warbler abundance by ungulate-induced reductions in horizontal shrub cover. IUU was inversely related to horizontal cover with shrub cover positively related to yellow warbler abundance.

High ungulate density has been shown to negatively impact neotropical bird density, including yellow warblers, where vegetation structure is altered by browsing (Berger *et al*. 2001; Olechnowski and Debinski 2008). However, moderate IUU may facilitate nesting opportunities for yellow warblers because short branches with overhead leaf cover create more suitable nest sites (Holt, Fuller & Doman 2011; Erin Bayne, *personal communication*). In general, dense understory is considered favourable to yellow warblers by reducing detectability of nest sites by predators and brood parasites (Knopf & Sedgwick 1992; Thompson 2007) thereby increasing bird productivity. However, yellow warblers select nest sites based on vegetation patterns at many scales and make decisions based on more than just information at the nesting shrub level (Stauffer & Best 1980; Knopf & Sedgwick 1992). In this study, ungulates reduced horizontal shrub cover due to heavy browsing and, because horizontal shrub patterns and density surrounding nests are critical to nest site selection by yellow warblers (Stauffer & Best 1980; Knopf & Sedgwick 1992), it is likely that the overall reduction in shrub cover at a patch scale supersedes any local beneficial effects associated with the creation of individual shrubs with more stable nest substrate.

As would be expected, there was an inverse relationship between canopy cover and amount of shrub habitat (Collins, James & Rixxer 1982). Because yellow warblers select for shrub habitat with open canopy cover (Hanski, Fenske & Niemi 1996), the expected inverse relationship between yellow warbler abundance and canopy was demonstrated. Likewise, a positive relationship between amount of shrub habitat and yellow warbler abundance was found and is supported by the findings of Knopf & Sedgwick (1992) where yellow warblers selected for areas with large area of shrubs. The yellow warbler SEM showed a positive relationship between canopy cover and horizontal cover and horizontal cover and yellow warbler abundance. If these effects were transitive, one would expect canopy cover to have a positive relationship with yellow warbler abundance, when in fact, a negative relationship was demonstrated. It is likely that, when holding horizontal cover constant, areas with higher canopy cover would have fewer yellow warblers. That is, a range of percent canopy cover will support 60% horizontal cover. Based on my SEM, yellow warblers will use areas of 60% horizontal cover that have the least amount of canopy cover.

It is widely recognized that canopy cover limits both light and moisture to understory plants thereby limiting understory development through bottom up processes. Increasing light intensity to forest floors increases herbaceous understory cover (Anderson, Loucks & Swain 1969) through photosynthesis. The hypothesized inverse relationship between canopy cover and horizontal cover was not, however, supported. In fact, as canopy cover increased, horizontal cover also increased. One of the most dominant shrubs for many of the study sites was beaked hazelnut which is shade-tolerant. Light intensity in the relatively open aspen forests seem to be high enough to not limit hazel growth and thus horizontal cover. Although light intensity was not directly measured at each site, the average canopy cover was 47.7% (range between 5.5 and 85.4%) with 8 to 17% of full sunlight considered necessary for understory plant growth (Swain 1964; Anderson, Loucks & Swain 1969). Light therefore may not be a limiting understory shrub development in the Beaver Hills area.

The Canadian tiger swallowtail cascade

Browse impact on chokecherry had a negative effect on Canadian tiger swallowtail abundance through reduction in chokecherry density. Herbivory can alter forage quality by increasing nitrogen and carbon content, chemicals that can enhance growth rates of Canadian tiger swallowtails (Scriber 1991), thereby increasing butterfly survival rates. Browsing may reduce, however, foliage available to leaf-eating caterpillars, which restricts carbon and nitrogen gain and thus caterpillar development (Ouellet, Boutin, & Heard 1994). In this study there wasn’t an indirect positive relationship between browse impact and Canadian tiger swallowtail abundance. Reductions in chokecherry foliage are therefore a more likely explanation for reductions in Canadian tiger swallowtail abundance. Chokecherry is highly palatable to ungulates (Holsworth 1960; Best et al 2003) and was expected to be severely impacted by intense and frequent year-round herbivory.

Browsing intensity and frequency, the type of herbivory, and the time of year vegetation is browsed all influence plant morphology and physiology (Danell, Bergström & Edenius 1994; Danell, Huss-Danell & Bergström 1985). Many shrub species respond to moderate defoliation due to herbivory by the development of new shoots and stems (Crawley 1983) which may contribute to the lack of relationship between willow and aspen browse and corresponding shrub densities. Furthermore, in response to herbivory, studies have demonstrated that resprouting juveniles of cottonwood (*Populus* spp.) and willow contained high levels of compounds that deter mammalian herbivores, which may also suggest limited effects of browsing on specific shrub species (Tahvanainen *et al.* 1985; Martinsen, Driebe & Whitham 1998). Willow and aspen stems are highly resilient to disturbance (vegetative resprouting) and can therefore rapidly increase when released from intensive browsing (Baker, Peinetti & Coughenour 2005). This supports the lack of relationships observed between IUU and shrub density for willow and aspen.

Beaked hazelnut has a high tolerance to browsing (Best et al 2003; Hood & Bayley 2009). Because beaked hazelnut is the dominant understory shrub at most sites within the study area, it may absorb the negative effects of intense browsing on other shrub species. Blyth *et al*. (1994) demonstrated that annual winter twig use of beaked hazelnut by ungulates in Elk Island ranged from 40-55%, which makes up a large portion of their winter diet. Because the effects of browsing on shrubs accumulates over multiple years, shrub density measured during a single year in summer, particularly for aspen and willow, may not be reflective of general year-round browsing pressure or pressure in different years.

The lack of relationship between willow and aspen density and Canadian tiger swallowtail abundance may mean that, at a small spatial scale, aspen and willow host plants are ubiquitous and thus not limiting Canadian tiger swallowtails (Rausher 1979b). It should be noted that Canadian tiger swallowtails were measured in their adult stage and because adults forage on a variety of flowering plants, habitat selection may shift for other life stages. Adults may have flown from their larval habitats to nearby areas containing high density of nectar plants. Future research should estimate adult butterfly flight distances or density estimates of Canadian tiger swallowtail caterpillars. Regardless, areas with a higher abundance of larval food plants would be expected on average to have higher local populations of dependent butterflies. Alternatively, however, chokecherry may act as a preferred larval host plant for Canadian tiger swallowtail that resulted in lower dependence or use of aspen and willow. Currently host preference hierarchy for most butterfly species in

Alberta is unclear. This research suggests that Canadian tiger swallowtail may depend more on chokecherry during their larval stages than other host plants.

