Evaluating trade-offs: the effects of foraging, biting flies, and footing on wood bison (*Bison bison athabascae*) habitat use

by

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Abstract

Understanding the distribution of forage is important in predicting the distribution, habitat use (behaviour), movements, and fitness-related traits of large, grazing ungulates. Although this bottom-up perspective provides a foundation for understanding habitat supply and thus nutrition, foraging decisions are also affected by among other things trade-offs with energy expenditure and predation risk. This includes energy expenditures associate with thermal stress, deep snow, and predation from biting flies and larger carnivores. The objectives of this study were to quantify trade-offs between summer forage availability for wood bison with that of biting fly abundance representing a form of predation, and soil firmness which affects movement and thus energy budgets and carnivore predation risk. Specifically, trade-offs were assessed for three habitat types and one landscape feature at nine replicate sites (*n* = 36 sites) utilized by bison in the Ronald Lake area of northeast Alberta, Canada in the summer of 2016. At each site dung counts (summer vs. winter) were quantified in belt transects to measure bison use, forage measured in quadrats as dry biomass of graminoids, soil firmness quantified along transects with a penetrometer, and biting flies trapped and netted throughout the summer. Structural equation models were used to relate summer and winter use of habitats by bison as dung counts with that of forage, footing, and biting flies. Graminoid availability was not related to summer wood bison use, but was related positively to winter use when biting insects were absent and footing was firm (frozen). Although summer bison use was not related to graminoid biomass, it was negatively related to biting fly abundance and positively related to sites with more firm footing. These results were consistent with diet and habitat selection studies of wood bison with summer diets generally more diverse than that of winter diets. Studies of bison habitat use in relation to forage are often descriptive and rarely quantitative, often reporting the effects between a single factor, either forage quality/quantity or land-cover types (vegetation types). This study provides a more comprehensive understanding of the factors that contribute to the dynamic nature of wood bison behaviour, habitat use, and fitness-related costs and benefits. A greater understanding of the factors and trade-offs influencing and limiting habitat use is fundamental to guiding the management and conservation of threatened bison populations, including the Ronald Lake herd that overlaps its territory with that of oil sand deposits.

Preface

This thesis is the original work of Robert Belanger. The aim of this thesis is to investigate the mechanisms, processes, and trade-offs influencing wood bison (*Bison bison athabascae*) habitat use in northeast Alberta, Canada. Land-cover data was provided by Ducks Unlimited Canada and were used for classifying habitat types and locating both study area and sample sites. I contributed to the concept formation and study design, and led work on field data collection, data analysis, and manuscript composition. Scott E. Nielsen and Mark A. Edwards contributed to the concept formation, study design, data analysis, and thesis edits. Lu N. Carbyn contributed to concept formation and study design.

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Chapter 1: General introduction

Habitat selection is a hierarchical, behavioural process by which animals select resources within a landscape, thereby affecting acquisition and competition for food and mates, reproductive success, and predator avoidance (Schaefer & Messier 1995; Rettie & Messier 2000; Dussault et al. 2005; Loiser et al. 2015; Long et al. 2016). Animal behavioural and functional responses are influenced by spatial and temporal variability in resources that relate to trade-offs associated with abiotic-biotic interactions, which are most apparent when resources are limiting (forage) or fitness-costs are high (predation) (Mysterud & Ims 1998; Godvik et al. 2009; Hebblewhite & Merrill 2009; Owen-Smith et al. 2010). Based on energy maximization principles within a heterogeneous landscape, we expect the distribution of large, grazing ungulates to match nutritious forage resources (Hanley 1982; Bergman et al. 2001; Fortin et al. 2003; Zweifel-Schielly et al. 2009; Wilmshurst et al. 2000; Beyar et al. 2010; Newmark & Rickart 2013; Shoenecker et al. 2015; Dupke et al. 2017). While attaining forage resources may be critical for meeting nutritional needs, foraging decisions by animals may be only one of several factors, including predation risk and energy budgets, which affect animal behaviour, habitat use and distributions, and ultimately fitness (Hanley 1982; Canon et al. 1987; Brown et al. 1999; Aublet & Festa-Bianchet 2009; Ahmad et al. 2016; Dupke et al. 2017). Examining the processes and trade-offs related to fitness is therefore important to understanding animal behaviour and habitat use, which is beneficial for the successful management of populations (Mysterud & Ims 1998; Brow et al 1999; Dussault et al. 2004; Schoenecker et al. 2015; Steenweg 2016; Yan et al 2016).

Much is known regarding habitat and resource selection of animals, where a myriad of studies has examined the effects of land-cover attributes and scale on the spatial and temporal distributions of animals (Boyce 2006; Hebblewhite et al. 2008; Zweifel-Schielly et al 2009; Owen-Smith et al. 2010; Shoenecker et al. 2015; Steenweg 2016). While models of habitat and resource selection can provide a basis for the conservation and management of populations, attributes in these models are rarely quantified resulting in speculation about the operative processes influencing the health and survival of animals (Brown et al. 1999; Joly 2008; Theuerkauf & Rouys 2008; Owe-Smith 2014: Schoenecker et al. 2015; Tan et al. 2015; Courbin et al 2017). Identifying, quantifying, and coupling land-cover attributes with biological and environmental processes can assist in more accurately modeling biotic-abiotic interactions and spatial and temporal distributions of animals. A more comprehensive understanding of habitat use can provide robust rationale for the conservation and management of habitats and resources within populations ranges', especially for those species that are rare or endangered, or whose habitats limit populations due to disturbance, fragmentation, and loss.

Biological and environmental factors influencing animal habitat use are generally regulated by bottom-up (primary production) or top-down (predation) processes. Trade-offs are common where predation risk or predator avoidance limits use of foraging areas composed of high quality/quantity forage and/or increase use of areas where prey are less vulnerable to predators (Canon et al. 1987; Fortin et al. 2002; Dussault et al. 2005; Brown et al. 2009; Hebblewhite & Merrill 2009; Witter et al. 2012: Dupke et al.2017). Behavioural responses to trade-offs in foraging and predations risk can have profound effects on animal distributions and habitat selection, such as avoidance of valleys and meadows where forage resources are abundant, but predation risk is high, and conversely selection for mountain ridges where risk of predation is low (Sih 1980; Hamel & Cote 2007; Fortin et al. 2009; Zweifel-Schielly et al. 2009; Newmare & Richart 2013; Schoenecker et al. 2015; Yan et al. 2016; Baruzzi et al. 2017).

Underlying mechanisms that affect habitat use include forage and water availability (Later & Gates 1991; Fortin et al. 2003; Acebes et al. 2013; Newmark & Rickart 2013; Long et al. 2014; Long et al. 2016; Ringinos 2016), predation risk (Brown 1999: Brown et al. 1999; Hammel & Cote 2007; Hebblewhite & Merrill 2009), and environmental components such as thermal stress (Mysterud & Ostby 1999: van beest et al. 2012; Dussault et al. 2004; Aublet & Festa-Bianchet 2009), and snow depth (Schaefer & Messier 1995; Mysterud et al. 1997; Brown 1999; Hebblewhite & Merrill 2009; Robinson & Merrill 2012). Examples of fitness-related trade-offs are often found in studies of large, grazing ungulates. For instance, elk (*Cervus canadensis*) and mountain goats (*Oreamnos americanus*) limiting use of areas of high forage quantity/quality to mediate predation risk by wolves by using areas of higher elevation (Fortin et al. 2002; Richard et al. 2014). Similarly, caribou (*Rangifer tarandus*) reduce time spent foraging to mediate predation by biting flies by seeking snow patches, open tundra, and hill-tops during summer months (Helle et al. 1992; Toupin 1996; Hagemoen & Reimers 2002; Rolf & Reimers 2000). Likewise, moose (*Alces alces*) and elk decrease time spent in open areas of higher forage availability during summer months to mediate thermal stress by using closed canopy, conifer forests (Dussault et al. 2004; van Beest et al. 2012; Mysterud & Ostby 1999). White-tail deer (*Odocoileus virginianus*), muskoxen (*Ovibos moschatus*), moose, caribou, and mountain goats adjust their forage preference and behaviour to mediate locomotive and energetic costs, and predation risk by diversifying foraging strategies and limiting their travel through areas of deeper snow (Pruitt 1960; Stardom 1977; Schmitz 1991; Schaefer & Messier 1995; Mysterud & Bjornsen 1997; Poole & Mowat 2005; Robinson & Merrill 2012; Richard et al. 2014; Courbin et al. 2017). Overall, animals use different habitat and feature types due to relationships with fitness by counterbalancing energy gains (forage) with predation risk and energy costs (Hanley 1982; Pepin et al. 2009; Shepard et al. 2013; Long et al. 2016). Better understanding of the processes and mechanisms that govern habitat use can benefit ecologists by better discerning animal behavioural and functional responses, and for land-use managers who are tasked with species-specific land-use planning to maintain and/or maximize populations.

Wood bison (*Bison bison athabascae*) are a large grazing ungulate (Knapp et al. 1999; Mendoza & Palmqvist 2008), and a close relative to European (*Bison. b. bonasus*), and plains (*Bison b. bison*) bison that once numbered in the tens of millions on the great plains of North America until the turn of the 20th century (SARA 2017). Wild and managed extant occurrences of wood bison are endemic to areas north of their plains relatives in the northern regions of the provinces and territories of Canada and the state of Alaska, and are classified as near threatened internationally (IUCN 2017), and threatened in Canada (SARA 2017). Bison diet and habitat selection have been well studied, with forage availability identified as a significant factor limiting bison populations, and a primary factor determining bison distributions and habitat use (Chowns 1987; Reynolds 1987; Larter & Gates 1991; Carbyn et al. 1993; Fortin et al. 2002; Fortin et al. 2009; Strong & Gates 2009; Jung 2015; Merkel et al. 2015; Steenweg et al. 2016). While many studies address bison habitat selection relative to forage, there is a lack of focus on trade-offs associated with foraging, and other mechanisms that may affect bison habitat use, including factors that may limit use of areas with high forage quality and quantity such as predation risk and energy costs (Carbyn & Trottier 1987; Theuerkauf & Rouys 2008). Comprehensive studies addressing top-down, bottom-up, biological and environmental factors regarding bison habitat use are rare and are needed to understand the factors influencing and limiting bison populations.

Wood bison, like other boreal ungulates, likely face similar trade-offs relative to their energy demands via foraging, such as predation risk by wolves and biting flies, thermal stress, and snow depth. While studies have speculated that bison are affected by factors other than forage, they have rarely been empirically quantified (Berezanski 1986; Morgan 1987; McMillian 2000; Fortin et al. 2009). A more comprehensive analysis of the mechanisms regulating bison habitat use is needed to improve our understanding of bison behavioural and functional responses to biological and environmental stimuli which in-turn affect the spatial and temporal distribution of individuals and populations. Progressive and comprehensive knowledge of the resources and habitat types and features needed for the maintenance and survival of wood bison populations is essential for the conservation and management of this species.

In this thesis I examine patterns in bison summer habitat use as it relates to the bottom-up factor of forage availability and two factors that may limit summer use of high forage value areas: biting fly activity and soil/ground firmness or footing. Insect harassment can negatively affect health and survival (Helle & Tarvainen 1984; Toupin et al. 1996; Rolf & Reimers 2002), while footing, like that of snow depth, can limit movement and thus positively affect predation risk by large carnivores, and negatively affect energy budgets (Pruitt 1960; Parker et al. 1984; Fancy & White 1986; Shepard et al. 2013). The remainder of thesis is comprised of a single 'data' chapter (Chapter 2) that relates to field work conducted to address the above question, a conclusion chapter that relates this work to management questions and future research needs, and lastly a supplemental appendix that supports the research. The style used in this thesis reflects formatting requirements for the Journal of Mammal Research.

Chapter 2: Evaluating the trade-offs influencing wood bison habitat use

1.0 Introduction

Wood bison are a large, grazing ruminant (Knapp et al. 1999; Mendoza & Palmqvist 2008) whose summer diets are diverse being composed of graminoids (primarily), forbs, and shrubs with winter diets being primarily graminoids, particularly sedges (Jung 2015; Fortin et al. 2003; Strong & Gates 2009; Bergman et al. 2015; Steenweg et al. 2016; Leonard et al. 2017). Numerous ecological studies of bison have focused on the diversity and seasonality of diets (Reynolds et al. 1987; Campbell & Hinks 1983; Larter & Gates 1991; Strong & Gates 2009; Bergmann et al. 2015; Jung 2015; Lenard et al. 2017), with seasonal selection of vegetation-cover types quantified during different seasons and life-stages (Schoenecker et al 2015; Tan et al. 2015; DeMars et al. 2016). Habitat selection of the Ronald Lake bison herd (Tan et al. 2015; DeMars et al. 2016) show results that are consistent with studies and observations of bison where sedge marshes are selected in both summer and winter months relative to other land-cover types (Chowns 1987; Larter & Gates 1991; Fortin et al. 2003; Jung 2015; Merkel et al. 2015). However, habitat selection is substantially lower for sedge marshes during summer compared to winter with a 1.5 to 4-fold decrease in use during summer from winter. The observed decrease in selection leads to complementary hypotheses: 1) forage availability and nutrition in sedge marshes, relative to other land-cover types, is greater during winter months (Larter & Gates 1991; Bergmann et al. 2015; Leonard et al. 2017), thus bison show greater selection for sedge marshes in winter, and/or 2) non-forage related factors contribute to declines in summer selection of sedge marshes, including availability of more nutritious forage resources (forbs, shrubs) (Larter & Gates 1991; Leonard et al. 2017) in other land-cover types (2a) and/or other mechanism(s), such as increased predation risk, contributing to lower use of sedge marshes (2b). Here, I evaluate these hypotheses by investigating bison use of sedge marshes, deciduous forests, jack pine forests, and an esker (prominent, high elevation geological feature). I examine these land-cover and feature types to contrast forage availability, predation risk by biting flies and large carnivores, and locomotion as mechanisms of habitat use within the Ronald Lake bison herd in northeast Alberta, Canada (Fig. 2.1). By examining this question, we will better understand factors affecting bison habitat use, thus providing insight into the possible mechanisms contributing to differences in habitat use between two seasonal extremes.

Ungulate foraging decisions are often discussed in the context of trade-offs, where predation risk and energy costs associated with locomotion and thermal conditions affect foraging behaviour, habitat use, and general spatial and temporal changes in their distributions. (Brown 1999; Fortin et al. 2001; Dussault et al. 2005; Hebblewhite & Merrill 2009; Zweifel-Schielly et al. 2009; Ahmad et al. 2015). While much is known regarding bison habitat use in the context of forage availability and nutrition, less is known regarding the trade-offs associated with foraging and abiotic and biotic stimuli, including predation and energetic costs that may affect bison foraging behaviour.

Wetlands in the boreal, particularly marshes, are areas of high primary productivity during summer months, where graminoids contribute a substantial portion of annual biomass (Gorham 1974). This productivity can be attributed to elevated levels of soil moisture content (Gorham 1974; Briggs & Knapp 1995; Duckworth et al. 2010). Despite contributing to considerable amounts of primary productivity, these wetlands also significantly shape other ecosystem functions, processes, and taxa, including provisioning of breeding sites and habitats for the lifecycles of many insects, including those of biting flies that prey on mammals for blood-meals (Danks 1981; Lewis 1987; Kozlov et al. 2005). Wetlands and graminoids are therefore important aspects of habitat supply and forage availability for bison. However, summer use of these areas may be limited due to 1) harassment by biting flies which may negatively affect the health and energy balance of bison, and 2) soft soil conditions which may limit the movement of bison thus affecting their energy balance and predation risk by wolves. To balance the trade-offs associated with these factors, like other ungulates, bison may 1) seek areas where alternate forage opportunities exist, such as other graminoids, forbs, and shrubs, 2) seek areas of refugia from biting flies, such as hill-tops and areas of lower insect activity and abundance, and 3) seek areas of firmer ground where energy costs associated with movement are lessened, and where bison are more readily able to defend themselves from large carnivores such as wolves. In this study I investigate the effects of forage availability, biting fly activity, and soil softness/firmness, or footing, on bison summer habitat use for the Ronald Lake bison herd. Forage resources may be important regarding bottom-up effects of bison habitat use. However, a more comprehensive understanding of bison summer habitat use is needed to address multiple factors and processes limiting bison habitat use/selection.

