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Evaluating trade-offs between forage, biting flies, and footing on habitat selection by wood bison (*Bison bison athabascae*)

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Abstract: Habitat selection is a behavioural process that ultimately affects animal fitness. Forage availability and predation risk are often studied in the context of habitat selection for large ungulates, while other biological and environmental factors such as insect harassment and footing are less studied. Here we examine trade-offs in summer habitat selection between forage availability for wood bison (*Bison bison athabascae* Rhoads, 1898) with that of biting-fly harassment and soil firmness, which affects activity budgets and predation risk, respectively, and contrast this to winter when flies are absent and soils frozen. Using path analysis, we demonstrate that graminoid availability was not related to habitat selection in summer, but was positively related to habitat selection in winter. Habitat selection in summer was negatively related to biting-fly abundance and positively related to firmer footing. Our results suggest that bison observe trade-offs in summer between maximizing forage intake and minimizing harassment from that of biting flies, while avoiding areas of soft substrates that affect locomotion and vulnerability to predators. In contrast, during the winter, bison focus on areas with greater graminoid availability. Although forage is a key aspect of habitat selection, our results illustrate the importance of considering direct and indirect effects of multiple biological and environmental factors related to ungulate habitat selection.

Key words: wood bison, *Bison bison athabascae*, ungulate, habitat selection, forage, insect harassment, footing.

Résumé : La sélection d'habitat est un processus comportemental qui, ultimement, influence l'aptitude des animaux. La disponibilité de nourriture et le risque de prédation sont souvent étudiés dans le contexte de la sélection d'habitat pour les grands ongulés, alors que d'autres facteurs biologiques ou environnementaux, comme le harcèlement par les insectes et la qualité de la surface du sol, le sont moins. Nous examinons les compromis dans le processus de sélection d'habitat en été par le bison des bois (*Bison bison athabascae* Rhoads, 1898) entre la disponibilité de nourriture et le harcèlement par des mouches piqueuses et la fermeté du sol, qui ont une incidence, respectivement, sur les budgets d'activité et le risque de prédation, et les comparons à ce qui se passe l'hiver, quand les mouches sont absentes et le sol est gelé. En utilisant l'analyse causale, nous démontrons que la disponibilité de graminoïdes n'est pas reliée à la sélection d'habitat en été, mais présente une relation positive avec la sélection en hiver. La sélection d'habitat en été est négativement reliée à l'abondance de mouches piqueuses et positivement reliée à la fermeté de la surface du sol. Nos résultats donnent à penser que les bisons font des compromis en été entre la maximisation de l'ingestion de nourriture et la minimisation du harcèlement par les mouches piqueuses, tout en évitant les zones de substrats mous qui influencent leur locomotion et leur vulnérabilité aux prédateurs. En comparaison, durant l'hiver, les bisons se concentrent sur des zones caractérisées par une plus grande disponibilité de nourriture. Si la nourriture est un aspect clé de la sélection d'habitat, nos résultats illustrent l'importance de tenir compte des effets directs et indirects de plusieurs facteurs biologiques et environnementaux associés à la sélection d'habitat chez les ongulés. [Traduit par la Rédaction]

Mots-clés : bison des bois, *Bison bison athabascae*, ongulé, sélection d'habitat, nourriture, harcèlement par les insectes, surface du sol.

Introduction

Habitat selection is a behavioural process by which animals select resources, thereby affecting acquisition and competition for food, mates, reproductive success, and ultimately fitness (Schaefer and Messier 1995; Dussault et al. 2005; Long et al. 2016). For ungulates, habitat selection is generally regulated via bottom-up constraints such as primary production (Ripple and Beschta 2006; Dupke et al. 2017) and top-down mechanisms such as predation (Hebblewhite and Merill 2009; Ahmad et al. 2016). The presence or perception of predation risk by large carnivores can influence ungulate foraging decisions and limit selection of forage-dense patches (Brown et al. 1999; Fortin et al. 2005; Hamel and Côté 2007; Acebes et al. 2013). Balancing the essential need of food with the risk of becoming food thus influences fitness and can represent a fundamental trade-off that affects foraging behaviour in ungulates (Brown et al. 1999; Riginos 2015; Long et al. 2016).