The positive relationship demonstrated between the proportion of grassland habitat and intensity of ungulate use is likely a result of high bison numbers. The hypothesized inverse relationship between proportion of shrub habitat and Canadian tiger swallowtail abundance was not supported. Swallowtail species lay eggs in sunny open habitats (Rauscher 1979b) and vegetation structure and composition surrounding host plants significantly influence a butterfly’s ability to locate host plants (Tahvanainen & Root 1972; Atsatt & O'Dowd 1976). Butterflies use chemical cues to locate host plants and thus in areas with high plant diversity the mixing of chemicals can breakdown patterns of orientation, making it difficult to locate host plants. Therefore more open areas may result in greater number of eggs. Other factors that influence butterfly search ability, such as host plant abundance or competition for oviposition sites (Rausher 1979b), are likely more important than the amount of shrub habitat in an area with high diversity of shrub species.

Although I demonstrated that chokecherry density influences swallowtail abundance, the method used to quantify chokecherry abundance is likely at too large of a scale to answer questions about host plant and butterfly larval behaviour. Many larva of butterfly species move relatively short distances when searching for suitable forage and host plants that provide sufficient foliage that limit larval movement to the host plant where oviposition occurred (Rausher 1979a).

Conclusion

Cascading effects across trophic levels are most common in systems with low diversity, food web complexity and productivity (Polis & Strong 1996; Schmitz, Hamback & Beckerman 2000). High productivity may weaken the interactions between species, thereby limiting cascading effects. The Beaver Hills ecosystem is considered productive and biologically diverse (Bork, Hudson & Bailey 1997) relative to other well-known terrestrial ecosystems in western North America where trophic cascades have been reported (e.g. Yellowstone and Zion National Parks). However, ungulate exclosures that have been in place in Elk Island since 1999 illustrate that even in this productive ecosystem characterized by wood species with vegetative resprouting capabilities, forest structure (succession) is limited by ungulate browsing. Shrub structure, however, often still persists albeit at low heights (Figure 3.2a).

Despite the theoretically low susceptibility to cascading effects in this ecosystem dominated by aspen, I provide evidence of a species-level cascade wherein high intensity of ungulate use decreases yellow warbler abundance likely through nest-site limitations or increased predation and limits butterfly abundance of Canadian tiger swallowtails through reduction of larval host plant densities. This study provides evidence of a trophic cascade, initiated by a combined effect of the loss of top predators and human management of ecosystems geared towards maintaining high ungulate densities.

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Table 3.1 Expected and observed outcomes including coefficients for direct, indirect and total effect for hypothesized causal relationships in the SEM for yellow warblers and Canadian tiger swallowtails.

Expected outcomes		Observed outcomes		
yellow warbler SEM		Direct paths	Indirect paths	Total effects
High IUU will	decrease horizontal cover	- 0.294**	None	- 0.294
	decrease proportion of shrub habitat	- 0.040 †	None	- 0.040
	reduce yellow warbler abundance	None	- 0.072 †	- 0.072
Reduced horizontal cover will	decrease yellow warbler relative abundance	0.196*	None	0.196
Increased canopy cover will	reduce horizontal cover	0.269**†	None	0.269
	reduce proportion of shrub habitat	- 0.630**	None	- 0.630
	reduce yellow warbler relative abundance	- 0.279**	- 0.163	- 0.442
Increased proportion of shrub habitat will	increase yellow warbler relative abundance	0.342**	None	0.342
Canadian tiger swallowtail SEM				
Increase browse impact of chokecherry will	decrease chokecherry density	- 0.792**	None	- 0.792
	reduce Canadian tiger swallowtail abundance	None	- 0.207	- 0.207
Increase browse impact of willow spp. will	decrease willow spp. density	- 0.186 †	None	- 0.186
	reduce Canadian tiger swallowtail abundance	None	- 0.036	- 0.036
Increase browse impact of aspen will	decrease aspen density	- 0.123 †	None	- 0.123
	reduce Canadian tiger swallowtail abundance	None	0.008	0.008
High IUU will	decrease chokecherry density	0.100 †	None	0.100
	decrease willow density	0.171 †	None	0.171
	decrease aspen density	0.255 †	None	0.255
High proportion of shrub will	increase Canadian tiger swallowtail abundance	0.084 †	None	0.084
High proportion of grass will	reduce Canadian tiger swallowtail abundance	0.214 †	None	0.214
Reduced willow spp. density will	decrease Canadian tiger swallowtail abundance	0.194†	None	0.194
Reduced chokecherry density will	decrease Canadian tiger swallowtail abundance	0.262*	None	0.262
Reduced aspen density will	decrease Canadian tiger swallowtail abundance	- 0.061 †	None	- 0.061

* = P <0.1, ** = P <0.05; † represents paths where the expected outcome is different from the observed outcome.

Table 3.2 Yellow warbler Structural Equation Model unstandardized and standardized direct path coefficients, standard error of the unstandardized coefficients and z test results. The paths are represented from the dependent variables (lower case) to the independent variable (*italicized*).

	Unstandardized path coefficients	Standard error	*z*-value	P-value	Standardized path coefficients
proportion of shrub habitat					
IUU	- 0.010	0.025	- 0.39	0.70	- 0.040
canopy cover	- 0.005	0.001	- 6.11	< 0.01	- 0.630
horizontal cover					
IUU	- 0.068	0.028	- 2.47	0.01	- 0.294
canopy cover	0.002	0.001	2.25	0.02	0.269
yellow warbler abundance					
horizontal cover	0.786	0.463	1.70	0.09	0.196
canopy cover	- 0.009	0.004	- 1.93	0.05	- 0.279
proportion of shrub habitat	1.322	0.542	2.44	0.02	0.342

Table 3.3 Canadian tiger swallowtail Structural Equation Model unstandardized and standardized direct path coefficients, the standard error of the unstandardized coefficients and z test results. The paths are represented from the dependent variable (lower case) to the independent variable (*italicized*).