Biting, blood-sucking flies from the order Diptera and families Simuliidae, Culicidae, Ceratopogonidae, and Tabanidae are some the most common and widespread biting flies in boreal environments (Lewis 1987; Kozlov et al. 2005; Krecmar 2005). Predation by biting flies have been shown to affect ungulate behaviour, health, distribution and migration patterns during summer and calving seasons (Helle & Tarvainen 1984; Morgan 1987; Thomas and Kiliaan 1990; Folstad et al. 1991; Toupin et al. 1996; Witter et al 2012 & 2014). Because of harassment by biting flies, ungulates reduce time foraging, while also expending more energy in response to irritation (harassment) by flies. Consequences of this harassment are blood and net energy loss, and decreased health and survival of adults and calves (Ralley 1985; Walsh et al. 1992; Morschel & Klein 1997; Hagemoen & Reimers 2002; Witter et al. 2014). To avoid or reduce predation by flies, animals seek habitat types and features including open tundra, hill-tops, and snow patches (Rolf & Reimers 2002), and time their migrations from areas of high insect load to areas of low insect load, including movements from inland to coastal areas, and lowlands to elevated areas (Folstad et al. 1991).

Observational studies of bison behaviour during summer months show that bison are affected by biting flies (Morgan 1987; Carbyn et al. 1993; McMillan et al. 2000), although quantitative studies of biting fly activity and/or abundance in relation to bison habitat use are rare. During times of high biting fly activity, bison spend less time foraging, more time lying, and more time using wallows to thwart the effects of biting flies (Morgan 1987; McMillan et al. 2000). Biting flies may negatively affect bison health and energy budgets, and may therefore be a key factor regarding bison foraging decisions, health, and habitat use. In contrast to summer, during winter the distribution and depth of snow affects ungulate foraging decisions, movement, distributions, and negatively affects energy budgets, and positively affects predation risk (Mysterud et al. 1997; Pool & Mowat 2005; Pepin et al. 2009; Robinson & Merrill 2012; Courbin et al. 2017).

Like that of snow cover, during summer months variation in soil softness/firmness may yield similar energy costs and risk to predation, and thus constrain foraging opportunities in highly productive areas such as wetlands and marshes where primary production is high (Murray 1991; Duckworth et al. 2010; Shepard et al. 2013). This has not, however, been quantitatively examined for wood bison. The objective of this study is to test trade-off hypotheses in the context of forage availability, predation risk by biting flies, and locomotive, energetic costs associated with abiotic elements of terrain affecting footing which may further relate to predation risk, during the summer period when forage is widely available. Specifically, I quantify wood bison habitat use with dung counts, summer forage (graminoid) biomass, biting fly abundance, and soil firmness/footing in three habitat types and one landscape feature for the Ronald Lake bison herd in northeast Alberta, Canada. This examination will improve our knowledge of the factors regulating bison foraging decisions and use of land-cover types important for habitat supply (forage).

2.0 Methods

2.1 Study area

The study area was selected based on the known distribution of bison in the Ronald Lake area (Tan et al. 2015; DeMars et al. 2016) in northeast Alberta, Canada approximately 15 km south of Wood Buffalo National Park (Fig. 2.1). I selected sampling sites within a 12-km radius of Ronald Lake and covering ~452 km^2 of boreal forest (57°58’ N, 111°40’ W). The area of Ronald Lake marks the approximate center of the herds’ known home-ranges which extend ~40 km to the north and south and ~30 km and ~15 km from western and eastern extents, respectively. The nearest whether station to the Ronald Lake area is Fort Chipewyan where mean annual temperature is -1.5° C, and a mean annual precipitation of 366 mm. Elevation within the study area vary between 222 to 325 m above sea-level. Land-cover types include a mosaic of upland aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and mixed-wood forests, and wetlands that include meadow and emergent marshes, treed swamps, and poor to rich treed and non-treed fens and bogs. Unlike much of the Lower Athabasca region, this area is more dominated by meadows and marshes than fens and bogs which are more common to other areas of the region. Bordered to the west and east of the study area are the Birch Mountains and the Athabasca River, respectfully. Active resource exploration, extraction, and development by forestry and energy industries have created a variety of anthropogenic disturbances including forestry, seismic lines, and temporary or season roads that occur mostly in the southern parts of the study area (Tan et al. 2015).

2.2 Sample site selection

I selected three land-cover types frequently used by bison, marsh meadows, deciduous forests, and jack pine forests, for study using previous information on Ronald Lake bison habitat selection (Tan et al. 2015; DeMars et al. 2016). In addition to land-cover types, I also included a large esker (surficial geological feature composed of alluvial sediments formed by under-glacial streams) (Storrar et al. 2015) that dissects the study area spanning ~15 km north-south ending in the north at Ronald Lake itself. The esker represents an area of higher elevation that is exposed to westerly winds which were hypothesized to be a potential refuge from biting insects and thus included in the study design. Here forth, I refer to land-cover types and land form features (esker) collectively as land-cover for simplicity.

I selected 9 representative field sites for each of the 4 land-cover types ($n = 36$) using the Ducks Unlimited Enhanced Wetland Classification (Ducks Unlimited Canada 2016) in ArcGIS 10.3 (ESRI 2014). Only sites having a minimum patch size of 1 ha (100 x 100 m) were considered, to avoid potential misclassification and to be large enough to accommodate our field sampling design. All sites were close to a ~18 km long, semi-maintained, trapper's access trail starting at the Athabasca River and ending at Ronald Lake. Final sample sites were based on stratification in ArcGIS (land cover type and patch size) and accessibility (within 3 km of the trail). Because the esker was a single landform in the area, the nine sampled esker sites were equally spaced along a 6-km section of the esker and thus ~750 m apart (Fig. 2.1).

2.3 Field methods

2.3.1 Transects

I established transects 60 m in length in the *center* of each site and sampled soils, biting flies, and vegetation. I selected the 60 m transect length to reduce edge effects given that some patches were as small as 1 ha with all transect ending >20 m from any visible edge. All transects were established along a north-south bearing, except in marshes where directionality and proximity of marshes to other land-cover types required an alternate bearing.

2.3.2 Bison activity

Bison summer and winter dung counts were used as a measure of bison summer and winter activity, respectively. I sampled dung counts at all sites between 16 and 18 August of 2016. At each sample site, dung were counted in 3 belt transects, 100 m in length and 4 m in width (2 m on either side of a tape), and parallel to each-other starting at the center of each site. A single dung count was recorded based on the assessment of an individual bison defecation event, i.e. a single or small grouping of dung patty(s) as summer dung, or grouping of droppings as winter dung with texture further used to differentiate seasons (Appendix 1). In total, 108 transects were sampled (4 landcover types × 9 sites per landcover type × 3 transects each) (Appendix 2).

Dung counts were assumed to be directly proportional to bison activity, and more specifically that decay rates for both summer and winter dung to be equal within land-cover types (Brodie 2006; Theurerkauf & Rouys 2008). Detectability of dung in marshes may be lower given the amount of biomass present obscuring visibility and moist conditions that may increase decomposition rates (Rodriguez et al. 1998; Brodie 2006). Substantial effort was given to fully searching each transect to minimize false absences due to poor visibility. Relative to length of time dung were assessed, decay rates of dung for cattle have been estimated at 180 to 240 days (Rodriguez et al. 1998). To help minimize bias associated with time since defecation, we counted only recent dung, or dung that did not look visibly decayed. Overall, dung counts represented the complete winter period (mid-November – March) and the summer (April – mid-August) cycle for up to 270 days. Dung encounter rates in this study were also consistent with studies of wood bison summer and winter diet elsewhere (Larter & Gates 1991; Jung 2015; Leonard et al. 2017) and importantly were similar in ranking to habitat selection values for this population of animals based on GPS-telemetry data (Tan et al. 2015; DeMars et al. 2016) that independently indexed use of habitats without potential biases associated with dung measures and redistribution of dung based on foraging, resting, and movement behaviours (Appendix 3).

2.3.4 Forage

I estimated biomass of plants by species, growth form, or genera at the end of the growing season between 9 and 15 August. Nine equally spaced 0.5 m^2 circular quadrats were alternatingly set at 2-m from the 60 m transect line starting at 0-m and ending at 60-m. In total, I sampled 324 plots (4 landcover types × 9 replicate sites × 9 quadrats per site/transect). All vegetation within quadrats were clipped with graminoids and forbs cut 2.5 cm above ground and only new growth of shrubs cut. Creeping shrubs, such as bearberry (*Arctostaphylos uva-ursi*), lichens, mosses, and trees were not collected due to 1) unlikeliness of being a component of bison diet (Jung 2015, Bergmann et al. 2015; Leonard et al. 2107), or 2) very low occurrences within plots. Clipped vegetation was separated by species, dried in a drying oven at 60° C for 48 hours, and weighed using a balance to the nearest 0.01 g. For final analysis vegetation was lumped into one of three growth forms based on previous studies of bison diet composition (Jung 2015, Bergmann et al. 2015; Leonard et al. 2107): graminoids, forbs, and shrubs (Appendix 4)

2.3.5 Biting flies

I sampled biting flies between 18 June and 16 August with a focus on groups of insects that are known to affect the behaviour of boreal ungulates, including caribou (Helle & Tarvainen 1984; Witter et al. 2014) and bison (Morgan 1987; McMillan et al; 2000). Specifically, 4 families of biting flies were assessed from the order Diptera: Tabanidae (horse-fly and allies), Simuliidae (black fly and allies), Culicidae (mosquito and allies), and Ceratopogonidae (biting midges and allies) (Lewis 1987; Walsh et al 1992; Pfannenstiel & Ruder 2015; Kozlov et al. 2015). I used 3 sampling methods to measure biting fly activity: 1) sweep netting (Rolf & Reimers 2002; Krcmar 2005); 2) tabanid traps (or modified Manitoba traps) (Thorsteinson et al. 1965; Morgan

1987; Duncan & Cowtan 1980; Schreck et al. 1993); and 3) Malaise traps (Schreck et al. 1993; Tunnakundacha et al. 2017). Each sampling method is described below.

Sweep netting

Sweep net sampling started 18 July and ended 16 August. Ten sampling days occurred in July and 8 days in August with 2 observers used. Sweep net samples occurred across the study period with 16 sites randomly selected for sampling each day (4 per land-cover type). A site was sampled at a minimum frequency of 2 to 3 days. Specifically, 30 full sweeps (180°) above graminoid vegetation height (~1 m above ground) were used while walking a 50-m transect with 12 transects completed per site. Total number of flies caught were recorded and the flies released. Time of day, average and maximum wind speed (m/s), temperature (°C), and relative humidity (%) were recorded using a handheld Kestral 3500 weather meter mounted to a stake at 1.3 m height at each sample site for the duration of sweep net sampling (~20 minutes). In total, 2837 sweep net events were conducted during 254 site visits at the 36 sites (Appendix 5).

Tabanid and Malaise traps

Tabanids were sampled in 2016 between 27 June and 16 August over five 7-day sampling periods using tabanid and Malaise traps. Three tabanid traps were spaced equally along the main 60 m transect at each of the 36 sites, while a single Malaise trap (4 per land-cover type) was set 15 m perpendicular to the center of each transect. Traps were set on day 1 and samples collected on day 7 of each sampling period. In total, 504 tabanid trap samples and 80 Malaise trap samples were collected over the 5-week sampling period or 108 samples per week. Of the 80 Malaise trap samples (16 per week), only 36 samples were fully collected due to high trap interference from wildlife. Given the loss of these data, Malaise trap information were removed from analyses due to low sample sizes (Appendix 5).

Tabanid traps were constructed using the design of Thorsteinson et al. (1965) to specifically target flies from the family Tabanidae (Thorsteinson et al. 1965). Traps were constructed of 6 mm transparent plastic cut into a cone shape measuring 13 cm diameter at the top and 76 cm diameter at the bottom, and at a 76-cm height. Half-inch plastic tubing was taped with weather resistant tape to the bottom of the cone for support. Two-liter soda bottles were used to capture tabanids with the top of soda bottles cut off, inverted, and glued inside the soda bottles. Soda bottle-capture units were attached to the top of the cone. Traps were fixed to a stake with the bottom 1 m above ground. A black ring measuring 50 cm in diameter x 12 cm in height, made of 3 mm black plastic was fixed to the stake just below the bottom cone opening to attract (lure) biting flies from the family Tabanidae (Appendix 6). No preservatives were used in traps. Tabanids from traps were preserved in 250 ml specimen cups filled with ethylene glycol (Schmidt et al. 2006) and brought back to lab for identification by family, and counted.

2.3.6 Footing

Ground footing by animals can be described by the firmness, strength, or shear resistance of soil when pressure is applied to it such as when an animal steps (Haranz et al. 2000). Three soil properties were used to index footing conditions – soil bulk density, soil moisture content, and soil penetration depth. All measures of soil properties were correlated ($r > 0.866$) with each other (Appendix 7). A more detailed description of each measure is provided below.

Soil bulk density

Soil bulk density describes the pore space within a specific volume of soil. Soils with lower bulk density have a greater amount of pore space (Hernanz et al. 2000). Soils with lower bulk density and greater pore space are often considered softer or less firm soils. Soil bulk density was measured using two cylindrical steel soil cores that each measured 70 mm x 150 mm. A 150-mm core was used to ensure that both organic and mineral horizons were obtained. At sites with shallow organic horizons, composed primarily of mineral soil, a core was pushed into to the soil to obtain a soil core. At sites with deep organic horizon, composed primarily of organic material, a core sharpened on one end was drilled into the soil to cut and obtain a soil core. Five soil cores were taken equally spaced along the main 60 m transect at each site. Soil cores were then placed into a double layer of plastic Ziploc bags to ensure that core moisture loss was minimal, and taken to lab for drying and weighing. Aluminum baking trays and a drying oven were used for drying the cores. Trays were dried and weighed using a balance before soil cores were placed on them. Soil cores were dried in a drying oven at 100 °C for 48 hours. A total of 180 soil bulk density cores were sampled (Appendix 8). Soil bulk density was then calculated on a volumetric basis using the following equation:

$$\rho_b = \frac{W_d}{mm^3}$$

Soil moisture content

Soil moisture content describes the water holding capacity of a soil as it is related to soil properties such as texture (sand, silt, clay). Water holding capacity of a soil increases as organic and/or clay content increases (Hernanz et al 2000). Soils with high moisture content are generally softer and thus less firm soils. Soil moisture content was measured here using two methods – in-situ and lab measurements. In-situ soil moisture content was measured using a PR2 soil moisture probe (Delta-T Devices Ltd. Cambridge, UK) at 7 locations equally spaced along the main 60 m transect starting at 0-m and ending at 60-m. Lab soil moisture content was measured using the same soil cores used for bulk density. In total, 756 in-situ measures and 180 lab-measures of soil moisture content were taken (Appendix 8). Percent soil moisture content was then calculated on a gravimetric, wet-weight basis using the following equation:

$$W_m = \frac{W_w - W_d}{W_w}$$

Soil penetration depth

Soil penetration depth describes soil strength as it relates to the shear strength and resistance of a soil which itself is related to soil bulk density and moisture content (Hermanz et al. 2000; Vaz & Hopmans 2001). Soil penetration is also often used as an index for soil compaction. Soils with low strength have lower bulk density, higher moisture content, less compaction, and therefore have higher penetration depths (Hermanz et al. 2000; Vaz & Hopmans 2001).