In addition to biotic elements of forage and predation, habitat selection for ungulates, such as caribou (*Rangifer tarandus* (Linnaeus, 1758)), is influenced by harassment from biting flies that affect foraging behaviour and spatial distributions (Helle et al. 1992; Hagemoen and Reimers 2002; Witter et al. 2012). Furthermore, selection by ungulates is influenced by abiotic–animal interactions, such as terrain ruggedness (Carbyn and Trottier 1987; Shepard et al. 2013) and snow depth (Parker et al. 1984; Mysterud

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et al. 1997; Pepin et al. 2009; Robinson and Merrill 2012), that affect energy expenditures and predation risk. The addition and interaction of biotic, abiotic, bottom-up, and top-down factors therefore contribute to a better understanding of the dynamic nature of habitat selection.

Wood bison (*Bison bison athabascae* Rhoads, 1898) diet is composed primarily of graminoids (particularly sedges), which comprise >95% of winter diet (Larter and Gates 1991; Strong and Gates 2009; Jung et al. 2015). Summer diet is more diverse, being composed of greater proportions of forbs and shrubs (Bergmann et al. 2015; Jung et al. 2015; Steenweg et al. 2016; Leonard et al. 2017). Bison habitat selection in relation to forage quantity and quality (Strong and Gates 2009; Jung et al. 2015; Leonard et al. 2017) and land-cover types (Schoenecker et al. 2015; DeMars et al. 2017; Jung et al. 2018) have been studied. Correspondingly, bison show high selection of sedge marshes, relative to other habitat types, in both winter and summer (Campbell and Hinks 1983; Larter and Gates 1991; Strong and Gates 2009), yet show higher selection of marshes in winter than in summer (DeMars et al. 2017). Although forage quantity, quality, and distribution are key elements of bison habitat selection, little is known regarding the simultaneous interactions between biotic and abiotic conditions that influence bison foraging decisions. In this study, we investigate the direct and indirect effects of multiple biological and environmental factors, including forage quantity, harassment from biting flies, and soil firmness (footing), on bison habitat selection.

Marshes in boreal wetlands, relative to bogs and fens, contribute significantly to aboveground net primary productivity (NPP), particularly graminoids (Gorham 1974; Thormann et al. 1997), resulting in large quantities of forage for ungulates (Larter and Gates 1991; Fortin et al. 2003; Merkle et al. 2015). In addition to high primary production, wetlands are breeding sites for the most common and widespread biting, blood-sucking flies in boreal environments, including flies from the families Simuliidae, Culicidae, Ceratopogonidae, and Tabanidae (Lewis 1987; Kozlov et al. 2005), which are known to affect the health, behaviour, and habitat selection of ungulates (Helle and Tarvainen 1984; Downes et al. 1986; Rolf and Reimers 2002). During spring and summer months, marshes are composed of wet, soft soils or peat that we hypothesize can have similar effects to that of snow cover in winter months. We hypothesize that soft soils, like deep snow cover, can affect the movement of ungulates (Telfer and Kelsall 1979; Mysterud et al. 1997; Courbin et al. 2017) by increasing energetic locomotion costs (Parker et al. 1984; Telfer and Kelsall 1984; Fancy and White 1987) and predation risk from large carnivores (Schaefer and Messier 1995; Robinson and Merrill 2012). The interaction of forage distribution, biting flies, and soft soil may directly and indirectly affect the energy balance of ungulates and represent trade-offs between maximizing forage returns in forage-dense patches (i.e., marshes) and minimizing harassment from biting flies, energetic costs, and predation risk.

Although trade-offs between foraging, biting flies, and snow depth have been studied in the context of habitat selection for several ungulates, they have rarely been studied for bison (Morgan 1987). Studies have shown ungulate adaptations for travel in snow (Telfer and Kelsall 1979, 1984), and others have shown habitat selection in relation to snow (Parker et al. 1984; Schaefer and Messier 1995; Robinson and Merrill 2012); however, movement and (or) habitat selection in relation to soft soil, or footing, has rarely been examined but may be an important factor for bison (Carbyn and Trottier 1987). A more comprehensive investigation is needed to provide a better understanding of the factors that contribute to ungulate habitat selection, including factors which affect foraging behaviour, predator avoidance, and fitness. In this study, we examined the direct and indirect effects of (*i*) forage biomass, (*ii*) biting-insect abundances, and (*iii*) soil firmness, or footing, on bison habitat selection in land-cover types used by bison. For wood bison, marshes are areas of high forage quantity; however, we expected to find summer bison selection of sedge marshes to be lower than winter due to (*i*) greater distribution of graminoids and alternative forage opportunities (forbs and shrubs) found in other habitat types, (*ii*) greater biting-insect abundance in marshes, and thus harassment, and (*iii*) softer footing in marshes. Figures 2*a* and 2*b* show a representation of our model predictions of the direct and indirect effects of forage, flies, and footing on bison summer and winter habitat selection, respectively.

