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Succession, herbicides, forage nutrition and elk body condition at Mount St. Helens, Washington

by

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ABSTRACT

Concerns have been voiced over recent reductions in forest cutting, herbicide spraying, and past heavy grazing on nutritional resources for elk (*Cervus elaphus*) and their body condition in the Pacific Northwest. I evaluated the effects of herbicides and herbivory on elk forage in a paired, retrospective vegetation sampling design for early seral (<13yrs) forests around Mount St. Helens (MSH), Washington. Common herbicide regimes reduced elk forage for <3 years after stand initiation and shortened the period of availability of the most nutritious forages prior to forest canopy closure. Herbicide-treated early seral stands provided higher nutritional resources for elk than mid and late-seral stands. Herbivory reduced biomass, primarily of highly palatable shrub species due to reductions in plant height rather than density. I related elk body fat derived from organs collected from hunter-harvested lactating elk in autumn 2011 at MSH (n=55) to the habitat surrounding kill locations. Probability of an elk being pregnant was related to body fat. Lactating females were not thinner than non-lactating female elk, and barren non-lactating individuals had the poorest body condition. The most supported model predicting body fat of lactating elk included harvest date, elevation, and elk density.

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CHAPTER 1

INTRODUCTION

The key role of habitat for wildlife management and conservation has long been recognized (Leopold, 1933; Odum and Barrett, 1971). Effective management of elk (*Cervus elaphus*) populations commonly addresses 3 major factors relating to habitat: (1) forage resources, (2) cover from disturbance, and (3) severe winter weather (Wisdom and Cook, 2000). In the maritime climates of the Pacific Northwest (PNW) severe weather is rarely limiting (Cook et al., 1998; Hanley, 1984; Merrill, 1991). Whereas heavily used roads can negatively impact elk habitat use (Rowland et al., 2000; Wisdom and Thomas, 1996), and therefore have been incorporated into elk habitat models and management plans (Rowland et al., 2005; Thomas, 1988; Wisdom, 1986). The role of nutrition in elk management has not been well addressed, largely because of the challenges in identifying meaningful metrics of forage availability and nutrition (Hobbs and Swift, 1985). However, recent declines in calf recruitment and population reductions in the PNW have been a catalyst for re-evaluating factors limiting elk productivity.

Experimental nutritional studies have shown that forage quality can inhibit ungulate performance and recent studies have helped to initially identify limiting factors in vegetation communities of the PNW. For example, Cook et al. (2004) fed elk ad libitum diets varying in quality between 2.90 (kcal/g) to less than 2.40 (kcal/g) of summer digestible energy (DE). In some cases this reduced the percent body fat of a lactating elk from 22% to less than 8%, and subsequently reduced the probability of being pregnant by more than 20%. More recently, Cook et al. (2013) measured autumn and spring body fat in free ranging elk from 21 herds measured in 5 western states between 2000 and 2009 and observed body fat ranging from 5.5 to 12.4%. Many of the herds in poorest condition were located in coastal Washington and Oregon (Cook et al., 2013). These fat levels were 30-75% of body fat levels observed in captive lactating elk being fed a high quality diet and indicate the potential for reduced pregnancy rates, later conception dates and reduced calf survival (Cook et al., 2004). Further, low body fat levels recorded in many Washington herds would suggest habitats are providing very poor forage conditions (Cook et al., 2004).

Forest succession is one of the most significant factors affecting plant communities and elk habitat within the PNW (Wisdom and Cook, 2000; Witmer et al., 1985). Inconsistent relationships have been found between forage biomass and either habitat use or diet selection in elk in west coast environments (Hanley, 1982; Janz, 1983; Leslie et al., 1984; Schoener, 1971). This suggests that forage production is not the only factor driving elk habitat use. Experimental studies with tame animals and modeling studies of forage intake by ungulates have shown that intake declines when forage availability drops below a critical threshold, but above this threshold intake is related to complex interactions among forage structure and plant quality that influence bite sizes, bite rates and energy intake (Gates and Hudson, 1979; Hudson and Watkins, 1986; Spalinger et al., 1988; Spalinger and Hobbs, 1992; Wickstrom et al., 1984). Studying these interactions in free-ranging animals is problematic, but forage selection reflects their integration and can lead to an assessment of the nutritional value of habitats for the animals that use them. For example, early studies of microhistological analysis of feces and associated plant quality in the PNW (Hanley, 1984; Janz, 1983; Leslie et al., 1984; Merrill et al., 1995) showed elk inhabiting the early seral areas created by the eruption of Mount St. Helens (MSH) had summer diets ~30% higher in dry matter digestibility than elk inhabiting either old-growth forest in the Hoh Valley of the Olympic Peninsula, WA or managed forests of Washington or Vancouver Island. Differences were due largely to elk selecting forbs in summer and grasses in autumn at MSH (Merrill et al., 1995), compared to evergreen ferns and conifers in old-growth forests of the Olympic Peninsula (Leslie et al., 1984) and shrubs in managed forest (Hanley, 1984; Janz, 1983).

More recently, Cook et al. (in review) used data collected in foraging trials with tame elk using standard bite count methodology (Collins and Urness, 1983; Wickstrom et al., 1984) across a set of environmental gradients in Oregon and Washington to identify *selected* and *neutral* plant species and used these species to assess nutritional resources by using algorithms to calculate dietary digestible energy (DDE). This allowed spatially explicit landscape predictions of nutritional resources (i.e., DDE) (kcal/g) to be mapped across a landscape. DDE was the metric of choice because it is most limiting to anabolic processes in ruminants (Holter and Hayes, 1977; Lyford, 1988; Parker et al., 1999). DDE also proved to be the most important variable for determining elk resource selection functions (RSF) for elk habitat management across Oregon and Washington (e.g., Westside Elk Habitat Model, WEHM). Assessment of WEHM using independent data sets has indicated highly successful prediction of elk selection patterns across Washington and Oregon, with Spearman rank r values >0.90 (Rowland et al., in prep.). Thus, these new models offer the potential to evaluate habitat conditions as land management regimes in the PNW continue to change.

Current habitat conditions for elk in the PNW have been influenced by land management regimes on United States Forest Service land, including declines in timber harvest and shifts away from early seral (ES) habitats (WDNR, 2012). With additional declines in timber harvest on private lands, elk herds now have far less access to early seral habitat (WDFW, 2006). Traditional silvicultural practices of site preparation relied on burning of stands prior to planting tree seedlings. This approach was associated with increased ungulate forage (Franklin and Dyrness, 1988). Use of herbicides during stand preparation has recently become more common to mitigate smoke disturbance on timberlands (M. Sheldahl pers. comm.) and to increase stand productivity (Wagner et al., 2004). Current declines in ES habitat and increased use of herbicides have raised the concern of wildlife managers and the hunting public over their long-term impacts on deer and elk populations due to a loss of forage value.

The MSH elk herd in south-western Washington is of particular interest in understanding nutritional dynamics in the PNW. The MSH elk herd has been identified as one of the most important elk herds in the state (WDFW, 2006). Populations of elk in portions of the MSH area are likely now at, or near, carrying capacity (K) and have been susceptible to localized high adult winter mortality (e.g., 1998-99, 2005-06, 2007-08). Indeed, more than thirty years after the eruption of MSH, a portion of the elk herd is now facing decline (WDFW, 2006). It has been suggested that declines in elk at MSH are related to reductions in the plant understory associated with canopy closure over extensive areas of the "blast zone", combined with high herbivory resulting from abundant elk since the eruption. Concerns have also been expressed by WDFW over the potential impacts of herbicide spraying in the timberlands to the west of MSH (WDFW, 2006).

The overall goal of this thesis is to address how changes in forest management practices and herbivory influence forage dynamics and to identify how these changes relate to nutritional condition of elk. I have focused on the environments in and adjacent to MSH because of existing broad-scale variation in forest conditions associated with natural and managed stages of succession. Such conditions are likely needed to see the effects of variable nutritional conditions on elk.

In Chapter 2, I quantified the effects of herbicide application using metrics of accepted biomass and DDE (kcal/g) *sensu* Cook et al. (in review) to compare forage and nutritional resources (a) between existing sites that had been clearcut and subsequently treated with herbicides to near-by sites paired by physiographic features that had not received herbicide treatments, and (b) among early seral sites treated with herbicide, early seral sites not treated with herbicide, and untreated mature forest stands on Forest Service land. Additionally, I compared the plant composition and nutritional resources (accepted biomass and DDE) inside and outside 16 fenced exclosures built from 1 to 6 years ago.

In Chapter 3, I evaluated differences in body fat of elk around MSH and related body fat in harvested female elk to habitat conditions and elk density within a summer “use-buffer” around harvest sites. I evaluated body fat of elk from harvested elk organs submitted by hunters and created a use-buffer from GPS collar data that reflected the area of habitat used by an average elk during summer months prior to the hunting season. I estimated accepted forage biomass (forage that elk will readily consume) and DDE across the study area and mapped relative elk abundance for the region using data from 1) aerial surveys and 2) elk pellet group counts. I compared habitat covariates in a model framework approach.

In Chapter 4, I summarize the results of my thesis and discuss implications for the management of elk in the PNW, and more specifically, at Mount St. Helens.

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CHAPTER 2

ELK NUTRITIONAL RESOURCES: HERBICIDES, HERBIVORY AND SUCCESSION AT MOUNT ST. HELENS

Introduction

Early seral forests (ES) are essential habitats for ungulate species in many parts of North America because available forage declines as forest canopy closes (Witmer et al., 1985). This is particularly true in forests of the Pacific Northwest (PNW) where understory biomass can exceed 4000 kg/ha during the first 10 years of stand establishment, but then decline to <100 kg/ha as the canopy closes (Alaback, 1982; Hanley, 1984; Harper, 1987; Jenkins and Starkey, 1996; Witmer et al., 1985). Wildfire and wind storms historically created most early seral forests in the PNW (Agee, 1993), but since the early 1950s, timber harvest has been the major disturbance creating ES forests in this region (Weisberg and Swanson, 2003). Over the last several decades increased use of wood aggregate products, competition with foreign markets, and protection of old-growth forests for spotted owl habitat has led to declines in timber harvest and the loss of ES forest in western Washington and Oregon, particularly on federal lands (Franklin, 1982; Franklin and Spies, 1991; Perez-Garcia and Barr, 2005)

The majority of ES stands in western Washington now exist mainly on private industrial timberlands (WDNR, 2012) where silvicultural herbicides are routinely used to offset reductions in fibre production resulting from increased import competition (Wagner et al., 2004). A suite of silvicultural herbicides are used operationally 1-2 times during an early window in succession to effectively reduce competing grass and broad-leaf woody plants (Blake et al., 1987; Brodie and Walstad, 1987; Freedman et al., 1993). Although the understory recovers post application (Blake et al., 1987; Brodie and Walstad, 1987; Stein, 1999), herbicide application may alter plant community composition and the long-term forage value of the understory community to ungulates (Strong and Gates, 2006). For example, swordfern (*Polystichum munitum*), a highly competitive but also highly unpalatable evergreen fern species for most ungulates, may be reduced for more than 5 years following herbicide application (Stein, 1995). In contrast, high-value forage species such as wooly catsear (*Hypocharis radicata*) and *Crepis* spp. may increase with the frequency of herbicide application because their short life cycle permits them to establish between treatments (Peter and Harrington, 2009). Reports of up to 50-70% reductions in the cover of palatable woody plant species with herbicide application have been documented, which may directly reduce browse availability but also indirectly alter the abundance of forbs and grasses due to reduced shading (Freedman et al., 1993; Stein, 1999). Although information on the effects of herbicide application on understory plant communities in the Pacific Northwest is accumulating (National Council for Air and Stream Improvement, 2009), no studies have assessed the effects of operational herbicide applications in terms of how they alter the nutritional resources available to ungulates.

Concerns have been raised over the combined effects of declining ES stands and routine herbicide application on black-tailed deer (*Odocoileus* *hemionus columbianus*) and elk (*Cervus elaphus*) habitats in the PNW (WDFW, 2006; ODFW, 2008). Black-tailed deer populations are regionally declining (ODFW, 2008), and low pregnancy rates and body fat levels have been reported for elk in western Oregon and Washington (Cook et al., 2013).

On commercial timberlands around Mount St. Helens I evaluated effects of operational herbicide application on nutritional resources for elk in ES stands ranging in age from 1 to 13 years. I used a nutritional approach modified from Cook et al. (in review), who classified plant species as selected, avoided, or neutral to elk based on foraging trials with tame elk in western hemlock (*Tsuga heterophylla*) forests of western Oregon and Washington. I focused on differences in understory biomass, standing digestible energy (DE), and dietary digestible energy (DDE) of these plant classes due to herbicide applications. I also evaluated the influences of herbivory by resident ungulate herds on each of my measures of nutritional resources, because ungulate herbivory may also play a key role in forest succession, and elk populations have been high in this area since the Mount St. Helens eruption (WDFW, 2006). Because of the high productivity of vegetation in the Pacific Northwest, I predicted that herbicide applications would (1) reduce swordfern and other shade-tolerant dominants that carry over from the harvested forest, allowing shade intolerant herbs and shrubs to develop rapidly improving nutritional resources for elk, but that (2) the early seral window of abundant forage would decline more quickly in treated sites because of the rapid growth of crop trees after herbicide application and ungulate browsing on competing deciduous woody species. Finally, I compared forage values for elk in

ES stands to that of late successional stands using information from this and other studies in the region.

Methods

STUDY AREA

The study was conducted near Mount St. Helens in southwest Washington in an area bordered by Swift reservoir in the south and Riffe Lake in the north (Fig. 2.1). The area includes private lands of the St. Helens Tree Farm operated by Weyerhaeuser Company (WeyCo, 70%), public lands under the jurisdiction of Washington Department of Natural Resources (WDNR, 10%), USFS MSH National Monument (MSHNM, 12%), State Wildlife Area managed by Washington Department of Fish and Wildlife (WMA), and a small percentage of small private landowners. The dominant land use is forestry with most of the study area managed for mid-succession Douglas fir (*Pseudotsuga menziesii*) stands harvested on 40-year cycles. Silvicultural management by WeyCo typically includes planting of conifer seedlings within 1 year of timber harvest. They typically use an initial application of herbicides prior to conifer planting as a chemical site preparation treatment and a second application sprayed during the second growing season to release conifers from competing graminoids and woody shrubs. Herbicide mixtures are variable but typically include combinations of glyphosate, sulfometuron methyl, atrazine, clopyralid, imazapyr, triclopyr and hexazinone. For example, a typical site preparation might include an aerially applied treatment of 1.5 quarts glyphosate and 3 ounces of sulfometuron methyl in 10 gallons of solution per acre. A typical site release treatment would include an aerially applied 3.5 pounds per acre of atrazine, 8 ounces of clopyralid per acre and 1 ounce of sulfometuron methyl in 10 gallons of solution per acre.

The climate is Pacific maritime with wet, mild winters and dry, cool summers (Franklin and Dyrness, 1988). Topography of the area is mountainous with elevations ranging from 240 m to 1200 m. The area supports 3 major forest zones including the western hemlock series (WHS, 75% of study area), Pacific silver fir series (PSS, 20%), and mountain hemlock series (MHS, < 1%). I limited my stand selection to the western hemlock swordfern series because it was the most common (Franklin and Dyrness, 1988). The area is inhabited by the MSH elk herd, which today is one of the largest herds in Washington (WDFW, 2006). After the MSH eruption, the elk population experienced a rapid initial recovery, which was attributed to rapid recovery of natural forage, broad-cast seeding of grass-legume mixes, along with initial restrictions on human access and harvest (Merrill, 1987; Merrill et al., 1995; Raedeke et al., 1986). Seeding of grass and legume forage species initially occurred in years following the eruption (1981-1985) in the northwest portion of the blast zone around Hofftstadt Bluff and on the MSH wildlife area along the North Fork Toutle River. Periodic seeding has continued on the MSH wildlife area and has included *Festuca rubra, Lolium* spp., *Phleum pretense, Dactylis glomerata* and *Trifolium* spp. The estimated elk population was 13,300 in 2005, with the highest densities of the population located in the central portions of the study area in timberlands north and south of the mudflow (WDFW, 2006). Additionally, the black-tailed deer (*Odocoileus* *hemionus columbianus*) population at MSH was estimated at 500 in 2000 (Davis et al., 2010), but higher numbers and densities exist in the southern portions of the study area closer to the Columbia River (WDFW, 2006).

FIELD DESIGN AND SAMPLING

To assess the influence of herbicide applications and ungulate herbivory on elk nutritional resources I sampled sites located in the western hemlock swordfern series (Franklin and Dyrness, 1988) ranging in elevation from 113 to 833 m using a retrospective approach. I used a case-controlled design for selecting 27 stands untreated with herbicides based on operational records and local guidance of forest managers, and selected the closest herbicide-treated stands (50- 6012 m) with similar stand age, elevation, aspect, slope, slope position, and soil type (See Appendix 3 for distances between paired sites). Sampling of vegetation biomass at herbicide-treated and untreated paired plots occurred between 30 July and 30 August in 2010 (n=12 pairs) and 1 July to 30 September in 2011 (n=15). To assess effects of herbivory on vegetation I sampled 16 established ungulate exclosures (See Appendix 5 for age and size) and unexclosed paired, adjacent plots within 50 m using the same selection criteria as described above. Exclosures ranged in size from 0.121 – 2.83 ha and were constructed of 4x4 wood fence posts and a heavy gauge steel fence 2 m high. Sites where exclosures occurred were subject to applications of herbicide within 1 year following clearcutting and a release treatment in the second year after seedlings were planted. Sampling at these sites occurred from 1 August to 30 September in 2011 with stand age (since crop trees were planted) at the time of sampling being 1-2, (n=3), 3-4 (n=7), and 5-6 (n=6) years. I note that all exclosure sites inside and outside of the exclosures were located in stands that had been treated with herbicides, limiting my ability to directly compare herbicide vs. herbivory effects on vegetation.

I followed the sampling design of Cook et al. (in review) to compare treatment differences. Briefly, I established a 0.4 ha macroplot with 5 parallel transects (45 m in length) systematically placed across the macroplot (Appendix 1). I clipped current annual growth (CAG) of forbs, graminoids, and shrubs, and standing biomass of ferns from 2 cm to a height of 2 m (reach of an elk) within two 2 m^2 circular plots along each transect for a total of 10 clipped plots per macroplot. For evergreen trees and shrubs I also clipped the previous year's growth (out to the second growth node), reflecting the fact that elk will sometimes consume older growth (Cook et al., in review). Harvested vegetation was sorted and bagged by plant species, oven dried at 60° C to constant weight, and weighed to nearest 0.1 g. Species biomass within each clip plot was averaged for each macroplot and converted to kg/ha. Along each transect, overstory canopy cover of trees was estimated at 10 points using an ocular sighting tube and averaged for the macroplot (Bunnell and Vales, 1990; Cook et al., 1995), and basal area was measured using an angle gauge from the center of each clip plot.

