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**Bottom-up Herbivore-Plant Feedbacks Trump Trophic Cascades in a
Wolf-Elk-Grassland System**

By Trevor C. Weeks

Undergraduate Thesis
Wildlife Biology Program
University of Montana

May 2020

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Bottom-up Herbivore-Plant Feedbacks Trump Trophic Cascades in a Wolf-Elk-Grassland System

Chairperson: Mark Hebblewhite

ABSTRACT

Top-down predator-prey effects that alter the abundance, biomass, or productivity of a population community across more than one link in a food web are referred to as trophic cascades. While these effects have been extensively studied in aquatic environments, fewer studies have examined trophic cascades in terrestrial ecosystems. And fewer still terrestrial studies have tested for trophic cascades between vertebrates and grassland vegetation. Across the globe, grassland plant biomass is driven by both precipitation and non-linear positive feedbacks between grazing and plant productivity, as predicted by the Intermediate Grazing Hypothesis. Yet little is known about the role that apex carnivores play in regard to trophic impacts on grassland biomass. We utilized a long-term dataset collected over the last two decades on a montane rough-fescue grassland adjacent to Banff National Park, Alberta, to test whether top-down effects regulate grassland biomass in a wolf-elk system. First, we measured annual growing season plant biomass from 2006 – 2018 at 61 repeat sampled plots in the grassland. Next, we measured wolf predation risk using a previously developed wolf resource selection function created from GPS radiocollar data from 5 wolf packs. Finally, we measured grazing intensity using Brownian Bridge Movement Models derived from GPS radiocollar data from 131 unique elk. We then tested top-down, bottom-up and abiotic hypotheses for grassland biomass over time in program R. The top model incorporated precipitation and positive non-linear effects of elk use, excluding predator effects and thus failing to support the trophic cascade hypothesis. This may be due to the observational nature of this study, or predation effects in this system may be obscured by human use. Alternatively, our results also support the hypothesis that intermediate grazing may outweigh the benefits of predation in grassland systems. Our study serves to help fill a gap in trophic cascade literature, and emphasizes that positive feedback between grazers and grasslands may trump top-down effects. Understanding when trophic cascade theory is or is not applicable is vital for carnivore management, conservation, and reintroduction efforts across North America.

Key Words: Trophic Cascades · Intermediate Grazing Hypothesis · Grassland · Herbivory · Predation · Elk · Wolf

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For his encouragement and guidance throughout this process, I'd like to thank my faculty mentor, Mark Hebblewhite. I'd like to extend my deepest thanks to Sara Williams for guiding me through R, always being willing to help me work through a tricky bit of code or do some last-minute troubleshooting. I'd like to thank all the members of the Hebblewhite lab, especially Tara Meyer and Hans Martin, for giving their time in emails and meetings to help an undergrad. I'd like to thank the Merrill lab and all of the Ya Ha Tinda technicians over the years, without whom this data would not exist. I'd especially like to thank Jacalyn Normandeau, Mateen Hessami, Monica Winkel, Andrea Baratte, Maddie Trottier, and Collen Sutheimer for helping to make field seasons at the YHT such an amazing experience. I'd like to thank Rick and Jean Smith, Tom McKenzie, and Tyler Ritchie for welcoming me to the ranch and for all of their support for us field techs throughout the years. For their support and feedback on this project, I'd like to thank my committee members, Evelyn Merrill and Jedediah Brodie. Lastly, I'd like to thank Kia Coon for her unwavering support throughout this entire process.

Finally, due to the span of the Ya Ha Tinda Long-term Elk Monitoring Project, and the fact that I myself only became involved in the project starting in 2018, I chose to use the “we” voice for the remainder of this paper.

INTRODUCTION

Top-down effects of predation that alter the abundance, biomass, or productivity of herbivores and plants across more than one link in a food web are referred to as trophic cascades (Pace et al. 1999). Robert Paine first coined the term “trophic cascade” in his experiments on predator exclusion in tidal pools (Paine 1980). Soon thereafter, the scientific community eagerly began to analyze these interactions across species and systems. For many years, scientists assumed that trophic cascades were “all-wet”, meaning that they primarily occurred in aquatic ecosystems (Paine 1980, Pace et al. 1999). However, as studies continued to analyze this newly identified phenomenon across ecosystems, they confirmed the existence of trophic cascades in environments ranging from montane, to semi-desert, to tropical forests, and beyond (Pace et al. 1999, Schmitz et al. 2000, Halaj & Wise 2001, Shurin et al. 2002). It is now widely accepted that trophic cascades are present in most environments. Yet there is little consensus as to the strength of these cascades, as it appears to vary significantly between habitats (Halaj & Wise 2001, Shurin et al. 2002, Borer et al. 2005, Leroux & Loreau 2008). Furthermore, trophic cascade studies performed in aquatic systems far outnumber those of terrestrial systems, and both aquatic and terrestrial studies are biased heavily towards invertebrates (Schmitz et al. 2000, Halaj & Wise 2001, Shurin et al. 2002, Borer et al. 2005).

The increase of studies involving terrestrial vertebrates has started to ameliorate this disparity in trophic cascade literature (Ripple et al. 2001, Hebblewhite et al. 2005, Beschta & Ripple 2009). In the 19th and early 20th century, large carnivores across North America were extirpated from much of their native range (Ripple et al. 2014), effectively removing the top-down constraints on herbivores in many ecosystems. Within the last few decades, these large carnivores have begun to recolonize some of their historic range throughout the globe. As large

carnivores recolonize or are reintroduced to the areas which they had previously inhabited, scientists are provided the serendipitous opportunity to study the reestablishment of trophic cascades that have been absent for generations. The most famous of these studies in recent years have been those involving wolves (*Canis lupus*), elk (*Cervus canadensis*), and aspen (*Populus tremuloides*) in Yellowstone National Park. Following the reintroduction of wolves to Yellowstone in 1995, scientists discovered that aspen recruitment in the park's northern range increased, where in some cases recruitment had been nonexistent for decades (Ripple et al. 2001, Beschta & Ripple 2009). While originally attributed to behaviorally-mediated trophic cascades caused by wolves, longer-term studies have cast doubt on this interpretation and instead have linked aspen responses to direct effects of predation, declining elk abundance, and abiotic drivers (Kauffman et al. 2010, Brodie et al. 2014). Hebblewhite et al. (2005) similarly took advantage of wolf exclusion around Banff township in Banff National Park and found strong support for wolf-caused trophic cascades. They reported dramatic differences in elk density, aspen and willow growth, beaver abundance, and songbird diversity between the high- and low- wolf use areas. Trophic cascades have also been studied between wolves, moose, and balsam fir in Isle Royale National Park (Peterson et al. 2014). These studies are vital to understanding and predicting how apex carnivores may alter an ecosystem. However, the majority of studies have focused exclusively on woody vegetation, ignoring grassland plant species.

The focus on woody vegetation over grasses can likely be attributed to the simplicity of the effects of herbivory on their productivity. Most researchers tend to agree that greater complexity leads to weaker cascading effects (Polis et al. 2000, Schmitz et al. 2000), although others have argued that trophic cascades are not restricted by complexity (Pace et al. 1999). While terrestrial systems as a whole are already far more complex than their aquatic counterparts (Polis et al.