Materials and methods

Study area

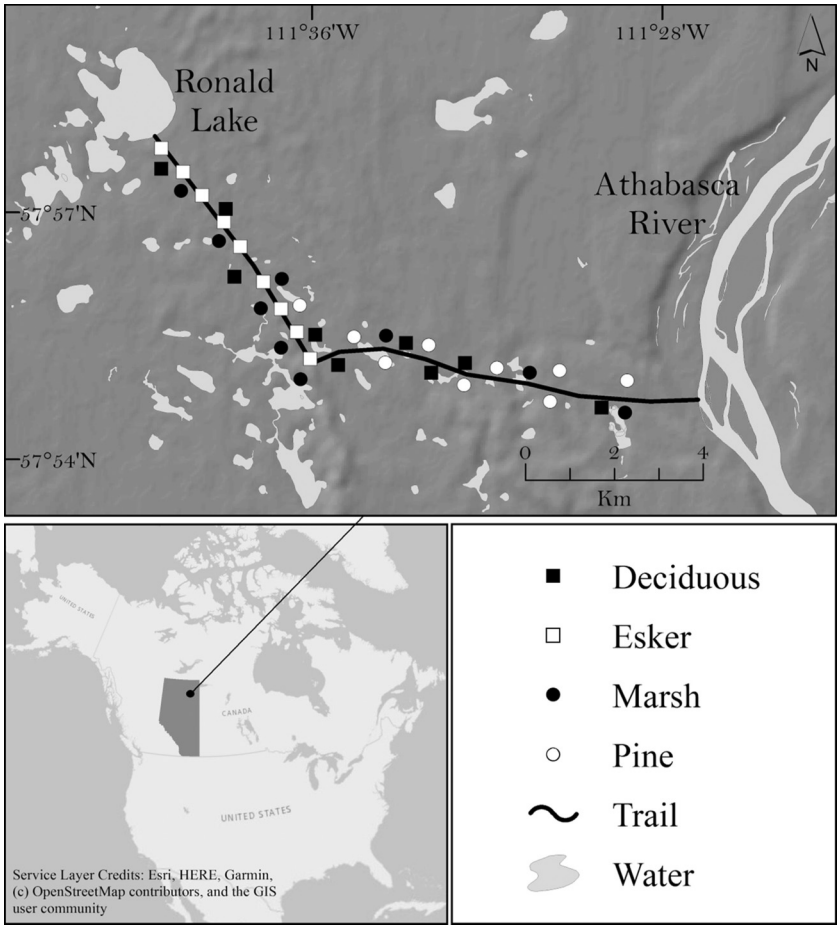
We selected the study area based on the known distribution of bison in the Ronald Lake area (Tan et al. 2014; DeMars et al. 2017) of northeast Alberta, Canada, ~15 km south of Wood Buffalo National Park. Field sampling sites were selected along a 16 km, poorly maintained trappers trail, southeast of Ronald Lake (59.97°N, 111.67°W). The area of Ronald Lake marks the approximate centre of the known home range of the herds, which extends ~40 km to the north and south and ~30 km and ~15 km from western and eastern extents, respectively. The nearest weather station is in Fort Chipewyan, Alberta, where mean annual temperature is –1.5 °C and mean annual precipitation is 366 mm (Environment and Climate Change Canada 2018). Elevation in the study area varies between 222 and 325 m above sea level. Land-cover types include a mosaic of upland trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb.), and mixed-wood forests, as well as wetlands that include meadow and emergent marshes, treed swamps, and poor- to rich-treed and non-treed fens and bogs (Ducks Unlimited Canada 2016). 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. Large tracts of burned forests and wetlands exist in the Ronald Lake area, notably burned area from the 2011 Richardson fire. 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 clearcuts, seismic lines, exploratory well pads, and temporary or seasonal roads that occur mostly in the southern parts of the study area (Tan et al. 2014).