	Unstandardized Path Coefficients	Standard Error	*z*-value	P-value	Standardized Path Coefficients
chokecherry density					
chokecherry browse impact	- 0.064	0.009	- 7.18	< 0.01	- 0.792
IUU	0.028	0.031	0.92	0.36	0.101
willow spp. density					
willow spp. browse impact	- 0.012	0.011	- 1.20	0.23	- 0.186
IUU	0.047	0.043	1.10	0.27	0.171
aspen density					
aspen browse impact	- 0.017	0.023	- 0.72	0.47	- 0.123
IUU	0.084	0.056	1.50	0.14	0.255
Canadian tiger swallowtail abundance					
chokecherry density	0.723	0.435	1.67	0.09	0.262
willow spp. density	0.554	0.438	1.27	0.21	0.194
aspen density	- 0.147	0.367	- 0.40	0.69	- 0.061
proportion of shrub habitat	0.004	0.001	0.55	0.59	0.084
proportion of grass habitat	0.683	0.507	1.35	0.18	0.214
IUU – chokecherry BI covariance	0.425	0.143	2.97	< 0.01	0.343
IUU – salix BI covariance	0.098	0.180	0.55	0.59	0.069
IUU – aspen BI covariance	0.347	0.094	3.70	< 0.01	0.409
IUU – proportion shrub habitat covariance	0.530	0.759	0.70	0.49	0.088
IUU – proportion grass habitat covariance	0.034	0.010	3.51	< 0.01	0.392

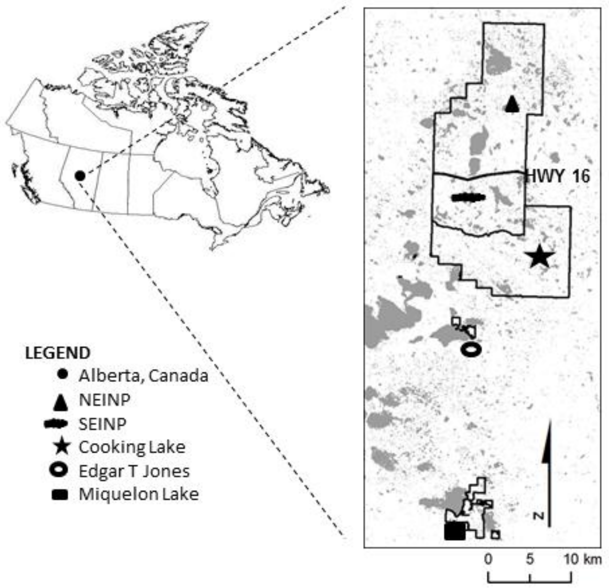

Figure 3.1 Location of study area in the Beaver Hills region of Alberta, Canada including Elk Island National Park, Cooking Lake-Blackfoot Provincial Recreation Area, Edgar T. Jones Natural Area and Miquelon Lake Provincial Park. Elk Island is divided by a major highway into north and south sections. Gray represents the lakes and other water bodies.