2000), in terms of trophic cascades, grasslands may be even more complex than other terrestrial habitats. This is primarily because many grasses and grass-like species are overcompensatory, meaning that in response to herbivory, the plant grows more tissue than it would have in the absence of herbivory (Frank et al. 1998). Grasses also are unique in storing much of their biomass, and thus energy reserves, below ground out of the reach of herbivory (Coughenour 1985, McInenly et al. 2010). Herbivory also provides nutrients through fecal deposition, and can benefit plants via the removal of standing dead biomass that may structurally compete with productivity and water-use efficiency (Hobbs 1996, Frank 2005). Thus, herbivory can stimulate plant productivity in grasslands (Hobbs 1996, Frank 2005). This characteristic informs the Intermediate Grazing Hypothesis, a variant of the Intermediate Disturbance Hypothesis (Grime 1973, Connell 1978, Frank et al. 1998). The Intermediate Grazing Hypothesis predicts that moderate grazing pressure will actually result in higher overall biomass and species diversity in grasslands. Studies performed in grasslands across the globe have consistently found evidence in support of the Intermediate Grazing Hypothesis, with herbivory playing key roles in nitrogen deposition, soil moisture, and overcompensatory shoot regrowth (Coughenour 1985, Hobbs 1996, Frank et al. 1998, Frank 2005, Frank 2008). This could conceivably make it quite difficult to isolate top-down effects in these systems, as moderate herbivory is expected to benefit, not harm, total biomass, as trophic cascade theory predicts. Additionally, grassland productivity around the globe is well known to be driven by precipitation (Frank et al. 1998, Fay et al. 2011, Robinson et al. 2013). As such, studies analyzing potential trophic cascades in grasslands must also isolate the effects of precipitation across the study area.

Ford and Goheen (2015) recently proposed a ‘golden-standard’ for trophic cascade studies, asserting that a complete study must demonstrate: i) reduction in herbivore abundance by

carnivores, ii) reduction of plant abundance by herbivores, and iii) indirect facilitation of plants by carnivores through the suppression of herbivory. Unfortunately, the majority of terrestrial trophic cascade studies fail to demonstrate all three components, instead settling for one or two components as evidence of trophic cascades. This not only fails to conclusively determine the prevalence and strength of trophic cascades in these systems, it also weakens the credibility of these studies (Peterson et al. 2014, Ford & Goheen 2015). To definitively quantify top-down effects in terrestrial systems, researchers must adhere to the tenets of the golden standard. While the Intermediate Grazing Hypothesis may complicate the application of the golden standard in grassland systems, it is nevertheless important that we understand the effects, or lack thereof, of carnivores in these systems.

The data collected through the Ya Ha Tinda (YHT) Long-term Elk Monitoring Project provide a unique opportunity to apply the golden standard for testing top-down trophic cascade theory in a complex wolf-elk-grassland system. The YHT Long-term Elk Monitoring Project includes over 20 years of elk, wolf, and vegetation data in a montane grassland ecosystem. Our objective was to utilize these data to determine what factors drive grassland biomass at the YHT. To that end, we tested four hypotheses: i) grassland biomass is driven by top-down effects, ii) grassland biomass is driven by bottom-up effects, iii) grassland biomass is driven by herbivory via the Intermediate Grazing Hypothesis, or iv) grassland biomass is driven by some combination of these covariates.

METHODS

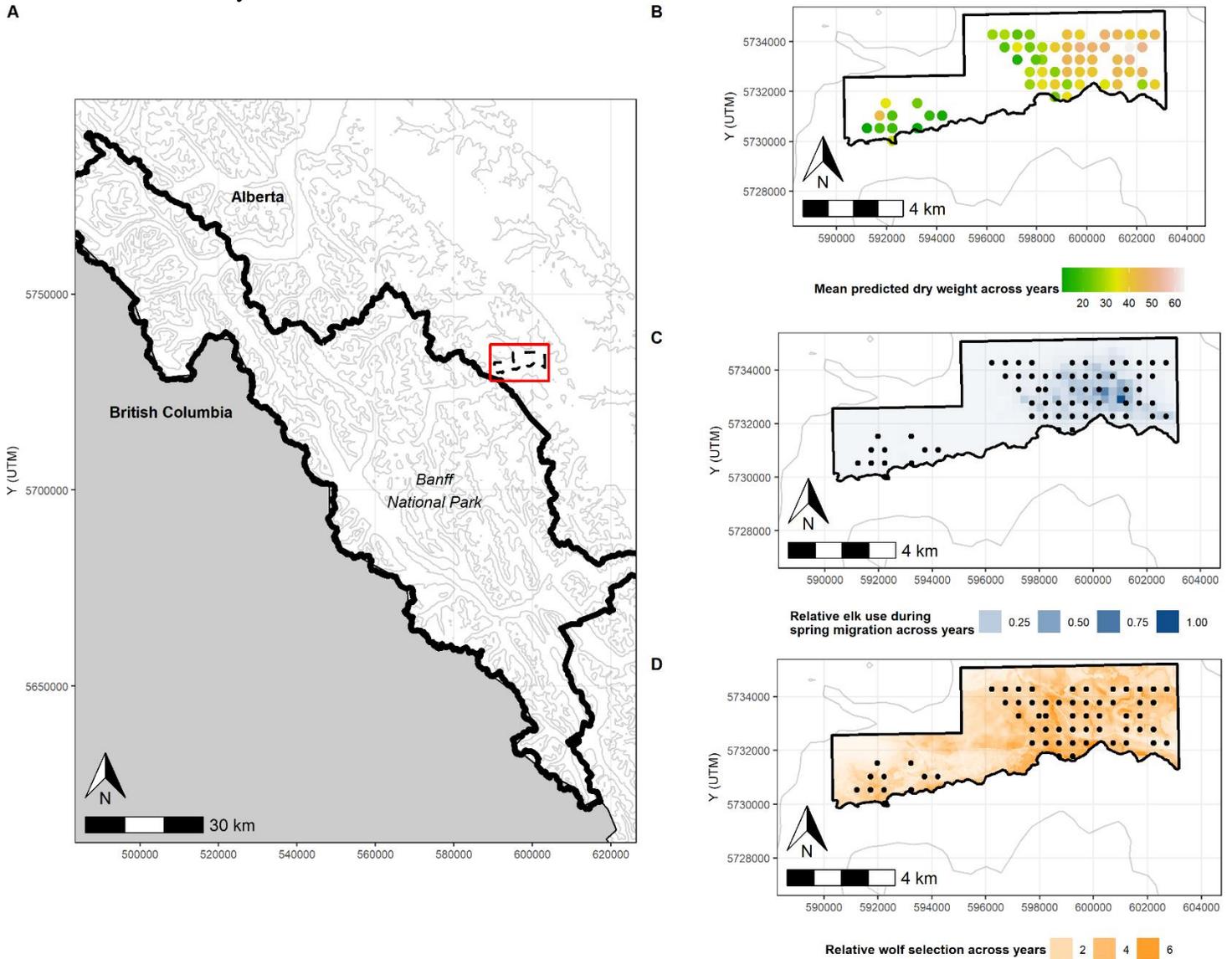
STUDY AREA

The study area was defined by the winter grazing range of the YHT elk herd, which coincides with the boundaries of the YHT ranch (~ 400 hectares) adjacent to Banff National Park (BNP; 51°30'N, 115°30'W), Alberta, Canada (Fig. 1A) (Hebblewhite et al. 2006). Meaning “mountain prairie” in the Stoney-Sioux language, the Ya Ha Tinda is one of the largest and most intact rough fescue (*Festuca campestris*) montane grasslands left in Alberta (Willoughby 2001). The montane grasslands are dominated by Fescue, but also include other graminoids such as *Helictotricon* spp., *Carex* spp., *Koeleria* spp., and *Bromus* spp.; dominant forbs included *Geum triflorum*, *Astragalus* spp., *Solidago* spp., *Achillea millefolium*, and *Potentilla* spp. (Glines 2012). Grassland shrub species included *Potentilla fruticosa*, *Salix* spp., *Betula glandulosa*, *Populus* spp., and *Rosa* spp. During the winter (October – April), all of the female elk in the study area (n ~ 400-500) congregate on the YHT. During the summer, approximately 70% of the population stay on the YHT as ‘residents’, while the remaining 30% either head west into Banff National Park or east onto provincial lands as ‘migrants’ (Ya Ha Tinda 2018-2019 Annual Report). An increasing proportion of residents over the last decade may have negative consequences for grassland biomass, as fescue is known to be sensitive to summer grazing (Johnston 1961, McInenly 2003). The study area is montane temperate, with an average of 319 mm of precipitation during summer months (May–Sept), and an average snowfall of 157 cm. Temperatures average 9°C during the summer, and –4.1°C during winter (source: Environment Canada Ya Ha Tinda weather station).