I designed a custom soil penetration device constructed of steel with the body of the penetrometer being 2 m in length and composed of 1.5” schedule 40 steel pipe (Appendix 9). A 1 m length penetration pin made from solid 1” round steel was then welded to the collar of the bottom of the body. A sliding weight around the penetrometer body of 7 kg was dropped from a height of 1.5 m onto the collar of the penetration pin. The penetration device was tested prior to field use on compacted and non-compacted soils of similar types, and modeled in relation to soil bulk density. Overall, there was a strong positive relationship between soil penetration depth and soil bulk density ($R^2 = 0.96$, SE = 0.12, $p < 0.001$). For each field site, 21 penetration measures were taken at 7 locations equally spaced along the main 60 m transect with 3 measurements per location. Penetration depth was recorded in cm. In total, 756 soil penetration measurements were taken (Appendix 8).

2.4 Analysis of the effects of land-cover type on bison summer and winter activity, footing, biting fly abundance, and forage biomass

All data were assessed for assumptions of parametric tests using Shapiro-Wilk’s test of normality, Bartlett’s test of variance, fitted residuals, and normal q-q plots. Data which violated assumptions for parametric tests were log10 transformed after adding a constant of 1 and then standardized. All analyses were performed in Stata version 15 (Stata. IC 2017), while all graphics were created in ggplot2 (Wickham 2016).

A series of linear regression models were first fit to independently test the effects of land-cover types on bison summer and winter activity, footing, biting fly abundance, and forage biomass. Land-cover type “marsh” was withheld as the reference category in all models to test the relative effects of other land-cover types to that of marsh. Adjusted R-squared was used to assess model fit. Zero inflated negative binomial (ZINB) models for bison summer and winter activity (dung counts) were fit, but were similar to those of linear regression and thus dropped.

2.5 Analysis of effects of footing, biting fly abundance, and forage biomass on summer and winter bison activity

A series of candidate, univariate, linear regression models were fit to test the effects of footing, biting fly abundance, and forage biomass on summer and winter bison activity (Appendix 11 & 12). Results from these analyses were used to guide the development of multivariate models of summer and winter bison activity, including relationships between footing, biting fly, and forage variables. Akaike's information criterion (AIC; Akaike 1974) ranking was used to compare support between a series of models that compared measures of biting flies and footing. Multivariate, linear regression models could not be used to test these combined relationships because of high collinearity among independent variables and in some cases multiple response variables (Table 2.1). Instead, structural equation modeling (SEM) was used to fit a series of multiple regressions that tested hypotheses of the direct, indirect, and total effects (direct + indirect) of footing, biting fly abundance, and forage biomass on summer and winter bison activity. Structural equation models are applicable for fitting multivariate, global (multi-faceted), regression models and data that are highly correlated (Bagozzi 1989), and were a suitable modeling approach for this study.

A series of global SEM models were then fit to test different measures of footing (soil bulk density, moisture content, and penetration depth) and biting fly abundance (sweep net and tabanid trap methods) on summer and winter bison activity. AIC was used to compare support between a series of models that compared types of measures and number of variables (Appendix 13 & 14). Model strength was then assessed for the most supported AIC model using root mean square error of approximation (RMSEA).

3.0 Results

3.1 Effects of land-cover type on summer and winter bison activity, footing, biting fly abundance, and forage biomass

Here, I report the results of linear regressions that I used to test the effects of land-cover type on summer and winter bison activity, footing, biting fly abundance, and forage biomass (Table 2.2). Relative to marsh, summer dung counts of bison did not differ significantly for deciduous forests ($\beta = 0.36$, S.E. = 0.34, $p = 0.291$), but were greater in pine forests ($\beta = 1.48$, S.E. = 0.34, $p < 0.001$), and the esker ($\beta = 1.71$, S.E. = 0.34, $p < 0.001$) (Fig. 2.2). Relative to marsh, winter dung counts of bison did not significantly differ from that of deciduous forests ($\beta = -0.39$, S.E. = 0.46, $p = 0.402$), pine forests ($\beta = -0.77$, S.E. = 0.46, $p = 0.105$), and the esker ($\beta = 0.13$, S.E. = 0.46, $p = 0.778$) (Fig. 2.2).

Marsh had softer footing relative to all land-cover types with greater soil moisture and penetration depth, and lower bulk density. Soil moisture content was significantly lower in deciduous forest ($\beta = -2.02$, S.E. = 0.16, $p < 0.001$), pine forest ($\beta = -2.16$, S.E. = 0.16, $p < 0.001$), and the esker ($\beta = -2.24$, S.E. = 0.16, $p < 0.001$) (Fig. 2.3), while marsh had greater abundance of biting flies, including horse flies, mosquitos, and midges with fewer biting flies in deciduous forest ($\beta = -1.29$, S.E. = 0.27, $p < 0.001$), pine forest ($\beta = -1.25$, S.E. = 0.27, $p < 0.001$), and the esker ($\beta = -2.33$, S.E. = 0.27, $p < 0.001$) (Fig. 2.4). And finally, there was less graminoid biomass in deciduous forest ($\beta = -2.18$, S.E. = 0.15, $p < 0.001$), pine forest ($\beta = -2.24$, S.E. = 0.15, $p < 0.001$), and the esker ($\beta = -2.05$, S.E. = 0.15, $p < 0.001$) than in marshes (Fig 2.5). Bison therefore use marshes less than deciduous and pine forests and the esker in summer, with winter use of land-cover types being more ubiquitous, but generally with greater use of marshes and esker, although not significantly different. These data also demonstrate that marshes have greater overall forage biomass primarily composed of preferred sedges, but also having softer soils and greater biting fly abundance than in nearby deciduous and pine forests and the esker sites. During summer months, it is apparent that bison used the esker more than marshes and deciduous and pine forests (Fig. 2.2). Overall, the esker had relatively firmer soils (Fig. 2.3), low abundance of biting flies (Fig. 2.4), and relatively greater graminoid biomass than deciduous and pine forests (Fig. 2.5).

3.2 Structural equation model of soil wetness, biting fly abundance, and forage biomass on summer and winter bison activity

Summer and winter structural equation models (Table 2.2 & 2.3) tested seasonal effects of measured covariates on bison activity (dung counts). The most supported summer model included covariates for soil moisture content from soil cores, biting fly abundance from sweep netting, and graminoid biomass (AIC = 340). When examining the total effects of summer bison activity, soil moisture ($\beta = -0.58$, S.E. = 0.14, $p < 0.001$) and biting flies ($\beta = -0.38$, S.E. = 0.19, $p = 0.046$) were negatively related to bison activity, while graminoid biomass (also, forbs and shrubs) had no overall effect ($\beta = 0.01$, S.E. 0.25, $p = 0.979$). The most supported winter model included only the covariate of graminoid biomass (AIC = 205) which was positively related to bison activity ($\beta = 0.28$, S.E. 0.15, $p = 0.062$).

4.0 Discussion

4.1 Trade-offs in summer bison habitat use

From my analysis, I find that bison habitat use in summer is not related to forage availability (quantity), however, is negatively related to 1) large abundances of biting flies which can negatively affect net energy budgets and health, and 2) soft soils that can hinder movement, increase energy expenditure, and increase vulnerability to large predators. During winter months when biting when fly abundance is low to nil, and ground conditions are frozen, I find that graminoid biomass has a strong positive effect on bison use of land-cover types. This analysis supports my hypotheses that bison habitat use, and summer distribution are affected by mechanisms other than forage, including biting flies and footing. In this section I will discuss the effects of forage, biting flies, and footing in the context of bison habitat use.

Energy maximizing principles state that bison should show high selection for areas composed of copious and nutritious food resources, such as marshes (Brown et al. 1999; Bergman et al. 2001; Fortin et al. 2003: Merkel et al. 2015). During summer months, however, bison show lower selection for marshes (Tan et al. 2015; DeMars et al. 2016), and do not follow energy maximizing principles but time minimizing principles, where bison spend shorter than expected bouts of time in marshes (Fortin et al. 2003; Merkel et al. 2015). During summer months bison use of marshes closely follow time minimizing principles potentially due to alternative, nutritious foraging opportunities in other land-cover types such as shrubs in forested areas (Larter & Gates 1991; Strong & Gates 2009; Bergmann et al. 2015; Leonard 2017). From our results, during summer months bison in the Ronald Lake area may be sourcing alternative forage opportunities in deciduous and pine forests due to increased availability of forbs and shrubs, and more widely distributed graminoids in land-cover types other than marshes. While forbs and shrubs may comprise a small proportion of bison summer diets (Larter & Gates 1991; Leonard et al. 2017), shrubs are found to be more nutritious (Larter and Gates 1991), with higher crude protein levels, thus may supplement as an alternative forage resource. My findings of forage biomass as a factor that does not affect bison habitat use is consistent with studies that show seasonal shifts in bison summer diet and use of land-cover types (Larter & Gates 1991; Bergmann et al. 2015; Leonard et al. 2017). While my estimation of bison forage in focal land-cover types is consistent with other studies, I suggest there is merit in further investigation to quantify Ronald Lake bison use of forage types, and diet diversity and composition to further our understanding of bison seasonal shifts in dietary preferences, and use of land-cover types.

The effect of biting flies on bison behaviour and habitat use has rarely been quantified. I use three methods to capture biting flies, each method differing in effectiveness. Sweep netting and Malaise traps are effective for capturing varieties of flying insects (Schreck et al. 1993; Rolf & Reimers 2002; Krecmar 2005; Bawm et al. 2015; Tunnakundacha et al. 2017), and tabanid traps are effective for capturing biting flies from the family Tabanidae (Thorsteinson et al. 1965; Duncan & Cowtan 1980; Hughes et al. 1981). Though I cannot speak on the effectiveness of Malaise traps in my study due to low sample size, the Malaise trap data (Appendix 1.1) reflects similar trends compared to the sweep net data (Fig. 2.4). In contrast to Malaise traps and sweep netting, the tabanid trap method likely introduced a bias towards attracting tabanids from surrounding land-cover types, and may be non-representative of tabanid, or insect, abundance within a land-cover type. Tabanids are known to travel up to 2.4 km (Thronhhill & Hays 1972; Cooksey & Wright 1987; Foil et al 1991), thus tabanid traps likely bias abundance estimates within a land-cover type. I tested the effects of bison habitat use between all methods and found the sweep net data to better fit the models. I am confident that my data are representative of insect loads within land-cover types, however, are indirect measures of the influence of flies on bison. I suggest that direct observations throughout the summer period and in various land-cover types are needed to better assess the effects of biting flies on bison habitat use.

Snow depth is an important factor that influences ungulate distributions, predation risk and energetic costs associate with locomotion (Mysterud et al. 1997; Pool & Mowat 2005; Pepin et al. 2009; Robinson & Merrill 2012; Courbin et al. 2017). Deeper snow conditions increase ungulate vulnerability to predators, (Fancy & White 1986; Carbyn et al. 1988; Carbyn et al. 1993), and can increase locomotive, energetic costs up by 7 times that of snow-free conditions (Stardom 1977; Parker et al. 1984; Schaefer & Messier 1995; Mysterud et al. 1997; Robinson & Merrill 2012). Like quantitative studies of snow depth in relation to ungulate habitat use, we tested the effects of summer soil conditions on bison habitat use. During summer months, bison can better escape predation when on firm ground (Carbyn & Forttier 1988) and thus avoid soft terrain that can limit movement and increase vulnerability to wolves. In addition to predation risk, energy expenditure in soft terrain is higher than that of more firm ground (Shepard et al. 2013). Our methods of quantifying soil conditions in the context of animal footing, predation risk, locomotion, and habitat use are novel and a step towards examining soil conditions as a mechanism affecting habitat use and distributions. More work is needed to address the influence of soil conditions in relation to predation risk and locomotive, energetic costs.

Like habitat use models that incorporate direct measurements of animal movements with the use of GPS radio telemetry, or aerial observations, here, I use indices of bison habitat use by using dung counts to quantify seasonal bison habitat use in three land-cover types and one landform feature. Using animal dung counts to measure relative use of different land-cover types is an effective method (Brodie 2006; Theurerkauf & Rouys 2008), but still has limitations. Dung counts are time consuming to establish, especially if year to year measurements are important. Measurement errors from dung surveys are affected by sample sizes, observer bias, and decay rates (Rodriguez et al. 1998; Brodie 2006; Alves et al. 2013). However, unlike radio telemetry or aerial surveys, where financial cost and logistics of collaring individuals and surveys can limit sampling effectiveness and success, dung surveys can be conducted at relatively low cost to budget and time, and account for population-level measures of habitat use. Use of dung counts to measure summer and winter bison use of land-cover types is consistent with other studies of bison diet (Larter & Gates 1991; Fortin et al. 2009; Jung 2015; Leonard et al. 2017), observations of bison (Carbyn & Trottier 1987; Carbyn et al. 1993), and telemetry-based habitat selection of the Ronald Lake bison herd (Tan et al. 2015; DeMars et al. 2016).

Th objective of this study was to investigate mechanisms, including forage, that effect ungulate habitat use. The results of my study are consistent with studies of the effects of forage (Larter & Gates 1991; Leonard et al. 2017), biting flies (Walsh et al. 1992; Witter et al. 2014), locomotion (Robinson & Merrill 2012; Shepard et al. 2013) on ungulate habitat use. I find that the effects of forage biomass on bison habitat use is less important during summer months than in winter months. This is because forage is more widely available across habitat types during summer months than winter months, thus bison are not constrained to habitats, such as marshes, where forage (graminoids) persist year-round. I find that biting flies and footing negatively affect summer habitat use, where bison reduce use of areas with greater biting fly abundances and softer footing. This is because biting flies can negatively affect health, survival, and energy budgets, and soft ground can reduce movement, and increase predation risk and locomotion costs. I find support for my hypotheses that bison habitat use is affected by mechanisms other than forage, and that bison observe trade-offs between forage, biting flies, and footing. The combination of forage, biting flies, and footing, influence a hierarchical behavioural construct between these factors, and bison balance energy demands and predation risk by using various habitat types.

Understanding the complex ecology and relationships between animals and their environment is challenging and often onerous, but necessary for filling our knowledge gaps related to animal behaviour, and the biological and environmental factors limiting individuals and populations. A comprehensive investigation of the processes contributing to the dynamic nature of animal habitat use will shed light on the factors and mechanisms that significantly affect animal temporal and spatial distributions, behaviour, and fitness-related costs and benefits. This includes not only proximate, descriptive explanations of habitat use, as they relate to attributes such as land-cover types and how these effect animal distributions, but also casual links of small and large-scale processes associated with those attributes and distributions. These observations are fundamental to our ability in the successful management of populations of animals, and are essential for the conservation of rare and endangered species.

4.2 Management implications

Bison once numbered in the tens of millions until the turn of the 20th century when they were nearly extirpated from North America. The establishment and recovery of bison populations to this point marks a major achievement for the conservation of this species. However, as land use expands further into pristine, natural environments, such as those surrounding Fort McMurray, habitat for threatened and endangered species will be more limited (SARA 2017).

Wood bison are now a threatened species in Canada with an estimated population of approximately 10,000 individuals across 12 wild subpopulations. In Alberta, free-roaming wood bison are primarily found in 2 subpopulations located in the Hay-Zama and Wood Buffalo National Park areas (SARA 2017). Current forestry, bitumen exploration, and proposed bitumen mining operations in the Ronald Lake area pose as potential impacts and direct loss of habitat to the Ronald Lake bison herd. This examination of the mechanisms that influence wood bison habitat use garners comprehensive knowledge of the factors affecting wood bison health and survival, and can provide guidance to better manage, conserve, and reclaim habitats and features important to the sustainability of the Ronald Lake bison herd and bison populations in free-ranging and managed herds.

Table 2.1: Pearson's correlation matrix of the most supported variables used in structural equation models of summer bison activity. Dung, soil moisture content, biting fly abundance, and graminoid biomass were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016 (*n* = 36).