At exclosure sites, macroplot dimensions were occasionally reduced to accommodate small exclosures resulting in a smaller area sampled and shorter transect lengths for overstory measurements, but clip plots remained the same size. A second approach was used to estimate shrub biomass at exclosures because clipping shrubs was not always feasible inside exclosures. I counted the number of shrub or deciduous tree stems (rooted stems) by species in 6 belt transects (2 x 15 m) and recorded the average of the crown height (cm) and 2 perpendicular cross-sectional diameters (cm) on up to 10 representative rooted stems for each species per shrub plot. Individual stem volume (height x mean diameter of cylindrical growth form, n ~60) was used to estimate mean CAG (g/stem) for a shrub species based on allometric relationships (Appendix 6) from Merrill (1985) and was multiplied by shrub density to estimate shrub CAG (kg/ha) by species in each macroplot. To compare differences in these approaches, I estimated shrub biomass with both methods using data from 16 of the unexclosed sites (1-6 yrs). I found using allometric predictions, that biomass of accepted shrubs was not significantly different between methods (*P*=0.58), but predictions using the allometric approach were higher than clip plot estimates for avoided shrub species, primarily salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*), by 1.9 ± 4.5 times (*P*=0.05). As a result, I adjusted allometric biomass predictions at exclosures for avoided shrubs when comparing between herbicide and herbivory treatments.

Finally, I used understory biomass and composition data from sites located in the western hemlock series in Washington and Oregon to describe nutritional resources for elk in pole (21-50 yrs, n=35), mature (51-150, 36) and old-growth stands (151-600, 8) (Cook et al., in review). Plot locations were selected using a random sampling approach in a GIS framework and placed within stands using a random starting point located at least 50 m from each stand edge and road to reduce potential road or edge effects (Cook et al., in review). Understory vegetation was sampled using the same sampling protocols as described at herbicide sites in this study.

FORAGE PREFERENCE CLASSES

I classified plant species found in herbicide and exclosure plots into two preference classes derived from the 3 classes used by Cook et al. (in review) for understory plants in the WHS series, which was based on 89 week-long foraging trials with tame elk (n=30) in early seral and closed canopy forests in the coastal and Cascade ranges of Oregon and Washington from 2000-2002. They collected diet composition data using standard bite count methodology (Collins and Urness, 1983; Wickstrom et al., 1984) and measured forage availability as described herein. Selection values of each plant species were based on the Ivlev index (I) derived as $(D_i - B_i)/(D_i + Bi)$ (Ivlev, 1961) where D and B are the proportions that the biomass of species *i* comprised either of the diet (D_i) or of the available biomass (B_i) in a pen during the foraging trial. Values ranged from -1 to +1 with "selected" plant species having $I > 0$ at a 90% confidence interval that excluded zero, "avoided" species having $I < 0$ with a 90% confidence interval that excluded zero, and "neutral" species were those species whose 90% confidence interval included zero. For this study, I retained the avoided category, but combined selected and neutral species into an "accepted" category. For the 31 species (16% of all species) found at Mount St. Helens that were not reported by Cook et al. (in review), I used results of elk fecal analyses from Mount St. Helens (Merrill, 1987), published literature (Jenkins and Starkey, 1996), and observations of feeding elk in the field to assign a forage preference class.

STANDING AND DIETARY DIGESTIBLE ENERGY

Standing digestible energy (DE, kg/ha) available in the understory at treatment sites was estimated from sampled biomass (kg/ha), gross energy values (GE, kcal/g) obtained from Cook et al. (in review), and digestible dry matter (DMD, %) of species. DMD values were from samples collected in late summer (August-October) when senescence can create a bottleneck effect in summer diet quality. I sampled 217 species across sites, but generally 21 species comprised the majority (more than 1% per species) of total biomass. DMD values for these species were known for all but 2 species which were unpalatable and only comprised between 4-7% of total biomass. Nevertheless, species DMD values across all sites were known for 83% ± 16 of total biomass. DMD values for the 217 species were obtained in 3 ways: (1) DMD of 12% of the species were estimated by collecting samples in the study area in August 2011; (2) DMD of 14% of the species were reported by Merrill et al. (1995), who collected the species in the area in August 1984; and (3) DMD values of 19% of species were reported in the literature for sampling that generally occurred between August and October (Canon et al., 1987; Damiran et al., 2002; Hanley and McKendrick, 1983; Jenkins and Starkey, 1996; Kirchhoff and Larsen, 1998; Leslie et al., 1984; Perez, 2006; Rhodes and Sharrow, 1990). For species collected in this study and by Merrill et al. (1995), samples were collected from 3-5 sites and included plant parts (buds and shoots) that were observed to be eaten during observations of foraging elk. To estimate DMD for those species for which no values were available, I used the mean DMD (Appendix 8) of all other species in the same vegetation class (forbs: 63.08% ± 9.31, mean ± SD > deciduous shrub leaves and twigs: 55.84% ± 11.21 > graminoids: 54.04% ± 8.40 > ferns: 39.63% ± 5.83 > evergreen trees/shrubs: 35.85% ± 7.24; ANOVA, df=4, P>0.01). Most vegetation classes were significantly different (BONFERRONI, P<0.05), but due to a small sample size, ferns were similar to all vegetation classes except forbs, and grass was equivalent to deciduous shrubs.

Plants collected in this study were analyzed using acid detergent fiber analysis at Washington State Habitat Nutrition Lab and DMD was calculated following methods of Robbins et al. (1987). Merrill et al. (1995) obtained DMD values at Washington State Habitat Nutrition Lab following methods of Tilley and Terry (1963) using inoculum from a rumen-fistulated elk maintained on an alfalfa diet. Values obtained from the literature used one of these two approaches. For GE (kcal/g) of plant classes, I used those provided by Cook et al. (in review): 4.80 ± 0.42, mean ± SD for evergreens plants (shrubs, trees, and ferns), 4.60 ± 0.19 for deciduous shrubs, 4.51 ± 0.35 for graminoids, and 4.50 ± 0.17 kcal/g for forbs. These gross energy values were marginally higher than plants sampled in other PNW studies (4.1-4.4 kcal/g [Hutchins, 2006]).

I estimated total available DE (kcal/ha) for accepted and avoided species per macroplot as the sum of the product of biomass, B_i, of the species and its respective DE_i (DDM of the species x GE of the respective forage class). DDE (kcal/g) of elk foraging at my sampled plots was derived using foraging trials with tame animals. Cook et al. (in review) determined that elk DDE was asymptotic at 2.72 kcal/g intake in WHS communities but that it dropped below this value when the biomass of accepted forage fell below 500 kg/ha. They hypothesized this decline occurred because encounter rates with accepted biomass declined and thus elk had to consume avoided species of lower quality to maintain intake rates. Therefore, I derived DDE (kcal/g) based only on encounters with accepted species when the biomass of accepted species was >600 kg/ha and on all species when accepted species biomass was <600 kg/ha as:

$$\text{DDE}j = \sum U_{ij} DE_i = \sum \frac{w_i A_{ij}}{\sum_i^n w_i A_{ij}} DE_i \qquad \text{eqn 2.1}$$

where U_i is the proportional use of plant species at site j based on encounter proportional to biomass availability (A_i) and selection given an encounter (Lele et al., 2013), and their respective DE_i. Elk selection was based on the mean selection ratio (w_i) for species i from tame elk foraging trials at 87 sites in WHS communities (Cook et al., in review) as % of the diet consumed of species i by an elk during a foraging trial divided by percent of species i of the total biomass available to the elk during a foraging trial (see Appendix 10 for species values).

STATISTICAL ANALYSIS

I tested for significant (α=0.05) main effects (age, treatment) and their interaction for biomass classes, DE and DDE using ANOVA based on a split-plot design because plots were paired within sites. All references to age and years refer to time since crop trees were planted, and crop trees were always planted within 1 year of the preceding harvest. Post-hoc tests of treatment differences were based on paired T-tests within stand ages. Early seral stands were compared to late seral stands using one-way ANOVA and BONFERONI post-hoc analysis. Square root or log transformations were used when data violated assumptions of normality or equality of variance. Pearson's product moment correlations were used to evaluate relationships between biomass categories and relationships between plant species and basal area. All statistical analyses were performed in STATA 12 (StataCorp, 2011).

Results

HERBICIDES

Biomass. Total biomass ranged from 98 kg/ha to 5148 kg/ha across sites. Biomass of avoided species comprised the greatest proportion (65% ± 22, mean ± SD) of the total biomass (2482 kg/ha ± 1249). As a result, biomass of avoided species was correlated with total biomass in herbicide-treated and untreated sites (r=0.77, P<0.01, Fig. 2.2a). In contrast, accepted biomass was positively correlated with total biomass only in herbicide-treated sites (Fig. 2.2b). Accepted and avoided biomass were related only in stands without herbicide application and the relationship was negative (Fig. 2.2c). Canopy cover was negatively related to accepted biomass in both treated (r=-0.39, P=0.05, n=27) and untreated sites (r=-0.37, P=0.06, n=27) between 1-13 years, whereas avoided biomass was positively related to overstory canopy cover only in untreated sites (r=0.50, P<0.01, n=27).

There was no year effect on biomass at sites within the same age class sampled in 2010 and 2011 (P>0.15) so data were combined across years for further analysis. Total, avoided, and accepted biomass was lower in herbicide-treated sites than untreated sites in the first two years after stand establishment (Fig. 2.3a, Table 2.1). The initial decline in biomass at treated sites was primarily related to a decline in biomass of ferns ($P<0.01$, paired T-test), graminoids ($P<0.01$), and *Rubus* spp. ($P<0.01$), particularly salmonberry (*Rubus spectabilis*), whereas forbs were not significantly different in biomass, but were higher at 3 out of 5 sites where woodland groundsel (*Senecio sylvaticus*) dominated (Table 2.2, Fig. 2.4).

After the first two years, accepted biomass was similar between herbicide treatments until year 13, but compositional differences remained (Fig. 2.3a, Table 2.1). The increase in biomass (Fig. 2.3a) in treated sites greater than 2 years old occurred because grasses such as velvet grass (*Holcus lanatus*) and *Agrostis* spp. became more abundant ($P<0.05$), whereas swordfern ($r=0.67$, $P<0.01$) and salal ($r=0.35$, $P=0.01$), which were correlated with increasing avoided forage, remained lower in biomass in treated sites after 2 years ($P<0.05$). Forbs and shrubs did not differ in biomass, but thistle species (*Cirsium* spp.) and trailing blackberry (*Rubus ursinus*) were found consistently more often in treated sites between 3-5 years, and evergreen shrubs (Oregon grape and salal) were found consistently less in herbicide-treated sites (Table 2.2, Fig. 2.4). Wooly catsear and smooth hawksbeard (*Crepis capillaris*) increased in both treatments. Between 6-9 years, biomass of grass remained higher in treated sites ($P<0.01$), but all other vegetation classes were similar. However, thistle and trailing blackberry continued to be more common in treated sites while swordfern remained less common (Table 2.2). After 9 years, biomass of accepted forage was similar between treatments, but higher biomass of avoided species, particularly swordfern, occurred in untreated sites ($P<0.05$) (Table 2.2, Fig. 2.4). The difference in total and avoided biomass between 10-13 years was associated with a decline in fern as canopy cover increased in treated sites ($r=-0.96$, $P<0.01$, n=5).

Digestible energy. DMD averaged higher in accepted species (57.5% ± 1.04, mean ± SD, n=164) than in avoided species (48.1% ± 1.48, n=53; $X^2=10.8$, $df=3$, $P=0.02$, Fig. 2.6). Standing DE in accepted species was lower in the first 1-2 years after herbicide treatment ($P=0.01$), which reflected reduced availability of accepted biomass (Fig. 2.7a). Standing DE in accepted species was highly variable in composition across sites between 3-9 years but trended higher in herbicide-treated sites. Standing DE in accepted species began to decline in treated sites in years 10-13 (Fig. 2.7a), but was similar between treated and control sites.

Estimated dietary digestible energy was higher in sites 1-2 years after herbicide treatment ($P=0.02$) because highly digestible species, including red huckleberry (*Vaccinium parvifolium*) and wooly catsear, were proportionally more abundant. DDE was higher in untreated stands in years 3-5 ($P=0.04$) due to a high diversity and proportion of digestible forbs and shrubs including snowberry (*Symphocarpus albus*), *Rosa* spp., *Viola* spp., wood rush (*Luzula* spp.), as well as some *Carex* species. In contrast, declines in DDE in treated sites were consistent with increases in lower digestibility grasses such as *Agrostis* spp. and velvet grass (Table 2.2, Fig. 2.4). After 5 years DDE declined and remained similar between treatments (Fig. 2.8a).

HERBIVORY

Biomass. Total biomass increased with age since harvest inside and outside exclosures (Table 2.3), and as expected, successional patterns of biomass outside enclosures were comparable to that of herbicide-treated sites of the same age (3-4 yrs: 1188.80 kg/ha ± 427.1 vs. 2006.15 ± 704.39, mean ± SD; 5-6 yrs: 2395.74 kg/ha ± 188.46 vs. 2708.56 ± 1265.03). Outside the exclosures, total biomass was 35% lower ($P<0.01$) and accepted species biomass was 49% lower ($P<0.01$) than inside the exclosures. Biomass of avoided species was similar inside and out after two years (Table 2.3, Fig. 2.3b). Lower accepted biomass outside the exclosures was due largely to less standing biomass of shrubs such as *Rubus* spp. ($P<0.01$), bitter cherry (*Prunus emarginata*), red alder (*Alnus rubra*), Cascara buckthorn (*Rhamnus purshiana*), *Ribes* spp., and red huckleberry at some sites (Table 2.4). Most of these shrubs were classified as accepted by elk (Appendix 10). The higher shrub biomass inside exclosures was the result of increased shrub biomass rather than increased shrub densities (all species, $P>0.01$, Table 2.5). In addition to shrubs, biomass of grass species, including velvet grass, *Agrostis* spp. and blue wild rye (*Elymus glaucus*), was higher outside exclosures between 3-4 years ($P=0.05$, Fig. 2.5), and these species remained higher at 4 of 6 sites between 5-6 years (Table 2.4). Douglas fir biomass was consistently higher inside exclosures between 3-4 years, but not thereafter. Between 5-6 years Douglas fir leader height inside exclosures was negatively associated with increasing avoided biomass ($P<0.01$, $r=-0.95$), whereas no relationship existed outside exclosures.

Digestible energy. Standing DE increased rapidly with stand age, particularly inside exclosures. Standing DE was similar between exclosed and unexclosed sites the first 2 years. But differences in total standing DE and that of accepted species between exclosure treatments increased markedly thereafter, indicating a strong suppressing effect of herbivory on accepted species as succession progressed (Table 2.6).

After 2 years, 76% of plots within exclosures had higher DDE values because biomass of palatable shrub species was proportionally higher, including red elderberry, cascara, and a palatable forb, fireweed (*Epilobium angustifolium*). The relatively low estimates of DDE in areas with herbivory were primarily due to the greater abundance of graminoids; these provided relatively low levels of DE in late summer. But high proportions of digestible forbs, particularly thistle, and wooly catsear kept DDE moderately high (Table 2.4, Fig. 2.8b). Nevertheless, I found no significant effects of exclosure treatment or age effects on DDE (Table 2.3), likely due to the relatively high abundance of grasses in 3 of 13 exclosures (Fig. 2.8b).

BIOMASS AND DDE IN LATER SERAL STANDS

Total understory biomass in late successional stages ranged from 248 kg/ha ± 395, mean ± SD in pole stage to 415 kg/ha ± 271 in old-growth. Accepted biomass in late seral stages was very low, never comprising more than 26% ± 18 of total forage. Total biomass was lower in all closed canopy forest (CCF) stages than in any of the herbicide-treated ES stands (ANOVA, $P<0.05$), except those <3 years old (Table 2.7, Fig. 2.3). Biomass of accepted species was lower in all CCF stages than in any of the herbicide-treated ES stands ($P<0.05$) (Fig. 2.3a). Standing DE was lower in late seral stands than early seral stages ($P<0.05$) except for 1-2 year stands treated with herbicide and 10-13 year stands treated or untreated with herbicide (Fig. 2.7a). Estimated DDE in late seral sites was lower compared to 1-2 year old herbicide-treated stands and 3-5 year old herbicide-untreated stands but was otherwise similar (Table 2.7, Fig. 2.8a).

Exclosure sites between 3-6 years old averaged 1232 kg/ha ± 805 higher in accepted biomass than late seral stands ($P<0.05$, Table 2.8). Standing DE of accepted species reflected differences in biomass and was greater in early seral sites between 3-6 years old ($P<0.05$, Fig. 2.7b).

DDE was lower in mature stands compared to 1-2 year old unexclosed and 3-4 year exclosed sites ($P<0.05$), but was otherwise similar to early seral herbivory sites. Late seral DDE was primarily comprised of *Vaccinium* spp. and vine maple, but remained relatively low because avoided biomass remained proportionally high (Table 2.8, Fig. 2.8b).

Discussion

The poor nutritional resources in late summer on timberlands at MSH and more generally the PNW pose significant challenges for maintaining productive elk populations in this region (Harper, 1987; Hutchins, 2006; Cook et al., 2013). Nutritional limitations in late summer and autumn have been shown to increase age at first reproduction, reduce adult female fecundity, and decrease juvenile body growth and juvenile survival (Cook et al., 2004). Maintaining ES habitat is considered a key management focus for supporting elk herds in the region largely because of their greater level of forage production (Hutchins, 2006; Merrill, 1987; Cook et al., in review). Peak biomass at MSH (~5000 kg/ha) averaged about 10 times that in closed canopy forests. Estimates for ES communities at MSH are similar to that reported previously in the WHS region, but higher than that reported by Cook et al., in review (2500 kg/ha up to 4500 kg/ha), and marginally lower than the 3853-7640 kg/ha range of biomass that is reached 10-15 years after timber harvest in other forests of the Pacific Northwest (Boldor, 2007; Karakatsoulis and Kimmins, 1993; Messier and Kimmins, 1990; Schoonmaker and McKee, 1988). Thus, I would predict that DDE of elk would be greater in ES habitats than in older stages with closed canopy forests, and previous studies support this contention (Cook et al., in review). Nevertheless, 65% ± 22 of the biomass in ES communities consisted of species that elk avoided, and these typically were low in digestible energy. My DDE estimates may be conservative and on average were about 10% ± 6 lower when using my approach (see DDE methods) to estimate DDE with plant biomass data from macroplots sampled by Cook et al. (in review), compared to DDE estimates for the same sites that were estimated by Cook et al. (in review) and based on observations of tame elk foraging in their experimental pens. My DDE estimation assumes elk encounter forage species randomly, whereas in spatially heterogeneous environments elk may forage in high quality patches until they are depleted (Jiang and Hudson, 1993). Even so, elk foraging at MSH may not be able to achieve a dietary maintenance level of 2.7 kcal/g, and typically their diets may be below 2.5

kcal/g where performance of lactating adults and their offspring decline (Cook et al., 2004).