While the predominant prey and predator species throughout the study area are elk

and wolves, the study area boasts a nearly full suite of North American megafauna. Other predators in this system include coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), cougars (*Puma concolor*), lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*); black bears (*Ursus americanus*) are rare in the study area (Steenweg 2016). Human harvest, both from licenses and First Nations Harvest, is also a factor on the YHT and surrounding provincial lands. Secondary ungulates in the system include white-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*, respectively), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), horses (*Equus ferus*), and most recently, bison (*Bison bison*), following their reintroduction to Banff National Park in the summer of 2018.

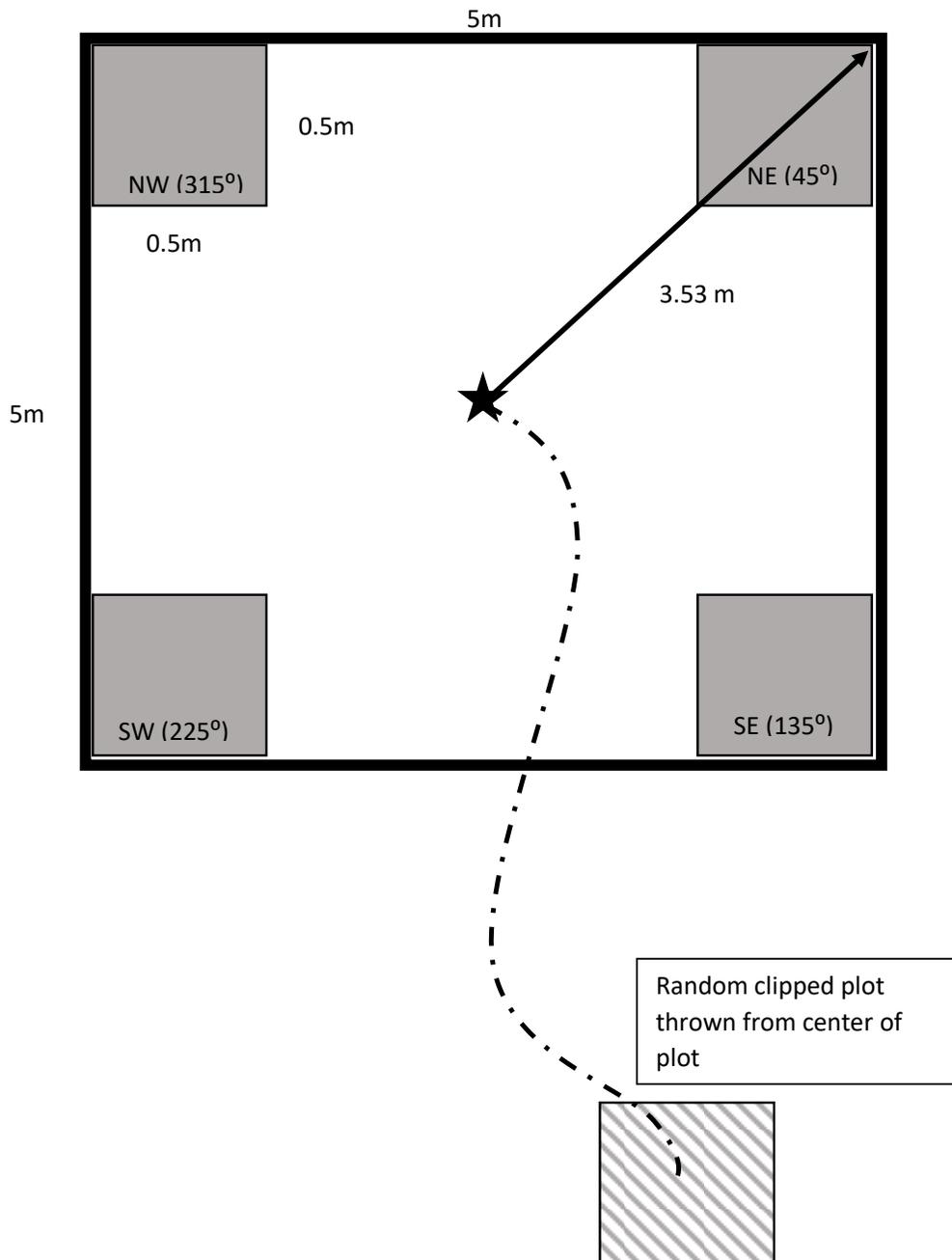
Figure 1: The study area. A) The Ya Ha Tinda Ranch is located just outside of Banff National Park (BNP; 51°30'N, 115°30'W), Alberta, Canada. B) Mean predicted biomass (g/0.25m²) from 2006 – 2018 at biomass plots (n = 61) located throughout the study area. C) Relative elk use from April 24th – June 17th, 2006 – 2018, across the YHT study area. D) Relative wolf resource selection from April 15th – October 15th, 2005 – 2018, across the YHT study area.



VEGETATION DATA COLLECTION

Biomass measurements were taken annually starting in 2006 at systematic grid-based plots established throughout the study area (Fig.1). In 2006, fewer plots were measured ($n=37$), but the number of plots gradually increased each year before plateauing at 61 plots (mean n across all years = 54). From 2006 – 2011, biomass measurements were taken every summer month (May – September). From 2012 to the present, measurements were taken only at the peak of growing season in late July or early August. For this reason, the only biomass data from 2006 – 2011 included in our analyses were the late July/early August measurements, representing peak of growing season plant biomass. At each plot, we measured standing biomass height at four subplots in the four corners of a 5m x 5m square (NE, SE, SW, and NW) (Fig. 2). We indirectly measured height using a disc-pasture-meter approach (Vartha & Matches 1977, Dörgeloh 2002) in a 0.5m x 0.5m quadrat, then visually estimated the percent cover of grasses, forbs, shrub, and bare ground within the quadrat. We also estimated percent old versus new growth, percent seeded, percent cured, and percent grazed. Additionally, at each plot we randomly selected and measured a fifth subplot (Fig. 2). At this fifth subplot, in addition to the above measurements, we clipped all vegetation down to a grazed level (~ 2 cm). We sorted all clipped vegetation into live or dead grass, live or dead forb, and live or dead shrub. We weighed each vegetation type in the field and recorded wet weights. Each sample was later dried in an oven at 100 °C for 24 hours and then weighed again to determine dry weights. All samples were stored and weighed in brown paper bags, so we removed 7g (the mean weight of a dry paper bag) from the final dry weight for every sample. We recorded the dry weight for each vegetation type for each clipped subplot as well as the total dry weight of the clipped subplot.