Site selection

Our study occurred between 12 June and 25 August 2016. Three land-cover types frequently used by Ronald Lake bison (Tan et al. 2014; DeMars et al. 2017) were selected for study: meadow marsh (1.2% of study area), deciduous forest (35.3%), and jack pine forest (12.7%). In addition to these three land-cover types, a large esker (0.3% of area) measuring ~15 km in length was selected for study. The esker represents a high-elevation landform that is exposed to westerly winds, which we hypothesized to be a potential refuge for bison from biting insects. Henceforth, we refer to land cover and landform collectively as land cover for simplicity.

Nine representative field sites for each land-cover type were randomly selected adjacent to and not farther than 1 km from the trail (n = 36) using Ducks Unlimited Enhanced Wetland Classification (Ducks Unlimited Canada 2016) in ArcGIS version 10.3 (ESRI 2014) (Fig. 1). To avoid potential misclassification and to be large enough to accommodate our field sampling design, only sites having a minimum patch size of 1 ha (100 m × 100 m) were considered. Sites were ground-truthed on the first visit. Because the esker was a single, linear landform, the nine sampled esker sites were equally spaced along a 6 km section of the esker and thus spaced ~750 m apart.

Fig. 1. Location of study area in northeastern Alberta (inset map), Canada, and the location of study sample sites in four land-cover types. Study sites were accessed using an existing trappers trail. Sample sites for deciduous, pine, and marsh were randomly selected and no farther than 1 km from the trail; sites for esker were equally spaced along a 6 km section of the esker. Note that some land-cover types were clustered due to natural concentration of those features in an area. Sample site locations and trail were recorded using a handheld GPS unit and subsequently mapped as a data layer using the GPX To Features (Conversion) tool in ArcMap (ESRI 2014). Base-map image is digital elevation model (DEM) converted to hillshade using the Hillshade (Spatial Analyst) tool in ArcMap (ESRI 2014). DEM data are from Alberta Environment and Sustainable Resource Development 2013. Inset base map is Light Grey Canvas Map. Sources: Esri, DeLorme, HERE, MapmyIndia.



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Field sampling

At each site, we established 60 m transects for soil, biting fly, and forage sampling. To reduce edge effects, we located all transects >30 m from any visible edge. We established transects along a north–south bearing, except in marshes where directionality and proximity to other land-cover types required an alternate bearing. In addition to the 60 m transects for soil, biting fly, and forage sampling, at each site we established three 100 m × 4 m transects adjacent to each other (0.12 ha area) for bison dung surveys. The 60 m transect for soil, biting fly, and forage sampling was established in the centre of the three 100 m × 4 m, bison dung transects, thus overlapped.

We used bison dung counts as an index of habitat selection between land-cover types and assumed dung counts to be directly proportional to bison selection of patches. Two observers surveyed transects and counted bison dung between 16 and 18 August. Surveying consisted of each observer independently walking transects and searching for bison dung. Counts between the two observers where compared. When discrepancies arose between counts, the observers re-surveyed transects until accurate counts of all bison dung were completed. We divided bison dung counts into two categories (summer dung and winter dung) being differentiated by texture and appearance: summer dung were more plop-shaped and winter dung were more clumped (L.N. Carbyn and T.C. Stitsen, personal observation). We assumed the detectability of dung to vary between land-cover types (Brodie 2006; Theuerkauf and Rouys 2008; Jung and Kukka 2016), thus extensive effort was given to detect dung where vegetation cover is dense and detectability low such as that in marshes. A single dung plop (summer) or pile of clumps (winter) was recorded as a single dung count. Moderately and heavily decayed dung was counted, but counts were not used in analyses due to the likelihood of dung being >1 year old. Results of summer and winter dung counts and corresponding habitat selection for marsh, deciduous forest, and pine forest corroborated with DeMars et al. (2016) and DeMars et al. (2017), where bison GPS locations were used to assess summer and winter habitat selection (Table 1). Thus, local counts reflect independent assessments of habitat selection.