HERBICIDES

The application of operational herbicides reduced nutritional resources both directly and indirectly. Herbicides reduced the available understory biomass during the initial 2 years of stand initiation by as much as 77% ± 13 with no discrimination between accepted species and avoided species. Comparable short-term reductions of plant understory of 54 to 84% after herbicide application have been reported in other studies in the PNW (Dinger, 2007; Harrington et al., 1995; Maguire et al., 2009; Stein, 1995). Initially elevated estimated DDE (~2.62 kcal/g) for elk occurred because herbicides removed most of the residual forest understory, and the remaining plants, including species such as wooly catsear and red huckleberry, were high in DE. Cook et al. (in review) similarly found elevated levels of DDE for tame elk when they foraged in a 2 year old stand that had considerable bare ground but where there were patches of green herbs due to autumn rains. While DE available per bite may be initially high, the majority of these sites had accepted biomass below the threshold of 150 kg/ha where instantaneous intake rates decline (Cook et al., in review). If elk avoid these very young stands (1-2 yrs) as they do clearcuts in the very early stages (Irwin and Peek, 1983), herbicide application essentially creates short-term habitat loss. However, data from Cook et al. (in review) indicated less reduction in biomass of accepted species after herbicide treatment than found here, suggesting that much variation may exist in the reduction of accepted biomass in the first year or two after herbicide application. Differences in herbicide mixes, application regimes, and a host of site conditions may contribute to these differences.

By reducing competition with understory species, application of herbicides facilitated the growth of trees and more rapid canopy closure than in other studies (Edwards et al., 2004; Miller et al., 1995). Cook et al. (in review) reported that canopy cover was the best predictor of accepted biomass in WHS communities across a wide range in stand ages and reported that canopy closure in WHS reached 20-40% by 9-11 years (consistent with my results) and 90% by 20-25 years. At MSH, by 10-13 years accepted species had declined and their biomass was similar in both treated and untreated sites despite differences in canopy cover of trees. However, accepted species within both treated and untreated stands of 10-13 years remained above the threshold (~500 kg/ha) where elk could maintain DDE. At the same time, biomass of avoided forages, primarily ferns and evergreen shrubs, remained lower on sites where herbicides were applied, and this difference was significant when stands reached 10-13 years. If the reduction in avoided species at these sites afforded better access to the remaining high quality forage, then herbicide application may have improved foraging opportunities in the period just prior to full canopy closure. Standing DE was higher in treated sites prior to the onset of canopy closure, but I found no evidence of elevated estimated DDE because of a high abundance of species with lower DE in both treatments.

Between stand initiation (1-2 yrs) and the beginning of canopy closure (3-9 yrs), biomass of accepted species recovered from the effects of herbicides, as did avoided species across all sites. During this period, fluctuation in DDE were largely because of variation in site-specific plant composition, where high DDE was associated with shrubs and forbs such as elderberry and wooly catsear, and lower DDE was often associated with velvet and *Agrostis* Spp. Sites not treated with herbicides typically had some of the highest abundance and diversity of accepted species, and my data indicated that in theory elk have the highest likelihood of achieving maintenance levels of DDE (>2.7 kcal/g) in these stands along the successional sequence. At the same time, I found lower DDE at some treated sites because of an abundance of velvet grass and *Agrostis* spp., which may persist after herbicide applications due to secondary disturbances like herbivory (see below). In late summer grasses typically are cured, and my estimates of DMD indicate their quality is low unless late summer rains promote regrowth.

HERBIVORY

My data also indicated that ungulate herbivory may further reduce the nutritional value of early seral stands at MSH. The reduction in availability of preferred shrub species, such as bitter cherry, elderberry, huckleberry and rose, represents a substantive loss of DE because shrub leaves in particular are often nutritionally superior to herbs in late summer when DE demands are high for lactation, juvenile growth, gaining body fat reserves, and breeding (Cook et al., 2004; Cook et al., 1996; Irwin et al., 1994; Noyes et al., 2002). Substantial reductions in the elk population likely would be necessary to eliminate these effects because herbivory on preferred browse species is not proportionally related to ungulate density (Hobbs, 1996; Nugent et al., 2001). Support for this conclusion in PNW systems comes from the low availability of these preferred species in areas where elk have not maintained high elk densities (Cook et al., in review). Reductions in herbivory also may be undesirable from a forestry perspective because there is little evidence that ungulate browsing eliminates shrubs, rather their height is suppressed (Table 2.5), and recovery of shrubs even where herbicides applications occur may hinder young conifer growth (Ristau et al., 2011). Similarly browsing by elk may prevent deciduous shrubs from shading out other understory species that may be important to ungulates (Hanley and Taber, 1980; Merrill, 1994; Riggs et al., 2000).

The most consistent impact of herbivory on the herbaceous understory was an increase in grass biomass and disturbance-tolerant species in unexclosed areas. Grasses that have evolved with herbivory have been shown to reallocate belowground resources and increase photosynthetic rates to successfully recoup tissue loss, or stimulate above ground production only under favorable conditions (Augustine and McNaughton, 1998; Strauss and Agrawal, 1999). Increases in graminoids outside exclosures have been reported in other studies from the PNW (Schreiner et al., 1996; Woodward et al., 1994) and in field observation where ungulate grazing is high (Harper, 1987). Although benefits of increased availability of grasses for improving diet quality may depend on micro-site condition or summer rains, grasses are key forages for elk in the PNW during winter and spring (Leslie et al., 1984; Merrill, 1994). A secondary effect proposed for increased graminoids is the potential to retard tree growth and prolong the ES window of high forage availability (Riggs et al., 2000). Such a grazing-mediated effect could be important particularly in the WHS communities where forest succession is rapid, but I found no evidence for such an effect, and even observed one site with complete canopy closure between 10-13 years. There is some evidence for an initial increase in forbs such as woodland groundsel, *Cirsium* spp., and wooly catsear, which are typically associated with disturbance. However, herbicide applications occurred at all exclosure sites so whether the effect of herbivory on these species is a secondary disturbance that is contingent on herbicides remains uncertain.

IMPLICATIONS FOR ELK NUTRITION

Studies on reproduction and lactation rates and their associated poor body condition of elk from PNW herds support the hypothesis of nutritional limitation in these systems (Cook et al., 2013; Harper, 1971; Stussy, 1993; Trainer, 1971). On managed lands west of Mount St. Helens where large portions of the area were affected by the 1980 eruption, forest canopies are now largely closed and operational herbicides are used widely. Segments of the Mount St. Helens elk population inhabiting this area have some of the lowest body condition and reproduction values measured through the PNW (Cook et al., 2013), and elk at MSH experience periodic die-offs (WDFW, 2006). A large-bodied ungulate like an elk, confronted with the poor nutritional conditions characteristic of PNW forests, is forced to make dietary trade-offs to meet total DE requirements and rumen function at multiple spatial scales (Hanley and Taber, 1980; Jenkins and Starkey, 1993; Leslie et al., 1984; Spalinger and Hobbs, 1992). At the scale of the landscape, early seral stands play an important role in providing abundant forages (Cook et al., in review; Hanley, 1984; Jenkins and Starkey, 1996; Witmer et al., 1985). Their use by elk is predictably high where human disturbance is low (Merrill, 1994) because thermal constraints in these open areas are rarely limiting (Cook et al., 1998; Merrill, 1991). Within a stand, Cook et al. (in review) reported elk maintained intake until biomass of accepted species dropped below 500 kg/ha by increasing their consumption of avoided species. Associated with this dietary shift were reduced bite rates, larger bite masses, and increases in feeding time, but behavioral shifts still lead to lower DDE and 24-hr DE intake. When avoided species were unavailable, elk were not able to maintain instantaneous DDE intake rates when biomass was below 120 kg/ha.

I have shown that herbicides and herbivory have the potential to alter the foraging opportunities for elk in early seral stand by altering the absolute and relative availability of preferred and avoided species. Herbicide application initially may equate to habitat loss but the loss is short-lived and spatial patterning of timber harvest on the landscape that staggers stand ages by even 2 years is likely to improve forage conditions on a local scale. More frequent application of herbicides than reflected in my data could severely disrupt understory recovery before canopy closure influences a shift toward lower quality, shade tolerant species.

The loss of forage occurs very rapidly at 12-15 years after stand initiation, and this probably represents the greatest loss, within stands, in nutritional resources across the successional sequence. Thus, extending the ES window has potential to substantially improve nutritional resources, and a number of options might exist to extend this period. Lower density of planted conifer seedlings, pre-commercial thinning with appropriate slash management, and commercial thinning have been promoted as options for off-setting forage losses due to rapid canopy closure (Raedeke and Lemkuhl, 1984). However, Cook et al. (in review) found that commercial thinning to 65% canopy closure increased abundance of palatable groups like forbs, deciduous shrubs, and grasses, but without a commensurate decline in ferns and evergreen shrubs. As a result, only moderate increases in DDE and DE intake levels were observed, and diets still did not achieve maintenance level DDE. Commercial thinning combined with judicious use of herbicides to reduce the dominance of unpalatable shade-tolerant species, such as swordfern, might offer better foraging options than thinning alone. I hypothesize there may be a period prior to canopy closure, where foraging opportunities for elk also may be improved moderately by herbicide application because dominant poor-quality residual forest species are reduced. Many options may exist for improving the forage base with or without the use of herbicides, but more work is needed to determine which silvicultural strategies would be most effective.

Site preparation with prescribed fire has also been promoted as a management tool to increase forage (ODFW, 2008; WDFW, 2006) and was commonly used prior to operational herbicide use (Wolters, 1981). Burning can increase forage by creating seed bed surfaces (Nguyen-Xuan et al., 2000), and increasing soil nitrogen (Hobbs and Gimingham, 1984), but herbicide applications can have similar effects on seed bed availability and nitrogen mineralization (Maguire et al., 2009; Vitousek et al., 1992). Vegetation recovery at MSH after herbicide application shares a number of similarities with recovery after prescribed burning and both disturbances initially cause a reduction of biomass, particularly residual species, followed by an increase of invader species including woodland groundsel, wall lettuce (*Lactuca muralis*), and thistle species (Franklin and Dyrness, 1988; Halpern, 1989). In both cases the greatest increase of vegetation occurs 2 years after disturbance and the timing of recovery is potentially similar because Cook et al. (in review) observed no differences between herbicide-treated sites and burned sites in 15 year old stands. I suggest stands treated with herbicide may be more similar to prescribed burning than stands untreated with herbicides.

Conclusions

I assessed the adequacy of forage resources for elk at MSH under current use of operational herbicides and elk herbivory using DDE. My approach relied on calculating diet choice based on forage abundance at a site and forage selection values averaged across many foraging trials with tame elk in experimental settings (Cook et al., in review). Despite the assumptions of my approach, it may be a meaningful metric for assessing stand conditions because total forage biomass, which is commonly used to assess forage availability, is most related to the abundance of forages that elk are unlikely to eat. Additionally, protein is not considered limiting in the PNW (Cook et al., in review; Jenkins and Starkey, 1996; Merrill, 1994), and there remains considerable variation in DE among forages that elk will consume. Although estimates of DDE derived using my approach are likely to be conservative, they also can be judged more readily in terms of animal performance (Cook et al., 2004).

At MSH early seral stands of WHS provide marginal resources in terms of DE for elk to meet energy requirements for maintenance. Operational herbicides may initially exacerbate these conditions due to the initial loss of forage. At the same time, harvest regimes on private industrial land in this region have relatively short rotations (~40 yrs) which, based on simulations of forage dynamics over the long-term, is expected to provide a potentially higher forage base that is temporally more stable (Hett et al., 1978; Visscher and Merrill, 2009). My results support the conclusion that wide-spread declines in the rate of timber harvest, which results in more late seral habitat (Jenkins and Starkey, 1996), is likely to have a relatively greater, long-term effect on the nutritional adequacy of PNW landscapes for elk than the use of operational herbicides if applications are restricted to stand initiation.

Anticipating the consequences of the long-term decline in nutritional resources due to reduced timber cutting on elk populations can be problematic because there is an asymmetry in the potential response of an ungulate population to a directional change in habitat conditions -- a population response to an increasing carrying capacity is limited by the maximum intrinsic growth rate of the species, while a population decline has no such constraint and can be dramatic. Interactions between long-term declines in carrying capacity and short-term stochastic variation in the environment (e.g., severe winters or summer drought) may periodically result in dramatic changes in fitness (Pettorelli et al., 2005), even in the face of population reductions. Similarly, harvested species may be more susceptible to being overharvested when habitat conditions are declining than when it is increasing. Quantifying these effects will require linking nutritionally based metrics of habitat-performance in the field.

Table 2.1. Treatment means by age class and test statistics for main effects (herbicide and age) and age x treatment interaction on biomass (kg/ha) of total plant understory, avoided or accepted biomass, biomass of vegetation classes, standing digestible energy of forage preference classes and dietary digestible energy. Note: Woody plants include deciduous trees and all shrubs excluding *Rubus* spp.

	1-2 years			3-5 years			6-9 years			10-13 years			Effect (p-value)		
Response	NH	H	SIG[c]	NH	H	SIG	NH	H	SIG	NH	H	SIG	Treat	Age	T*A
Total	2663	700	**	2371	2119		3566	3061		3615	2001	*	<0.01	0.02	0.05
Avoided	1407	486	*	1643	1236		2519	1832		3285	1741	*	<0.01	0.05	0.23
Accepted	1256	214	*	728	883		1047	1229		330	260		0.07	<0.01	<0.01
Conifer	16	23		139	346		1043	573		790	279		0.43	<0.01	0.24
Ferns	830	9	**	801	323	**	777	666		1926	908		<0.01	0.03	0.17
Forbs	585	553		453	462		331	397		80	113		0.67	<0.01	0.69
Graminoids	590	84	**	154	419	*	35	597	**	76	71		0.24	0.2	<0.01
Rubus Spp.	450	12	**	222	380		384	365		333	279		0.07	0.14	0.04
Total DE[a]	5159	1881	**	4434	4495		5764	6100		5001	3195		<0.01	0.02	<0.01
Avoid DE[a]	2109	1286		2458	2170		3388	2922		4250	2495		0.02	0.19	0.32
Accept DE[a]	2929	516	**	1898	2186		2262	3076	*	731	676		<0.01	0.08	<0.01
DDE[b]	2.60	2.67	*	2.62	2.50	*	2.51	2.50		2.50	2.52		0.69	0.21	0.18

[a] DE is kcal/ha*1000

[b] DDE is kcal/g

[c] SIG represents a pairwise significant difference (T-test) with one star denoting a p-value below 0.05 and two stars denoting a p-value below 0.01.

Table 2.2. Species consistently higher or lower at herbicide-treated or untreated sites within stand age class. Species characteristics are presented with mean biomass (kg/ha) difference between treatments, percent (%) of sites where species abundance was higher or lower, and number of sites (n) where a biomass difference was calculated. Positive mean values indicate lower biomass in herbicide-treated sites and negative mean values indicate a lower biomass in herbicide-untreated sites.

	Higher biomass in untreated sites								Lower biomass in untreated sites						
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	Species	Class	Pref	Type	Mean	SD	%	n
1-2 Years								1-2 Years							
Polystichum munitum	FE	A	RE	797	460	100	5	*Senecio sylvaticus*	F	A	RU	-258	265	100	5
Holcus lanatus	G	N	RU	395	382	100	5	*Galium triflorum*	F	N	RE	-2	3	80	5
Rubus spectabilis	MS	N	RE	300	260	100	3	3-5 Years							
Rubus discolor	MS	A	RU	221	207	100	3	*Pseudotsuga menziesii*	CT	A	RE	-364	411	70	10
Hypochaeris radicata	F	S	RU	217	331	80	5	*Holcus lanatus*	G	N	RU	-230	215	90	10
3-5 Years								*Rubus ursinus*	MS	A	RE	-194	150	82	11
Pteridium aquilinum	FE	A	RU	781	848	88	8	*Agrostis* spp.	G	N	RU	-129	98	91	11
Gaultheria shallon	S	A	RE	444	547	83	6	*Cirsium* spp.	F	N	RU	-107	94	64	11
Alnus rubra	DT	S		178	385	83	6	6-9 Years							
Berberis nervosa	S	A	RE	167	212	71	7	*Holcus lanatus*	G	N	RU	-777	633	67	6
6-9 years								*Rubus ursinus*	MS	A	RE	-299	247	67	6
Polystichum munitum	FE	A	RE	526	596	67	6	*Cirsium* spp.	F	N	RU	-120	70	67	6
Rubus spectabilis	MS	N	RE	169	89	100	5	*Acer circinatum*	S	S	RE	-74	77	80	5

[a] Classes: Carex (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), *Rubus* spp. (MS), and Shrubs (S).

[b] Forage preference: Avoided (A), Neutral (N), and Selected (S).

[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE).

[d] Mean and SD for higher biomass species calculated from all sites where species "x" was more abundant, and lower biomass mean and SD calculated from all sites where species were less abundant.

Table 2.2. Continued

	Higher biomass in untreated sites								Lower biomass in untreated sites						
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	Species	Class	Pref	Type	Mean	SD	%	n
Rubus parviflorus	MS	S	RE	38	59	100	5	*Digitalis purpurea*	F	A	RU	-69	66	83	6
Oxalis oregana	F	S	RE	17	6	100	4	10-13 years							
Stellaria borealis	F	N	RU	16	18	100	3	*Pteridium aquilinum*	FE	A	RU	-77	70	60	5
10-13 years								*Holcus lanatus*	G	N	RU	-56	50	75	4
Polystichum munitum	FE	A	RE	1364	1481	80	5	*Vaccinium parvifolium*	S	S	RE	-45	50	80	5
								Sambucus racemosa	S	N	RE	-41	67	100	3
								Acer circinatum	S	S	RE	-30	24	100	3

[a] Classes: Carex (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), *Rubus* spp. (MS), and Shrubs (S).