Figure 2: Illustration of the five subplots sampled at each biomass plot at the Ya Ha Tinda grassland, Alberta, Canada, 2006 – 2018. At the four subplots in each corner of the 5m x 5m square, we measured height and percent cover type. At the fifth subplot, in addition to the above measurements, we clipped and sorted all biomass >2cm.



VEGETATION DROP-DISC MODEL SELECTION

To estimate dry weight values for the drop-disc-only readings, we used the data from the clipped plots to create a model predicting dry weight values (e.g., Dörgeloh 2002, Hebblewhite et al. 2008). We used the MASS package in program R to run backward stepwise model selection starting with a model that incorporated height, percent grass cover, percent forb cover, percent shrub cover, and percent bare cover. The top model identified via stepwise selection incorporated height ($\beta = 1.67$, $p < 2e-16$), percent shrub cover ($\beta = -0.26$, $p = 1.60e-08$), and percent bare cover ($\beta = -0.29$, $p < 2e-16$) (intercept = 19.72, $r^2 = 0.54$). We applied this model to the drop-disc-only data, and then took the mean predicted dry weight across the four subplots in each plot each year for use in analyses.

ELK DATA COLLECTION

We quantified relative elk use as a proxy for herbivory pressure at each plot using data from GPS radiocollars on 131 unique adult female elk from 2002 – 2018. We captured adult female elk during the winter months between February 2002 and March 2018, using a mixture of corral trapping, helicopter net gunning, and darting from horseback (Animal Care Protocols: University of Alberta 353212, 611812, 000624 and University of Montana AUP 004-16). We fitted each captured elk with either a GPS (Lotek GPS 3300, 4400, 7000; LOTEK Inc., Aurora, Ontario, Canada) or VHF (LMRT-4; LOTEK Inc., Aurora, Ontario, Canada) collar. We collected a total of 447,896 GPS fixes from 2002 – 2018. Previous analyses at the YHT have shown that both location error (~34m) and fix rate bias (< 10%) are negligible (Hebblewhite & Merrill 2007). See Eggeman et al. (2016) for more details about animal capture, handling, and radiocollaring.

BROWNIAN BRIDGE MOVEMENT MODELS

We estimated relative elk use as a proxy for herbivory pressure during the spring and summer months using Brownian Bridge Movement models (BBMMs). BBMMs (Kranstauber et al. 2012) estimated the relative spatial use of each individual GPS radiocollared elk during spring and summer migration (April 24th to June 17th). We focused on this spring and early summer period as a proxy for grazing pressure because of the sensitivity of rough fescue and perennial forbs to grazing during the spring and summer growing season (Johnston 1961, McInenly 2003). Using the BBMM package in program R, we created utilization distributions that detail the time each elk spent in locations across the study area. We then combined the BBMMs for all individuals in a given year, scaled these values from 0 to 1 for relative use, and extracted the relative use value at each biomass plot each year. We excluded the years 2008 and 2012 from our analyses because we had no elk with GPS collars in those years, and thus no way to quantify relative use.

WOLF PREDATION RISK

We quantified wolf predation risk at each plot using a previously developed wolf resource selection function (RSF) by Hebblewhite and Merrill (2008). This RSF was created using GPS and VHF data from 5 wolf packs (n = 46 wolves) located on YHT lands or in nearby Banff National Park. The RSF predicts summer (April 15th – October 15th) resource selection, and is further modified by diurnal cycles and pack size-driven changes in kill rate. Previous studies have demonstrated that this RSF model predicts independent elk mortality locations very well (Hebblewhite & Merrill 2007). By incorporating annual changes in land cover, we were able to extend the RSF estimates to 2005 – 2018. This approach assumes that the patterns driving wolf selection did not change over time in our long-term study area. We created raster

layers of wolf resource selection across the YHT each year. We then extracted the wolf RSF value at each biomass plot each year.

PRECIPITATION

We used the Northern Pacific Oscillation (NPO) index between November 1 and March 31 as a proxy for precipitation. Driven by anomalies in sea-surface temperature over the North Pacific Ocean, the NPO is known to be related to winter and spring precipitation (rain and snowfall) and local weather data in the Rocky Mountains (Trenberth & Hurrell 1994, Hebblewhite 2005). This is especially the case in the Canadian Rockies, where NPO has the strongest correlation with local climate factors (Trenberth & Hurrell 1994).

STATISTICAL ANALYSIS

We developed competing *a-priori* models using Generalized Linear Models (GLMs) with biomass (g/0.25m²) as a function of our different covariates using a Poisson log link GLM (McCullough & Nelder 1989). Since the Poisson distribution requires whole numbers in order to perform analyses such as AIC, we rounded the predicted biomass values to integers. We used this log-link Poisson model following previous studies (e.g., Hebblewhite et al. 2008), and because goodness of fit testing confirmed that Poisson models fit our biomass data better than Gaussian linear regression (T. Weeks, unpublished data). We tested 11 competing *a-priori* models of trophic relationships (top-down, bottom-up, abiotic) in the following general format:

$$\text{Grassland Biomass}_{it} \text{ (g/0.25m}^2\text{)} = \exp(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \varepsilon) \quad \text{Eqn 1}$$

where β_0 is the log transformed average biomass, β_n is the coefficient effect of each covariate, and ε is Poisson-distributed error variance. Our 11 different competing models were: 1)

grassland biomass is best explained by precipitation, 2) grassland biomass is best explained by wolf predation risk effects, 3) grassland biomass is best explained by elk herbivory effects, 4) grassland biomass is best explained by precipitation and elk herbivory, 5) grassland biomass is best explained by elk herbivory and wolf predation risk, 6) grassland biomass is best explained by precipitation and wolf predation risk, 7) grassland biomass is best explained by precipitation, elk herbivory, and wolf predation risk, 8) grassland biomass is best explained by non-linear intermediate herbivory effects, 9) grassland biomass is best explained by precipitation and non-linear intermediate herbivory effects, 10) grassland biomass is best explained by precipitation, non-linear intermediate herbivory effects, and wolf predation risk, 11) grassland biomass is constant. We also generated models that incorporated random effect by year, but chose not to include them in this paper because we discovered that almost all of the annual variation in the models was already absorbed by our annually-varying NPO (T. Weeks, unpublished data). We used the `cor()` function in program R to screen against collinearity in our covariates. We then conducted model selection by comparing AIC values (Burnham & Anderson 1998). We also compared BIC values, as the BIC test imposes stricter penalties against multiple parameters.

RESULTS

Grassland biomass, relative elk use, and relative wolf resource selection varied spatially across the study area (Fig. 1). We found significant variation in biomass between plots, with mean biomass from all years at individual plots ranging from 7.30 g/0.25m² (standard deviation = 7.675) to 66.55 g/0.25m² (standard deviation = 26.474) (Fig. 3). Total biomass throughout the study area remained relatively constant across years, ranging from a mean of 26.43 g/0.25m² (standard deviation = 11.897) in 2016 to a mean of 43.97 g/0.25m² (standard deviation = 16.446) in 2014 (Fig. 4). Relative elk use of biomass plots each year decreased from 2006 – 2011, then increased from 2014 – 2018 (Fig. 5). Elk use and wolf resource selection were not correlated ($r^2 = 0.012$).