	Dung summer	**Soil moisture**	**Biting flies (Sweep net)**	**Graminoid biomass**
Dung summer	1			
Soil moisture	-0.576	1		
Biting flies (Sweep net)	-0.573	0.692	1	
Graminoid biomass	-0.477	0.831	0.706	1

Table 2.2: Univariate, linear regression models relating land-cover type on measured variables of summer bison activity (*n* = 108), winter bison activity (*n* = 108), soil moisture content (lab measured; *n* = 180), biting fly abundance (sweep net method; *n* = 2837), and graminoid biomass (*n* = 324). Land-cover type 'marsh' was withheld as the reference category in all models and thus significance based on their comparison (difference). Dung, soil moisture content, biting fly abundance, and graminoid biomass were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016.

Model #	**Dependent**	**Independent**	**β**	**S.E.**	**C.I.**		***p***
1	**Bison summer activity** $R^2 = 0.49$	Deciduous	0.36	0.34	-0.32	1.04	0.291
		Pine	1.48	0.34	0.80	2.17	< 0.001
		Esker	1.71	0.34	1.02	2.39	< 0.001
2	**Bison winter activity** $R^2 = 0.05$	Deciduous	-0.39	0.46	-1.33	0.55	0.402
		Pine	-0.77	0.46	-1.71	0.17	0.105
		Esker	0.13	0.46	-0.81	1.07	0.778
3	**Soil moisture content** $R^2 = 0.88$	Deciduous	-2.02	0.16	-2.35	-1.69	< 0.001
		Pine	-2.16	0.16	-2.49	-1.83	< 0.001
		Esker	-2.24	0.16	-2.57	-1.91	< 0.001
4	**Biting fly abundance** $R^2 = 0.68$	Deciduous	-1.29	0.27	-1.84	-0.75	< 0.001
		Pine	-1.25	0.27	-1.80	-0.70	< 0.001
		Esker	-2.33	0.27	-2.88	-1.78	< 0.001
5	**Graminoid Biomass** $R^2 = 0.90$	Deciduous	-2.18	0.15	-2.50	-1.87	< 0.001
		Pine	-2.24	0.15	-2.55	-1.93	< 0.001
		Esker	-2.05	0.15	-2.36	-1.74	< 0.001

Table 2.3: Best fit structural equation model of direct, indirect, and total effects of soil moisture content, biting fly abundance (sweep net method), and graminoid biomass on summer bison activity. Soil moisture content, biting fly abundance, and graminoid biomass were measured in 4 land-cover types (*n* = 36) near Ronald Lake, Alberta between June and August 2016. Root mean squared error of approximation, RMSEA < 0.0001.

Dependent	**Independent**	**β**	**S.E.**	**C.I.**		***p***
Direct effects						
Summer bison activity	Soil Moisture	-0.45	0.24	-0.93	0.02	0.061
	Biting fly abundance	-0.38	0.19	-0.75	-0.01	0.046
	Graminoid biomass	0.17	0.25	-0.32	0.65	0.498
Biting fly abundance	Soil Moisture	0.34	0.20	-0.06	0.74	0.098
	Graminoid biomass	0.42	0.20	0.02	0.83	0.038
Graminoid biomass	Soil Moisture	0.83	0.09	0.65	1.01	< 0.001
Indirect effects						
Summer bison activity	Soil Moisture	-0.12	0.21	-0.53	0.29	0.557
	Graminoid biomass	-0.16	0.11	-0.38	0.06	0.151
Biting fly abundance	Soil Moisture	0.35	0.17	0.01	0.70	0.043
Total effects						
Summer bison activity	Soil moisture	-0.58	0.14	-0.84	-0.31	< 0.001
	Biting fly abundance	-0.38	0.19	-0.75	-0.01	0.046
	Graminoid biomass	0.01	0.25	-0.47	0.49	0.979
Biting fly abundance	Soil moisture	0.69	0.12	0.46	0.93	< 0.001
	Graminoid biomass	0.42	0.20	0.02	0.83	0.038
Graminoid biomass	Soil moisture	0.83	0.09	0.65	1.01	< 0.001

Table 2.4: Best fit structural equation model of direct total effects of graminoid biomass on winter bison activity (dung). Graminoid biomass was measured in 4 land-cover types (n = 36) near Ronald Lake, Alberta in August 2016. Root mean squared error of approximation, RMSEA < 0.0001.

Dependent	**Independent**	**β**	**S.E.**	**C.I.**		***p***
Direct and total effects						
Bison winter activity	Graminoid biomass	0.28	0.15	-0.01	0.58	0.062

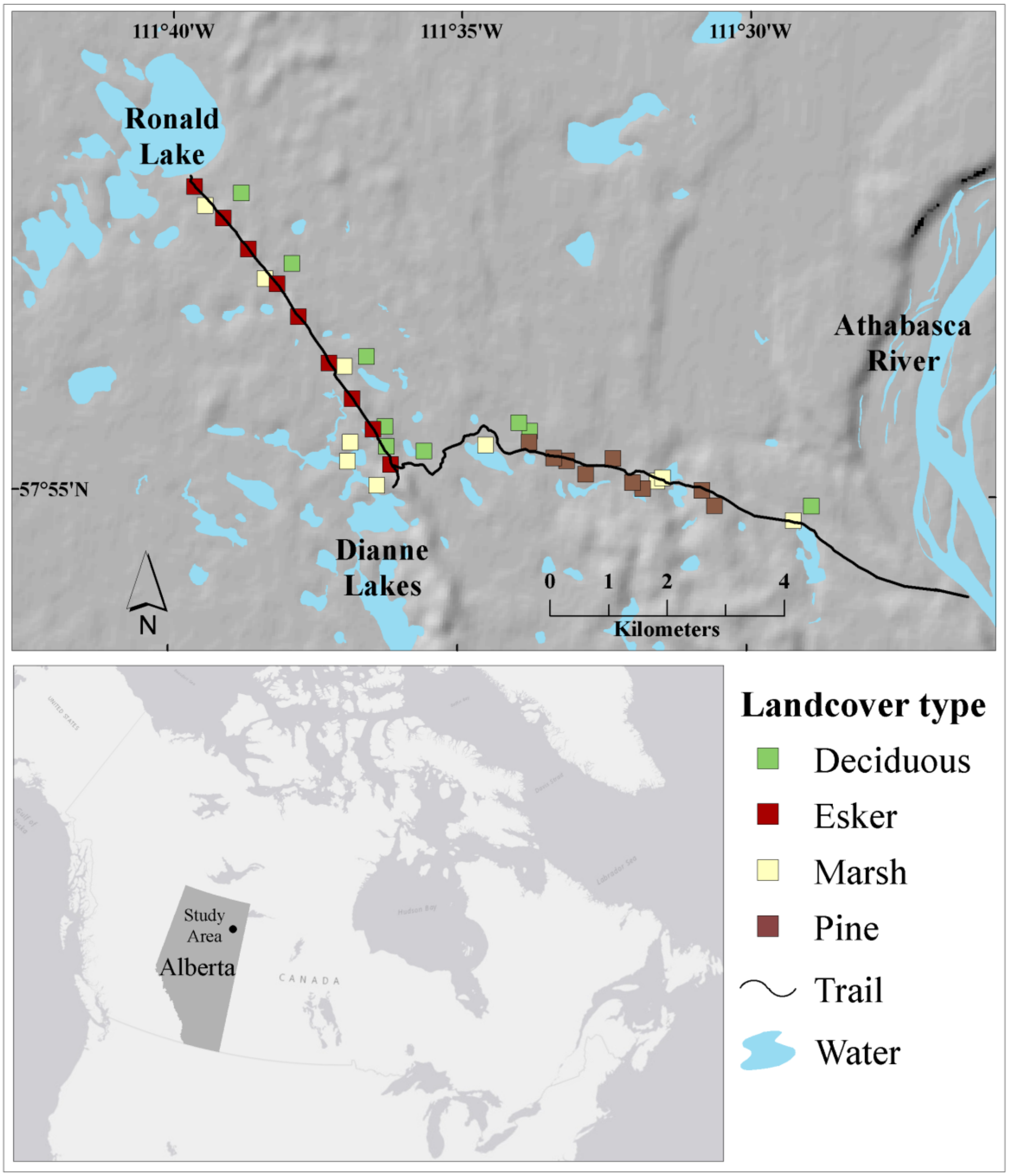

Figure 2.1: Map of study area and study sites in north-eastern Alberta near Ronald Lake, Alberta, ~ 150 km north of Fort McMurray and ~15 km south of Wood Buffalo National Park. Study sites were located adjacent to an ~18 km trapper's trail that starts at the Athabasca River and ends at Ronald Lake.

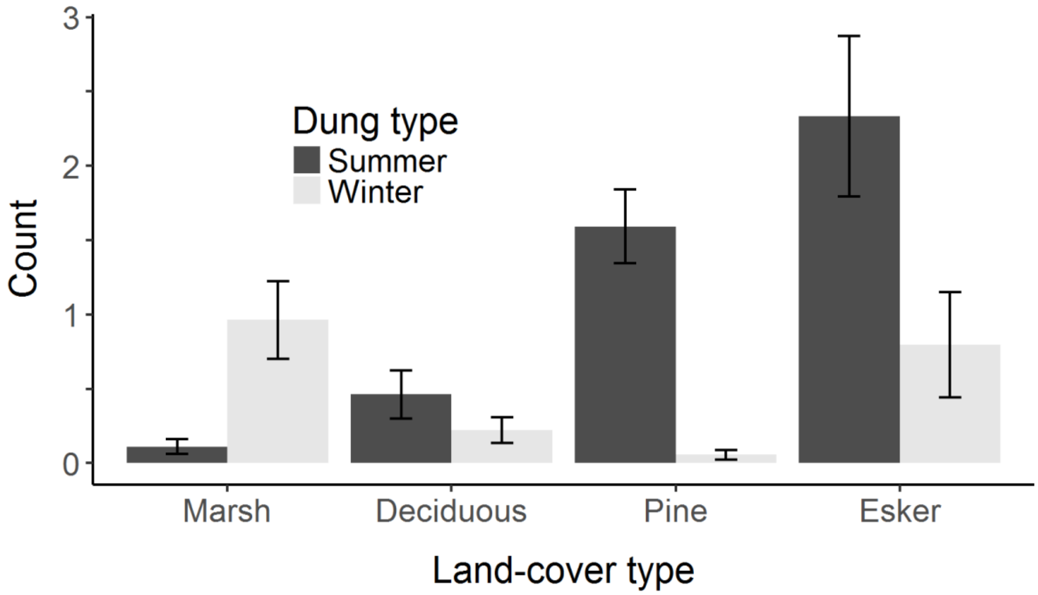

Figure 2.2: Mean dung count estimates in 4 land-cover types near Ronald Lake, Alberta (*n* = 108). Dung counts were measured in August 2016. Relative to marsh, summer bison activity (dung counts) did not differ significantly from deciduous forest (β = 0.36, S.E. = 0.34, p = 0.291), while being higher in pine forests (β = 1.48, S.E. = 0.34, $p < 0.001$) and the esker habitat (β = 1.71, S.E. = 0.34, $p < 0.001$). In contrast to summer, winter bison activity (dung counts) were not significantly differ from marsh in all three habitats of deciduous forest (β = -0.39, S.E. = 0.46, p = 0.402), pine forest (β = -0.77, S.E. = 0.46, p = 0.105), and the esker habitat (β = 0.13, S.E. = 0.46, p = 0.778).

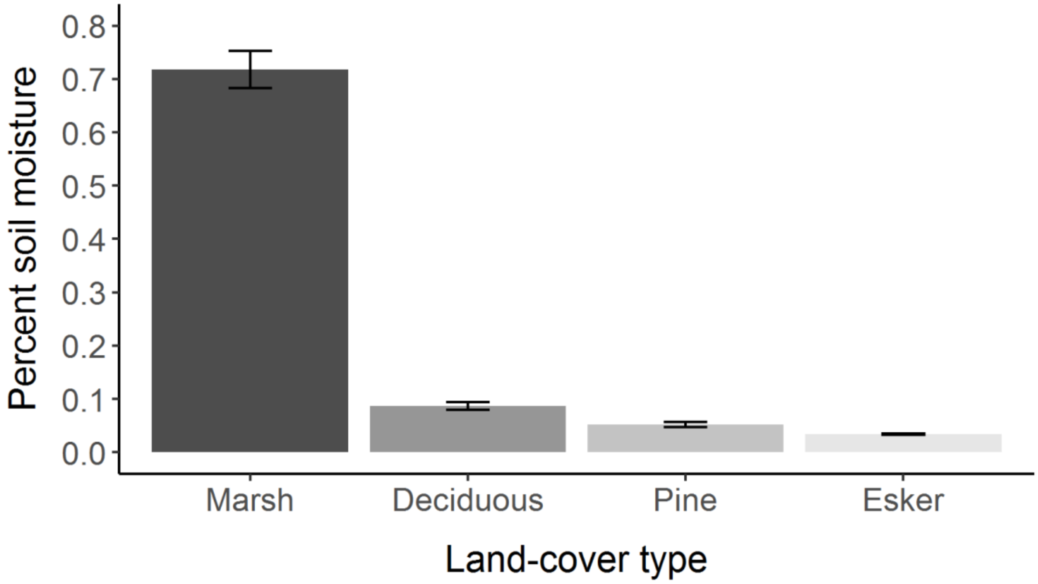

Figure 2.3: Mean percent soil moisture content across 4 land-cover types near Ronald Lake, Alberta (*n* = 180). Soil moisture content was measured using a 577 cm^3 (15 cm height x 7 cm round) soil core. Soil cores were dried in a drying oven at 100°C for 48 hours and weighed. Relative to marsh habitats, soil moisture content was always significantly lower for deciduous forest (β = -2.02, S.E. = 0.16, $p < 0.001$), pine forest (β = -2.16, S.E. = 0.16, $p < 0.001$), and the esker habitat (β = -2.24, S.E. = 0.16, $p < 0.001$).

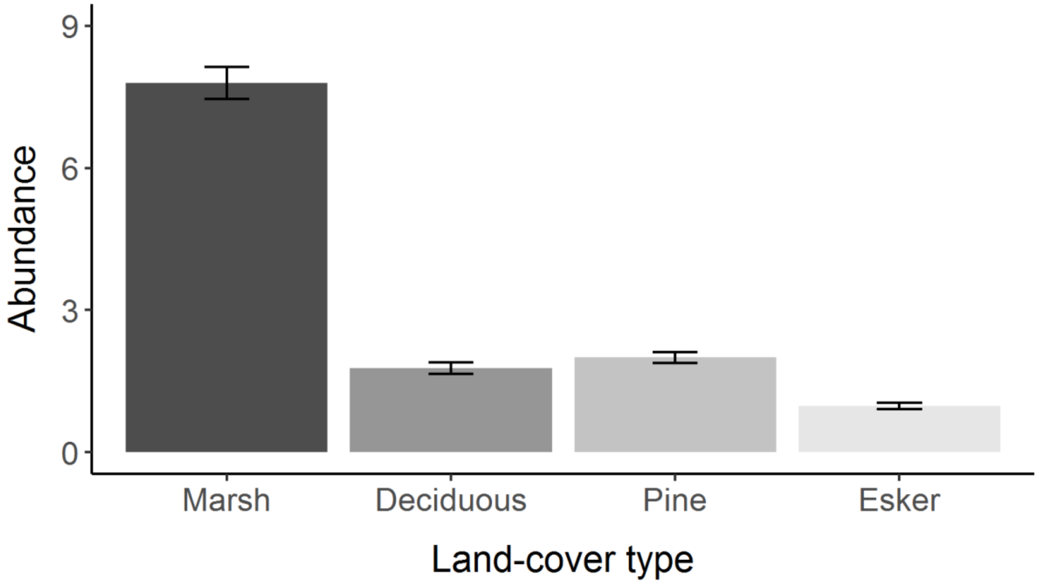

Figure 2.4: Mean biting fly abundance estimates from sweep nets for tabanids, mosquitos, and midges across 4 different land-cover types near Ronald Lake, Alberta. Graph is of mean number of flies caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect ($n = 2837$). Flies were caught between June and August of 2016. See appendices 21, 22 and 23 for individual abundances of tabanids, mosquitoes, and midges. Relative to marshes, there were significantly fewer biting flies in deciduous forest ($\beta = -1.29$, S.E. = 0.27, $p < 0.001$), pine forest ($\beta = -1.25$, S.E. = 0.27, $p < 0.001$), and the esker habitat ($\beta = -2.33$, S.E. = 0.27, $p < 0.001$).