We estimated biomass of plants at each site by species, growth form, or genera at the end of the growing season between 9 and 15 August. We alternatingly set nine equally spaced 0.5 m^2 circular quadrats at a 2 m distance from the 60 m transect line starting at 0 m and ending at 60 m. In total, we sampled 324 quadrats for biomass (4 landcover types × 9 replicate sites × 9 quadrats per site/transect). We clipped all vegetation within quadrats, with graminoids and forbs cut 2.5 cm above ground, and only new growth of shrubs. Creeping shrubs, such as bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), lichens, mosses, and trees were not collected due to (*i*) un-

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Table 1. Standardized β estimates from zero-inflated negative binomial models using wood bison (*Bison bison athabascae*) dung counts from this study (n = 36 sites) and resource selection function models from DeMars et al. (2016) and DeMars et al. (2017) for two different land-cover types for both summer and winter seasons.

Land-cover type	Season	β	SE	p	Source
Marsh	Summer	–1.43	0.45	0.002	This study
		0.68	0.03	<0.001	DeMars et al. 2016
		0.85	0.04	<0.001	DeMars et al. 2017
	Winter	1.45	0.32	<0.001	This study
		3.32	0.03	<0.001	DeMars et al. 2016
		3.36	0.03	<0.001	DeMars et al. 2017
Pine	Summer	1.24	0.23	<0.001	This study
		0.74	0.01	<0.001	DeMars et al. 2016
		0.75	0.03	<0.001	DeMars et al. 2017
	Winter	–1.39	0.65	<0.001	This study
		–1.15	0.03	<0.001	DeMars et al. 2016
		–0.53	0.06	<0.001	DeMars et al. 2017

Note: In all models, the land-cover category "deciduous" was the reference category.

likeliness of being a component of bison diet (Bergmann et al. 2015; Jung et al. 2015; Leonard et al. 2017) or (*ii*) very few occurrences within plots. We separated clipped vegetation by species, growth form, or genera, dried vegetation in a drying oven at 60° C for 48 h, and weighed vegetation using a balance (±0.01). For final analysis, we lumped vegetation into one of three growth forms based on previous studies of bison diet composition: graminoids, forbs, and shrubs (Bergmann et al. 2015; Jung et al. 2015; Leonard et al. 2017).

We used three methods to sample biting flies between 18 June and 16 August: (1) sweep netting, (2) tabanid traps (modified Manitoba traps following Bracken and Thorsteinson 1965), and (3) Malaise traps. All methods performed well at capturing biting insects of interest; however, due to potential sampling bias and lack of model support observed with tabanid (n = 504 samples) and Malaise traps (n = 80 samples), only our sweep net methods are described here. Sweep net sampling started 18 July and ended 16 August. Ten sampling days occurred in July and eight sampling days occurred in August. We randomly selected 16 sites for sampling each day (4 sites per land-cover type). A site was sampled at a minimum frequency of 2 days. Specifically, sweep nets measuring 38 cm in diameter were used to make 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. We recorded the total number of flies caught and released flies. In total, we conducted 2837 sweep net transects during 254 site visits at the 36 sites. We counted and used in our analyses only biting flies from four families: Tabanidae (horse fly and allies), Simuliidae (black fly and allies), Culicidae (mosquito and allies), and Ceratopogonidae (biting midges and allies).

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 (Hernanz et al. 2000; Vaz and Hopmans 2001). We measured three soil properties as an index of footing conditions: (1) soil bulk density, (2) soil moisture content, and (3) soil penetration depth. In total, we obtained 180 soil bulk density, 756 soil moisture, and 756 soil penetration depth measurements along the 60 m transect. Only methods for soil moisture content are described due to greater model support, although all three soil properties were highly correlated. As such, only methods for soil moisture content are described. Specifically, we obtained three soil moisture content measurements, using a PR2 soil moisture probe (Delta-T Devices Ltd. 2004), at seven locations equally spaced along the main 60 m transect starting at 0 m and ending at 60 m at each site.

Data analyses

We assessed all data for assumptions of parametric tests using Shapiro–Wilk's test of normality, Bartlett's test of variance, fitted residuals, and normal q–q plots. We applied a $\log_{10}$ transformation after adding a constant of 1 for data that violated assumptions for parametric tests. We performed all analyses in Stata release 15 (StataCorp LLC 2017).