The top model was:

$$\text{Grassland Biomass}_{it} \text{ (g/0.25m}^2\text{)} = \exp^{(-22.91 + 1.42*\text{elk use} + -2.34*\text{elk use}^2 + 0.03*\text{NPO} + \varepsilon)} \quad \text{Eqn 2}$$

where ε is Poisson-distributed error variance. The top model had both the lowest AIC score and BIC score (Table 1). The top model incorporated non-linear effects of herbivory (Elk Use $\beta = 1.42$, $p < 2e-16$; Elk Use ² $\beta = -2.34$, $p = 4.59e-12$) and precipitation ($\beta = 0.03$, $p = 2.61e-13$) (Table 2). The model incorporating non-linear herbivory effects (Elk Use $\beta = 1.42$, $p < 2e-16$; Elk Use ² $\beta = -2.34$, $p = 4.61e-12$), precipitation ($\beta = 0.03$, $p = 3.92e-13$), and wolf predation risk ($\beta = -0.0001$, $p = 0.99$) had $\Delta\text{AIC} = 2$ (Table 1), indicating that it may be just as relevant as the top model. However, $\Delta\text{BIC} > 2$, and the wolf covariate was not significant, therefore we chose the above model in favor of the one incorporating wolf effects. We exponentiated the predictions of the top model in order to return values in g/0.25m². The top model clearly

illustrates a strong non-linear effect of herbivory on grassland biomass, modified by positive effects of precipitation (Fig. 6).

Table 1: List of *a-priori* models explaining grassland biomass and associated AIC and BIC values at the Ya Ha Tinda grassland, Alberta, Canada, 2006 - 2018. Models were created using a Poisson log link GLM. The BIC test inflicts stricter penalties against the number of parameters (K) than the AIC test. The values for the top model are bolded.

Model Covariates	K	AIC	BIC
1. <i>Precipitation only</i>	2	5821.747	5830.078
2. <i>Wolves only</i>	2	5876.661	5884.992
3. <i>Elk only</i>	2	5833.880	5842.211
4. <i>Precipitation & Elk</i>	3	5778.522	5791.018
5. <i>Elk & Wolves</i>	3	5835.281	5847.777
6. <i>Precipitation & Wolves</i>	3	5823.260	5835.756
7. <i>Precipitation, Elk, & Wolves</i>	4	5780.514	5797.175
8. <i>Quadratic Elk</i>	3	5779.923	5792.420
9. <i>Precipitation & Quadratic Elk</i>	4	5728.599	5745.261
10. <i>Precipitation, Quadratic Elk, & Wolves</i>	5	5730.599	5751.426
11. $y \sim 1$	1	5876.993	5881.158

Table 2: Summary statistics of the top model explaining grassland biomass at the Ya Ha Tinda grassland, Alberta, Canada, 2006 - 2018. Note that the model was created using a Poisson log link GLM, so the effects of the β coefficients are unintuitive.

Covariate	β Coefficient	Standard Error	z value	p value
Intercept	-22.91	3.609	-6.35	2.17e-10
Elk Use	1.42	0.153	9.29	< 2e-16
Elk Use ^ 2	-2.34	0.338	-6.92	4.59e-12
NPO	0.03	0.004	7.31	2.61e-13

Figure 3: Grassland biomass at the Ya Ha Tinda grassland, Alberta, Canada, 2006 – 2018, showing biomass across all years grouped by plot ID. There was significant spatial variation in grassland biomass. Plot 695 had the lowest biomass over the study period (mean = 7.30, sd = 7.675), and Plot 232 had the highest levels of biomass (mean = 66.55, sd = 26.474).

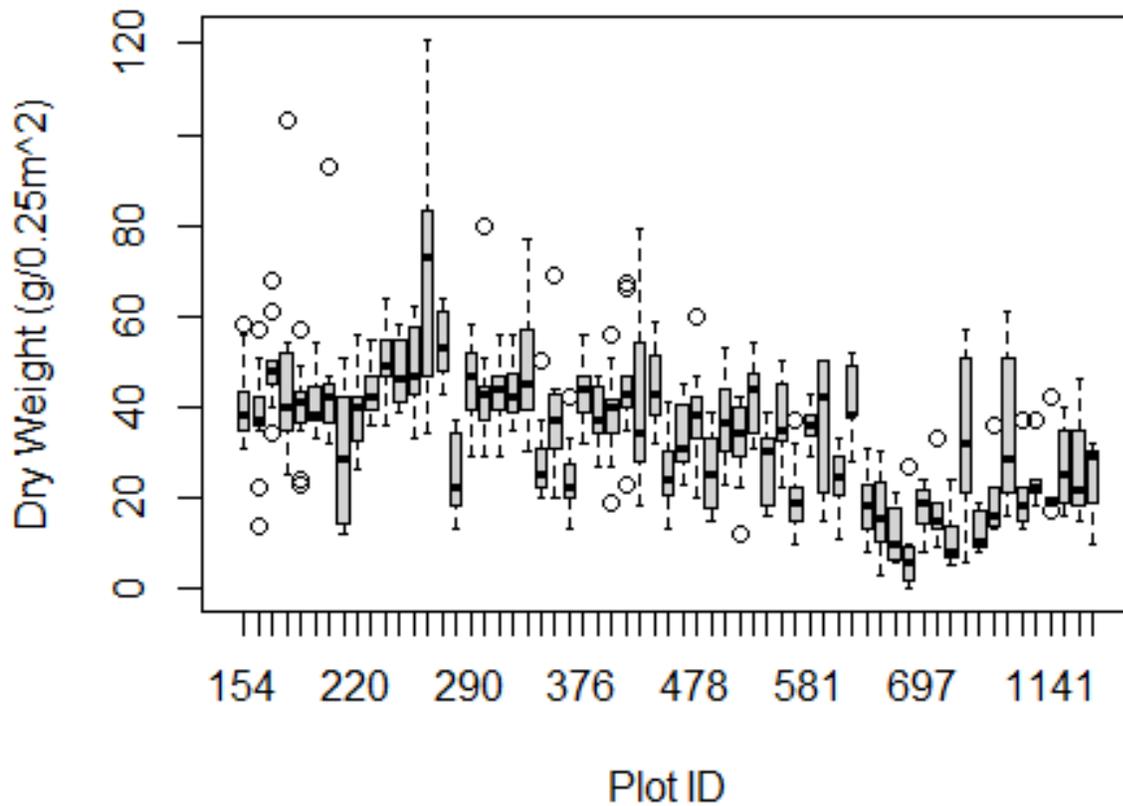


Figure 4: Grassland biomass of all plots grouped by year at the Ya Ha Tinda grassland, Alberta, Canada, 2006 - 2018. Years 2008 and 2012 were not included in my analyses (see Methods - Brownian Bridge Movement Models). Biomass remained relatively constant across the study area between years. 2016 was the lowest biomass year (mean = 26.43, sd = 11.897), and 2014 was the highest biomass year (mean = 43.97, sd = 16.446).