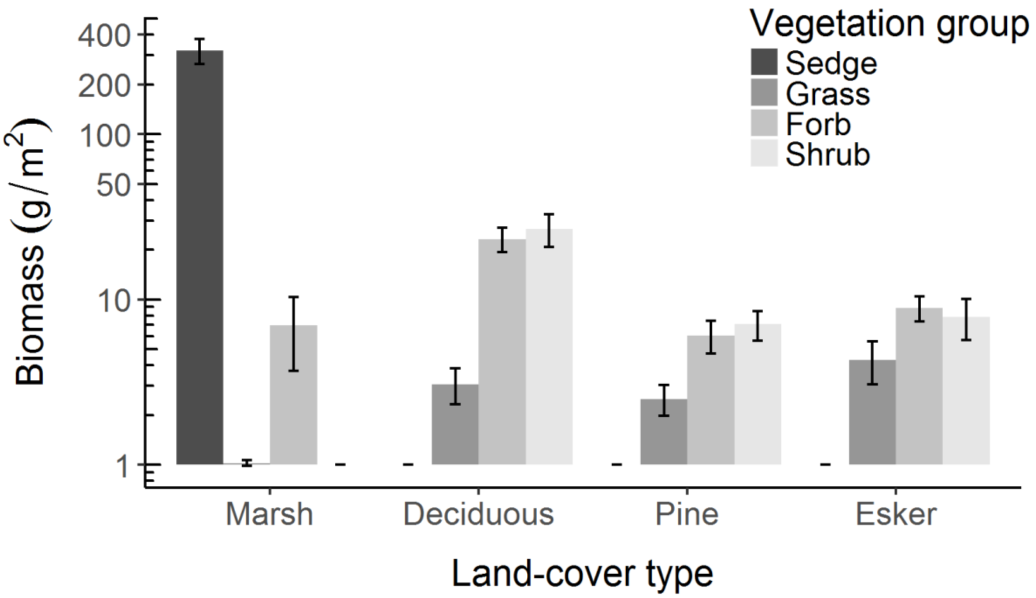

Figure 2.5: Mean forage biomass for 4 growth forms in 4 land-cover types near Ronald Lake, Alberta. Forage was estimated at the end of the growing season (August 2016) in multiple 0.5 m^2 circular quadrats per site (n = 324). Relative to marshes, graminoid biomass was lower in deciduous forests ($\beta = -2.18$, S.E. = 0.15, $p < 0.001$), pine forests ($\beta = -2.24$, S.E. = 0.15, $p < 0.001$), and the esker habitat ($\beta = -2.05$, S.E. = 0.15, $p < 0.001$).

Chapter 3: General conclusions

Realization of forage resources as a principle component of habitat use is integral for understanding prerequisites of ungulate fitness-related traits, behaviour, and distributions (Hanley 1982; Bergman et al. 2001; Fortin et al. 2003; Pool & Mowat 2005; Long et al. 2014; Long et al. 2016). Forage, however, is one of several factors that affect health and survival. Ungulates observe a diverse set of challenges that differ among seasons with trade-offs affecting behaviour, health, and survival being common (Brown et al. 1999; Dussault et al. 2005; Witter et al. 2012; Yan et al. 2016). Land-cover types that supply abundant forage are critical to supplying basic and essential needs for maintenance of large grazing ruminants (Larter & Gates 1991; Carbyn et al. 1993; Fortin et al. 2002), but they may also be areas where predation risk and energetic costs are high (Brown et al. 1999; Hebblewhite & Merrill 2009; Zweifel-Schielly et al. 2009; Courbin et al. 2017). A heterogenous landscape provides animals with a variety of forage opportunities, as well as attributes that reduce predation risk and energetic costs (Dussault et al. 2004; Pepin et al. 2009; Robinson & Merrill 2012; Shepard et al. 2013).

By focusing on the mechanisms that are important to the fitness and subsequently the distribution of individuals and populations, a better understanding of the factors and trade-offs influencing and limiting habitat use can be made. This understanding is fundamental to the successful management of animal populations, and in particular the conservation of rare and endangered species.

Wood bison are endemic to northern regions of the provinces and territories of Canada and the state of Alaska, and are extant in a small fraction of their native habitat. Our findings contribute towards a better understanding of wood bison behaviour, habitat use, and fitness-related costs and benefits associated with forage, insect harassment, and footing. This information can be used to guide the maintenance, (re)introduction, and conservation of this IUCN Red Listed species within extant, historic, and novel wild and managed areas. In particular, this herd overlaps with possible future oil sands developments that require information on the habitat types important to the Ronald Lake wood bison herd. Little knowledge exists regarding habitat supply (forage) for land-cover types in the Ronald Lake area. This study helps to quantify forage resource abundance within bison home ranges and identifies land-cover types important for supplying forage resources. This study can also contribute to a more comprehensive knowledge of the biological and environmental factors that affect bison health and survival, and provide rational for the conservation and reclamation of land-cover types and features within and surrounding Ronald Lake bison home ranges.

Marshes in the Ronald Lake area are dominated by graminoids, especially sedges (*Carex* spp.), that comprise a large portion of a wood bison's diet (Larter & Gates 1991; Steenweg 2016). In this study I found that marshes supply ~100-fold more graminoid forage than deciduous and pine forests, and esker. Unlike other habitats used by Ronald Lake bison, I found soil in marshes are ~10-fold softer, and have ~13-fold greater abundance of biting flies than deciduous and pine forests, and esker. In this study, I observed low bison activity in marshes during summer months, but high activity during winter months. During summer months, marshes are important regarding habitat supply for bison, but a diversity of habitat types is important for suppling alternate foraging opportunities, escapement of harassment by biting flies, and reduction of predation risk and energetic costs. During winter months, marshes are a critically important for providing forage resource for bison.

Direct loss of habitat is a consequence of potential bitumen mining in the Ronald Lake area. This study provides understanding of the mechanisms of habitat use and provides rational for the conservation and reclamation of habitat types within Ronald Lake bison home ranges. Marshes comprise ~1 percent of the study are with deciduous and pine forest, and esker comprising ~35, ~13, and < 1 percent, respectively. The conservation and reclamation of marshes that supply critically important winter forage, the esker that provides bison relief from biting flies, and forests that supply alternate forage and frim footing, are important for the maintenance and conservation of wood bison in this area.

This study builds on pre-existing knowledge of the effects of forage on bison seasonal habitat use and is the first comprehensive, quantitative examination of the effects of biting flies and footing on bison habitat use, and trade-offs associated with foraging. This improves our understanding of bison ecology and can direct attention towards mechanisms that effect the health and survival of other large ungulates. Examining the causal factors that affect bison use of land-cover types can help identify areas important to bison, and can assist with management decisions for among other things the 1) prioritization and protection and conservation of habitat for threatened and endangered species; 2) reclamation of habitat from land-use activities; and 3) identification of habitat suitability for the (re)-introduction of species to native or novel environments

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Appendix

Appendix 1: Bison dung during summer (left) and winter (right). Summer and winter dung are differentiated by texture and is largely influenced by moisture content influenced by both direct water consumption and water content in forage. During summer months, bison are better hydrated, thus summer dung is moister and more ‘plop’-shaped. In contrast, during winter months bison are more dehydrated, thus winter dung is less moist and is more block-shaped (Carbyn pres. comm.).

Appendix 2: Bison total dung counts for 4 land-cover types (*n* = 36). Dung was counted in 3, 100-m belt transects of 4-m width at each site in August 2016. Dung was divided into summer and winter dung based on dung texture.

Land-cover	**Site #**	**Summer Count**	**Winter Count**
Marsh	1	0	0
Marsh	2	0	0
Marsh	3	0	0
Marsh	4	1	0
Marsh	5	0	0
Marsh	6	0	8
Marsh	7	0	0
Marsh	8	3	25
Marsh	9	2	19
Deciduous	1	4	0
Deciduous	2	16	7
Deciduous	3	0	0
Deciduous	4	3	1
Deciduous	5	0	1
Deciduous	6	0	0
Deciduous	7	0	0
Deciduous	8	2	0
Deciduous	9	0	3
Pine	1	9	0
Pine	2	4	0
Pine	3	11	0
Pine	4	20	0
Pine	5	12	0
Pine	6	3	0
Pine	7	1	0
Pine	8	3	3
Pine	9	23	0
Esker	1	8	2
Esker	2	17	30
Esker	3	3	1
Esker	4	9	2
Esker	5	63	6
Esker	6	8	1
Esker	7	5	1
Esker	8	6	0
Esker	9	7	0

Appendix 3: Habitat selection coefficients for bison from the Ronald Lake herd from Tan et al. (2015) and DeMars et al. (2016). Deciduous forest was held constant in both reports (reference habitat). Seasons defined by: winter (Nov – Apr), spring (Apr – May), calving (May – Jun), summer (Jun – Sept), and fall (Sept – Nov). In the DeMars et al. (2016) report, the season summer + fall was defined as June – November.

Tan et al. 2015				
Land-cover	**Winter**	**Spring**	**Summer (calving)**	**Fall**
Marsh	3.001	1.840	1.969	-0.450
Conifer	-0.141	1.663	-3.478	0.482
Pine	2.135	2.059	-4.054	3.094

DeMars et al. 2016				
Land-cover	**Winter**	**Spring**	**Calving**	**Summer + Fall**
Marsh	3.360	1.830	1.570	0.850
Conifer	-0.530	-0.660	-3.440	0.750

Appendix 4: Mean forage biomass (g/m^2) (n = 324) for three forage groups for 4 land-cover types (n = 36) measured in August 2016.

		Graminoid		**Forb**		**Shrub**	
Land-cover	**Site #**	**(g/m^2)**	**S.E**	**(g/m^2)**	**S.E**	**(g/m^2)**	**S.E**
Marsh	1	46.92	10.22	0	0	0	0
Marsh	2	42.19	7.22	0.64	0.59	0	0
Marsh	3	31.45	4.21	0.60	1.07	0	0
Marsh	4	158.10	44.41	1.71	1.10	0	0
Marsh	5	156.79	58.02	9.22	9.08	0	0
Marsh	6	326.33	50.83	10.82	9.65	0	0
Marsh	7	70.45	9.28	0.81	1.63	0	0
Marsh	8	289.43	22.47	0.34	0.50	0	0
Marsh	9	318.80	63.76	2.83	2.54	0	0
Deciduous	1	1.97	1.36	20.61	6.02	12.55	6.85
Deciduous	2	2.05	1.60	11.27	3.91	18.64	12.81
Deciduous	3	1.34	1.20	19.78	4.99	13.39	7.58
Deciduous	4	0.03	0.03	3.58	2.51	0.90	0.53
Deciduous	5	0.30	0.29	13.74	5.34	8.19	4.18
Deciduous	6	0.36	0.45	13.80	6.46	25.97	13.37
Deciduous	7	2.81	1.62	4.83	2.44	14.30	7.80
Deciduous	8	0.07	0.15	7.04	4.82	13.74	9.12
Deciduous	9	0.37	0.26	4.84	2.38	7.95	4.89
Pine	1	0.12	0.17	1.32	0.87	1.23	0.68
Pine	2	0.11	0.15	2.72	1.18	4.10	2.34
Pine	3	0.95	0.84	2.27	1.22	1.67	1.41
Pine	4	0.21	0.17	0.54	0.57	0.73	0.81
Pine	5	0.04	0.04	0.44	0.40	0.84	0.97
Pine	6	0.85	0.78	2.85	1.15	3.33	2.03
Pine	7	1.57	1.21	7.60	3.67	5.01	1.84
Pine	8	2.10	1.18	3.25	1.94	6.11	3.42
Pine	9	0.78	0.44	1.69	1.42	4.26	1.67
Esker	1	2.00	1.23	5.83	2.22	5.36	5.71
Esker	2	1.11	0.84	1.06	0.81	4.34	3.37
Esker	3	3.53	3.37	5.85	3.24	3.98	2.58
Esker	4	0.96	0.67	5.08	2.27	4.65	2.57
Esker	5	0.25	0.21	3.25	2.61	0.82	0.84
Esker	6	1.00	0.79	4.80	1.86	3.99	2.06
Esker	7	0.53	0.57	1.45	0.56	3.78	5.54
Esker	8	4.86	3.40	5.60	2.60	3.50	2.36
Esker	9	0.66	0.23	2.42	1.31	0.36	0.35

Appendix 5: Mean biting fly abundance (count) from June to August 2016 for three sampling methods across 4 land-cover types: sweep netting (*n* = 2837), tabanid traps (*n* = 540), and Malaise traps (*n* = 80).

		Sweep net		**Tabanid trap**		**Malaise trap**	
Land-cover	**Site #**	**Count**	**S.E.**	**Count**	**S.E.**	**Count**	**S.E**
Marsh	1	7.86	0.69	24.27	12.27	No trap set	
Marsh	2	4.30	0.50	12.67	6.42	No trap set	
Marsh	3	8.94	0.85	15.00	7.45	24.60	24.35
Marsh	4	7.11	0.73	29.93	19.74	No trap set	
Marsh	5	19.51	1.86	7.69	5.95	No trap set	
Marsh	6	8.95	1.21	14.80	8.60	38.00	38.00
Marsh	7	13.65	1.46	41.20	22.31	No trap set	
Marsh	8	14.03	1.53	16.53	8.65	38.80	38.05
Marsh	9	10.11	1.30	10.73	5.95	193.20	191.20
Deciduous	1	4.51	0.60	8.13	4.23	Trap destroyed	
Deciduous	2	2.12	0.30	3.60	1.75	No trap set	
Deciduous	3	5.03	0.79	1.67	1.53	No trap set	
Deciduous	4	0.99	0.20	23.60	19.84	No trap set	
Deciduous	5	2.37	0.30	4.73	2.70	Trap destroyed	
Deciduous	6	2.72	0.39	2.00	1.24	No trap set	
Deciduous	7	1.63	0.25	6.67	3.85	No trap set	
Deciduous	8	7.02	0.59	1.36	1.11	6.20	5.95
Deciduous	9	1.15	0.18	9.07	5.72	23.00	21.76
Pine	1	1.55	0.30	24.67	15.80	60.20	60.20
Pine	2	1.93	0.36	20.67	12.25	No trap set	
Pine	3	2.75	0.44	22.80	13.07	0.60	0.40
Pine	4	1.38	0.22	29.80	17.03	No trap set	
Pine	5	3.78	0.46	9.67	5.52	10.20	10.20
Pine	6	3.24	0.37	9.33	6.02	No trap set	
Pine	7	3.26	0.53	4.00	2.51	No trap set	
Pine	8	4.18	0.50	9.40	4.92	28.00	27.26
Pine	9	3.22	0.52	19.13	12.15	No trap set	
Esker	1	1.59	0.29	28.29	13.39	9.60	9.35
Esker	2	0.76	0.17	6.07	4.62	No trap set	
Esker	3	0.76	0.20	10.60	5.49	No trap set	
Esker	4	1.52	0.24	43.33	24.55	0.40	0.40
Esker	5	0.21	0.11	15.40	9.21	No trap set	
Esker	6	2.46	0.38	7.40	4.10	4.20	4.20
Esker	7	0.46	0.10	11.27	6.59	No trap set	
Esker	8	1.53	0.25	18.93	10.80	No trap set	
Esker	9	0.50	0.12	15.33	7.99	19.80	19.55