We used zero-inflated negative binomial (ZINB) model to estimate bison habitat selection based on dung counts. In these models, land-cover type was a single variable with four categories and was also the independent variable, and summer and winter bison dung counts were each a dependent variable. We used univariate, general linear models (GLM) to compare soil moisture, biting-fly abundances, and forage biomass between land-cover types. In these models, land-cover type was a single variable with four categories and was also the independent variable, and soil moisture, biting-fly abundances, and forage biomass were each a dependent variable. The land-cover category marsh was withheld in all models. Finally, we used path analyses, a form of structural equation modeling (SEM), to estimate the direct and indirect pathways in which soil moisture, biting-fly abundance, and forage biomass affect bison summer and winter habitat selection. A path analysis is an appropriate model when it is desirable to investigate relationships between both independent and depended variables in which strong relationships exist (Bagozzi and Youjae 1989; Acock 2013). A series of global path analyses were fit to test the different measures of footing (soil bulk density, moisture content, and penetration depth) and biting-fly abundance (sweep net, tabanid trap, and Malaise trap methods) on summer and winter bison activity (dung). Where appropriate, we used Akaike's information criterion and Pearson's r^2 to compare support between methods and strength of models.

Results

Bison habitat selection based on dung counts

We found that marshes had lower summer dung counts compared with all land-cover types and significantly differed from deciduous forests, pine forests, and the esker. Marshes had greater winter dung counts compared with all land-cover types and significantly differed from that of deciduous forests, pine forests, and the esker (Table 2). These results suggest that bison selection of marshes differ depending on season. In addition, we found that summer dung counts on the esker were greater than all land-cover types, suggesting greater bison selection of the esker than other land-cover types during summer.

Comparing soil properties, biting-fly abundances, and forage biomass to land-cover types

We found that marshes had softer footing relative to all land-cover types with greater soil moisture content. We found that soil moisture content was strongly, positively correlated with soil penetration depth (r^2 = 0.942, SE = 0.006, p < 0.001), and strongly, negatively correlated with bulk density (r^2 = 0.921, SE = 0.005, p < 0.001). In addition, soil penetration depth was strongly, negatively correlated with bulk density (r^2 = 0.916, SE = 0.007, p < 0.001). Compared with marshes, soil moisture content was significantly lower in deciduous and pine forests, and the esker. Marshes had greater abundance of biting flies relative to all land-cover types, with fewer biting flies in deciduous and pine forests, and the esker. Finally, marshes had greater graminoid biomass than all land-cover types, with less graminoid biomass in deciduous and pine forests, and the esker (Table 2). These data demonstrate that marshes have softer soils, greater biting-fly abundance, and greater overall forage biomass, primarily composed of preferred sedges, than in nearby deciduous and pine forests, as well as the esker sites. In addition, the esker had relatively firmer soils, low

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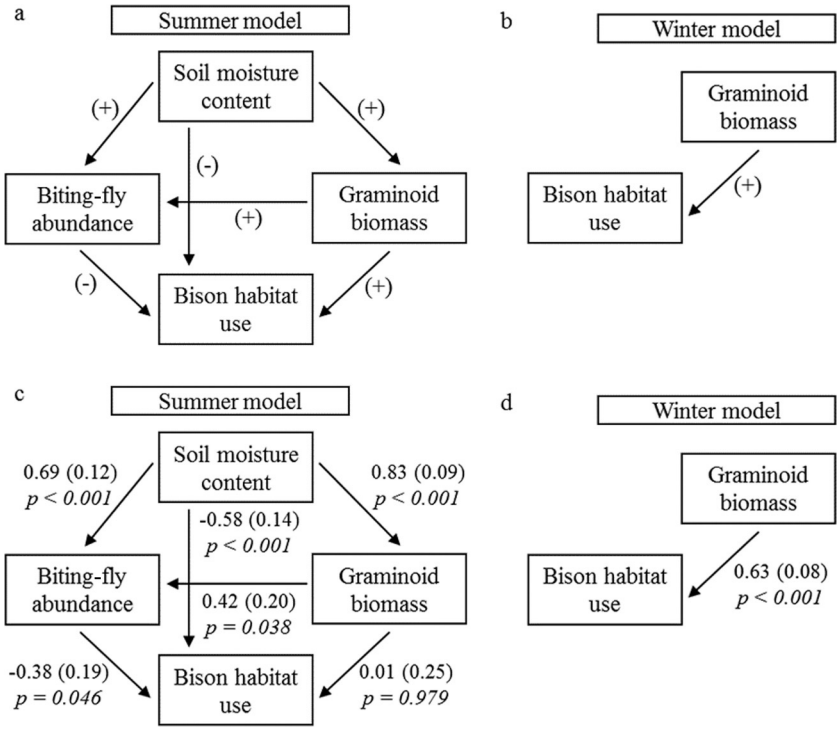
Table 2. Standardized β estimates of univariate zero-inflated negative binomial (ZNIB) models and general linear models (GLM) examining the effect of land-cover type on summer and winter wood bison (*Bison bison athabascae*) dung counts, soil moisture, biting-fly abundance, and graminoid biomass.