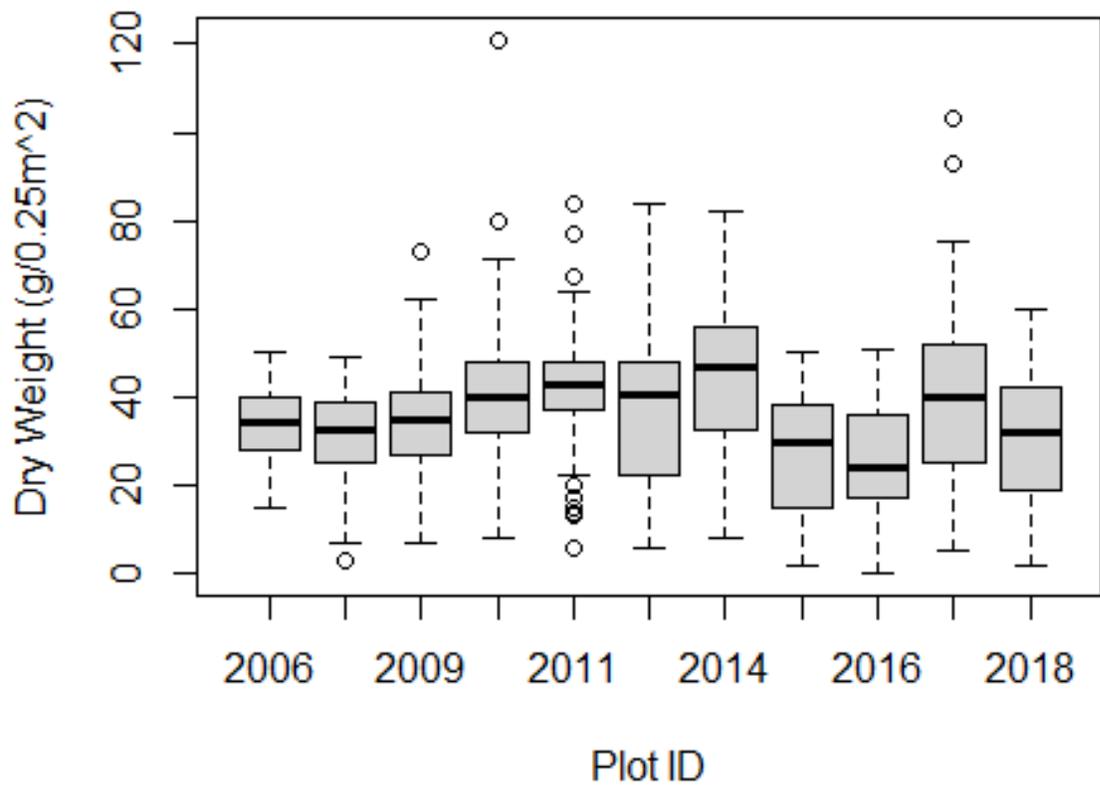


Figure 5: Relative elk use across all plots grouped by year at the Ya Ha Tinda grassland, Alberta, Canada, 2006 - 2018. Relative elk use decreased in the early years of the study (2006 – 2011), but then increased in recent years (2014 – 2018). This suggests that changing elk use over time is not driving variation in biomass, but rather that spatial hotspots (Fig. 3) are driving variation in biomass (Anderson et al. 2010).

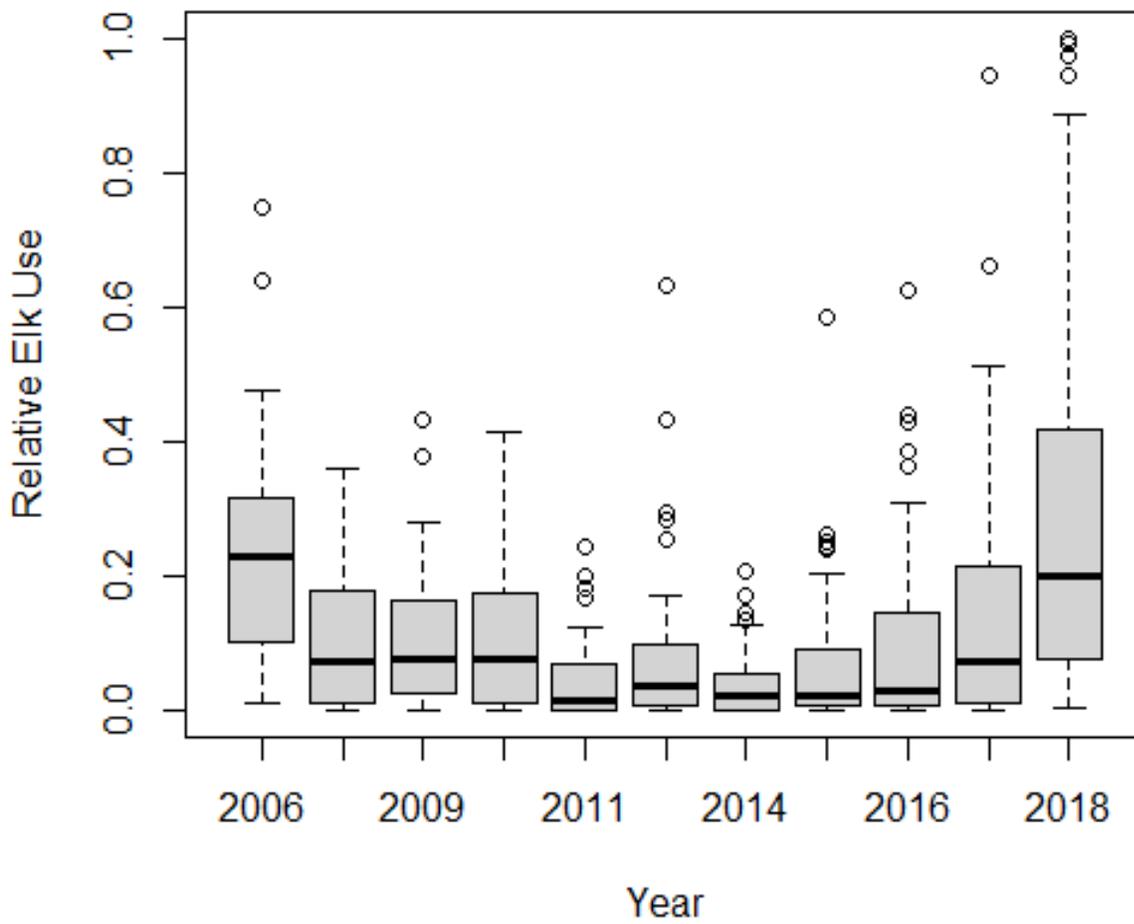
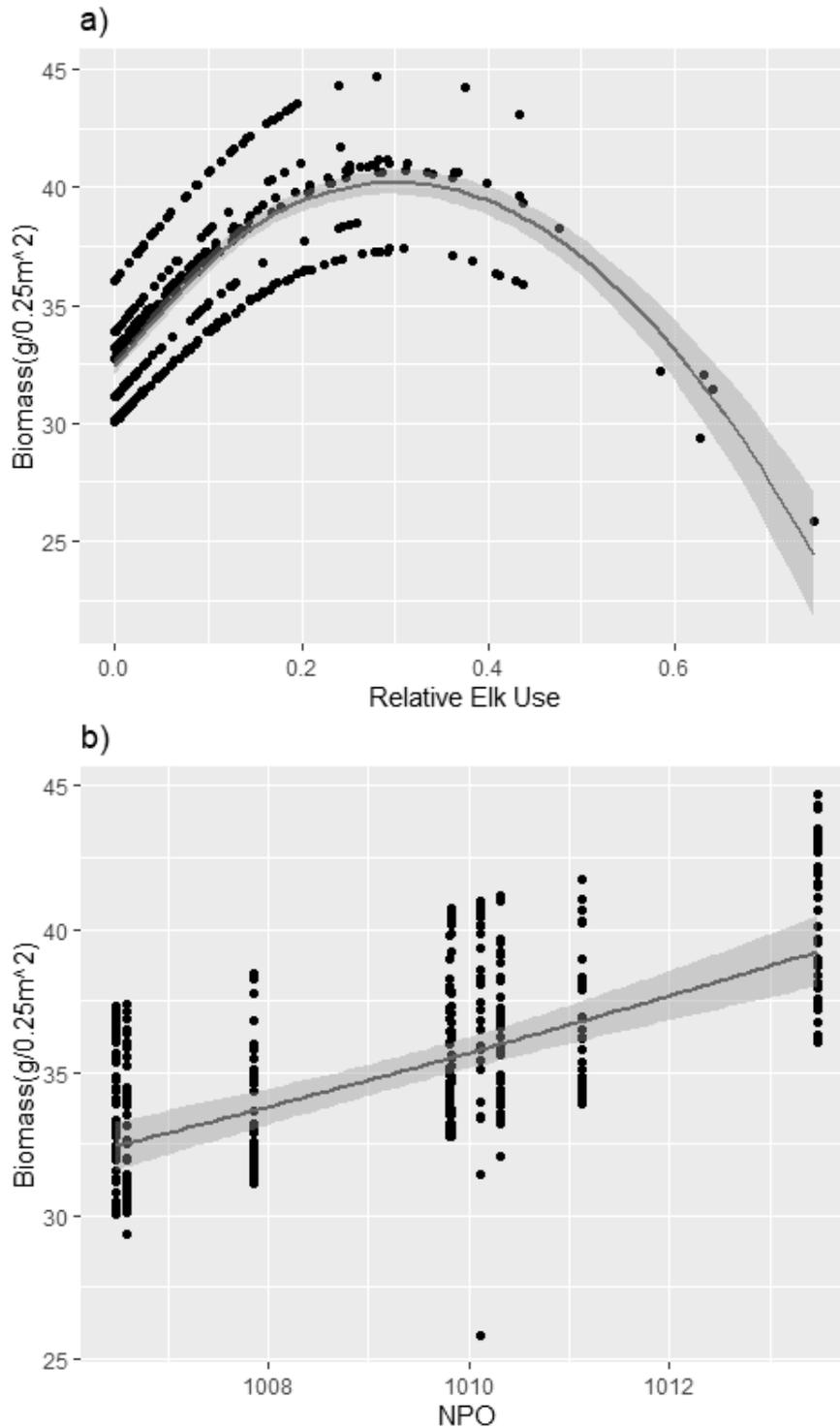