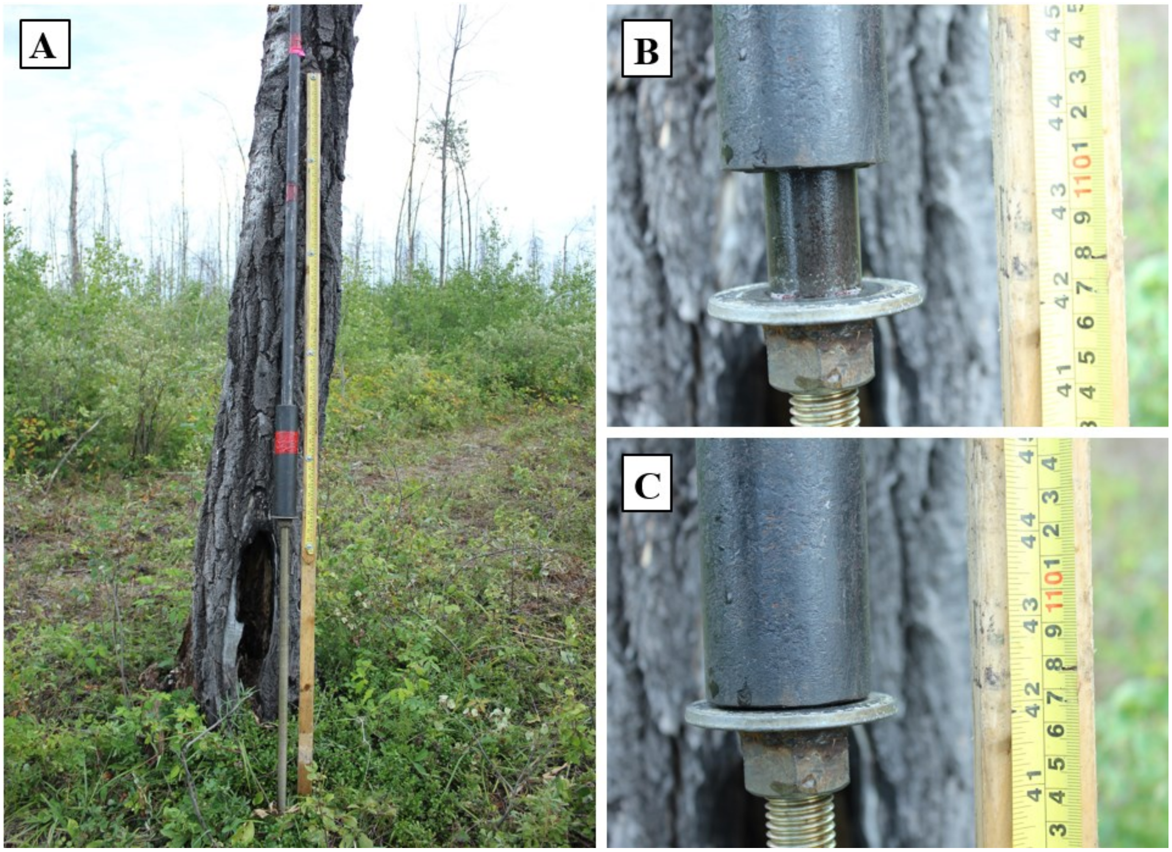
Appendix 6: Tabanid trap developed for this thesis based on design of Thorsteinson et al. (1965). Traps were designed to catch flies from the family Tabanidae (description in section: Field methods).

Appendix 7: Correlation matrix of measured soil properties for 180 soil moisture and bulk density samples and 756 penetration depth measures taken in 4 land-cover types (marsh, deciduous, pine, and esker) in the summer of 2016 near Ronald Lake, Alberta.

	Soil moisture (lab %)	**Bulk density (g/mm^3)**	**Penetration depth (cm)**
Soil moisture (lab %)	1		
Bulk density (g/mm^3)	-0.980	1	
Penetration depth (cm)	0.889	-0.866	1

Appendix 8: Mean penetration depth (*n* = 756), bulk density (*n* = 180), in-situ soil moisture (*n* = 756), and lab measured soil moisture (*n* = 180), for 4 land-cover types (*n* = 36). Soil parameters were measured in July 2016.

		Penetration depth		**Bulk density**		**Moisture in-situ**		**Moisture lab**	
Land-cover	**Site #**	**(cm)**	**S.E.**	**(g/mm^3)**	**S.E.**	**(%)**	**S.E.**	**(%)**	**S.E.**
Marsh	1	42.76	4.76	0.09	0.01	1.00	0	0.89	0.01
Marsh	2	43.76	4.03	0.07	0.01	0.99	0.01	0.91	0
Marsh	3	36.81	4.25	0.04	0	1.00	0	0.94	0
Marsh	4	17.86	1.06	0.12	0	0.81	0.05	0.84	0
Marsh	5	17.55	0.83	0.56	0.09	0.68	0.07	0.57	0.06
Marsh	6	7.31	0.38	0.41	0.05	0.37	0.04	0.53	0.02
Marsh	7	31.60	3.33	0.07	0	0.97	0.03	0.91	0.01
Marsh	8	3.83	0.26	0.86	0.04	0.37	0.03	0.27	0.01
Marsh	9	12.86	0.99	0.48	0.15	0.54	0.04	0.61	0.08
Deciduous	1	3.86	0.18	1.23	0.04	0.11	0.01	0.08	0.01
Deciduous	2	4.19	0.30	1.25	0.04	0.15	0.01	0.10	0.01
Deciduous	3	4.74	0.20	1.10	0.05	0.10	0.01	0.09	0.01
Deciduous	4	4.45	0.24	1.28	0.02	0.10	0.01	0.06	0
Deciduous	5	5.26	0.28	1.01	0.03	0.12	0.01	0.09	0
Deciduous	6	4.36	0.20	0.97	0.03	0.13	0.01	0.09	0.01
Deciduous	7	5.07	0.24	1.17	0.04	0.11	0.01	0.04	0
Deciduous	8	5.43	0.31	0.75	0.07	0.17	0.02	0.19	0.03
Deciduous	9	6.19	0.38	1.22	0.03	0.12	0.01	0.05	0.01
Pine	1	6.86	0.39	1.41	0.05	0.10	0.01	0.04	0.01
Pine	2	6.38	0.38	1.35	0.03	0.11	0.01	0.03	0
Pine	3	5.95	0.28	1.30	0.07	0.10	0.01	0.04	0.01
Pine	4	6.95	0.28	1.44	0.04	0.07	0	0.02	0
Pine	5	6.81	0.35	1.38	0.02	0.07	0.01	0.03	0
Pine	6	5.69	0.75	1.26	0.05	0.11	0.01	0.05	0.01
Pine	7	4.74	0.26	1.23	0.05	0.10	0.01	0.06	0.01
Pine	8	5.57	0.32	1.29	0.02	0.10	0.01	0.11	0.01
Pine	9	4.12	0.23	1.32	0.04	0.11	0.01	0.09	0.01
Esker	1	4.55	0.24	1.34	0.03	0.08	0.01	0.03	0
Esker	2	4.17	0.17	1.35	0.02	0.06	0.01	0.03	0
Esker	3	3.81	0.23	1.27	0.03	0.11	0.01	0.04	0
Esker	4	4.14	0.18	1.30	0.04	0.08	0	0.04	0
Esker	5	3.90	0.21	1.40	0.02	0.05	0.01	0.02	0
Esker	6	4.00	0.22	1.34	0.02	0.07	0.01	0.03	0
Esker	7	3.95	0.16	1.33	0.04	0.06	0.01	0.03	0
Esker	8	3.64	0.20	1.32	0.05	0.08	0.01	0.03	0
Esker	9	4.40	0.20	1.32	0.05	0.10	0.01	0.04	0



Appendix 9: Soil penetrometer developed for this thesis and used to measure soil resistance and strength (description in section: Field methods). Penetrometer body constructed of 2 m length, 1.5” schedule 40 steel pipe, and 1 m length penetration pin constructed of 1” solid steel (A). A sliding weight (7 kg) was dropped from 1.5 m height onto the collar of the penetration pin (B & C). A tape measure fixed to a stake was used to measure penetration depth to the nearest 0.5 cm.

Table 10: Univariate, linear regression models testing the effects of soil parameters (footing), biting fly abundance, and forage biomass on summer bison activity (dung). Candidate, univariate models were used for selection of variables to be used in multivariate, structural equation models. Bison dung counts, soil parameters (soil moisture, bulk density, and penetration depth), biting fly abundance (using two methods: sweep net and tabanid traps), and forage biomass (divided into three groups: graminoids, forbs, and shrubs) were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016.

Model I.D.	**Model form**	***df***	**AIC**	**Δ AIC**
7	Dung ~ Plant Biomass (Total)	2	87.6	-
10	Dung ~ (Graminoid + Shrub Biomass)	2	88.5	0.9
9	Dung ~ (Graminoid + Forb Biomass)	2	89.4	1.8
4	Dung ~ Soil Moisture (Lab)	2	90.7	3.1
3	Dung ~ Soil Moisture (In-situ)	2	90.8	3.3
5	Dung ~ Sweep Net	2	90.8	3.3
2	Dung ~ Soil Bulk Density (Inverse)	2	93.2	5.6
1	Dung ~ Soil Penetration	2	93.4	5.9
8	Dung ~ Graminoid Biomass	2	95.9	8.3
6	Dung ~ Tabanid Trap	2	102.7	15.1

Table 11: Univariate, linear regression models testing the effects of different forms of forage biomass on winter bison activity (dung). Candidate, univariate models were used for selection of variables to be used in multivariate, structural equation models. Bison dung counts and forage biomass (divided into three groups: graminoids, forbs, and shrubs) were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016.

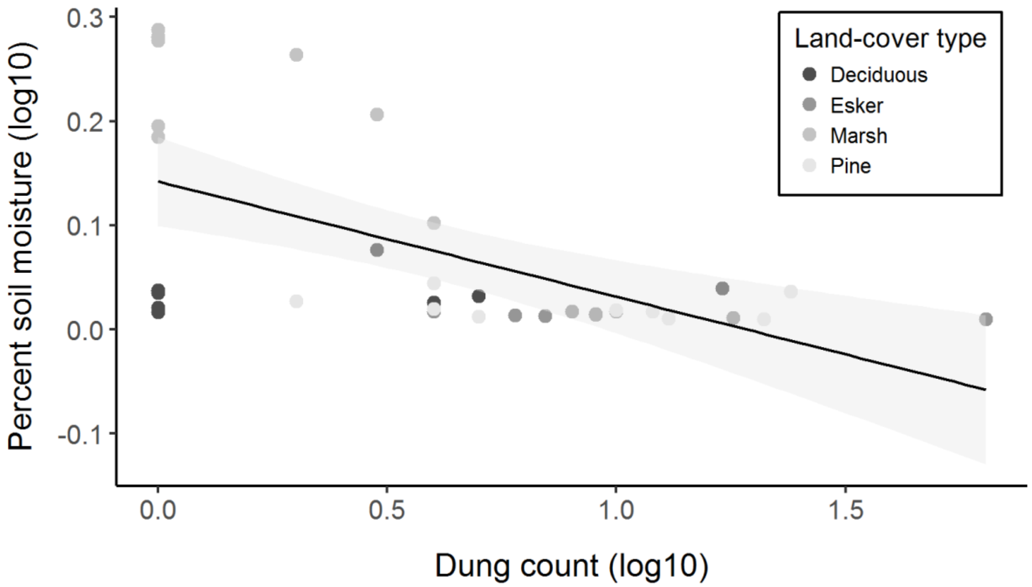
Model I.D.	**Model form**	***df***	**AIC**	**Δ AIC**
4	Dung ~ (Graminoid + Shrub Biomass)	2	101.8	-
1	Dung ~ Vegetation Biomass (total)	2	102.2	0.4
2	Dung ~ Graminoid Biomass	2	102.2	0.4
3	Dung ~ (Graminoid + Forb Biomass)	2	102.3	0.5

Table 12: Structural equation models testing the effects soil parameters (footing), biting fly abundance, and forage biomass on summer bison activity (dung). Candidate, multivariate models were used for selection of best fit structural equation model. Bison dung counts, soil parameters (soil moisture, bulk density, and penetration depth), biting fly abundance (using two methods: sweep net and tabanid traps), and forage biomass (divided into three groups: graminoids, forbs, and shrubs) were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016.

Model I.D.	**Model form**	***df***	**AIC**	**Δ AIC**
3	Dung ~ Soil Moisture (Lab) + Sweep Net + Graminoid Biomass	12	340.5	-
5	Dung ~ Soil Moisture (Lab) + Sweep Net + (Graminoid + Shrub Biomass)	12	344.9	4.3
4	Dung ~ Soil Moisture (Lab) + Sweep Net + (Graminoid + Forb Biomass)	12	347.3	6.7
1	Dung ~ Soil Moisture (Lab) + Sweep Net + Plant Biomass (Total)	12	351.0	10.5
2	Dung ~ Soil Moisture (Lab) + Tabanid Trap + Plant Biomass (total)	12	370.7	30.1

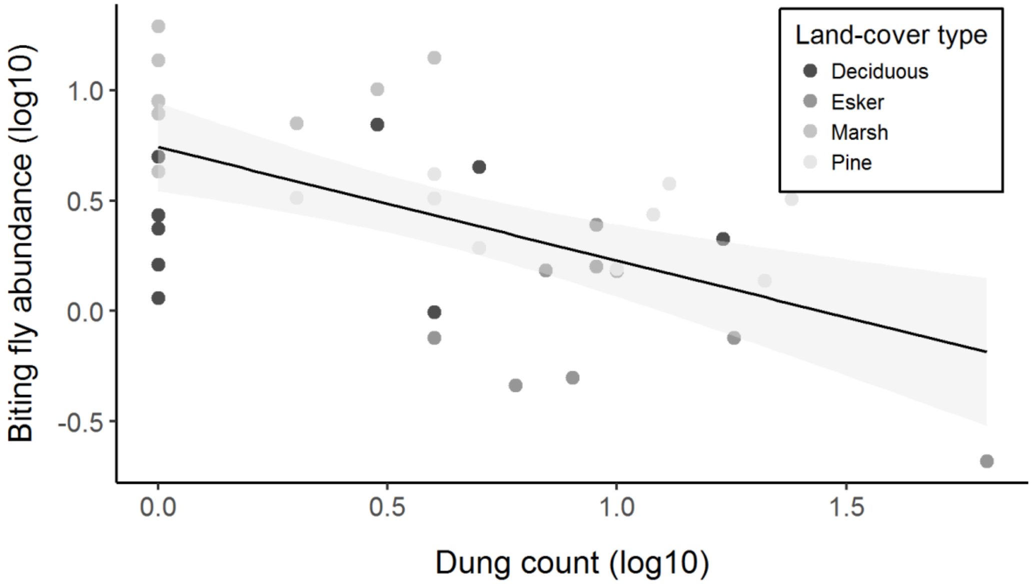
Table 13: Structural equation model testing the effects soil parameters (indirect effect) and forage biomass (direct effect) on winter bison activity (dung). Candidate, multivariate models were used for selection of best fit structural equation model. Bison dung counts, soil parameters (soil moisture, bulk density, and penetration depth), and forage biomass (divided into three groups: graminoids, forbs, and shrubs) were measured in 4 land-cover types near Ronald Lake, Alberta between June and August 2016.