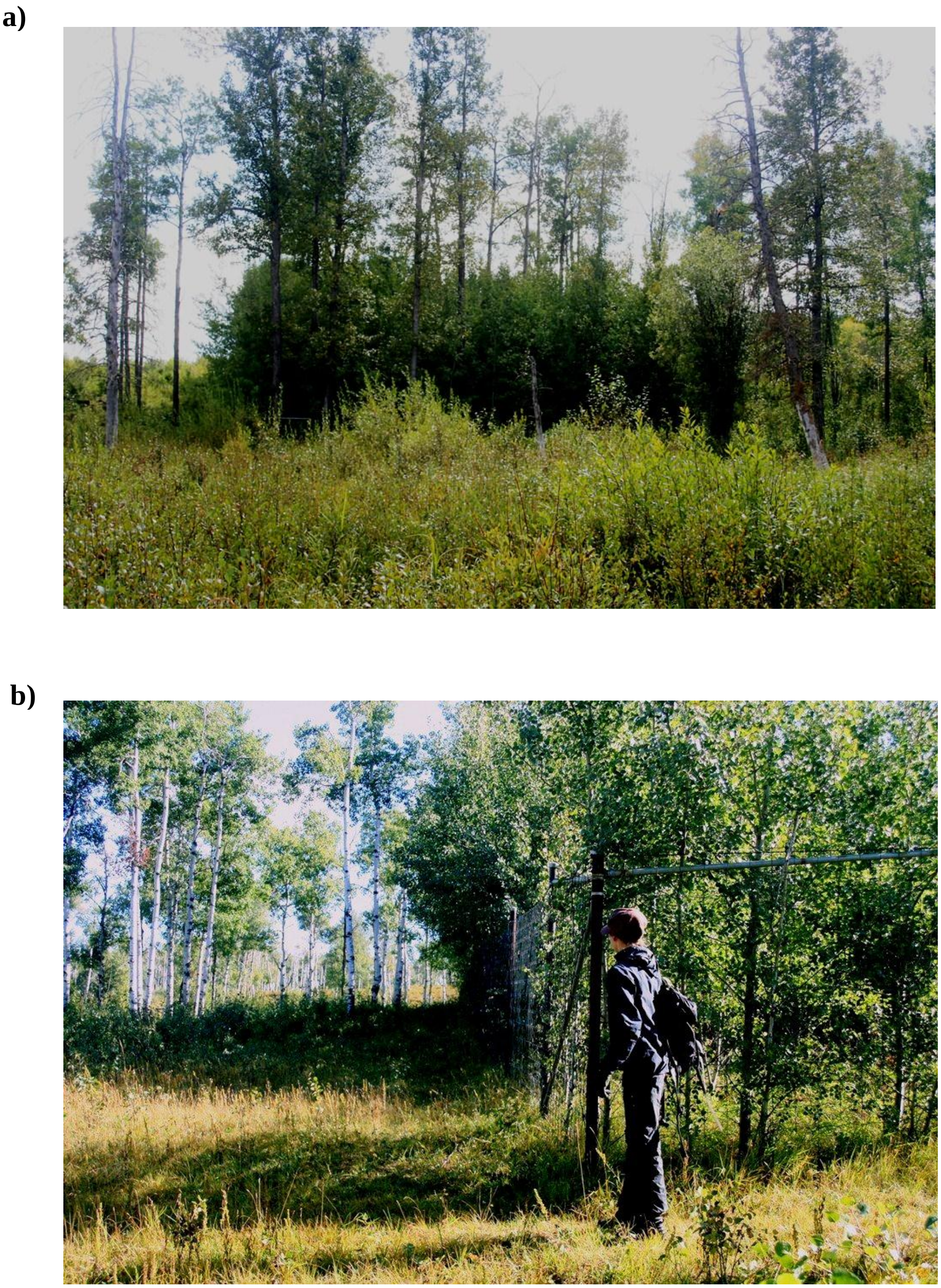

Figure 3.2a-b Photos from the south part of Elk Island National Park illustrating change in shrub structure and composition after 13 years (since 1999) of ungulate exclusion.

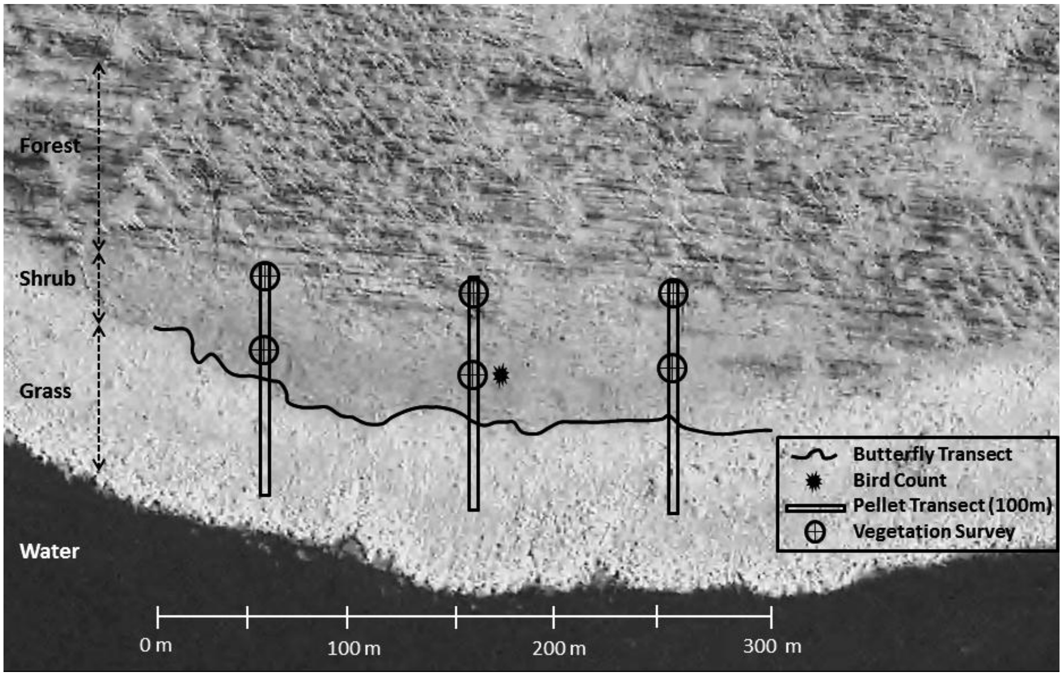

Figure 3.3 Ungulate pellets, vegetation characteristics, and relative abundance of yellow warbler and Canadian tiger swallowtail were quantified at 59 sites. Pellet transects were perpendicular to the wetland thus crossing grass, shrub, and forest zones. Vegetation surveys were conducted in the shrub and forest areas for a maximum 6 surveys per site. Yellow warbler playbacks were performed in the middle of the shrub zone while butterfly transects occurred parallel to the wetland along the grass-shrub interface.