Figure 6: Predictions of the top model explaining grassland biomass at the Ya Ha Tinda grassland, Alberta, Canada, 2006 - 2018. The model was selected via AIC and BIC values. a) There is a strong non-linear effect of elk herbivory (Elk Use $\beta = 1.42$, $p < 2e-16$; Elk Use $^2 \beta = -2.34$, $p = 4.59e-12$), consistent with the Intermediate Grazing Hypothesis. b) There is also a positive linear effect of precipitation ($\beta = 0.03$, $p = 2.61e-13$). NPO is used as a proxy for precipitation (see Methods – Precipitation).



DISCUSSION

Overall, our results did not support the presence of a trophic cascade in this system. The first tenet of the golden standard (Ford & Goheen 2015) states that a complete trophic cascade study must demonstrate a reduction in herbivore abundance by carnivores. In their test of the trophic cascade hypothesis in nearby Banff National Park, Hebblewhite et al. (2005) reported negative relationships between wolf and elk abundance. Another study performed at the Ya Ha Tinda showed negative relationships in spatial distribution between wolves and elk (Hebblewhite et al. 2009). Our results, however, did not demonstrate this, as elk use and wolf resource selection were uncorrelated ($r^2 = 0.012$). The second tenet states that a study must demonstrate a reduction of plant abundance by herbivores. Our results showed that at high levels of herbivory (relative elk use ≥ 0.30 , Fig. 6), grassland plant biomass declines in response to herbivory pressure. However, intermediate levels of herbivory appear to promote, not reduce, grassland biomass. The third tenet of the golden standard states that a trophic cascade study must demonstrate indirect facilitation of plants by carnivores through the suppression of herbivory. Not only did our results fail to demonstrate the suppression of herbivory by carnivores, as stated above, but in the second-best model, which incorporated wolf predation risk, the beta coefficient for the wolf covariate was negative ($\beta = -0.0001$). This was the opposite effect that we would expect given trophic cascade theory (later in the Discussion we expand on potential explanations for this). As the three tenets of the golden standard were not all demonstrated, the hypotheses proposing the existence of trophic cascades on grassland biomass at the YHT were not supported. We did, however, find support for the hypothesis that grassland biomass was driven by a combination of precipitation and non-linear herbivory effects via the Intermediate Grazing Hypothesis. The complexity of herbivore-plant feedbacks in grassland systems suggests that the golden standard

proposed by Ford and Goheen (2015) may need to be revised in order to accommodate grasslands.

The relationship between relative elk use and grassland biomass illustrated the predictions of the Intermediate Grazing Hypothesis. It is likely that bottom-up factors may initially drive the model, with elk preferentially selecting areas of greater biomass, but then at a certain density of elk use, heavy grazing leads to reductions in overall biomass and herbivory becomes the causal factor driving the model. The Intermediate Grazing Hypothesis (Grime 1973, Connell 1978, Frank et al. 1998) predicts that grasslands will respond non-linearly to grazing intensity, with the highest levels of grassland biomass at intermediate grazing intensity. Our top model clearly demonstrated this type of relationship between grassland biomass and herbivory pressure (Fig. 5a), for which we used relative elk use as a proxy. Several different mechanisms have been proposed to explain this relationship. These mechanisms include the facilitation of overcompensatory shoot regrowth, the improvement of soil moisture and plant water-use efficiency via the removal of old tissue, and the deposition of fecal nitrogen (Hobbs 1996, Frank et al. 1998). Previous work by McInenly et al. (2010) performed on rough fescue collected from the Ya Ha Tinda showed that defoliation coupled with high nitrogen return led to increased plant N uptake and preferential allocation to aboveground rather than belowground growth. This suggests that fecal nitrogen deposition by elk may be the primary mechanism driving the intermediate grazing response observed in our system.

The top model also included a positive linear effect of precipitation (Fig. 5b), for which we used the NPO index as a proxy. The Northern Pacific Oscillation is strongly correlated with winter and spring precipitation and mean temperatures, especially in the Canadian Rocky Mountains (Trenberth and Hurrell 1994, Hebblewhite 2005). Hebblewhite (2005) reported a

strong positive correlation ($r = 0.61$, $p=0.005$) between the NPO index and snowfall in Banff National Park. As such, we feel that the NPO index acts as an appropriate proxy for precipitation in our system. We used values from the NPO index that covered only winter (November 1st – March 31st) index values, but research has shown correlations between winter precipitation and summer moisture conditions (Quiring & Kluver 2009). The positive effect of precipitation on biomass in the model was unsurprising, as precipitation is known to drive grassland biomass globally (Frank et al. 1998, Fay et al. 2011, Robinson et al. 2013). Also, research performed by Brodie et al. (2012, 2014) in Yellowstone has demonstrated snowpack to mediate herbivore impacts on vegetation. They found that higher snowpack significantly lowered elk use at sites, resulting in reduced browse intensity and increased recruitment of aspen saplings (Brodie et al. 2012). Their results suggested that snowpack had much stronger effects on trophic dynamics in the system than did wolf predation (Brodie et al. 2014).