[b] Forage preference: Avoided (A), Neutral (N), and Selected (S).

[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE).

[d] Mean and SD for higher biomass species calculated from all sites where species "x" was more abundant, and lower biomass mean and SD calculated from all sites where species were less abundant.

Table 2.3. Treatment means by age class and test statistics for main effects (herbivory and age) and age x treatment interaction on biomass (kg/ha) of total plant understory, avoided or accepted biomass, biomass of vegetation classes, and standing digestible energy of forage preference classes and dietary digestible energy. Note: Woody plants include deciduous trees and all shrubs excluding *Rubus* spp.

	1-2 years			3-4 years			5-6 years			Effects (p-value)		
Response	E[a]	U[a]	SIG[b]	E	U	SIG	E	U	SIG	Treat	Age	T*A
Total	954	913		3138	2212	*	5186	3397	**	<0.01	<0.01	0.07
Avoided	915	812		1241	989		2691	2116		0.13	<0.01	0.79
Accepted	39	101		1897	1223	*	2495	1282	**	<0.01	<0.01	0.03
Conifer	14	7		399	251		1055	1092		0.63	<0.01	0.86
Fern	16	45		181	134		450	525		0.82	0.08	0.75
Forb	856	802		1220	1015		890	615		0.15	0.42	0.87
Graminoid	1	4		120	258	*	343	705		0.07	<0.01	0.56
Rubus spp.	4	32		261	121		846	232	**	0.07	<0.01	0.13
Woody plants	64	23		952	424	**	1596	209	**	<0.01	<0.01	0.29
Total DE[c]	2498	2378		8407	5126	**	10800	6892	**	<0.01	<0.01	0.12
Avoid DE[c]	2388	2388		2623	2236		4746	3465		0.08	0.02	0.45
Accept DE[c]	111	294		5452	3665	*	6668	3350	*	<0.01	<0.01	0.05
DDE[d]	2.71	2.73		2.70	2.68		2.61	2.58		0.834	0.1094	0.882

[a] E represents forage inside exclosures and U represents forage in unexclosed areas.

[b] SIG represents a pairwise significant difference (T-test) with one star denoting a p-value below 0.05 and two stars denoting a p-value below 0.01.

[c] DE is kcal/ha*1000

[d] DDE is kcal/g

Table 2.4. Species consistently higher or lower inside or outside of exclosures within stand age class. Species characteristics are presented with mean biomass (kg/ha) difference between treatments, percent (%) of sites where species abundance was higher or lower, and number of sites (n) where a biomass difference was calculated. Positive mean values indicate higher biomass inside exclosures and negative mean values indicate a lower biomass inside exclosures.

	Higher biomass inside exclosures								Lower biomass inside exclosures						
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	**Species**	Class	Pref	Type	Mean	SD	%	n
3-4 years								1-2 years							
Sambucus racemosa	S	N	RE	752	1008	71	7	*Polystichum munitum*	FE	A	RE	-27	24	100	3
Epilobium angustifolium	F	N	RU	436	436	71	7	*Cirsium* spp.	F	N	RU	-12	13	100	3
Prunus emarginata	S	N	RE	419	707	71	7	3-4 years							
Pseudotsuga menziesii	CT	A	RE	268	197	71	7	*Cirsium* spp.	F	N	RU	-348	461	86	7
Epilobium watsonii	F	A	RU	157	157	71	7	*Elymus glaucus*	G	N	RE	-173	282	75	4
Crepis capillaris	F	N	RU	148	207	80	5	*Holcus lanatus*	G	N	RU	-83	89	67	6
Rubus ursinus	MS	A	RE	83	87	83	6	*Berberis nervosa*	S	A	RE	-57	49	83	6
C. leucanthemum	F	N	RU	18	30	100	3	*Agrostis* spp.	G	N	RU	-45	58	83	6
Dicentra formosa	F	N	RE	14	23	75	4	*Deschampsia elongata*	G	A	RU	-25	22	100	7
Hypericum perforatum	F	S	RU	12	20	75	4	*Poa* spp.	G	A	RU	-11	8	100	3
5-6 years								5-6 years							
Pseudotsuga menziesii	CT	A	RE	711	631	67	6	*Holcus lanatus*	G	N	RU	-516	467	67	6
Rubus ursinus	MS	A	RE	676	769	67	6	*Cirsium* spp.	F	N	RU	-188	158	83	6

[a] Classes: Carex (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), *Rubus* spp. (MS), and Shrubs (S)

[b] Forage preference: Avoided (A), Neutral (N), and Selected (S)

[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE)

[d] Mean and SD for higher biomass species calculated from all sites where species "x" was more abundant, and lower biomass mean and SD calculated from all sites where species were less abundant.

Table 2.4. Continued

	Higher biomass inside exclosures								Lower biomass inside exclosures						
Species	Class[a]	Pref[b]	Type[c]	Mean[d]	SD	%	n	**Species**	Class	Pref	Type	Mean	SD	%	n
Prunus emarginata	S	N	RE	645	687	100	6	*Hypochaeris radicata*	F	S	RU	-172	282	83	6
Epilobium angustifolium	F	N	RU	445	584	100	6	*Elymus glaucus*	G	N	RU	-163	163	67	6
Polystichum munitum	FE	A	RE	298	213	67	6	*Berberis nervosa*	S	A	RE	-85	71	67	6
Alnus rubra	DT	S	RE	289	285	100	4	*Digitalis purpurea*	F	A	RU	-62	73	83	6
Vaccinium parvifolium	S	S	RE	208	213	67	6	*Agrostis* spp.	G	N	RU	-61	68	67	6
Sambucus racemosa	S	N	RE	182	209	83	6	*Senecio sylvaticus*	F	A	RU	-24	46	100	4
Rhamnus purshiana	S	S	RE	153	86	75	4	*Crepis capillaris*	F	N	RU	-22	25	83	6
Anaphalis margaritacea	F	S	RE	104	59	100	4	*Veronica officinalis*	F	N	RU	-18	11	67	6
Rubus laciniatus	MS	A	RU	97	72	83	6	*Carex* spp.	CA	S	RE	-12	17	67	6
Hypericum perforatum	F	S	RU	39	32	75	4								
Ribes spp.	S	N	RE	26	20	75	4								
Rubus parviflorus	MS	S	RE	10	12	75	4								

[a] Classes: Carex (CA), Conifer trees (CT), Deciduous trees (DT), Grass (G), Forb (F), Fern (FE), *Rubus* spp. (MS), and Shrubs (S)

[b] Forage preference: Avoided (A), Neutral (N), and Selected (S)

[c] Type: invader species called ruderals (RU), and species that carryover from before a disturbance called residual species (RE)

[d] Mean and SD for higher biomass species calculated from all sites where species "x" was more abundant, and lower biomass mean and SD calculated from all sites where species were less abundant.

Table 2.5. Mean and standard deviation (SD) of predicted biomass (kg/ha), height (cm), density (no./m^2), and percent browsed (% of stems) by species for accepted and avoided shrubs *sensu* Cook et al. (in review) inside (exclosed) and outside (unexclosed) 16 exclosures near Mount St. Helens, WA. Each * indicates significant (*P*=0.05, or *P*=0.01) pairwise (S), main effect and interaction (E, E*A), or stand age (A) effect.

	1-2 years					3-4 years					5-6 years							
	Exclosed		Unexclosed			Exclosed		Unexclosed			Exclosed		Unexclosed					
Biomass	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	E	A	E*A
Accepted total	5.5	4.2	4.3	3.8		997.1	1054.3	35.9	21.7	**	867.9	618.6	68.9	71.6	**	**	**	*
Avoided total	29.4	27.6	18.6	14.2		33.2	48.2	82.4	79.0	*	279.8	370.2	139.2	104.9				
Total	34.9	30.2	23.0	16.7		1030.2	1087.6	118.3	84.2	*	1147.7	688.6	208.0	156.5	**	**	**	
ACCI	2.7	4.2	3.3	3.8		54.9	85.4	8.5	12.5		16.1	39.0	25.1	41.2				
PREM	0.7	0.9	0.2	0.4		254.0	383.9	5.5	11.2	*	473.0	441.0	5.2	5.3	*	*	*	*
RHPU	0.3	0.6	0.3	0.5		3.1	6.0	3.7	7.4		67.4	87.3	3.7	7.4				
Ribes spp.	0.0	0.0	0.0	0.0		3.5	8.2	0.3	0.6		11.2	15.7	0.1	0.3				
ROGY	0.0	0.0	0.0	0.0		2.3	6.0	1.4	2.4		27.4	43.7	2.8	6.0				
SARA	1.4	1.6	0.4	0.4		663.3	784.8	5.1	3.3	*	115.9	148.4	8.7	8.1		*	*	
VAPA	0.3	0.5	0.1	0.2		16.0	25.3	11.5	11.2		156.7	208.5	23.3	19.0			*	
BENE	28.0	27.6	15.7	12.9		32.9	48.0	76.6	81.8	*	279.8	370.2	139.2	104.9				
GASH	1.4	2.4	2.9	5.1		0.2	0.5	5.8	14.6		0.0	0.0	0.0	0.0				
Height																		
ACCI	19.0	7.6	20.8	6.6		87.2	47.5	38.8	15.2		102.1	5.2	57.9	6.7	*		**	
PREM	14.3	2.7	8.6	1.4		134.0	61.6	32.2	7.6	**	194.7	62.9	48.7	18.9	*	**	**	*
RHPU	16.0	-	23.2	-		122.4	35.9	39.8	28.6		133.9	37.7	49.8	21.5		*		
Ribes spp.	6.4	-	-	-		89.2	57.8	34.4	12.7		178.1	59.4	43.2	-				
ROGY	-	-	-	-		87.0	-	41.7	5.9		70.3	22.2	40.9	27.1				
SARA	22.0	4.2	16.8	6.8		154.8	55.8	30.6	26.1	**	163.9	120.7	36.3	11.1	*	**	**	
VAPA	17.3	-	8.2	-		45.4	16.5	32.4	16.3		90.5	28.5	41.9	13.1	*	**	**	
BENE	13.8	3.6	15.9	3.8		28.1	4.9	23.4	2.3		35.3	3.9	28.7	3.0		*	**	

Species abbreviations are ACCI: *Acer circinatum*, PREM: *Prunus emarginata*, RHPU: *Rhamnus purshiana*, ROGY: *Rosa gymnocarpa*, SARA: *Sambucus racemosa*, VAPA: *Vaccinium parvifolium*, BENE: *Berberis nervosa*, and GASH: *Gaultheria shallon*

Table 2.5. Continued.

	1-2 years					3-4 years					5-6 years							
	Exclosed		Unexclosed			Exclosed		Unexclosed			Exclosed		Unexclosed					
Height cont.	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	$\bar{X}$	SD	$\bar{X}$	SD	S	E	A	E*A
GASH	13.7	-	14.2	-		30.0	4.3	19.4	3.2		-	-	-	-				
Density																		
ACCI	0.1	0.1	0.1	0.1		0.1	0.1	0.1	0.1		0.0	0.1	0.2	0.4				
PREM	0.1	0.1	0.0	0.1		0.2	0.2	0.1	0.1	*	0.3	0.2	0.1	0.1		*		
RHPU	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0		0.1	0.1	0.0	0.0				
Ribes spp.	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0				
ROGY	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0		0.2	0.3	0.0	0.0				
SARA	0.0	0.0	0.0	0.0		0.2	0.3	0.1	0.1		0.1	0.1	0.0	0.0				
VAPA	0.0	0.0	0.0	0.0		0.1	0.2	0.2	0.2		0.4	0.5	0.2	0.1				
BENE	0.6	0.5	0.3	0.2		0.2	0.3	0.8	0.8		1.3	1.7	1.0	0.7				
GASH	0.1	0.1	0.1	0.2		0.0	0.0	0.1	0.3		0.0	0.0	0.0	0.0				
Browsed																		
ACCI	16.7		91.8		*	20.5		70.5		**	0.0		85.1		**			
PREM	0.0		24.2		*	1.0		60.0		**	0.6		59.8		**			
RHPU	0.0		30.0			16.7		87.1		**	NP		NP					
Ribes spp.	0.0		NP			0.0		30.0			0.0		0.0					
ROGY	NP[a]		NP			0.0		66.0		**	0.0		77.8		**			
SARA	0.0		50.0		*	3.8		64.2		**	0.0		51.9		**			
VAPA	0.0		33.3			5.2		88.0		**	0.0		92.0		**			
BENE	1.3		44.3		*	0.0		24.1		**	0.0		21.5		**			
GASH	0.0		78.6		*	0.0		0.0			NP		NP					

Species abbreviations are ACCI: *Acer circinatum*, PREM: *Prunus emarginata*, RHPU: *Rhamnus purshiana*, ROGY: *Rosa gymnocarpa*, SARA: *Sambucus racemosa*, VAPA: *Vaccinium parvifolium*, BENE: *Berberis nervosa*, and GASH: *Gaultheria shallon*

[a] NP signifies the species was not present in the shrub plots.

Table 2.6. Test statistics for treatment main effects (herbicide application and age or herbivory and age) and age x treatment interaction for standing digestible energy (DE, kcal/ha) of all plant species, total biomass (kg/ha) avoided plant biomass, and accepted plant biomass.

	Treatment		Age		Interaction	
	F-value	*P*	F-value	*P*	F-value	*P*
Herbicides						
Total DE	8.96	0.01	4.06	0.02	4.85	0.01
Avoided DE	6.42	0.02	1.85	0.17	1.22	0.32
Accepted DE	3.33	0.08	7.31	<0.01	8.97	<0.01
Herbivory						
Total DE	26.08	<0.01	15.67	<0.01	2.36	0.12
Avoided DE	3.61	0.08	5.47	0.02	0.86	0.45
Accepted DE	9.96	0.01	10.01	<0.01	3.87	0.05

Table 2.7. Difference between biomass (kg/ha), Digestible Energy (kcal/ha), and Dietary Digestible Energy in late seral forest stands versus herbicide-treated and untreated early seral stands. Early seral pairs (n=27) were sampled around Mount St. Helens in 2010-2011 and later seral stands (n=85) are from Cook et al. (in review) and were sampled throughout Washington and Oregon in 2002. Differences calculated as: (early seral [1-13yrs]) - (later seral [>pole]).

	1-2 years		3-5 years		6-9 years		10-13 years	
	H	NH	H	NH	H	NH	H	NH
Biomass								
Avoided								
Pole	260	1181	**1010**	1418	**1606**	**2294**	**1515**	**3059**
Mature	7	928	757	**1165**	**1353**	**2040**	**1262**	**2806**
Oldgrowth	171	1093	921	**1329**	**1517**	**2205**	**1426**	**2971**
Accepted								
Pole	193	**1235**	**862**	**707**	**1208**	**1026**	239	309
Mature	192	**1234**	**861**	**706**	**1207**	**1025**	238	308
Oldgrowth	113	**1155**	**782**	**627**	**1128**	**946**	159	229
Total								
Pole	453	**2416**	**1872**	**2124**	**2814**	**3320**	**1754**	**3368**
Mature	199	**2162**	**1618**	**1870**	**2560**	**3065**	**1500**	**3114**
Oldgrowth	284	**2247**	**1703**	**1956**	**2645**	**3151**	**1586**	**3200**
Digestible Energy								
Avoided								
Pole	988	**1811**	**1872**	**2160**	**2623**	**3090**	**2196**	**3952**
Mature	756	1579	**1640**	**1928**	**2392**	**2858**	**1965**	**3720**
Oldgrowth	829	1651	**1712**	**2001**	**2464**	**2930**	**2037**	**3793**
Accepted								
Pole	465	**2879**	**2136**	**1848**	**3026**	**2212**	625	680
Mature	461	**2874**	**2131**	**1843**	**3021**	**2207**	621	676
Oldgrowth	278	**2691**	**1948**	**1660**	**2838**	**2024**	438	492
Total								
Pole	1454	**4689**	**4007**	**4008**	**5649**	**5301**	**2822**	**4632**
Mature	1217	**4453**	**3771**	**3772**	**5413**	**5065**	**2585**	**4396**
Oldgrowth	1107	**4342**	**3660**	**3661**	**5302**	**4954**	**2475**	**4285**
DDE								
Pole	**0.22**	0.14	0.33	0.16	0.04	0.05	0.06	0.04
Mature	**0.17**	0.10	0.28	**0.12**	0.00	0.01	0.01	0.00
Oldgrowth	**0.18**	0.11	0.29	**0.13**	0.01	0.02	0.02	0.01

*Bold values represent a significance difference ($p<0.05$)

[a] DE is kcal/ha*1000

[b]DDE is kcal/g

Table 2.8. Difference between biomass (kg/ha), Digestible Energy (kcal/ha), and Dietary Digestible Energy in late seral forest stands versus exclosed and unexclosed early seral stands. Early seral pairs (n=16) were sampled around Mount St. Helens in 2010-2011 and later seral stands (n=85) are from Cook et al. (in review) and were sampled throughout Washington and Oregon in 2002. Differences calculated as: (early seral [1-13yrs]) - (later seral [>pole]).

	1-2 years		3-4 years		5-6 years	
	E	UN	E	UN	E	UN
Biomass						
Avoided						
Pole	565	499	**1267**	**918**	**2464**	**1888**
Mature	313	247	**1015**	666	**2212**	**1637**
Oldgrowth	478	412	**1180**	831	**2377**	**1801**
Accepted						
Pole	471	262	**2276**	**1041**	**2241**	**1261**
Mature	470	262	**2275**	**1040**	**2240**	**1260**
Old-growth	-391	-183	**2196**	**961**	**2161**	**1181**
Total						
Pole	**1036**	761	**3542**	**1958**	**4705**	**3150**
Mature	783	509	**3290**	**1706**	**4452**	**2897**
Oldgrowth	869	594	**3375**	**1791**	**4538**	**2982**
Digestible Energy[a]						
Avoided						
Pole	**2092**	**1781**	**2206**	**1750**	**4374**	**3090**
Mature	**1860**	**1549**	**1974**	**1518**	**4142**	2858
Oldgrowth	**1933**	1622	**2047**	**1591**	**4215**	**2930**
Accepted						
Pole	61	243	**5401**	**3615**	**6618**	**3299**
Mature	56	239	**5397**	**3610**	**6614**	**3295**
Oldgrowth	-127	-56	**5214**	**3427**	**6430**	**3112**
Total						
Pole	2152	2024	**7607**	**5365**	**10992**	**6389**
Mature	1916	1788	**7371**	**5128**	**10756**	**6153**
Oldgrowth	1805	1677	**7260**	**5018**	**10645**	**6042**
DDE[b]						
Pole	0.09	**0.20**	**0.24**	0.11	0.10	0.07
Mature	**0.14**	**0.25**	**0.28**	0.16	**0.14**	**0.12**
Oldgrowth	0.10	**0.21**	**0.25**	0.12	0.11	0.08

*Bold values represent a significance difference (*a*=0.05).