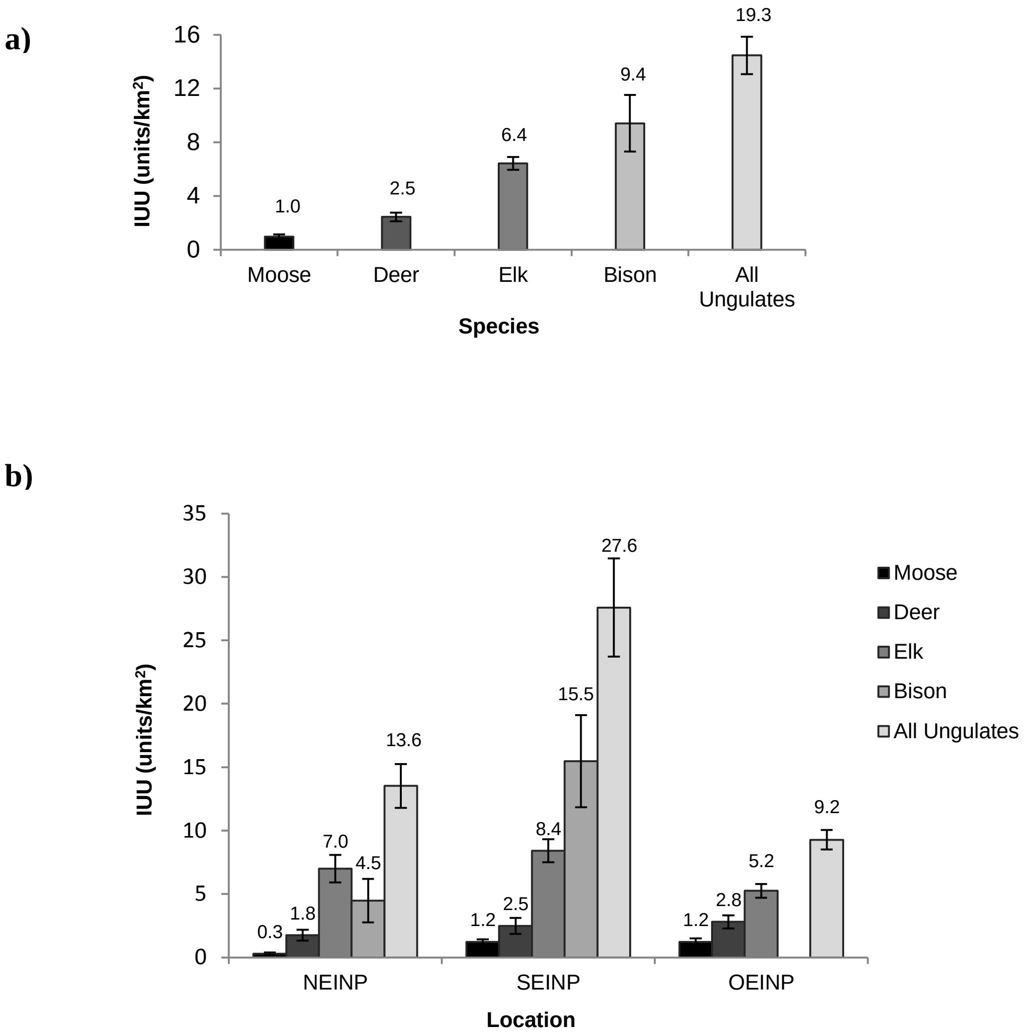

Figure 3.4a-b Average IUU for a) study area and b) by study sites for north Elk Island National Park (NEINP), south Elk Island National Park (SEINP) and outside Elk Island National Park (OEINP).

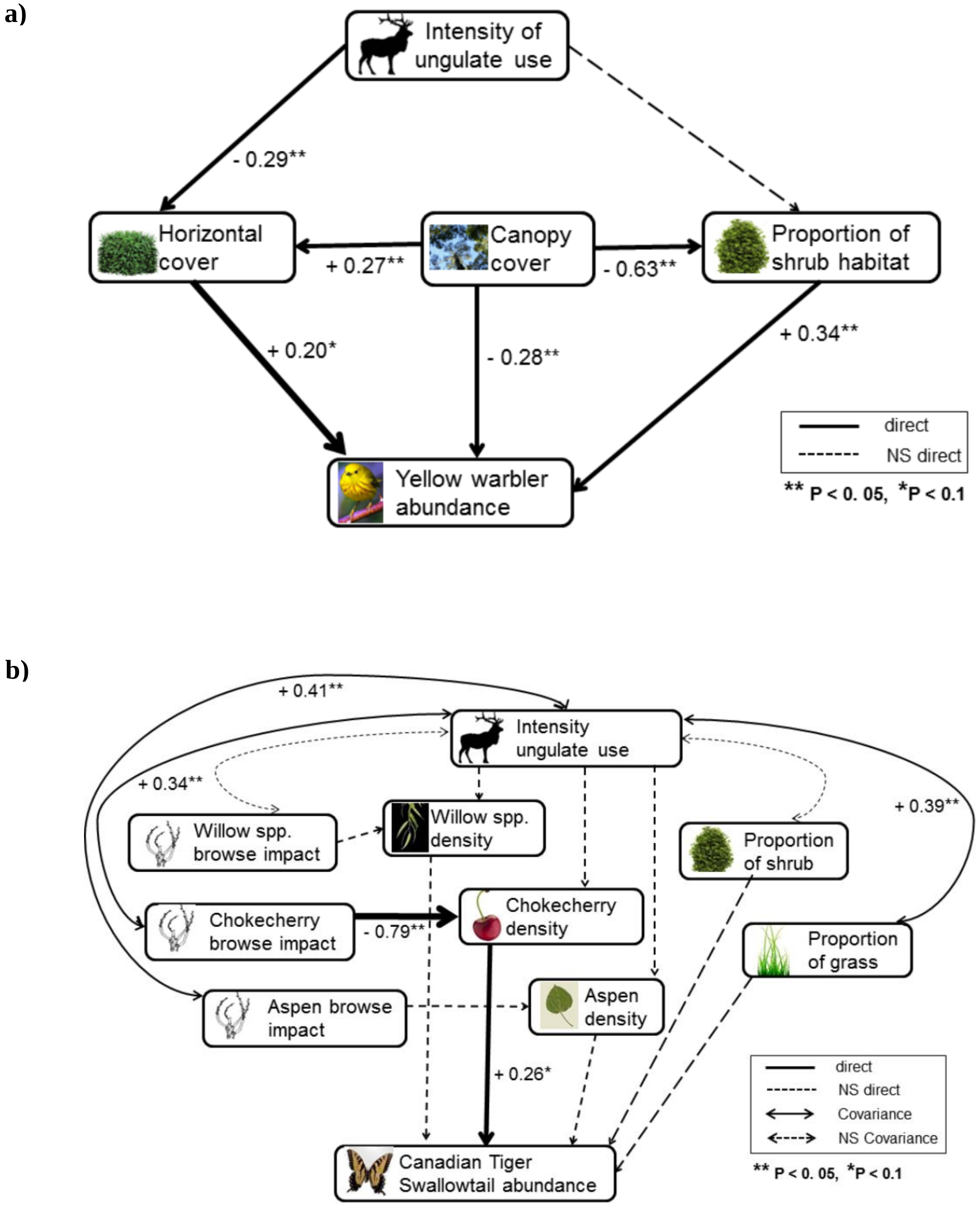

Figure 3.5 Structural Equation Model for a) yellow warbler (*Dendroica petechia*) and b) Canadian tiger swallowtail (*Papilio canadensis*). Thickness of the solid (direct effect) line represents the strength of the standardized path coefficients. A dotted line represents non-significant results**.** * = P <0.1, ** = P <0.05.

CHAPTER 4

GENERAL CONCLUSIONS

Since its establishment in 1906, Elk Island National Park has approached ungulate management by using multiple tools including fire suppression or, conversely, prescribed fires, supplemental feeding, culling and animal relocation (Blyth & Hudson 1987). Despite these management efforts, ungulates remain at some of the highest densities reported in Canada (Blyth & Hudson 1987; Hood & Bayley 2008), driven largely by bison and elk. Although elk are primarily grazers (Gordon 2003), in Elk Island, they used forested habitat with no apparent preference for grass, shrub or forest outside the park. Given that bison are present only inside Elk Island and mostly use grassland habitat, this finding suggests a behaviourally-mediated shift in habitat use by elk in Elk Island towards forested areas, likely due to the dominance of bison (Holsworth 1960; Stewart *et al*. 2002). In turn, elk browsing pressure on shrub understory is likely higher than in mixed-wood boreal forests exempt of bison.