Model I.D.	Model name	*df*	AIC	Δ AIC
5	Dung ~ Graminoid Biomass	3	205	-
1	Dung ~ Soil Moisture (Lab) + Graminoid Biomass	6	270.2	65.2
2	Dung ~ Soil Moisture (Lab) + (Graminoid + Forb Biomass)	6	281.6	76.6
3	Dung ~ Soil Moisture (Lab) + (Graminoid + Shrub Biomass)	6	282.3	77.3
4	Dung ~ Soil Moisture (Lab) + Plant Biomass (Total)	6	288.1	83.1

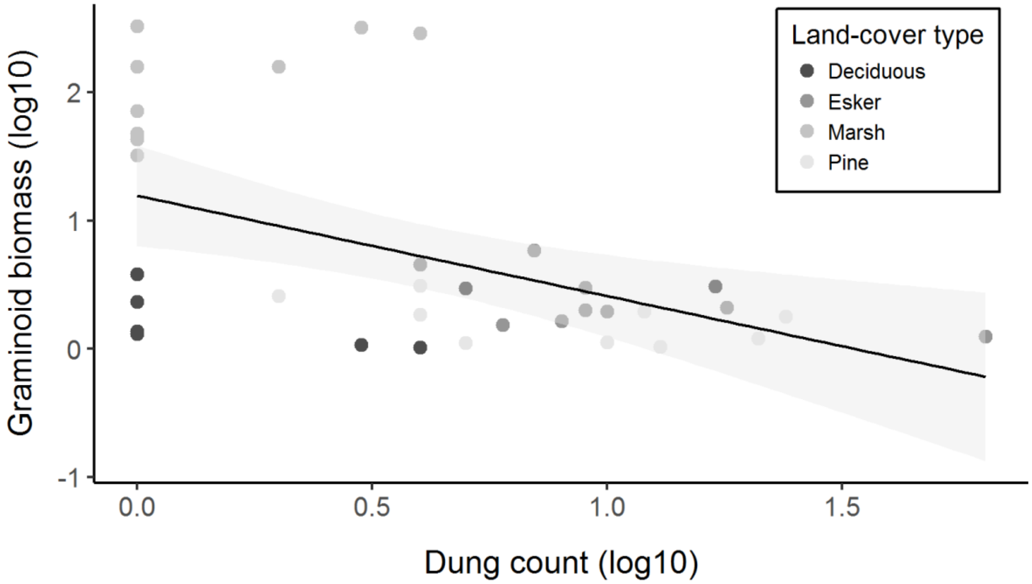


Appendix 14: Linear regression of the effect of soil moisture content on bison summer activity (dung). Soil moisture content and dung counts were measured from June to August 2016 for 4 land-cover types (*n* = 36) near Ronald Lake, Alberta.

A linear regression of summer dung count and percent soil moisture. Bison summer activity (dung) was significantly negatively related to soil moisture ($F_{1,34} = 16.84$, S.E. = 0.83, $R^2 = 0.33$, $p < 0.001$).

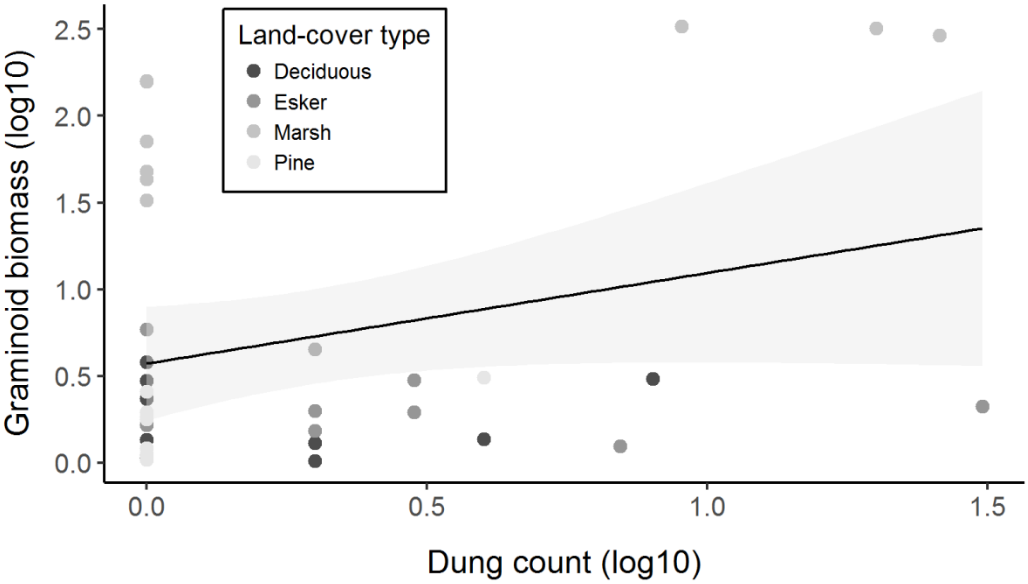


Appendix 15: Linear regression of the effect of biting flies: tabanids, mosquitos, and midges (sweep net total) on bison summer activity (dung). Biting fly abundance and dung counts were measured from June to August 2016 for 4 land-cover types ($n = 36$) near Ronald Lake, Alberta.
A linear regression of summer dung count and biting fly abundance. Bison summer activity (dung) was significantly negatively related to biting fly abundance ($F_{1,34} = 16.64$, S.E. = 0.83, $R^2 = 0.33$, $p < 0.001$).



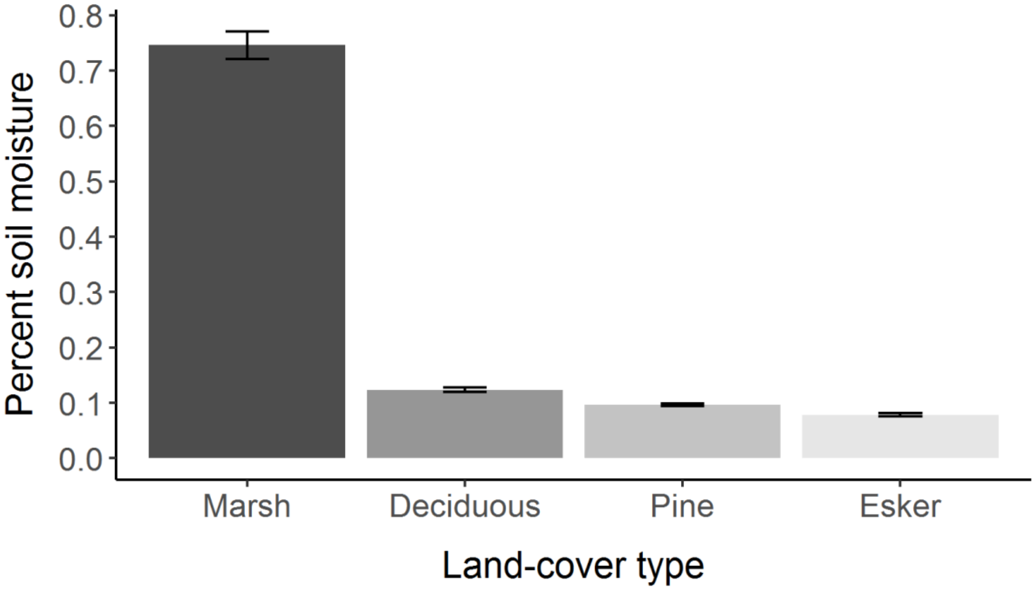
Appendix 16: Linear regression of the effect of graminoid biomass on bison summer activity (dung). Graminoid biomass and dung counts were measured in August 2016 for 4 land-cover types (*n* = 36) near Ronald Lake, Alberta.

A linear regression of summer dung count and graminoid biomass. Bison summer activity (dung) was significantly negatively related to graminoid biomass ($F_{1,34} = 9.99$, S.E. = 0.89, $R^2 = 0.45$, $p = 0.003$).

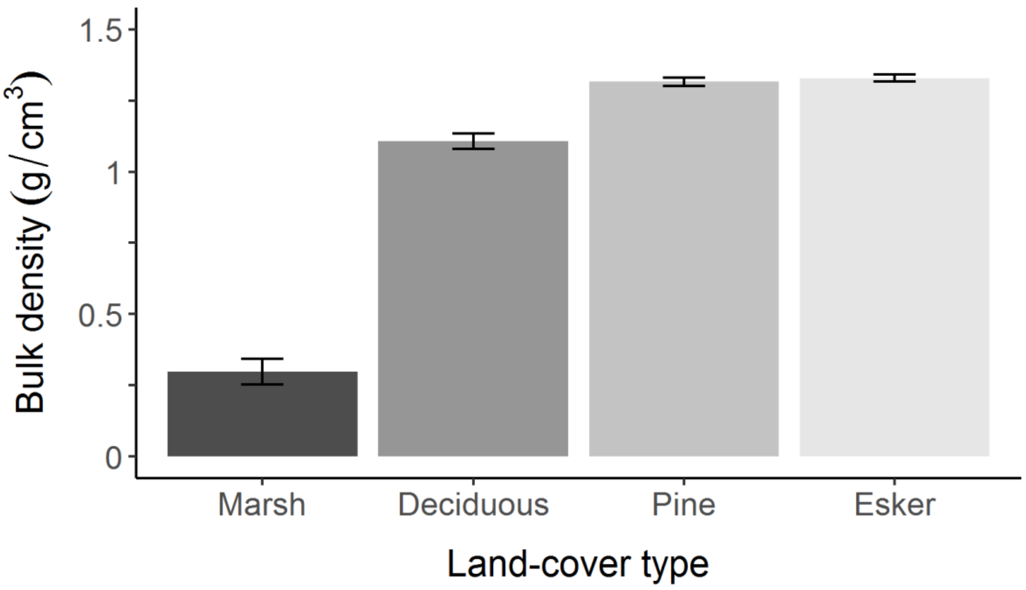


Appendix 17: Linear regression of the effect of graminoid biomass on bison winter activity (dung). Graminoid biomass and dung counts were measured from June to August 2016 for 4 land-cover types (*n* = 36) near Ronald Lake, Alberta.

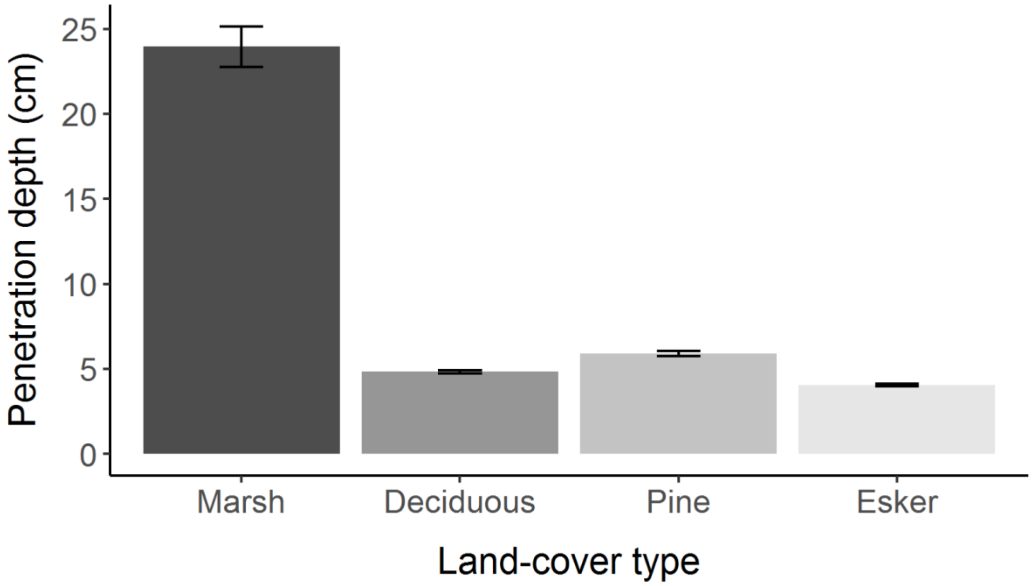
A linear regression of winter dung count and graminoid biomass. Bison winter activity (dung) was not significantly related to graminoid biomass ($F_{1,34}$ = 2.92, SE = 0.43, R^2 = 0.08, *p* = 0.097).



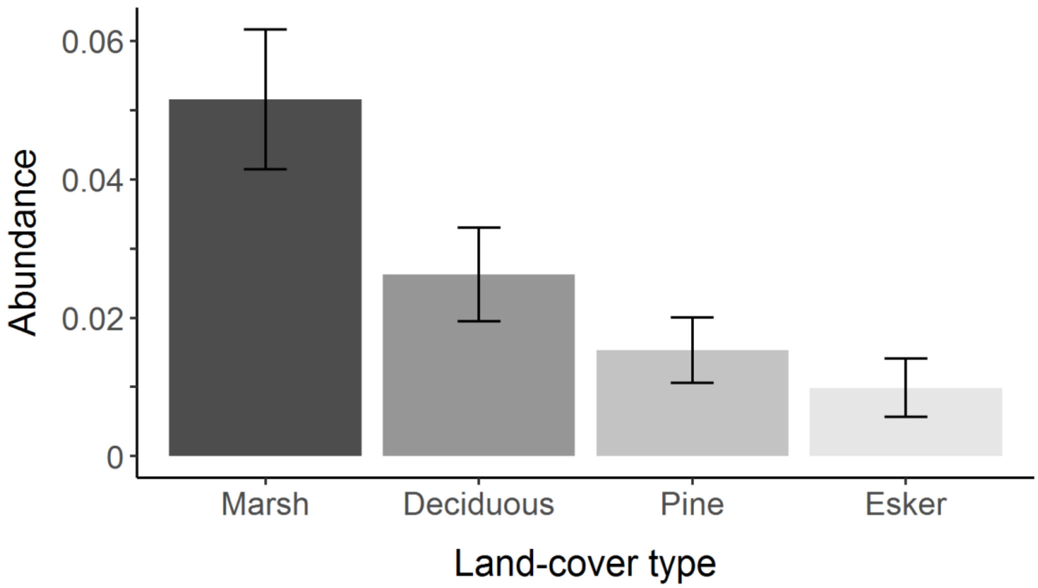
Appendix 18: Mean percent soil moisture content for 4 land-cover types near Ronald Lake, Alberta (*n* = 756). Soil moisture content was measured using a soil moisture probe (TDR) in July 2016.



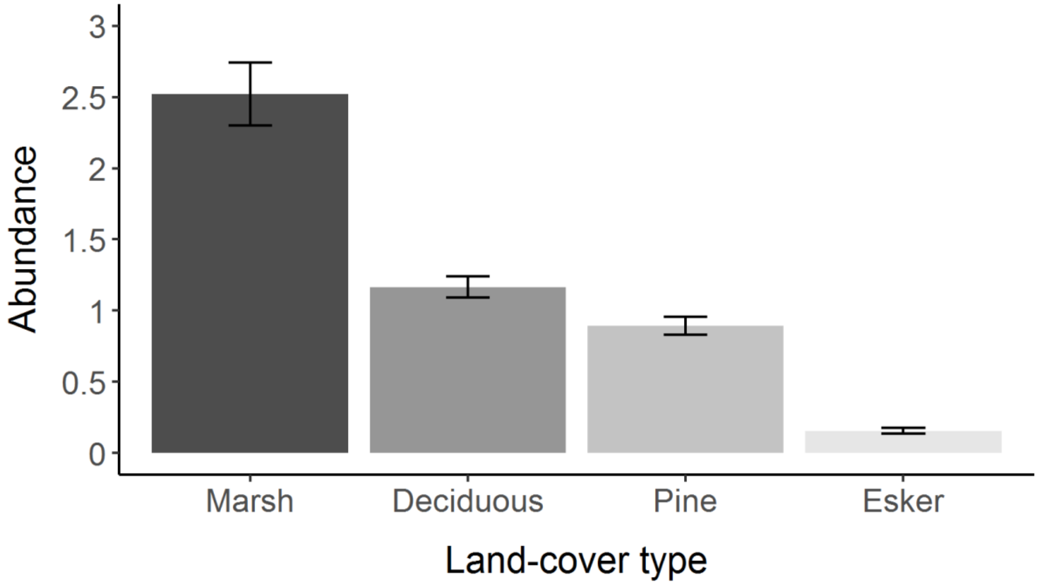
Appendix 19: Mean soil bulk density estimate for 4 land-cover types near Ronald Lake, Alberta (*n* = 180). Soil bulk density was measured using a 577 cm^3 soil core measuring 15 cm in height x 7 cm in diameter. Soil cores were dried in a drying oven at 95°C for 48 hours and weighed.