[a] DE is kcal/ha*1000

[b] DDE is kcal/g

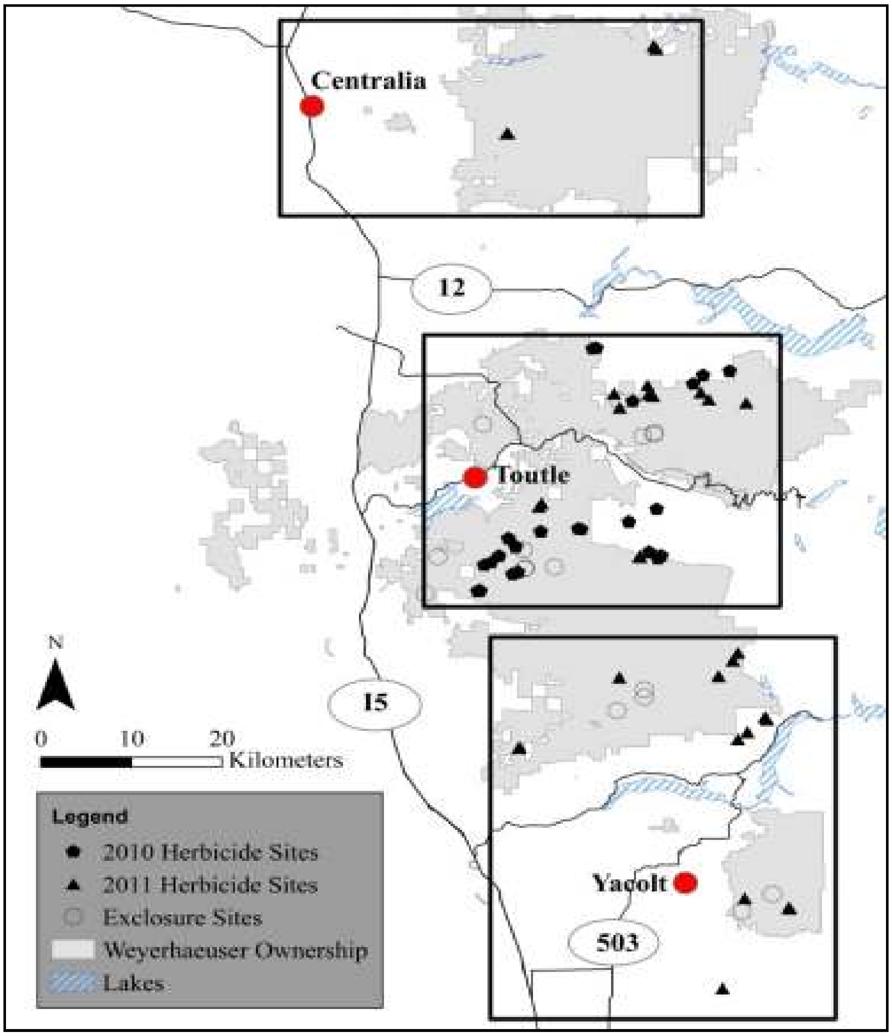

Figure 2.1. Location of herbicide and exclosure sites sampled in 2010-2011. Exclosure sites represent 1 site sampled inside, and 1 site sampled outside of exclosure. See Appendix 2 for detailed locations in study area.

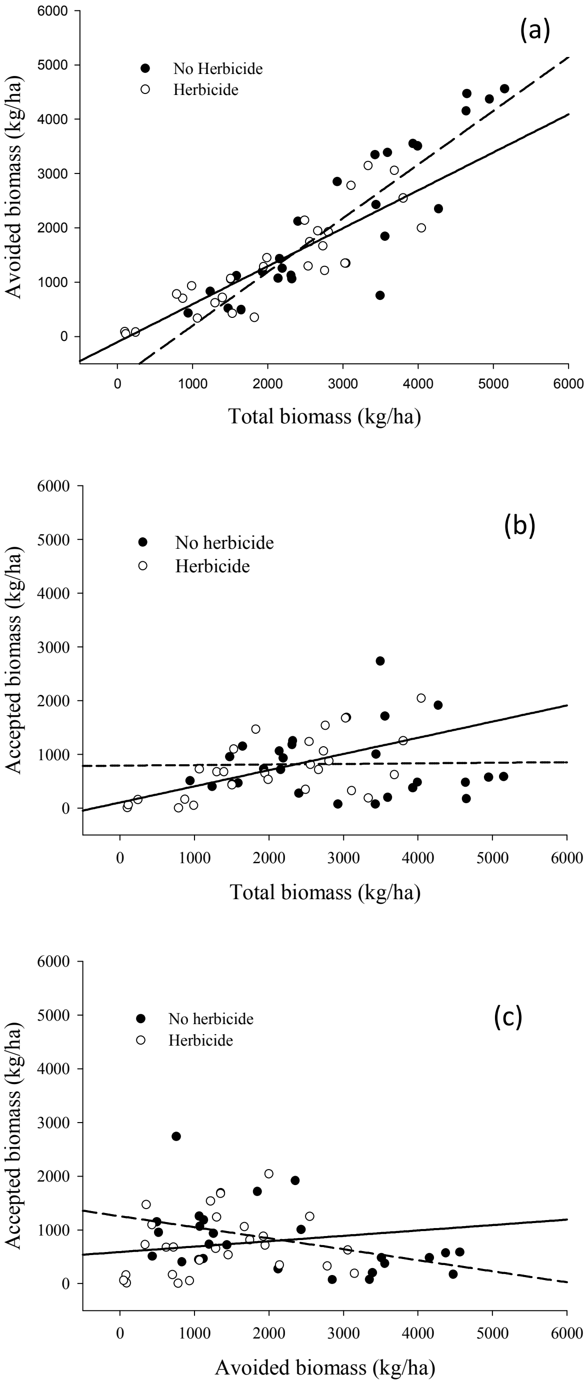

Figure 2.2. The relationship between total biomass and (a) avoided biomass, (b) accepted biomass or (c) accepted versus avoided biomass in stand ages < 13 years near Mount St. Helens sampled in 2010-2011. Straight lines are: (a) herbicide (solid line, *P*<0.01, *r*=0.62) and no herbicide (short dash, *P*=0.91, *r*=0.02); (b) herbicide (solid line, *P*<0.01, *r*=0.88) and no herbicide (short dash, *P*<0.01, *r*=0.89); (c) herbicide (solid line), and no herbicide (short dash, *P*=0.02, *r*=0.44).

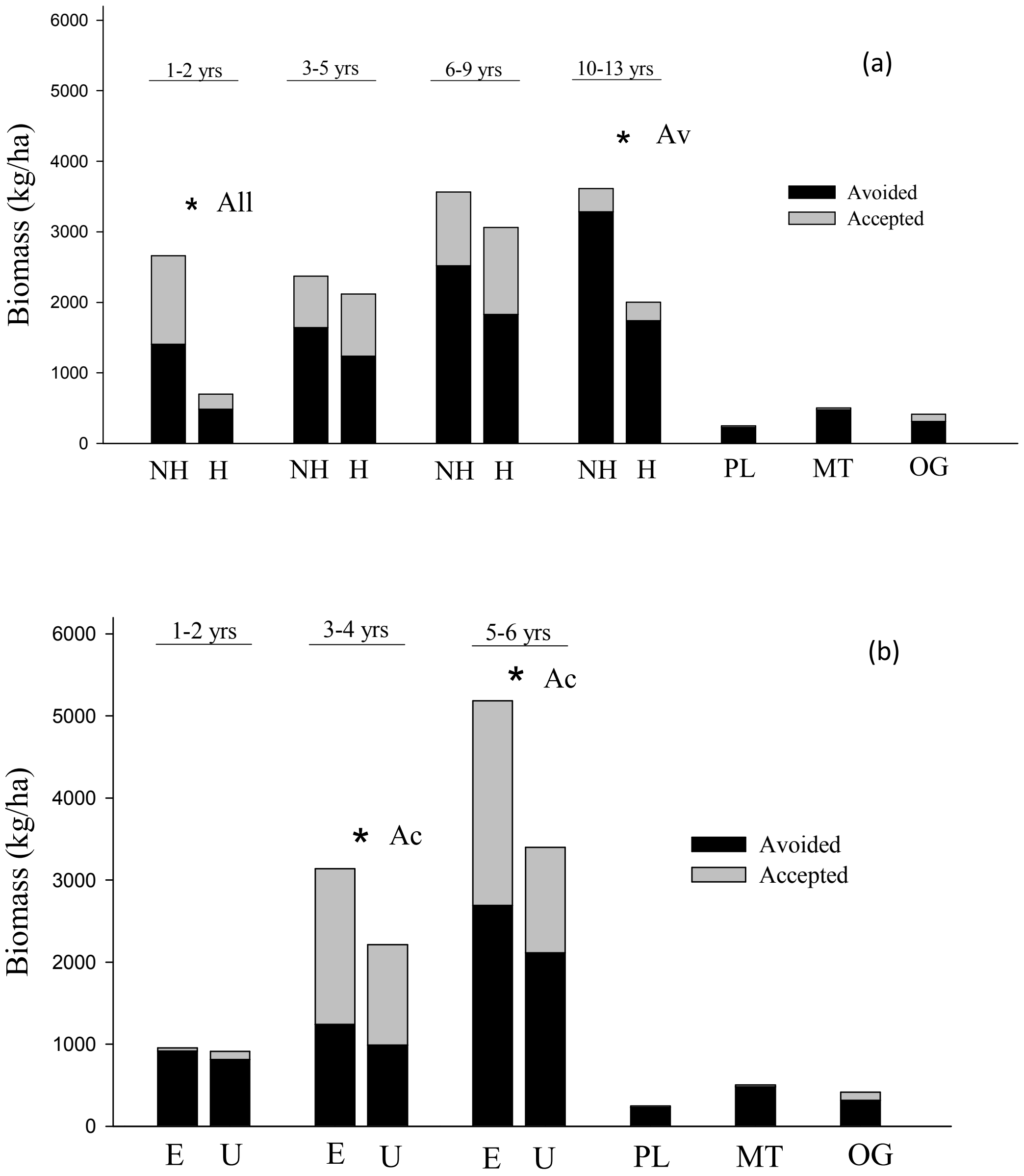

Figure 2.3. Mean forage biomass of total, avoided and accepted forages within (a) herbicide or (b) herbivory treatment (E=exclosed and U=unexclosed) in early stand ages including 1-2 (n=5), 3-5 (11), 6-9 (6); 10-13 (5); and later seral stages including pole stage (21-50yrs, PL, n=43), mature stand (51-150 yrs, MT, 37) and old-growth (151- 600, OG, 8). * indicates a significant difference in early seral accepted or avoided biomass between paired plot treatments within an age class 1-13 yrs at $P<0.05$. The superscript above the star indicates which group is different: 1) All: total, avoided, and accepted 2) Av: avoided 3) Ac: accepted.

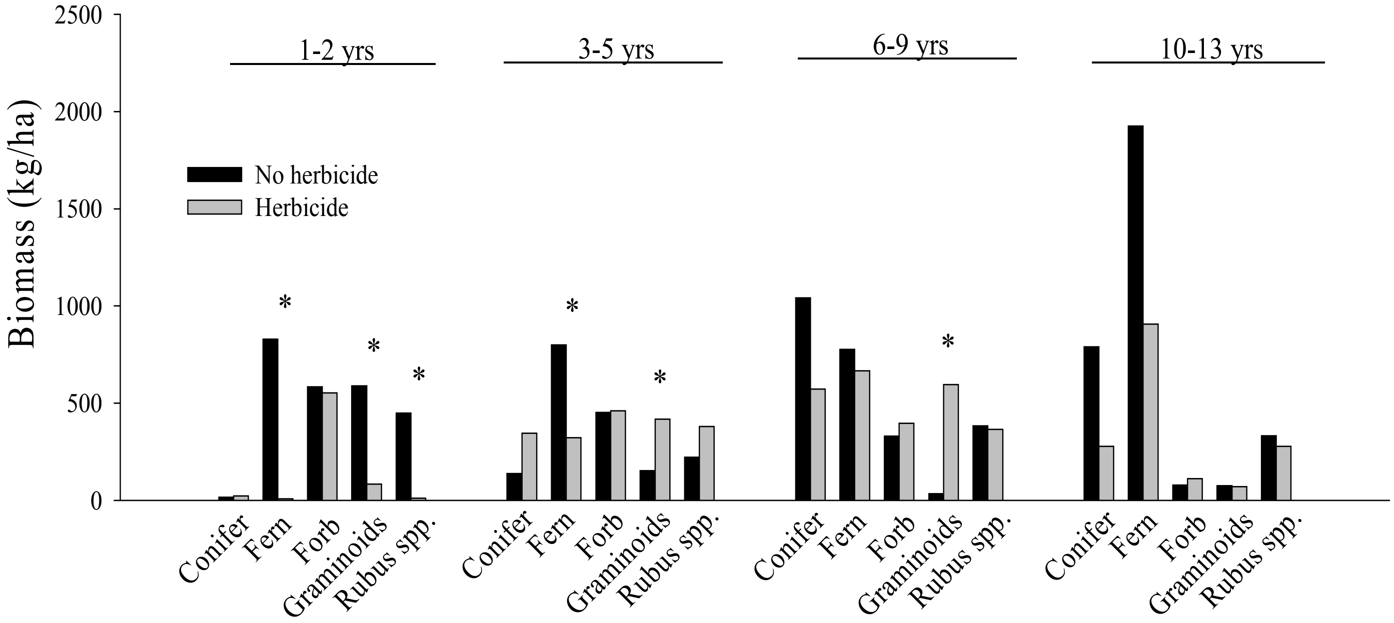

Figure 2.4. Mean forage biomass of vegetation classes by herbicide treatment and stand age (1-2 yrs, n=5; 3-5 yrs, n=11; 6-9 yrs, n=6; and 10-13 yrs, n=5). * indicates a significant pairwise difference between herbicide treatments within age class at α≤0.05.

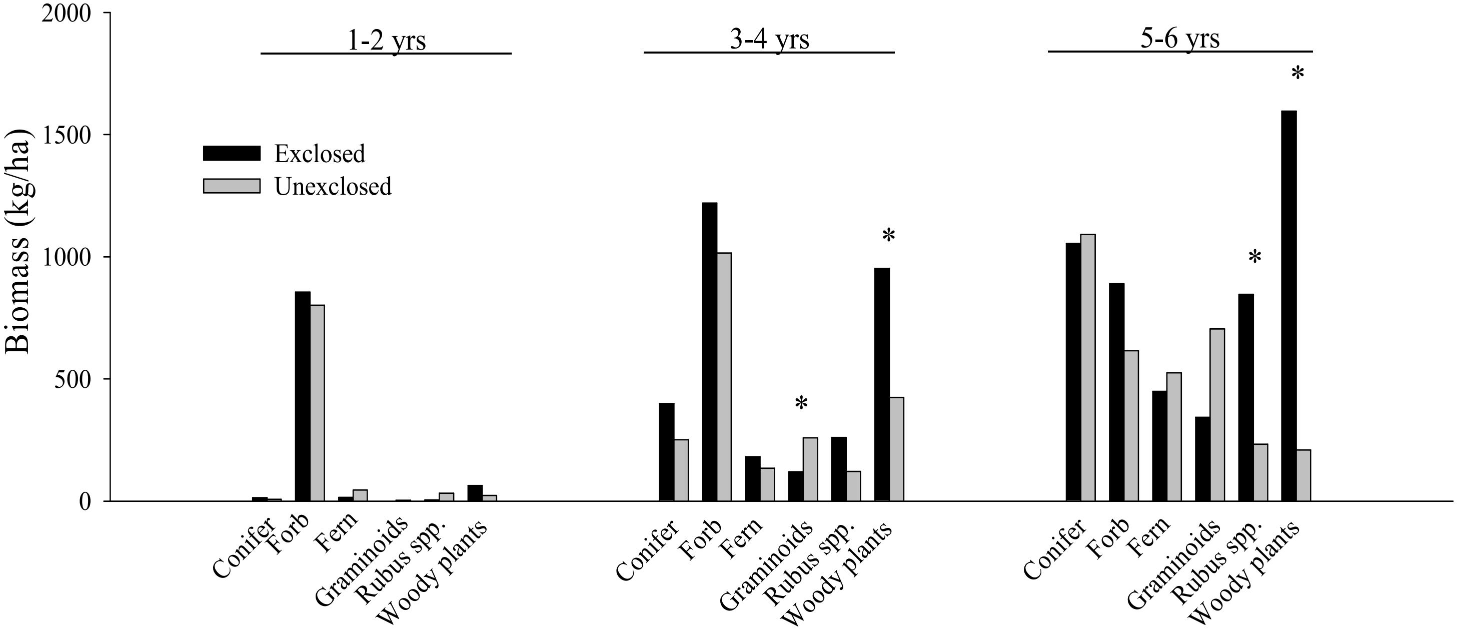

Figure 2.5. Mean forage biomass of vegetation classes by exclosure treatment and stand age (1-2 yrs, n=3; 3-4 yrs, n=7; and 5-6 yrs, n=6). * indicates a significant pairwise difference between herbicide treatments within age class at α≤0.05.