Model type	Dependent variable	Land-cover type	β	SE	p	AIC	Null AIC
ZINB	Summer dung	Deciduous	1.43	0.66	0.031	185.19	272.51
		Pine	2.66	0.64	<0.001		
		Esker	3.04	0.64	<0.001		
ZINB	Winter dung	Deciduous	–2.24	0.87	0.010	197.38	254.38
		Pine	–3.64	1.09	<0.001		
		Esker	–1.18	0.82	0.028		
GLM	Soil moisture	Deciduous	–2.02	0.18	<0.001	38.68	105.15
		Pine	–2.16	0.18	<0.001		
		Esker	–2.25	0.18	<0.001		
GLM	Biting flies	Deciduous	–1.29	0.27	<0.001	67.64	105.15
		Pine	–1.26	0.27	<0.001		
		Esker	–2.33	0.27	<0.001		
GLM	Graminoid biomass	Deciduous	–2.18	0.24	<0.001	60.64	105.15
		Pine	–2.24	0.24	<0.001		
		Esker	–2.06	0.24	<0.001		

Note: In all models, land-cover type was the independent variable and the land-cover category "marsh" was the reference category (n = 36). AIC is Akaike's information criterion.

Fig. 2. Model predictions of the direct and indirect effects of soil moisture content (footing), biting-fly abundance, and graminoid biomass on wood bison (*Bison bison athabascae*) summer (*a*) and winter (*b*) habitat selection in the Ronald Lake region of northeastern Alberta, Canada. Standardized β coefficients, SE (in parenthesis), and p values of paths for the best-fit model describing bison summer (*c*) and winter (*d*) habitat use.



abundance of biting flies, and relatively greater graminoid biomass than deciduous and pine forests.

Relating forage, biting flies, and footing to bison habitat selection using path analysis

Results for the summer path analysis (Fig. 2*c*) illustrate that forage biomass had no relationship with bison summer habitat selection and was not significant, suggesting that during summer the distribution of forage in different land-cover types had no influence on the distribution of bison. Soil moisture had a significant positive relationship with graminoid biomass (β = 0.83, SE = 0.09, p < 0.001) and biting-fly abundance (β = 0.69, SE = 0.12, p < 0.001). These results suggest that interactions exist between soils, flies, and forage. Regarding the influence of footing and biting flies on bison summer habitat selection, our results show that both soil moisture and biting flies have a strong negative relationship with bison habitat selection. Conversely, in winter (Fig. 2*d*), when soils are frozen and biting flies are not present, graminoid biomass had a significant positive relationship with bison habitat selection.

Discussion

Our results support our predictions that bison would have lower summer selection of forage-dense land-cover types due to

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trade-offs with insect harassment and footing compared with winter when bison rely on these areas for forage without insects and poor footing. We posit that bison selection of marshes is reduced in summer due to (*i*) forage being more widely distributed across land-cover types and not limiting (Leonard et al. 2017); (*ii*) higher abundance of biting flies that increase energy expenditure and negatively affect bison health (Morgan 1987; Rolf and Reimers 2002; Witter et al. 2012); and (*iii*) soft soil conditions that, like deep snow, increase bison energy expenditure and risk to predation (Parker et al. 1984; Carbyn and Trottier 1987; Schaefer and Messier 1995; Courbin et al. 2017). Furthermore, during summer when forage is more accessible across land-cover types, bison increase selection of land-cover types that have firmer footing and fewer biting flies. In particular, areas of higher elevation (esker) are used more than other land-cover types ($\beta = 2.639$, SE = 0.351, $p < 0.001$). We suggest that during summer, bison selection of higher elevation features not only provide a foraging area with fewer biting flies due to exposure to prevailing westerly winds, but also act as a corridor for movement.