Building on my findings regarding high ungulate numbers within the study area, I addressed the impacts of high intensity of ungulate use (IUU) on lower trophic levels. Classic food chain models (Oksanen et al 1981) predict that primary production is profoundly impacted by interactions among higher trophic levels. However, relationships within a food web depend on whether or not multiple species coexist at each trophic level and how species interact within the food web (Abrams 1993). The presence or absence of single consumers can have large ecosystem effects (Huntly 1991). Systems involving predation by a single predator are more likely to cascade compared to systems with predator diversity where trophic cascades are dampened (Fink & Denno 2004). Predator diversity can enhance food web complexity because predators may feed on each other and on shared prey (Polis, Myers & Holt 1989; Crooks & Soule 1999) thereby relaxing the impact of predation on herbivores and the associated cascading effects on primary producers (McCann, Hastings & Huxel 1998). I addressed cascading effects due to the historical functional loss of wolves, cougars and grizzly bears with humans being the only remaining functional predator. However, counter to 'natural' predation, one of the causes of the trophic cascades demonstrated in this work is that a single remaining 'predator' (human) increased prey (ungulate), thereby resulting in indirect negative impacts on lower trophic levels.

To determine whether cascading effects between ungulates and vegetation result in changes to populations of shrub-dependent yellow warblers and Canadian tiger swallowtails, a negative relationship must first be demonstrated between intensity of ungulate use (IUU) and/or browsing pressure and measured vegetation characteristics (composition and structure). Secondly, a negative relationship must be shown between changes in vegetation and, in this case, yellow warbler and Canadian tiger swallowtail abundances.

I demonstrated an inverse relationship between IUU and horizontal (shrub) cover and a positive relationship between horizontal cover and yellow warbler abundance which revealed negative cascading effect of high ungulate populations. Areas with high ungulate use may limit suitable nest sites and increase predation risk for shrub-nesting bird species (Knopf & Sedgwick 1992). Although covariance paths could be considered biologically plausible they were not fit in SEM models, particularly between IUU and horizontal shrub cover and IUU and proportion of shrub habitat because SEM cannot correlate endogenous and exogenous variables (program STATA/SE-64). It is likely that ungulates affect and are affected by vegetation characteristics including horizontal shrub cover and amount of shrub habitat in a given area. For example, ungulates may deplete a shrub patch before moving to another high forage quality area, which would ultimately create a lag time between heavily browsed areas and IUU. Future work could test this hypothesis by monitoring spatial and temporal fine-scale ungulate movement decisions using GPS telemetry.

A trophic cascade was shown for Canadian tiger swallowtail butterflies where browsing pressure reduced chokecherry density one of their preferred larval host plants. This suggests that Canadian tiger swallowtail larvae are partly dependent on chokecherry populations. More investigation on the mechanism of these responses is needed.

Most reported terrestrial cascades have been observed at small spatial scales that involve invertebrate predators such as spiders and ants (Schmitz, Hamba &

Beckerman 2000). Reports of terrestrial cascades initiated by large mammalian predators are, however, becoming more common. My findings supporting a trophic cascade are similar to other studies that tested the indirect effects of ungulates on other trophic levels (Hebblewhite *et al.* 2005; Ripple & Beschta 2006). It is often unclear, however, whether observed trophic cascades are density-dependent or trait-mediated (Schmitz 2000; Kaufmann, Brodie & Jules 2010). My study demonstrated a true density-dependent response of ungulates due to the absence of functional top predators in the mixed-wood boreal forest.

The shrub understory in the mixed-wood boreal forest of this study is comprised of several species that predominantly reproduce vegetatively including aspen (Myking *et al*. 2011), chokecherry (Schier 1983), and beaked hazelnut (Maini & Horton 1966). Although ungulate browsing can negatively impact both vegetative and sexual reproducing plant species, seed production is considered more nutrient-demanding than vegetative reproduction (Watson 1984), therefore ramet production appears to be the most efficient way of achieving high reproductive success (Eriksson 1989). Furthermore, long term plant densities may exceed those of plants that depend on seed dispersal, because clonal plants can remain in the ground for decades and are not dependent on variations in wind, pollinators, animal vectors and other abiotic and biotic factors required for propagation (Bergman 2001). All of these factors suggest that plants that reproduce vegetatively would be more resilient to browsing pressure than sexually reproducing plant species. Despite the resiliency of shrub understory, coupled with the biological diversity of the study system (Bork, Hudson & Bailey 1997; White, Olmsted & Kay 1998), I found a species-level cascade where vegetation structure and composition played a key role.

Interactions within a food web are complex. Given that ecosystems today are rapidly changing due to direct and indirect effects of humans, research is needed to better understand and predict their consequences. Understanding the effect of overabundant ungulates on plant communities and subsequently other trophic levels is critical for management because manipulations of ungulate numbers is a common wildlife management tool used to manage ecosystems. By better understanding trophic interactions, management can better target ecosystem function rather than the management of a single species or trophic level.

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APPENDIX I

Results from a literature review of defecation rates of *Alces alces* (moose), *Odocoileus spp* (deer), *Cervus elaphus* (elk) and *Bison bison* (bison).