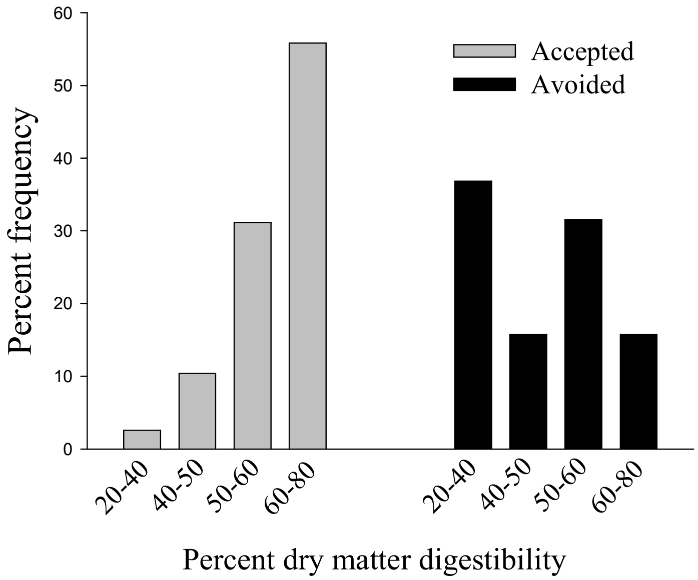

Figure 2.6. Percent frequency of accepted and avoided forages within 4 different percent dry matter digestibility (DMD %) classes. DMD distributions of forages differ between forage preference classes (X^2=24.55, *df*=3, *P*<0.01).

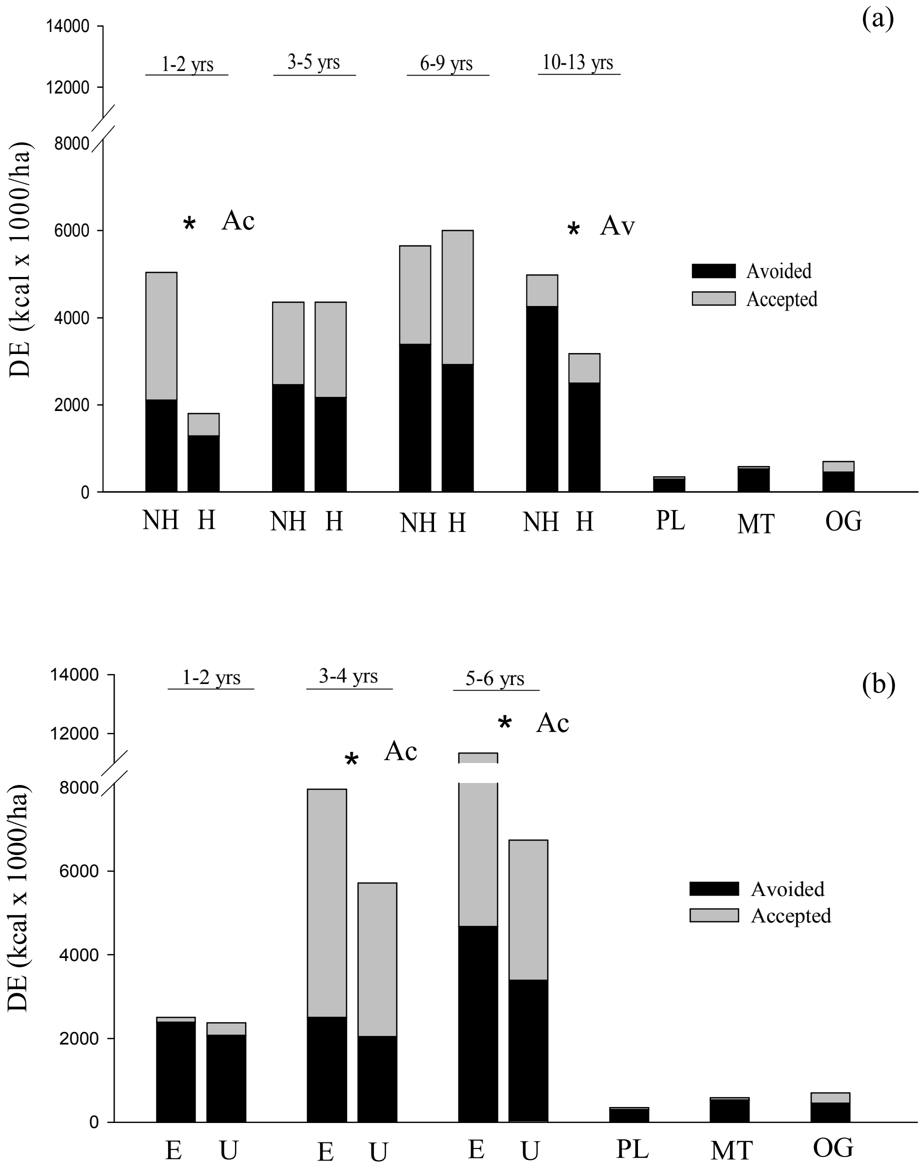

Figure 2.7. Standing digestible energy (DE, kcal x1000/ha) available in accepted and avoided elk forages within (a) herbicide or (b) herbivory treatment (E=exclosed and U=unexclosed) by stand age in western hemlock communities in southwestern Washington. * indicates significant difference within an age class at α≤0.05 based on a paired T-test. The superscript above the star indicates which group is different: 1) All: total, avoided, and accepted 2) Av: avoided 3) Ac: accepted.

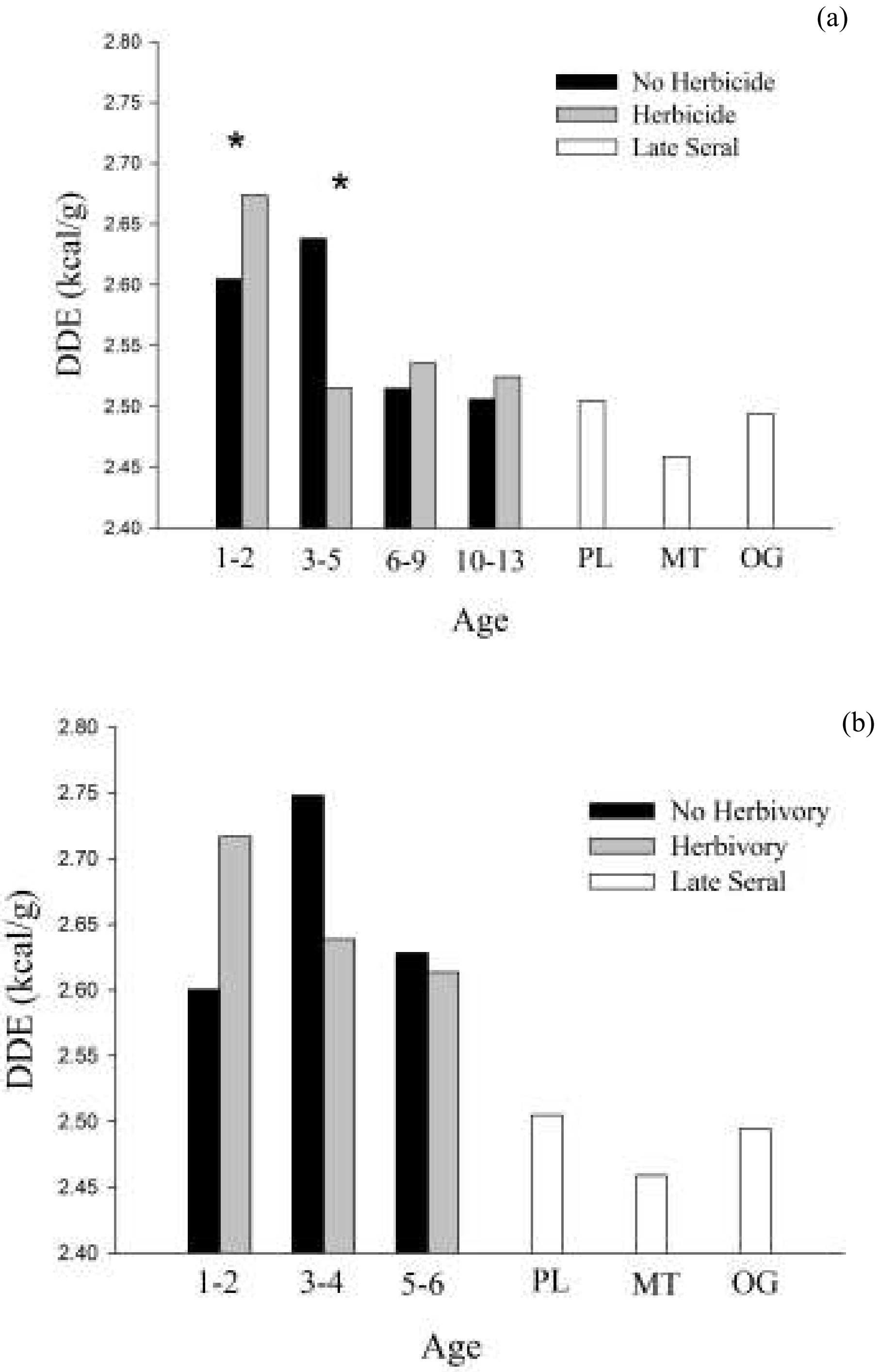

Figure 2.8. Dietary digestible energy (kcal/g) of an elk foraging within (a) herbicide or (b) herbivory treatments by stand age in western hemlock communities in southwestern Washington. * indicates significant difference within an age class at α≤0.05 based on a paired T-test.

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CHAPTER 3:

ELK BODY FAT-HABITAT RELATIONSHIPS AT MOUNT ST. HELENS, WASHINGTON

Introduction

The link between habitat quality and sustainable wildlife populations has been well recognized in wildlife management (Rodwell et al., 2003; Morrison et al., 2006; Wallisdevries, 1996), but the best method to evaluate habitat remains uncertain (Gaillard et al., 2010). In the past, two general approaches have been used to relate animal performance to habitats. When long-term data on population numbers are available, per capita growth rates have been related to animal density, weather, or plant phenology (Merrill and Boyce, 1991; Langvatn et al., 1996; Post and Stenseth, 1999; Mysterud et al., 2000; Forchhmamer et al., 2001; Pettorelli et al., 2005; Hebblewhite et al., 2006). More recently, with the advent of GPS it has been possible to relate performance of individuals or groups of individuals to habitats (Bender et al., 2007; Frair et al., 2007; Hutchins, 2006; McLoughlin et al., 2007). For instance, Bender et al. (2007) noted body fat of radio-collared mule deer in New Mexico was negatively related to the amount of pinyon-juniper in an individual's home range, and pinyon-juniper reflected poor forage conditions.

These two approaches require either long-term data sets or a large sample size, which can be costly. Alternatively, body mass and fat indices from organs of harvested animals, for which large number of samples can be obtained, have been related to elevation and habitat diversity (effects attributed to phenological effects on forage) (Hebblewhite et al., 2008; Mysterud et al., 2001; Wang et al., 2009). Nutritional adequacy of habitats reported in these studies may also be influenced through density-dependent mechanisms (Fowler, 1987; Mcloughlin et al., 2008; Mysterud, 2000). For example, Hjeljord and Histol (1999) found regional body mass of harvested moose in Norway was strongly dependent on habitat but was also negatively related to moose density. Finally, energy lost from movements associated with human disturbance in areas of high road density may also influence body condition. In his simulations, Rumble et al. (2005) showed elk needed an additional 30-46 minutes per day of foraging time to account for energy lost from movements associated with human disturbance on roads. This change in foraging behaviour suggests elk are negatively influenced by elk but this has not been successfully related to elk performance.

In this Chapter I assess the relationship between habitat conditions used by elk in summer and fall to late autumn ingesta-free body fat (IFBF, %) of harvested elk at Mount St. Helens, Washington. I focused on female elk and the habitats they used in summer-autumn because studies of elk (Cook et al., 2004), red deer (Loudon et al., 1983), and white tailed deer (*Odocoilus virginianus;* Verme, 1969) have all shown nutritional intake during this period is important to reproductive success. Additionally, the female segment of the population has a disproportionally high influence on population growth rates (Gaillard et al., 2000). Cook et al. (2013) also reported high variation among IFBF measurements of elk in Washington and Oregon that they attributed to variation in available nutritional resources influenced by forest succession and management. In fact, in foraging trials with tame elk in common habitats of the Pacific Northwest, they found that dietary digestible energy (DDE) of adult female elk was directly related to the rate of decline in IFBF of each female and rate of growth of their calf (Cook et al., in review). It is unknown whether similar results exist for wild elk feeding in these habitats. I focused on the environments in and adjacent to Mount St. Helens because there was broad-scale variation in forest conditions associated with varying natural and managed stages of succession, which provided variation in nutritional resources needed to evaluate the relationship between habitat conditions and elk IFBF.

My objective in this Chapter was to test the prediction that elk using areas of high nutritional resources during the summer-autumn period would have high IFBF. I evaluated this prediction using an estimate of IFBF based on the Kistner Subset Score (Cook et al., 2001) derived from organs of elk harvested by hunters in autumn 2011. I related IFBF to availability of accepted biomass (referred to as AccpBio in this Chapter) and DDE derived using the predictive algorithms of Cook et al. (in review) and 2 indices of elk abundance based on winter aerial surveys and summer elk pellet group counts. I also evaluated habitat characteristics, including human disturbances, slope, and distance to edge because they were found to be related to the intensity of elk use by the U.S. Forest Service (USFS) as part of their development of the West Coast Elk Habitat Model. Human disturbance at MSH is primarily related to vehicular road use, which is greatest during summer and autumn when tourists and hunters frequent the area

(WDFW, 2006; McCorquodale, 2013). The impacts of roads can be variable depending on location and type of use, but a number of studies have shown vehicle disturbance can increase glucocorticoid stress hormones in elk (Millspaugh et al., 2001; Creel et al., 2002) and energetics and foraging time can be negatively influenced by increased flight response and greater movement rates in the presence of busy roads (Stankowich, 2008; Cole et al., 1997; Rumble et al., 2005).

Materials and Methods

STUDY AREA

The study area was located west of Mount St. Helens in Southwest Washington (Fig. 3.1) with data collected in 5 WDFW Game management units: Winston (520), Margaret (524), Loo-wit (522), Toutle (556), and Coweeman (550). The study area boundary matched the extent of digital maps of habitat covariates, specifically the extent of area sampled for winter elk density by WDFW. The area includes private lands of the St. Helens Tree Farm operated by Weyerhaeuser Company (78%) and public lands under the jurisdiction of the Department of Natural Resources (10%), USFS MSH National Monument (5%), State Wildlife Area managed by Washington Department of Fish and Wildlife (<1%), and some small private landowners (~6%). Dominant land use in the area is forestry with the majority of the study area managed for mid-succession Douglas fir (*Pseudotsuga menziesii*) stands harvested on 40-year cycles. A small amount of land (<1%) is used for agriculture along the periphery of the study area. High road density in the study area is associated with the logging industry and tourism, but use of roads varies greatly depending on land ownership and land-use. Additionally, summer recreation is commonly associated with visitors traveling along major highways (HWY 504) towards the MSH blast zone and autumn recreation is primarily related to elk hunting between late August and mid-January.

The climate is Pacific maritime with wet, mild winters and dry, cool summers (Franklin and Dyrness, 1988). Topography of the area is mountainous and elevation increases from west to east ranging from 240 m to 1200 m. The area supports 3 major forest zones related to elevation including the low elevation (0 - 640 m) western hemlock series (WHS, 75% of study area), the mid-elevation (641 -1280 m) Pacific silver fir series (PSS, 20%), and the high elevation (>1280 m) mountain hemlock series (MHS, < 1%). The PSS and MHS are generally cooler and moister than the WHS and have later phenology and slower rates of succession. Thus, higher elevation vegetation zones can offer better elk forage and subsequently these forest zones have been considered in my analysis and have been incorporated into the models of Cook et al. (in review) that I used to predict forage at MSH. Within the study area, the western portion is primarily lower elevation WHS, whereas the eastern third of the study area is primarily PSS with some MHS (Fig. 3.1).

The MSH elk herd is currently one of the largest herds in Washington (WDFW, 2006). After the eruption, the elk population had a rapid initial recovery, which was attributed to rapid recovery of natural forage, broad-cast seeding of grass-legume mixes, and initial restrictions on human access and harvest (Merrill, 1987; Merrill et al., 1995; Raedeke et al., 1986). The estimated elk population was 13,300 in 2005, but lower numbers exist in the northern and southern portions of the study area (WDFW, 2006). Additionally, the black-tailed deer (*Odocoileus hemionus columbianus*) population at MSH was estimated at 500 in 2000 (Davis et al., 2010), but higher numbers and densities exist in the southern portions of the study area closer to the Columbia River (WDFW, 2006).

The role that natural predators play in elk mortality at Mount St. Helens is unknown (WDFW, 2006). Big game hunting season starts 13 August with the opening of autumn bear hunts. Elk archery season starts in early September, while the rifle season is a combination of general and special permit hunts with seasons from 6 September to 16 January but the primary hunts for female elk are in November. Based on mandatory WDFW hunter questionnaires, annual hunter participation between 1995 and 2005 averaged 20,111 hunters in the GMUs comprising the MSH elk herd. This was associated with an average 111,318 hunter days per year, and an average of 1786 elk harvested annually (WDFW, 2006).

FIELD DESIGN AND SAMPLING

I determined whether summer nutritional resources, elk density, and habitat conditions were related to autumn indices of body condition of elk in four steps. First, I collected data on IFBF, lactation, and pregnancy rates of elk harvested across the study area in autumn 2011. Second, I calculated AccpBio and DDE (Table 3.2) for unique areas inside the Mount St. Helens eruption “blast” zone (Table 3.1, Appendix 13) using methods outlined in Chapter 2. For all other areas I used the algorithms from Cook et al. (in review) to estimate AccpBio and DDE in 30 m cells to map summer nutritional resources across the study area. I used these two metrics of nutritional resources because they have been linked directly to elk IFBF (Cook et al., 2013). Third, I mapped indices of elk abundance based on late-winter aerial surveys correcting for the amount of visible area actually surveyed, and also evaluated summer pellet counts as an independent metric of summer elk abundance. Finally, I evaluated a set of competing models for predicting the IFBF value of each harvested elk based on availability of nutritional resources, elk density, and other physiographic landscape covariates within a "use-buffer" around the kill site using a model selection approach, and based on the final model I mapped this "fitness-based" metric of habitat condition across the study area.

ELK BODY FAT, LACTATION AND PREGNANCY

Sample collection. Female elk organs and reproductive tracts were collected during antlerless elk hunts from 1 October 2011 to 15 December 2011 in 5 GMUs across the study area. Hunters (n=1212) received collection bags, instructions, and figures (Appendix 11.A to 11.F) in the mail and successful hunters voluntarily submitted samples to collection barrels located along 9 major transportation routes in the study area. Each hunter was asked to submit the kill location (GPS coordinates), the heart, pericardium, both kidneys, reproductive tract, piece of the udder and 2 front incisors. Efforts to collect samples included a dedicated website, posters and flyers, voluntary check-points and an incentive program with prizes. All submitted samples were frozen until February 2012 when they were thawed and analyzed.