Although it is clear that the availability of forage (quantity and quality) is important to the health of bison (Larter and Gates 1991; Jung et al. 2015; Leonard et al. 2017) and that both forage and land-cover types influence bison spatial and temporal distributions (Merkle et al. 2015; Schoenecker et al. 2015; DeMars et al. 2017), examining the interaction between forage, land-cover types, and other factors that influence fitness provides a more comprehensive understanding of bison habitat selection (Fortin et al. 2003; Schoenecker et al. 2015). This study demonstrates that other fitness-related factors interact with forge availability thus creating trade-offs that influence bison habitat selection. Though bison select forage dense patches (i.e., sedge marshes) year-round, greater distribution of forage, harassment from biting flies, and soil conditions are important factors in the dynamic nature of bison habitat selection.

Optimal foraging theory state that bison should select for areas composed of large quantities of food resources, such as sedge-dominant marshes (Brown et al. 1999; Bergman et al. 2001; Fortin et al. 2003: Merkle et al. 2015), and indeed bison do show greater selection of marshes relative to other land-cover types both in summer and winter (Fortin et al. 2003; DeMars et al. 2017). However, during summer months, others have found that bison show lower selection for marshes compared with winter (DeMars et al. 2016, 2017), and during summer, do not follow energy maximizing principles but rather time minimizing principles, where bison spend shorter than expected bouts of time in marshes (Fortin et al. 2003; Merkle et al. 2015). This suggests that there are other potential causes for reduced selection of marshes during summer by bison despite high quantity and quality of forage.

All ungulates require forage intake for survival. In the search and acquisition of forage resources, the influence of biotic and abiotic factors affect ungulate foraging decisions and, ultimately, fitness (Dussault et al. 2005; Ripple and Bescheta 2006; Long et al. 2016; Riginos 2015). Trade-offs between foraging and predation have been shown for many ungulate species. Ungulate selection of vegetation-dense patches can be reduced by the presence and (or) perception of large predators, and the use of more rugged, vegetation-poor patches increased (Brown et al. 1999; Ripple and Beschta 2006; Hebblewhite and Merrill 2009; Acebes et al. 2013; Ahmad et al. 2016). Likewise, the spatial distribution of snow, high temperatures, and biting flies has shown to affect ungulate distributions (Schaefer and Messier 1995; Poole and Mowat 2005), time spent foraging (Dussault et al. 2005; Aublet et al. 2009; van Beest et al. 2012), and habitat selection (Walsh et al. 1992; Rolf and Reimers 2002), respectively. These factors also affect ungulate health and fitness, and thereby present trade-offs. Though forage availability and predation are dominant factors (Brown et al. 1999; Ripple and Beschta 2006; Acebes et al. 2013; Long et al. 2016), we demonstrate that other factors should also be considered when examining ungulate behaviour and habitat selection.

The objective of this study was to investigate factors that influence bison selection of land-cover types in the Ronald Lake region that (*i*) are an important food resource (marshes), (*ii*) form a large proportion of bison habitat (deciduous and pine forests), and (*iii*) are a high-elevation landform (esker), which together comprise ~50% of the study area. We demonstrate here that bison selection of forage dense patches is important, especially during winter months when forage resources are more limiting, and that interactions are observed between summer forage availability, biting-fly abundance, and soil firmness. In our examination, we found that soft footing and harassment from biting flies may be causal factors that reduce bison selection of forage-dense areas; however, the interactions and correlations between factors make it difficult to determine, and examine, to what extent they influence bison foraging decisions. Although our data suggest a strong, negative relationship between footing and bison summer habitat section, a broader examination of a greater number of land-cover types, including areas with soft footing, and lower abundances of flies and forage (e.g., bogs and fens) will enable researchers to better parse the relationships between these factors. Furthermore, the relationship between these factors is less understood for other boreal ungulates. This study provides insight into the complex nature of habitat selection, including biotic and abiotic interactions, and can provide rational for the examination of these and other factors (e.g., temperature, weather, snow depth) in relation to habitat selection for bison and other ungulates.

Understanding the ecology and relationships between animals and their environment is challenging, but necessary for understanding animal behaviour, and the biological and environmental factors limiting individuals and populations (Dussault et al. 2005; Hebblewhite and Merrill 2009; Long et al. 2016). An in-depth examination of habitat selection can provide guidance to better manage, conserve, and reclaim habitats and features important to the sustainability of populations, especially for those species that are rare or endangered, or whose habitats are limiting due to disturbance, fragmentation, and loss.

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