Species	Defecation rate	Pen/ wild/acre	Method	N	Habitat/ Diet	Season	Location	Authours
Alces alces	17.64	Penned (dimensions unknown) Kenai moose research center	24 hour tracking	8	Unknown	Feb/March 1975	Alaska	Franzmann, Arneson & Oldermeyer 1976
Alces alces	12.7	Free ranging	Driven slowly in unbrowsed sites and then backtracked after periods varying from 23-96 h	16	Fir/hobblebush/ virburnum/maple birch/aspen/ birch	Jan/March 1982-84	Quebec	Joyal & Ricard 1986
Alces alces	13.89	Free ranging	Aerial surveys and pellet counts	194	Pine/birch/aspen/willow	Winter	Sweden	Ronnegard *et al.* 2008
Alces alces	18.43	Free ranging	Tracked radiocollared moose and collected pellets in a 24 hour period	58	Pine/birch	Winter 1984-87	Norway	Andersen & Hjeljord 1992
Alces alces	16.7	Pens	Known # of moose/cleared pellet transects, then counted	7	MRC	Oct-May	Alaska	Oldermeyer & Franzmann
Bison bison	9	9000 ha enclosure	Observation/normalized to avoid time of day biases	~7	70% grasses, 20% forbs, 10% wood	May-Sept 1978-82	Montana	Belovsky & Slade 1986
Odocoileus hemionus	15.21	90-160 acres	Known deer and pellet counts	----	Good browse	Winter 1951-55	Colorado	Rogers 1958
Odocoileus spp	12.7	741 acres	----	172	Depleted winter range	Aug-Oct	Utah	McCain (1948) using Rasmussen & Doman data 1943
Odocoileus spp	12	Pens	----	36	----	Feb/ March	----	Eberhardt and Vanelten 1956
Odocoileus hemionus	13.2	2-4 acres	----	320	Pine/ Juniper	Winter	Colorado	Mckean 1965
Odocoileus spp	34	Free ranging	Radio-collared/observation	7	Conifer/deciduous	Winter	Minnesota	Rogers 1987
Odocoileus spp	31.8	Free ranging	Radio-collared/observation	4	Confier/deciduous	Oct 15-April 30	Georgia	Sawyer 1990
Odocoileus virginianus	19.8	9000 ha enclosure	Observation/ Normalized to avoid time of day biases	----	70% grasses, 20% forbs, 10% wood	May-Sept 1978-83	Montana	Belovsky & Slade 1987
Odocoileus hemionus	14.9	9000 ha enclosure	Observation/ Normalized to avoid time of day biases	----	70% grasses, 20% forbs, 10% wood	May-Sept 1978-84	Montana	Belovsky & Slade 1988
Odocoileus hemionus	14.9	Pasture	----	3-40	Winter browse	Over winter	Colorado	Rogers *et al.* 1958
Odocoileus hemionus	14.7	Pens	----	30	Native forage	Various	Utah	Smith 1964
Cervus elaphus	18.8	9000 ha enclosure	Observation/ Normalized to avoid time of day biases	~35	70% grasses, 20% forbs, 10% wood	May-Sept 1978-82	Montana	Belovsky & Slade 1989
Cervus elaphus	12.52	9.16 acre enclosure	Known # of elk and pellet counts	10	Wheatgrass, blue grama, blk dropseed etc.	Feb-June 1964	Arizona	Neff *et al.* 1965
Cervus elaphus	11	----	----	10	----	3 days	Montana	Morris (in Neff 1968)

APPENDIX II

A priori candidate model selection for determining IUU

Competing sets of models included location models, habitat models and combined location-habitat models. Location was divided into four treatments including north Elk Island National Park, south Elk Island National Park, burned areas in Elk Island and areas outside of Elk Island. Because north and south units of Elk Island are both fenced and are separated by a major highway, I considered these areas as two separate locations with potential differences in IUU. Areas within the park that are managed by prescribed burning were included as a separate treatment due to potential differences in forage quality and palatability for ungulates (Hood *et al.* 2007) and vegetation structure and composition (Bork, Hudson & Bailey 1997) compared to all other areas. With the exception of bison models, all models that included location variables were compared to outside Elk Island. Because bison are limited to inside Elk Island, I used north Elk Island to compare against other locations (south Elk Island and burned areas in Elk Island).

Vegetation patterns were categorized as grassland, shrub and forest habitat along wetlands to delineate patterns of forage material for moose, deer, elk and bison.

Moose and deer

Competing sets of models for moose and deer included location models (n = 1) habitat models (n = 4) and combined location-habitat models (n = 4). I included only shrub and/or forest habitat variables in these models based on moose and deer foraging requirements. Because moose and deer are browsers, I hypothesized that increases in shrub and/or forest (shrub understory) habitat would increase the intensity of moose and deer use.

Elk

Competing sets of models for elk included location models (n = 1), habitat models (n = 7) and combined location-habitat models (n = 7). Combinations of grassland, shrub and forest habitat were included in the elk models because, although elk are predominantly grazers (Gordon 2003), they have been shown to browse (Holsworth 1960; Hebblewhite *et al.* 2005). Therefore, I expected elk use to be potentially influenced by proportion of grassland, shrub and forest habitat. Furthermore, possible competition with bison for grassland in winter, when food is scarce, may also influence habitat use by elk, (Holsworth 1960; Stewart *et al*. 2002), shifting elk into nearby shrub and forest areas.

Bison

Competing sets of models for bison included location models (n = 1), habitat models (n = 7) and combined location-habitat models (n = 7). Bison are primarily grazers and were expected to be influenced most by proportion of grassland. Proportion of shrub habitat was also included as a vegetation variable because bison have been shown to browse (Holsworth 1960; Hood & Bayley 2008). Although forest understory is comprised of shrub, bison are primarily found in forested areas along bison trails (Holsworth 1960) in Elk Island and are therefore in transit from one habitat patch to another. Furthermore, shrub habitat is more easily accessible to large-bodied bison compared to forested areas so I did not expect proportion of forest habitat to influence the intensity of bison use.

Table 1 *A priori* candidate ΔAICc Explained Generalized Linear Models (GLM) for determining intensity of moose use. Model description, number of estimated parameters (K), model log-likelihood (LL), Akaike's Information Criterion (AIC), small sample size corrected AIC (AICc), AICc difference (ΔAICc), AIC weight (w), and % deviance explained are shown.