Analysis of Samples. Pregnancy was determined by inspecting the uteri for a fetus (0/1) and lactation status was assessed by inspecting the mammary tissue. Lactation status was primarily assessed by WDFW personnel by cutting an incision into the udder and identifying if there was clear or milky fluid or if it was dry. A small percentage of samples (less than 20%) were visually assessed for lactation status by hunters in the field. Lactation status was initially classified as (1) milk, (2) some clear liquid, and (3) dry, but only milk and dry status were used for any analysis requiring lactation status. Clear fluid samples (n=15, 12% of all lactation) were not used in analyses requiring lactation status because animals with clear fluid may have lactated for varying periods of time due to calf survival. For body condition, visual estimates by trained WDFW personnel were used to give the heart, pericardium, and kidneys a fat score ranging between 1 for minimal fat to 20 for maximum fat based on the modified Kistner-subset score (Cook et al., 2001). The score of each kidney is averaged and the modified Kistner score (KISThpk) is the sum of all organ scores. Percent IFBF was calculated from KISThpk using a linear equation of the form (Cook et al., 2001):

$$y = \beta_1 x + \beta_\sigma \qquad \text{eqn 3.1}$$

where β_1 and β_σ are specific to the KISThpk score and are 0.405 and -4.469, respectively, and x is Kistner score from the visual estimates of individual organs. Incisors of harvested elk were collected and sent to Matson's Lab in Missoula, Montana for aging by counting cementum annuli (Hamlin et al., 2000).

MAPPING ENVIRONMENTAL COVARIATES

Forage abundance and quality. Forage quantity and quality were characterised across the study area using biomass of AccpBio (kg/ha) and DDE (kcal/g). Two methods were used to estimate forage resources across the study area and values from each approach were merged to create maps of AccpBio and DDE, which were then used as inputs for modeling. First, vegetation biomass was directly sampled to estimate AccpBio and DDE in unique plant communities that were severely disturbed by the MSH eruption (Appendix 13). This included 6 distinct vegetation types (Charlie Crisafulli, 2011, pers.comm., Table 3.1) located along the North Fork Toutle River and pumice plains north of the MSH crater. I sampled plant species biomass (kg/ha) at 3-6 sites in each type using the macroplot sampling approach described in Chapter 2.

In brief, a 0.4-ha macroplot consisting of 5 transects 45 m in length was sampled at each site. Biomass of understory vegetation in each macroplot was clipped in 2, 2 m^2 circular plots per transect between 2 cm stubble height up to 2 m in height (reach of elk) providing a total of 10 clipped plots per macroplot. Clipped vegetation was sorted, bagged by plant species, and oven dried at 60^o C for at least 48 hrs. Forage species were classified into accepted or avoided based on diet selection during the elk forage trials outlined in Chapter 2 (Cook et al., in review), and AccpBio was calculated as the sum of biomass from all accepted species at a site. Species digestibility values were taken from the literature (see Appendix 10) or from analysed samples collected in 2011, and gross energy values for plant vegetation classes (forbs, fern, grass, shrubs and evergreens) were from Cook et al. (in review). DDE (kcal/g) was calculated using the same approach as Chapter 2, where DDE was calculated based on encounters with accepted species when the biomass of accepted species was > 600 kg/ha and on all species when accepted species biomass was < 600 kg/ha as:

$$\mathrm{DDE}j = \sum U_{ij} DE_i = \sum \frac{w_i A_{ij}}{\sum_i^n w_i A_{ij}} DE_i \qquad \text{eqn 3.2}$$

where U_i is the proportional use of plant species at site j based on encounters proportional to biomass availability (A_i) and selection given an encounter (Lele et al., 2013), and their respective DE_i. Selection was based on the mean selection ratio (w_i) for species i from tame elk in 87 elk foraging trials in western hemlock communities (Cook et al., in review). The w_i is derived as the percent of the diet consumed of species i by an elk during a foraging trial divided by percent of species i of the total biomass available to the elk during a foraging trial (see Appendix 10 for species values). Values of AccpBio and DDE were averaged across macroplots for each unique vegetation type and mean values were used to map DDE in 30 m cells of all unique vegetation types across the study area (Appendix 13).

AccpBio and DDE for the WHS and PSS (See STUDY AREA, Fig. 3.1) in the study area were estimated using the recently developed USFS Westside nutritional model (WEHM, Rowland et al., 2013; Cook et al., in review). Predictive algorithms for AccpBio and DDE used in these models were derived from data on measures of AccpBio and DDE based on tame elk foraging trials (Cook et al., in review) and environmental conditions of the pens in which the foraging trials occurred. Algorithms (for each vegetation series), found to be the best predictors of AccpBio, included the covariates percent canopy cover and proportion of total live trees (>2.5 cm dbh), and DDE was found to be asymptotically related to AccpBio (Cook et al., in review). I used the following WEHM equations to predict AccpBio (eqn 3.3a/b) and DDE (eqn 3.4a/b) in 30 m cells across the landscape for the low elevation WHS and high elevation PSS/MHS that were derived for the northern Cascade region:

$$AB_{WH} = 707.3 - 12.93(CC) + 0.0731(CC^2) + 383.17(HW) \qquad \text{eqn 3.3a}$$

$$AB_{PSF} = 657.6 - 11.28(CC) + 0.0458(CC^2) + 553.06(HW) \qquad \text{eqn 3.3b}$$

$$DE_{WH} = 0.47(5.755 - e^{-0.0041(AccpBio)}) \qquad \text{eqn 3.4a}$$

$$DE_{PSF} = 0.92(3.218 - e^{-0.0052(AccpBio)}) \qquad \text{eqn 3.4b}$$

For mapping AccpBio, canopy cover (CC) and hardwood values (HW) were based on the Gradient Nearest Neighbor layer (GNN, http://www.fsl.orst.edu/lemma/), which is a map derived from field data and remote sensing that used multivariate statistics and unit imputation to extrapolate values across study areas larger than 10000 ha (Lemma, 2013).

Elk abundance. Summer elk abundance was characterized across the study area using data collected from pellet counts and winter elk surveys. Elk pellet groups were counted between 1 October and 5 November 2011 at 231 plots with starting locations that were randomly selected from a 1-km grid using the random point function of Hawth's Tools (http://www.spatialecology.com). Each plot consisted of three 200 x 2 m transects in a triangle layout where each side consisted of eight 25 m sections. For each 25 m section of transect, observers recorded the number of elk pellet groups, ground level visibility (1 to 4, with 1 corresponding to bare ground and 4 corresponding to dense ground vegetation), and observer experience. Pellet groups were defined as consisting of at least 5 pellets and were counted if more than 50% of the pellet group was inside the sampling area. It was assumed all observed pellets were from the summer period because in the PNW Lehmkuhl et al. (1994) observed more than 50% of pellets exposed to high winter precipitation and moderate temperatures had severely deteriorated 4 months after deposition. To correct for detection bias, I used intensive recounts within 592, 25 m sections at 206 sites (1-3 per site) to estimate the proportion of pellets missed during the initial count. I considered the results of the recounts independent across sections even at the same sites. I used Beta regression to model the proportion of pellet groups counted in the initial count as a function of observer experience (1=inexperienced; 2=experienced) because I used volunteers to help with these counts, and as a function of relative visibility coded as an index (1-4) reflecting vegetation cover. I excluded 21 sites (<4%) where pellet groups were initially higher than in the recount. Because I found observer experience (P=0.04), but not visibility (P>0.67), influenced pellet group detection probability, which I attributed to inexperience of volunteers and complexity of ranking visibility, I corrected pellet counts only for observer effects. I used a correction inflation factor of 1/0.78 for experienced observers and 1/0.74 for inexperienced observers based on the recounts of these two types of observers. I used inverse distance weighting and empirical Bayesian kriging (Pilz and Spöck, 2007) to interpolate corrected pellet counts across the study area.

Aerial surveys to count elk were completed by Washington Department of Fish and Wildlife in a 2-week period during the weeks of 14-18 March and 28 March to 1 April 2011, with a Bell 206 Jet Ranger helicopter (Bell Helicopter Textron Inc., FortWorth, TX). Surveys occurred daily between 0800 to1600 and 19 survey units were systematically surveyed across 5 GMUs (520, 522, 524, 550, 556) by a 4-person crew at an altitude of 40-70 m above ground level, flying at 80-110 km/hr. Every large opening and clearcut within the survey units was surveyed. When an elk was spotted the pilot deviated from the transect and circled the elk group to record group location (GPS coordinates) and number of elk. I grouped elk counts from the 19 WDFW survey units into grid cells of 9.9 km^2, which is the average annual home range of an elk at MSH based on GPS collar movement data collected in 2009-2012. Because elk in closed canopy forests of the PNW are not visible during aerial surveys, I calculated density of elk in each grid cell in 3 steps. First, elk density in clearcuts (#/km^2) was calculated for each grid cell as the sum of elk counted in every clearcut within a grid cell divided by the area (km^2) of clearcuts within that same grid cell. Next, because elk use clearcuts and covered forest differently depending on season and time of day (Ager et al., 2003), movement data from 31 elk outfitted with GPS collars between 2009 and 2012 for the dates between 15 March and 15 April was used to calculate the ratio of elk in clearcuts versus closed canopy forest for 3 geographic regions in the study area (north of the Toutle river, mudflow, south of the Toutle river) and 3 survey time periods per day (0800-1300, 1301-1500,1501-1700). Observed number of elk in a 9.9 km^2 cell (adjusted for extent of clearcuts) was further adjusted based on the ratios of elk in clearcuts versus closed canopy forest for each region and time period (Appendix 15).

Human disturbances. Influence of roads was calculated in 3 ways to reflect varying levels of human disturbance. I used distance (m) and density (km/km^2) to 1) all public roads where a public road was defined as any road that could be freely accessed without needing gate access, 2) major logging roads and highways where major logging roads were those classified as “main lines” by Weyerhaeuser and highways were roads classified as highways by the State of Washington, and 3) all roads.

Physiography and vegetation types. I obtained a digital elevation model for southwest Washington (30 m cell size) from the USGS Geospatial Data Gateway (http://datagateway.nrcs.usda.gov/). Slope and terrain ruggedness were calculated in ArcGIS 10. Slope (%) was derived from a 30 m digital elevation model within each 30 m cell. Terrain ruggedness was calculated as the mean standard deviation of elevation (m) within a 1 km buffer around each 30 m cell and was derived from a 30 m digital elevation model. Distance to edge was calculated as the Euclidean distance to the nearest forest edge (Hanley, 1983). A clearcut index was created by identifying forest stands less than or equal to 15 years old in three ways: 1) using stand age information from Weyerhaeuser and DNR, 2) visually identifying clearcuts from 2011 satellite images, and 3) using the 2006 GNN layer to identify stand age (Table 3.2). To create the index, 30 m cells that were identified as closed canopy were coded with a value of 1 and were summed within the use-buffer of each harvested elk.

SUMMER HABITAT USE BUFFER

Habitat conditions surrounding the locations of harvested elk were measured within a circular buffer where buffer size was chosen to best reflect the habitat used by a harvested elk during the summer months (June-October) when they accrued IFBF (Cook et al., 2004). I evaluated varying buffer sizes based on the movements of GPS collared elk (n=31). Collared elk used in the analysis were helicopter darted with a carfentanil-xylazine mixture each February from 2009 - 2011. Elk were outfitted with either Telonics TGW-4700-3 or Lotek 3300 store-on-board collars collecting location data on 2- or 3-hour fix schedules, and were scheduled to drop from animals 13 months after deployment. Animal handling protocols followed procedures in compliance with WDFW's Animal Restraint and Chemical Immobilization Policy.

For each set of GPS locations of an elk, I randomly selected a hypothetical harvest location from locations in late autumn (1 October – 30 November). Then, placing varying buffer sizes (0.1 – 25 km^2) around that location I calculated what proportion of locations from the previous summer (1 June – 31 October) were within each buffer size. The buffer size was chosen to include the highest proportion of summer locations while minimizing the inclusion of areas not used by elk. All programing and script to identify optimal buffer sizes was created in r (version 2.13.1, R Development Core Team 2011).

STATISTICAL ANALYSIS AND MODELING

I first tested whether variation in body fat was explained by harvest date (Julian date) and elk age using a simple linear regression on the full data set or subsets when some months or ages were removed. I examined whether natural log transformations of IFBF improved the model fit. Differences in IFBF of elk collected from different GMUs were tested with ANOVA and BONFERRONI post-hoc tests. Differences in body fat between 2 reproductive categories (pregnant vs. non-pregnant; lactating vs. non-lactating) were tested using Students T-test, while differences between 4 reproductive classes (nonpregnant/nonlactating [NP-NL], pregnant/non-lactating [P-NL], non-pregnant/lactating [NP-L], pregnant/lactating [P-L]) were tested with ANOVA and BONFERRONI post-hoc tests, while controlling for harvest date. I used logistic regression to test whether the probability of being pregnant was related to IFBF in adults between 2 and 14 years old. Because of low sample sizes, I accepted a significant difference at α=0.10. Unless stated otherwise, I report standard deviations of the mean (SD).

Covariate reduction. An initial list of possible covariates (Table 3.2) was compiled prior to creating *a priori* models. Covariates were dropped when there were data missing. The final list of forage covariates included: DDE, AccpBio, and Clearcuts (Cook et al., in review). Disturbance covariates included: All Roads, and Main Roads (Rowland et al., in prep.). Physical covariates included: Elevation, Slope, and Terrain Ruggedness (Rowland et al., in prep.). Elk density was also included because Johnson et al. (2012) found relationships between density and reproductive rates in northwestern Oregon. Animal-specific covariates included lactation status, harvest date, and elk age, (Cook et al., 2013). I Note that elk age can influence animal performance due to stage of life (prime versus juvenile or old [Cook et al., 2013]), or through cohort effects (Gaillard et al., 1998b).

Covariates were further reduced to avoid collinearity using Pearson product-moment correlation ($r \geq 0.60$, $P<0.05$). I selected between covariates that were collinear by evaluating the AIC values for each covariate independently.

Model approach. I used a model selection framework based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) following Burnham & Anderson (2002). I compared *a priori* models that were combinations of forage resources, elk density, human disturbance, physiogeographic covariates reflecting conditions within the 9.2 km^2 buffers surrounding the kill site, and animal specific covariates including elk age and harvest date. I used a general linear model with maximum likelihood optimization. After selection of the best model, I compared the ΔAIC_c substituting in different metrics for the same 5 concepts to assist in refining the best supported model. Top models (< 2 AIC points from best model) were averaged if the top ranked model lacked strong support (AIC_c weight < 70%), but competing models with uninformative covariates (i.e., the best model but with one extra variable) were excluded when model averaging (Arnold, 2010; Anderson, 2008). I did not include both AccpBio and DDE when model averaging because they were correlated (r=0.66). All samples used for model selection were collected in 2011, so cohort effects on IFBF were not expected. Model selection and correlations were done in STATA® 12 (StataCorp, 2011).

I used the best model to predict the body fat value for each 30 m cell across the study area using a mean value for harvest date or elk age. I then averaged the landscape body fat values by GMU.

Model validation. Observed body fat values from organs collected in 2010 were compared to model predictions using 2 approaches. Body fat values from lactating elk collected in 2010 that were not used during model development and thus represented an "independent" data set were used for the first validation. Locations of these 16 samples were plotted on the landscape body fat map and for each sample I calculated the landscape body fat value within a 9.2 km^2 area centered on the location of the sample. Observed and predicted fat values of individual elk were plotted and compared with a paired T-test. Second, I used the values of a larger sample (n=46) of observed body fat measures from lactating elk whose locations were known only as to GMU, and therefore, were not used in model development. I took the mean values of observed field samples by GMU and plotted them against the mean predicted landscape body fat for each GMU. Due to the small number of sample points, my evaluation was based on visually inspecting the plot. Statistical tests were done in STATA® 12 (StataCorp, 2011).

Results

HABITAT USE BUFFER

The minimum convex polygon for female elk at Mount St. Helens between June and October was 9.2 ± 1.2 km^2 for elk off the mudflow and 12.0 ± 2.9 km^2 for elk on the mudflow. A buffer of 9.2 km^2 included 58% of a radio-collared elk's GPS locations between June and October (peak period of IFBF accumulation) and was chosen as the elk use buffer to characterize habitat covariates around the harvest site (Fig. 3.2).

BODY FAT, LACTATION AND PREGNANCY

Between 1 October and 15 December 2011, 133 elk organ samples were collected from harvested female elk within the study area. This constituted a return rate on mailings of 11%. Incomplete samples (i.e., missing harvest location info, or organs such as heart and kidney) were removed from the dataset prior to analysis resulting in 102 samples. The greatest number of samples were collected from GMU 556 (n=40) and fewest samples were collected in GMU 522 (n=6). The majority of harvest locations from organ samples collected in 2011 were evenly dispersed throughout the study area, however, fewer samples were submitted from regions close to the edge of the study area (Fig. 3.1, Fig. 3.3).

Sample collection peaked in early November with 76% of samples being harvested between 5 November and 2 December. I found no relationship between harvest date and adult (2-14yr) female IFBF (P=0.18, n=81). Harvested elk ranged in age from 1 to 16 years with a mean age of 5.7 years (SD=3.7, n=99). There was no relationship between age of adult elk (2-16yr) and IFBF (r=-0.03), P=0.78, n=85), but yearlings had significantly lower IFBF ($\bar{x}$=3.18, SD=3.02, n=13) compared to adult elk ($\bar{x}$=8.66, SD=5.66, f=6.38, df=96, P<0.01), whereas the sample size for older aged animals (>14yr) was too small to compare with other age groups ($\bar{x}$=6.33, SD=4.46, n=3).

Excluding yearling elk, there was a 0.63 (n=67) lactation rate for adult elk (2-14yr), which was not related to date (P=0.49), IFBF (P=0.77), or age (P=0.29). In contrast, the probability of an elk being pregnant increased with harvest date (r^2=0.51, P<0.01). Pregnancy rate in October (0.06) was lower than all other months combined (X^2=7.85, P<0.01) and was responsible for this pattern. Pregnancy rate of adult elk after 5 November was 0.51 (n=35) and 0.64 (n=22) from 22 November to 15 December (X^2=0.8176, P<0.37, Table 3.3). Between 5 November and 15 December 56% of the pregnant individuals were also lactating (n=28).

When I compared samples classified by pregnancy and lactation status (Fig. 3.4), females that were non-lactating and barren had the lowest mean IFBF (P=0.01, n=35, Fig. 3.4). IFBF explained the probability of being pregnant (r^2=0.23, P<0.01, Fig. 3.5).