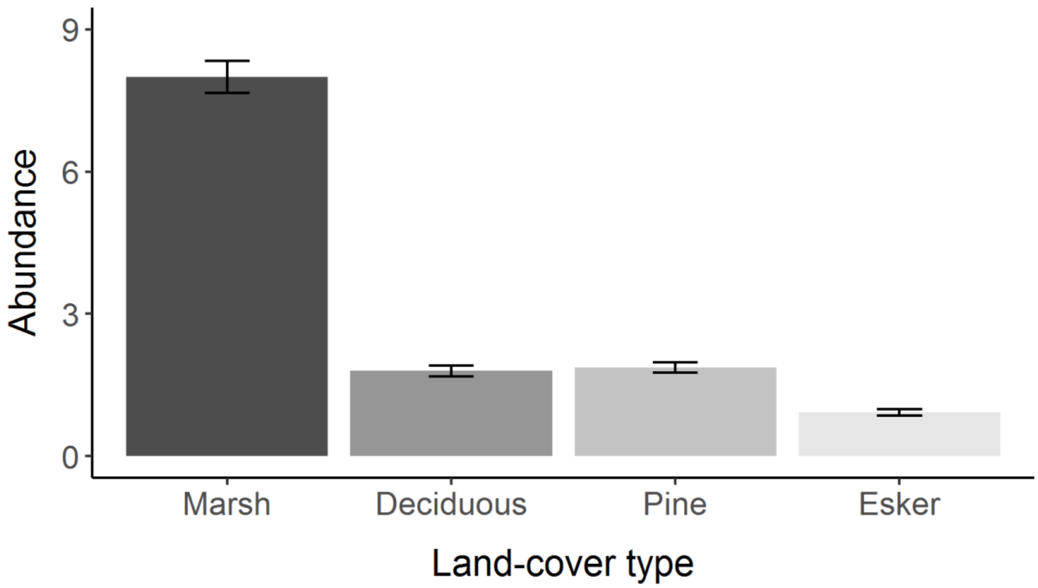
Appendix 20: Mean soil penetration depth for 4 land-cover types near Ronald Lake, Alberta (*n* = 756). Soil penetration depth was measured using a custom-designed soil penetrometer described in Appendix 9.



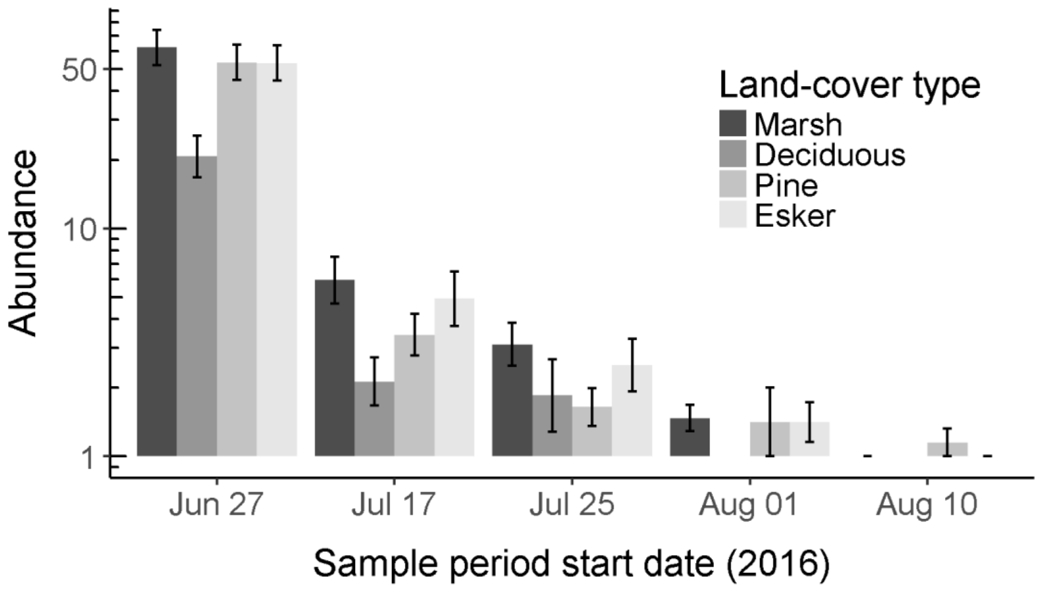
Appendix 21: Mean tabanid (Diptera: Tabanidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of horse flies (tabanids) caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (*n* = 2837).



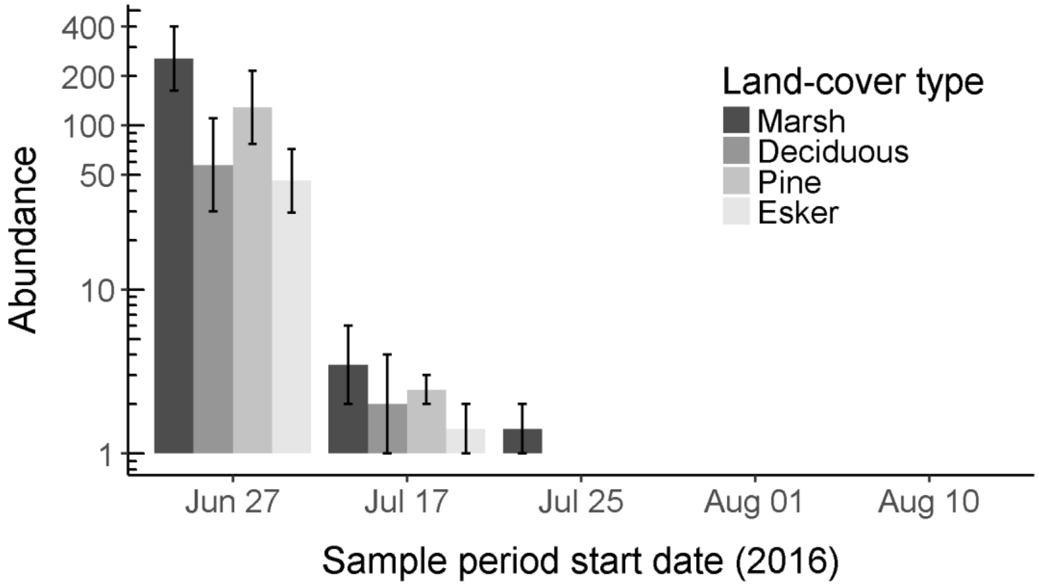
Appendix 22: Mean mosquito (Diptera: Culicidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of mosquitos caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (*n* = 2837).



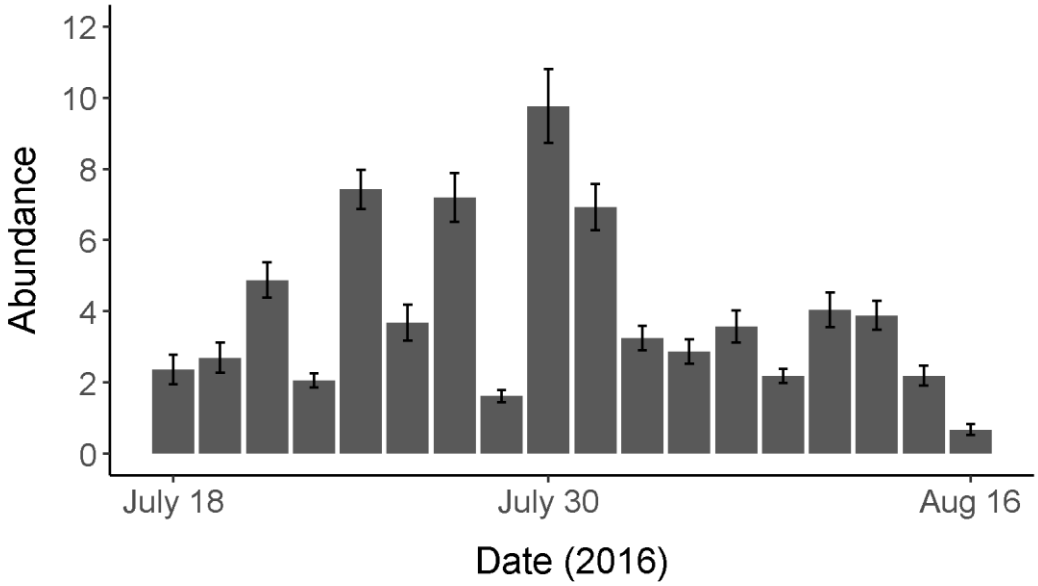
Appendix 23: Mean midge (Diptera: Ceratopogonidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of midges caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (*n* = 2837).



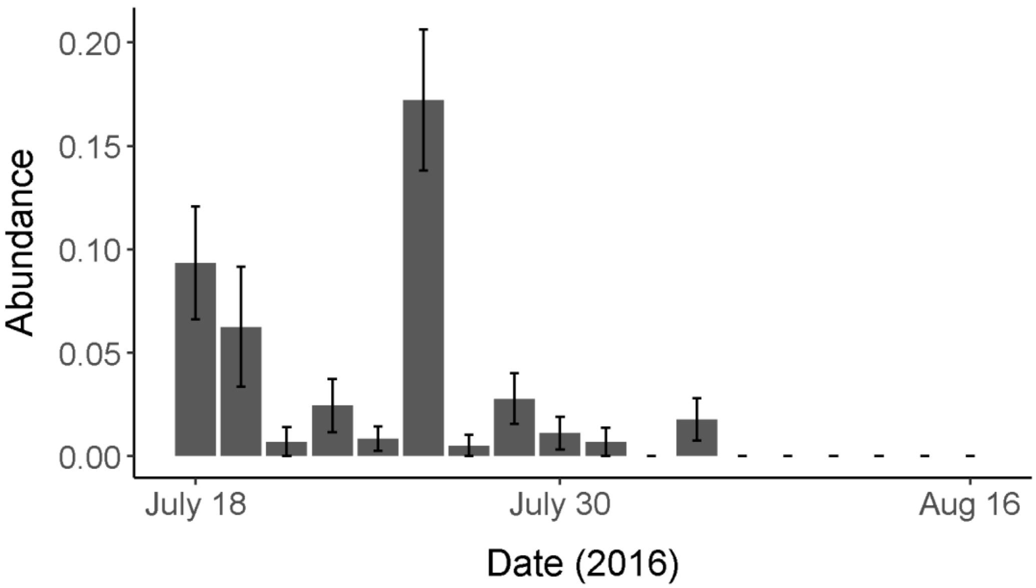
Appendix 24: Mean tabanid (Diptera: Tabanidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of tabanids caught in tabanid traps over 5, 7-day periods (*n* = 540).



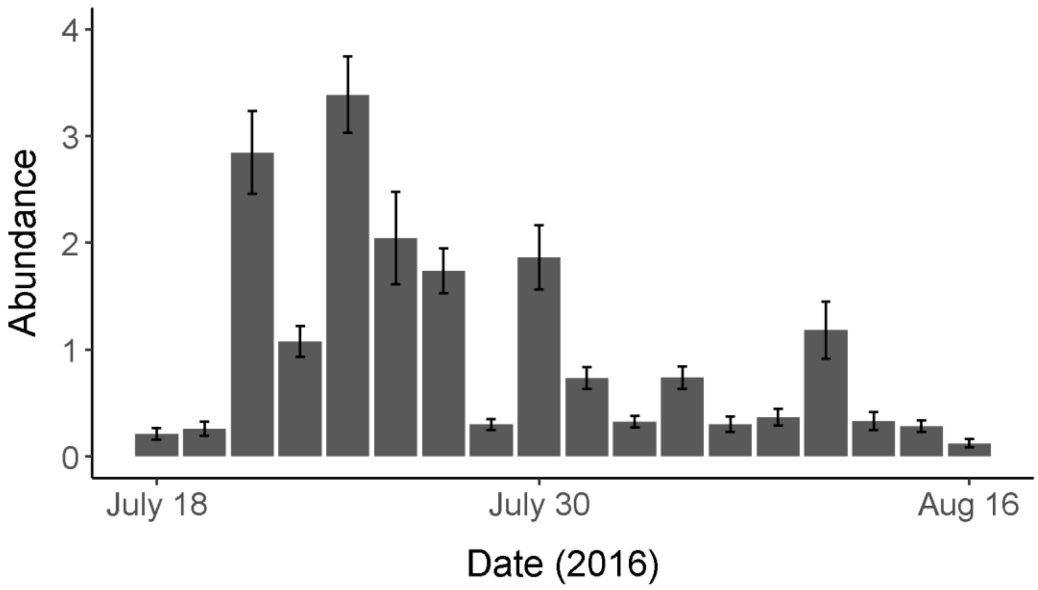
Appendix 25: Mean tabanid (Diptera: Tabanidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of tabanids caught in Malaise traps over 5, 7-day periods (*n* = 36).



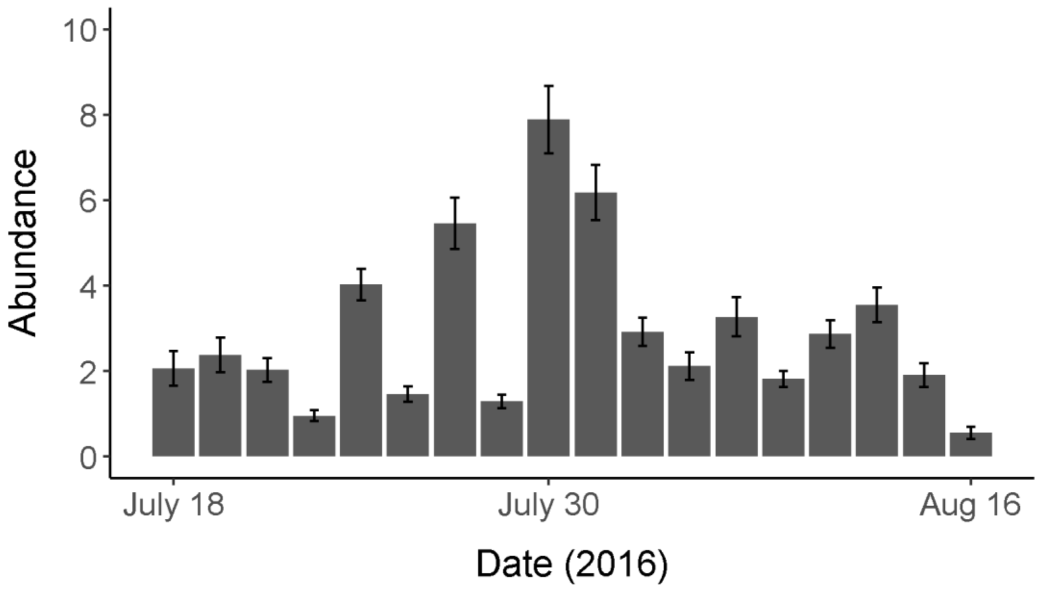
Appendix 26: Mean abundance of tabanids, mosquitos, and midges (total) from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of flies caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (n = 2837).



Appendix 27: Mean tabanid (Diptera: Tabanidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of horse flies caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (*n* = 2837).



Appendix 28: Mean mosquito (Diptera: Culicidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of horse flies caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (n = 2837).



Appendix 29: Mean midge (Diptera: Ceratopogonidae) abundance from June to August 2016 for 4 land-cover types near Ronald Lake, Alberta. Graph is of mean number of horse flies caught during a single sweep net event which consisted of 30 sweeps while walking a 50 m transect (*n* = 2837).