There are several possible explanations for why we did not identify predator effects on biomass in our system. For one, we may have failed to identify predator effects because of a failure in experimental design. In addition to proposing their golden standard, Ford and Goheen (2015) outlined the strengths and weaknesses of different experimental designs for trophic cascade studies. In our study, we did not experimentally manipulate predator or herbivore abundance, but rather observed correlations in use across natural gradients throughout the study area. Thus, we may have failed to detect the effects of wolf predation in our system.

Alternatively, trophic cascades caused by wolves may have been obscured by high human use at the Ya Ha Tinda. The Ya Ha Tinda is a popular destination for hikers and horse riders, and the grasslands see high levels of daytime human use (Hebblewhite & Merrill 2008). Previous work has shown that wolves avoid areas of high human use during the day (Hebblewhite et al. 2005,

Hebblewhite & Merrill 2008). These “human shield” effects have been identified in other systems as well, such as with moose and bears in Grand Teton National Park (Berger 2007). This diurnal avoidance of grasslands suggests that the effects of wolf resource selection on the model may differ if daytime and nighttime wolf resource selection were separate covariates. Future analyses may benefit from testing whether day or night wolf predation risk is more strongly correlated with trophic responses in our system. Another possible explanation that we find particularly intriguing is that the Intermediate Grazing Hypothesis may preclude the presence of trophic cascades in grasslands. As we discussed above, intermediate levels of grazing stimulate plant growth in grassland systems. It is possible that in our system, the benefits of moderate grazing on plant biomass may outweigh the negative effects of heavy grazing. Predation in such a system would therefore be of no benefit to plants, as it would diminish the benefits received via herbivory. Frank’s (2008) work in Yellowstone may support this interpretation. Frank (2008) found that high wolf use in Yellowstone’s grasslands was correlated with decreased net N mineralization and a disruption of beneficial grazer-associated processes. Thus, it is possible that trophic cascades in grasslands may be precluded by the effects of positive herbivore-plant feedbacks.

As large carnivores recolonize or are reintroduced to areas of their historic range, it is important that we understand the differing impacts that they may or may not have on different ecosystems. The previous body of literature regarding the role of large carnivores in triggering trophic cascades indicates that carnivores convey positive effects on woody plant biomass (Ripple et al. 2001, Hebblewhite et al. 2005, Beschta & Ripple 2009, Peterson et al. 2014), yet largely ignores the effects of carnivores on herbaceous grassland biomass. Our results suggest that the effects of carnivores may vary between ecosystems, and that trophic cascade theory may

not be applicable in grassland systems. At the very least, our results demonstrate the need for revised standards of trophic cascade studies that include considerations for the complex herbivore-plant feedbacks found in grasslands. Further research on the effects of large carnivores on non-woody vegetation will help to fill this gap in trophic cascade literature, and will help inform the management and conservation of large carnivores throughout North America.

LITERATURE CITED

- Anderson, T. M., J. G. C. Hopcraft, S. Eby, M. Ritchie, J. B. Grace, and H. Olf. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology* 91:1519-1529.
- Berger, J. 2007. Fear, human shields, and the re-distribution of prey and predators in protected areas. *Biology Letters* 3:620-623.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142:2401-2414.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528-537.
- Brodie, J. F., E. Post, F. Watson, and J. Berger. 2012. Climate change intensification of herbivore impacts on tree recruitment. *Proceedings: Biological Sciences* 279:1366-1370.
- Brodie, J. F., E. S. Post, J. Berger, and F. G. R. Watson. 2014. Trophic interactions and dynamic herbivore responses to snowpack. *Climate Change Responses* 1:1-8.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Coughenour, M. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* 72:852-863.
- Dörgeleh, W. G. 2002. Calibrating a disc pasture meter to estimate above-ground standing biomass in mixed bushveld, South Africa. *African Journal of Ecology* 40:100-102.
- Grime, J. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:44-347.
- Glines, L. M. 2012. Woody plant encroachment into grasslands within the red deer drainage, Alberta. University of Alberta, Edmonton.
- Eggeman, S. L., M. Hebblewhite, H. Bohm, J. Whittington, and E. H. Merrill. 2016. Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *Journal of Animal Ecology* 85:785-797.
- Fay, P. A., J. M. Blair, M. D. Smith, J. B. Nippert, J. D. Carlisle, and A. K. Knapp. 2011. Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences* 8:3053-3068.
- Ford, A. T., and J. R. Goheen. 2015. Trophic cascades by large carnivores: a case for strong inference and mechanism. *Trends in Ecology & Evolution* 30:725-735.
- Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the Earth's grazing ecosystems. *Bioscience* 48:513-521.

- Frank, D. A. 2005. The interactive effects of grazing ungulates and aboveground production on grassland diversity. *Oecologia* 143:629-634.
- Frank, D. A. 2008. Evidence for top predator control of a grazing ecosystem. *Oikos* 117:1718-1724.
- Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *The American Naturalist* 157:262.
- Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology* 74:226-233.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135-2144.
- Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. *Wildlife Society Bulletin* 34:1280-1295.
- Hebblewhite, M., and E. H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:377-387.
- Hebblewhite, M., and E. H. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834-844.
- Hebblewhite, M., E. H. Merrill, and G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis for a partially migratory montane elk population. *Ecological Monographs* 78:141-166.
- Hebblewhite, M., R. H. Munro, and E. H. Merrill. 2009. Trophic consequences of postfire logging in a wolf-ungulate system. *Forest Ecology and Management* 257:1053-1062.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695-713.
- Johnston, A. 1961. Comparison of lightly grazed and ungrazed range in the fescue grassland of southwestern Alberta. *Canadian Journal of Plant Science* 41:615-622.
- Kauffman, M. J., J. F. Brodie, and E. S. Lues. 2010. Are wolves saving Yellowstone's Aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742-2755.
- Kranstauber B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* 81:738-746
- Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147-1156.
- Martin, H., M. Hebblewhite, J. Normandeau, M. Trottier, M. Flowers, and E. H. Merrill. 2019. Ya Ha Tinda annual report 2018-2019. University of Montana & University of Alberta.

- McCullough, P., and J. A. Nelder. 1989. Generalized linear models. Second edition. Chapman and Hall, London, UK.
- McInenly, L. E. 2003. Seasonal effects of defoliation on montane Rough Fescue (*Festuca campestris* Rydb.). University of Alberta, Edmonton, Alberta.
- McInenly, L. E., E. H. Merrill, J. F. Cahill, and N. G. Juma. 2010. *Festuca campestris* alters root morphology and growth in response to simulated grazing and nitrogen form. *Functional Ecology* 24:283-292.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14:483-488.
- Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. *The Journal of Animal Ecology* 49:666.
- Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. *Annual Review of Ecology, Evolution, and Systematics* 45:325-345.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology & Evolution* 15:473-475.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227-234.
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnik, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:123148.
- Robinson, T. M. P., K. J. La Pierre, M. A. Vadeboncoeur, K. M. Byrne, M. L. Thomey, and S. E. Colby. 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. *Oikos* 122:727-738
- Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist* 155:141-153.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785-791.
- Steenweg, R. 2016. Large-scale camera trapping and large-carnivore monitoring, occupancy-abundance relationships, and food-webs. University of Montana, Missoula, MT.
- Trenberth, K. E. and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* 9:303-319.
- Vartha, E. W. and A. G. Matches. 1977. Use of a weighted-disc measure as an aid in sampling herbage yield on tall fescue pastures grazed by cattle. *Agronomy Journal* 69:888-890.

Willoughby, M. 2001. The rough fescue dominated community types in the foothills of north-central Alberta. Volume T/017. Public Lands Division, Sustainable Resource Development, Edmonton, Alberta, Canada.