	Model Description	**K**	**LL**	**AIC**	**AICc**	**ΔAICc**	**exp(-1/2Ai)**	**w**	**% Deviance Explained**
	null model	1	-50.17	102.3	102.4	3.8	0.15	0.03	0
a	prop shrub	2	-48.27	100.55	100.9	2.2	0.34	0.07	3.7
b	prop_shrb prop_frst	3	-46.42	98.84	99.5	0.8	0.67	0.14	7.4
c	prop_shrb prop_frst prop_shrb*prop_frst	4	-45.3	98.62	99.7	1.0	0.59	0.12	9.6
d	prop_frst	2	-50.13	104.25	104.6	5.9	0.05	0.01	0.05
e*	location (OEINP, BEINP,SEINP)	4	-44.79	97.58	98.7	0.0	1.00	0.21	10.7
f	prop_shrb location	5	-44.48	98.96	100.7	2.0	0.37	0.08	11.3
g	prop_shrb prop_frst location	6	-42.30	96.60	99.1	0.4	0.83	0.17	15.6
h	prop_shrb prop_frst prop_shrb*prop_frst location	7	-41.95	97.90	101.3	2.6	0.27	0.06	16.4
i	prop_frst location	5	-44.00	98.01	99.7	1.0	0.60	0.12	12.3

* Best model

Table 2 *A priori* candidate ΔAICc Generalized Linear Models (GLM) for determining intensity of deer use. Model description, number of estimated parameters (K), model log-likelihood (LL), Akaike's Information Criterion (AIC), small sample size corrected AIC (AICc), AICc difference (ΔAICc), AIC weight (w), and % deviance explained are shown.

	Model Description	**K**	**LL**	**AIC**	**AICc**	**ΔAICc**	**exp(-1/2Ai)**	**w**	**% Deviance Explained**
*	null model	1	-55.19	112.39	112.5	0.0	1.00	0.38	0
a	prop shrub	2	-55.19	114.38	114.7	2.2	0.33	0.13	0.0
b	prop_shrb prop_frst	3	-55.08	116.17	116.8	4.3	0.11	0.04	0.2
c	prop_shrb prop_frst prop_shrb*prop_frst	4	-54.16	116.32	117.4	4.9	0.08	0.03	1.9
d	prop_frst	2	-55.15	114.30	114.6	2.1	0.35	0.13	0.1
e	location	4	-52.68	113.37	114.5	2.0	0.37	0.14	4.5
f	prop_shrb location	5	-52.42	114.8	116.6	4.1	0.13	0.05	5.0
g	prop_shrb prop_frst location	6	-52.36	116.72	119.2	6.7	0.04	0.01	5.1
h	prop_shrb prop_frst prop_shrb*prop_frst location	7	-50.33	114.66	118.1	5.6	0.06	0.02	8.8
i	prop_frst location	5	-52.44	114.88	116.6	4.1	0.13	0.05	5.0

* Best model

Table 3 *A priori* candidate ΔAICc Generalized Linear Models (GLM) for determining intensity of elk use. Model description, number of estimated parameters (K), model log-likelihood (LL), Akaike's Information Criterion (AIC), small sample size corrected AIC (AICc), AICc difference (ΔAICc), AIC weight (w), and % deviance explained are shown.

	Model Description	**K**	**LL**	**AIC**	**AICc**	**ΔAICc**	**exp(-1/2Ai)**	**w**	**% Deviance Explained**
	null model	1	-59.55	121.10	121.2	19.8	0.00	0.00	0
a	prop grass	2	-58.08	120.16	120.5	19.0	0.00	0.00	2.5
b	prop grass propshrub	3	-56.49	118.99	119.6	18.2	0.00	0.00	5.1
c	prop grass prop_shrub prop_grass_shrub	4	-56.44	120.87	122.0	20.5	0.00	0.00	5.2
d	prop_shrub	2	-58.48	120.96	121.3	19.8	0.00	0.00	1.8
e	prop_shrub prop_frst	3	-56.15	118.30	119.0	17.5	0.00	0.00	5.7
f	prop shrub prop_frst prop_shrb_frst	4	-54.75	117.51	118.6	17.2	0.00	0.00	8.1
g	prop_forest	2	-56.16	116.32	116.6	15.2	0.00	0.00	5.7
h	location	4	-55.87	119.74	120.9	19.4	0.00	0.00	6.2
i	prop grass location	5	-50.05	110.09	111.8	10.4	0.01	0.00	16.0
j	prop_grass prop_shrub location	6	-45.00	102.00	104.5	3.0	0.22	0.09	24.4
k	prop_grass prop_shrub prop_grass_shrub location	7	-44.93	103.86	107.3	5.8	0.05	0.02	24.6
l	prop_shrub location	5	-53.87	117.74	119.5	18.0	0.00	0.00	9.5
m	prop_shrub prop_frst location	6	-44.63	101.26	103.7	2.3	0.32	0.13	25.1
n	prop shrub prop_frst prop_shrb_frst location	7	-42.22	98.45	101.8	0.4	0.82	0.34	29.1
o*	prop_forest location	5	-44.87	99.74	101.4	0.0	1.00	0.41	24.7

* Best model

Table 4 *A priori* candidate ΔAICc Generalized Linear Models (GLM) for determining intensity of bison use. Model description, number of estimated parameters (K), model log-likelihood (LL), Akaike's Information Criterion (AIC), small sample size corrected AIC (AICc), AICc difference (ΔAICc), AIC weight (w), and % deviance explained are shown.

	Model Description	K	LL	**AIC**	**AICc**	**ΔAICc**	**exp(-1/2Ai)**	**w**	**% Deviance Explained**
	null model	1	-57.93	117.86	118.0	26.0	0.00	0.00	0.0
a	prop grass	2	-49.30	102.61	102.9	11.0	0.00	0.00	14.9
b	prop_grass prop_shrub	3	-46.68	99.37	100.0	8.0	0.02	0.01	19.4
c	prop_grass prop_shrub prop_grass_shrub	4	-46.66	101.32	102.4	10.5	0.01	0.00	19.5
d	prop_shrub	2	-57.06	118.14	118.4	26.5	0.00	0.00	1.5
e	location (compared to NEINP)	3	-49.22	104.44	105.1	13.1	0.00	0.00	15.1
f	prop grass location	4	-41.72	91.45	92.6	0.6	0.74	0.27	28.0
g*	prop_grass prop_shrub location	5	-40.13	90.25	92.0	0.0	1.00	0.36	30.8
h	prop_grass prop_shrub prop_grass_shrub location	6	-38.78	89.56	92.0	0.1	0.97	0.35	33.1
i	prop_shrub location	4	-49.19	106.37	107.5	15.5	0.00	0.00	15.1

* Best model

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