INFLUENCE OF HABITAT ON BODY FAT

I used 38 lactating adults out of the 102 samples for modeling the influence of habitat on IFBF. Non-lactating individuals were not used for this analysis because some of these females may have nursed for only part of the summer and I was unable to account for this variability in energetic demand (but see Appendix 17 where I present an additional analysis with all female elk where lactation status was used as a covariate, n=55). Lactating individuals were used for analysis if the sample had information on harvest location, harvest date, and samples were from elk older than 1 year and less than 14 years.

I excluded 5 covariates (terrain ruggedness, slope, clearcuts, public roads, and pellet count density) from being included in models because they were highly correlated, specifically: elevation, ruggedness, slope ($r>0.60$), AccpBio and clearcuts ($r=0.83$), main roads and public roads ($r=0.57$), and late winter elk density estimates from aerial surveys versus summer elk density estimates from pellet surveys ($r=0.58$). After model selection, I evaluated their effect in the top model by substitution and found little support for the inclusion of any of the 5 covariates.

The top 2 models explained from 14 to 20% of the total variation in IFBF (Table 3.4) and the confidence limits of β coefficients for date of harvest, elevation, and elk density overlapped with zero (Table 3.5). The top 2 equally supported models were model averaged resulting in date of harvest showing a negative relationship to IFBF of lactating elk in autumn, while elevation and elk density the previous winter (Fig. 3.6) had a positive effect on IFBF of lactating elk (Table 3.5, Fig. 3.7). Winter elk density was not correlated with any forage or habitat covariates ($P>0.38$, n=39), whereas Elevation was correlated with main road density ($r=-0.59$, $P<0.01$, n=39).

I was able to use organ samples from 16 lactating elk collected in 2010 (with known harvest locations) to evaluate the model predictions at the scale of the 9.2 km^2 buffer. IFBF values predicted by the model (Fig. 3.8) from habitat conditions were not correlated with the observed values from the 16 cows harvested in 2010 (r=0.14, P=0.62). I also used the model to predict the mean IFBF for 5 GMUs in the study area (Fig. 3.9) and compared the mean values of IFBF of 55 elk collected across each GMU. I found that at the scale of the GMU, model predicted and observed values were still not closely correlated (r=0.47, P=0.42, Fig. 3.9).

Discussion

The 11% return rate on organ information packages mailed to eligible hunters (n=1212) in 2011 was within the range of 10-18% for sampling return rates observed in 2009 and 2010 when 424 hunters were contacted each year. The total number of samples collected at MSH in 2011 (n=133) was on average 13% higher than the total number of samples collected in 2009 and 2010 when reproductive organs and harvest coordinates were not collected. Samples collected in 2009-2010 were not included in this analysis because locations of kill sites were generally unknown. Despite the relatively low sample size in 2011 this collection effort produced one of the largest datasets with body condition, pregnancy, and lactation status collected in a single year from hunter-harvested elk in the PNW. I attribute this not only to the large number of packages WDFW mailed to hunters, but to having technicians in the field during the hunting season to assist hunters. Nonetheless, it is clear that long-term efforts are necessary to obtain large samples sizes. For example, 500 to 2000 samples of kidneys were reported in 13- to 31-year sampling efforts in Oregon (Johnson et al., 2013; Davidson et al., 2012; Kohlmann, 1999).

BODY FAT, LACTATION AND PREGNANCY

Date of collection of samples for assessing IFBF can add to the variation in characterizing body condition of herds. IFBF values reported from organ collections in Oregon and Washington declined by as much as 1.3 to 7.3% IFBF during autumn sampling periods that ranged from October to December (Kohlman, 1999; McCorquodale, 2008). Such declines in autumn IFBF have been attributed to waning forage quality that occurs under the continued demands of lactation and perhaps hunting pressure (Cook et al., 2013). Correlation between date of collection at MSH and IFBF of adult elk was variable, but non-lactating-barren females evidently had the lowest IFBF in autumn. IFBF and pregnancy rates of elk varied among age classes as has been reported in other studies where sample sizes were 482 to 861 elk (Cook et al., 2013; Morano et al., 2013). The 75% lower IFBF in yearlings compared to prime adults is likely related to the different energetic constraints of age classes because yearlings are still allocating resources to somatic growth (Atwood and Weeks, 2002). Thus their inclusion into herd-level indices of body condition may confound the interpretation unless the age structure of the population is known. Declines in IFBF of old animals typically are less apparent than in yearlings (Cook et al., 2004), but a decrease in IFBF can occur when elk past their prime struggle to maintain energy reserves because tooth wear decreases mastication efficiency (Young and Marty, 1986). I also did not observe a difference in IFBF between lactating and non-lactating individuals, which has been consistently reported for captive and free ranging elk (Stussy, 1993; Trainer, 1971; Kohlman, 1999; Cook et al., 2004; Davidson et al., 2012; Cook et al., 2013). I propose two explanations. First, lactation status may have been misjudged during organ scoring. To reduce mistakes I removed samples from the dataset prior to analysis when a cow had clear fluid in their udder because this status can bias the assessment of lactation during organ scoring. Nevertheless, misjudgement of lactation status may still have introduced an observer bias.

Second, some elk at MSH may be low enough in nutritional condition that they are unable to breed or lactate. This may be the result of extremely poor habitat, such as those areas along the North Fork Toutle River where minimal forage grows because of high volcanic ash deposition. Alternatively, hoof rot is becoming an increasing problem at MSH and in some cases hoof rot can cause 30-90% of afflicted animals to suffer from deformed hooves or lameness (WDFW, 2011), which potentially prevents adequate forage intake when habitat conditions are poor. To date, necropsies of afflicted elk from southwest Washington have been inconclusive, but deficiencies in trace minerals have been ruled out (WDFW, 2011).

Direct comparisons of body fat from elk obtained in this study to others are difficult because of the different indices used to measure body fat, the nature of the samples used, and variation in when samples were collected. Early studies assessing body fat of hunter-harvested elk in the PNW used kidney fat indices (KFI) based either on full kidney fat weight (Trainer, 1971) or trimmed kidney fat weight (Merrill, 1987; *sensu* Riney, 1955). In this study I used the Kistner subset score to assess organs (Cook et al., 2001), which may become more commonly used for harvested animals in the future because of its strong linear relationship to fat (Cook et al., 2001). For live elk, a recent study has promoted the use of scaledLIVINDEX, which combines rump fat score and maximum rump fat thickness and is scaled to an elk's surface area (Cook et al., 2010). For comparisons I converted body fat indices from different methods to IFBF using the equations of Cook et al. (2001), but recognize the limitations when comparing KFI to more recent approaches.

Lactating adult elk harvested at MSH in this study averaged slightly lower IFBF in the autumn (IFBF=8.64% ± 5.5, n=65) than reported for lactating female elk of the same age group collected in the MSH blast zone during autumn of 1983 and 1984 (Merrill, 1987: 9.27% ± 4.96, n=12), slightly higher than lactating elk in coastal Oregon in autumn of 1967-1968 (Trainer, 1971: 7.47% ± 3.26, n=31), but considerably higher than elk harvested in 1988 and 1989 in the Oregon coastal range, although these samples were collected in January and February (Stussy, 1993: IFBF=3.5%, n=29). Because the latter samples were collected during mid to late winter (31 Dec to 27 Feb) and declines in the order of 4% would be expected for a coastal herds (Cook et al., 2013), summer IFBF levels corrected for this decline may have been ~7.3%. If these IFBF estimates are roughly correct, they would indicate that IFBF of coastal elk may be slightly lower than in the

MSH elk population inhabiting the Cascades, a trend supported by more recent studies. Cook et al. (2013) reported higher IFBF based on scaledLIVINDEX of live elk in the Washington Cascades region (11.39-13.31%) than in the coastal regions (6.89-8.45%) of Washington and Oregon. Experimental foraging trials with tame elk support these findings because female elk showed lower dietary digestible energy intake and calves exhibited slower rates of growth in habitats characteristic of coastal forests compared to the habitats of the Cascades (Cook et al., in review).

The relationship between IFBF indices and pregnancy that I observed in elk (Fig. 3.5) has been reported widely (Davidson et al., 2012; Stewart et al., 2005). Sampling date significantly influenced the probability of a harvested female being pregnant. Low pregnancy rate prior to 1 November is consistent with mean conception dates of 27 September reported for elk in Oregon (age >2) (Noyes et al., 2002) and within the range of reported conception dates for elk in the PNW between 13 September and 5 November (Noyes et al., 2002; Trainer, 1971; Merrill, 1987).

Based on uteri collections after 1 November, adult pregnancy rates of all females (lactating and non-lactating) at MSH in 2011 was low (0.51) but consistent with rates reported for elk in coastal Oregon (Trainer, 1971: 0.50) and Washington (Kuttel, 1975: 0.69) 3 decades earlier. However, the 2011 pregnancy rate at MSH likely represents a minimum value because detection error of small fetuses, as well as late conception dates, can reduce pregnancy estimates based on analysis of reproductive tracts. In fact, the pregnancy rate from samples collected between 5 November and 15 December (0.51) was 20% lower than samples collected between 22 November and 15 December (0.64, n=22). Although this was not statistically different it potentially indicates fewer fetuses were observed earlier in the autumn when they were less developed, and some elk were potentially still breeding. Additionally, if the 2011 lactation rate (0.63, n=67) reflects percent of cows pregnant in 2010 then there is more support for 2011 pregnancy rates of ~0.60, which is higher than estimates based on all samples but still relatively low. Cook et al. (2013) reported average pregnancy rates of all prime-aged female elk to be 0.93 for elk herds in the WA Cascades between 2000 to 2009 and generally >0.80 in the Oregon Cascades south of MSH, however Trainer (1971) observed pregnancy rates of 0.50 in reproductive tracts collected between November and January of 1964 to 1968 in Western Oregon. Between 5 November and 15 December no yearlings at MSH were pregnant (n=5), which was consistent with the findings of Stussy (1993) from coastal Oregon in 1987-1988. Yearling pregnancy rates reported by Trainer (1971) in Western Oregon were typically below 0.20, whereas Cook et al. (2013) reported pregnancy rates of 0.20-0.34 for various herds in the PNW based on sample sizes between 5 and 23. I did not find strong support for alternate year breeding at the herd level because adult (2-14 yrs) lactating elk had a 48% (n=21) pregnancy rate and adult non-lactating elk had a 53% (n=15) pregnancy rate based on samples collected after 1 November. However, pregnancy rates suggest reproductive pause is not uncommon.

BODY FAT- HABITAT RELATIONSHIPS

I did not find strong evidence that either DDE or AccpBio were good predictors of IFBF in lactating elk, but my sample size was small (i.e., n=38). Including the extent of clearcuts, which reflects total forage biomass, also was not supported. Clearcuts commonly have been identified as key foraging areas for elk (Irwin and Peek, 1983; Witmer et al., 1985), and DDE was a key habitat covariate in the recent PNW elk habitat use models (Rowland et al., in prep.). There may be several explanations for not finding a relationship.

First, forestry practices around MSH and the residual effects of the 1980 eruption have produced a range of landscape conditions. This spatial variation initially was thought to be an advantage because it provided variation in forage conditions that I expected to lead to variation in elk performance (i.e., IFBF). The buffer size (~9.2 km^2) I used around a kill location to relate forage resources to IFBF was a compromise between including too many unused areas while not excluding important foraging sites. Use of too large a buffer size may not be a disadvantage in environments where resources are homogeneous. However, in averaging over an area approximately the size of an elk's home range, I found the mean DDE from each use buffer had a range of only 0.41 kcal/g (CV = 0.03) across all elk samples used in the analysis (Appendix 14, Appendix 16). In fact 82% of harvested elk had foraged in areas with mean DDE values within the range (2.5-2.7 kcal/g) that Cook et al. (2004) found to be associated with similar levels of autumn body fat in lactating females (8-12%). Other studies that have successfully related habitat to body condition have been based either on more detailed studies of ungulate movements (Mcloughlin et al., 2007; Bender et al.,

2007) or on hunter harvested red deer (*Cervus elaphus*) during long-term government programs with very large sample sizes (n > 20,000, Mysterud et al., 2001).

Second, factors related to forage resources other than DDE or AccpBio that better explained the variation in IFBF may have reflected forage quality. For example, I found elevation was positively related to autumn IFBF. Higher elevations can offer important forage resources because lower temperatures and higher moisture compared to lower elevations may provide access to lagged growing season conditions offering higher quality forage later in the summer (Mysterud et al., 2001; Hebblewhite et al., 2008; Cook et al., in review). Cook et al. (in review) sampled forage resources in western Washington and Oregon across sites representing a gradient of elevations: Nooksack, Springfield, and Willapa Hills. They found that DE was often 25% greater in high elevation PSS and MHS zones at Nooksack and these were among the only sites that provided adequate levels of DE (2.7 kcal/g). This supports my observations at Mount St. Helens that IFBF of lactating elk increases with elevation.

Alternatively, elevation also was negatively correlated with main roads (r=-0.56, P<0.01). Previous studies have suggested roads may potentially influence elk body condition by increasing energetic costs or by displacing elk from preferred habitat (Rumble et al., 2005; Ward and Cupal, 1979; Millspaugh et al., 2001; Cole et al., 1997). For example, Benhaiem et al. (2008) reported roe deer in active hunting areas increased vigilance and decreased foraging efficiency during the hunting season often selecting areas farther from disturbance with lower quality forage, and Davidson et al. (2012) attributed lower pregnancy rates of lactating elk to increased disturbance from archery hunters in areas of marginal forage. Nevertheless, there was more model support for elevation than roads ($\Delta AIC_c = 2$) for lactating elk at MSH.

In contrast to my original expectation, I found a positive relationship between winter density and body condition at MSH. This was unexpected because density-dependent recruitment and survival have commonly been reported for elk in the Rocky Mountains (Merrill and Boyce, 1991; Houston, 1982; Johnson et al., 2013; Keech et al., 2000; Simard et al., 2010; Stewart et al., 2011). A positive relationship between winter density and body condition could have reflected that elk congregated in areas offering better resources because density of ungulates has been positively related directly or indirectly to forage availability (Pettorelli et al., 2009; Suring and Vohs, 1979), and forage quality (DE, Mereszczak et al., 1981). However, recent research also indicates spring IFBF of elk in western Washington is most related to IFBF from the previous autumn, which reflects summer nutrition, while December through February weather (precipitation and temperature) potentially have very minimal influence on elk body condition (Cook et al., 2013). In fact, evidence is accumulating that summer nutrition is the most influential season for reproduction (Cook et al., 2004; Stewart et al., 2005; Therrien et al., 2007; Mahoney and Schaefer, 2002; Cook et al., in review; Cook et al., 2013).

Nevertheless, two other reasons may explain the positive relationship between winter elk density and nutrition. First, telemetry data of MSH elk indicate elk remain in the same general area and do not seasonally migrate (unpublished data, WDFW). Thus, areas with high winter densities of elk may reflect the same areas used during summer. Alternatively, conditions of winter range may be related to elk performance at MSH because summer and winter habitat conditions may interact to influence annual nutrition levels - a process described by the equilibrium hypothesis. Cook et al. (2013) described this hypothesis as the interaction between winter, spring, summer, and autumn nutrition such that each season's relative effect can vary among ecological settings and herbivore densities. Cook et al. (2013) also noted this interaction is made more complex by an interaction between pregnancy, lactation, body fat, and reproductive pause. For instance, even though annual nutrition rates may be influenced by the interaction between winter and summer habitat, Cook et al. (2013) generally observed that lactating elk undergo declines in their nutritional condition each winter (the step-down hypothesis: Cameron, 1994; Parker et al., 2009), with fatter elk losing body fat more rapidly in winter than thin elk. Low body fat of elk exiting winter in poor condition can be recovered when summer nutrition is adequate eliminating lingering effects of the previous winter. If summer nutrition is adequate lactating elk can recover fat reserves to become pregnant, whereas if summer range conditions are poor, elk with low spring IFBF that lactated in the previous year may not recover sufficiently while non-lactating elk may become pregnant.

Model validation provided little support for the top model based on predicted and observed values of an independent dataset collected in 2010. Weak model validation could not be explained by differences in habitat condition or sampling regimes between November 2010 and 2011. Specifically, hunting pressure and weather conditions were comparable between years, and the geographic distribution of organ samples collected in the study area was similar across GMUs for 2010 and 2011. Also, organs were scored for organ fat using the same sampling protocol each year. Nevertheless, IFBF estimates for samples collected in GMU 524 (n=3) and GMU 556 (n=7) were consistently lower than model predicted IFBF values. Both of these GMUs are higher in elevation and GMU 524 also has high elk density, suggesting these model parameters may overinflate IFBF predictions when elevation and elk density are extremely high. Additionally, the relationship between predicted and observed IFBF was variable partly because of a small sample size (n=16), which made outliers highly influential. Using the average observed and predicted IFBF values across each GMU allowed more samples to be used because many samples had a GMU location, but no coordinates. This minimized the influence of outliers, but predicted values in GMU 524 and GMU 556 remained high compared to observed values. These regions of the study area may be an important area of focus for future research.

It remains unclear why elk in areas of MSH are in poorer nutritional condition and have lower pregnancy rates than other elk herds in the Cascades. One possible reason may be that most elk I sampled were harvested from low elevation areas in the western portion of the MSH elk herd range rather than from the higher elevation areas within the Mount St. Helens National Monument where hunting is not allowed. The western low elevation habitat at MSH shares similarities with some coastal hills elk herds, and this may also result in more similar forage quality between the western portions of the MSH elk herd range and some coastal hills elk herds compared to higher elevation Cascade elk herds. For example, the elevation in the western two-thirds of the core MSH elk herd (356m ± 215) is 16 m lower than Willapa Hills elk herd (372m ± 189) and both areas have similar mean annual precipitation (MSH: 192cm ± 61 and Willapa Hills: 202cm ± 47). These similarities are not necessarily surprising because the northwestern herd boundary of my study area is only 10 km from the coastal Willapa Hills region delineated by Cook et al. (in review) for comparing herd productivity. Additionally, using organ samples collected from MSH between 2009-2011 (see Appendix 12), I did find some indication that there was a west to east difference in IFBF estimates of all female elk (T-test, $P<0.01$, n=116), which corresponded to the elevation transition from the WHS to the PSS zone (Fig. 3.1 [Franklin and Dyrness, 1988]). My sample of hunter-harvested elk may not reflect the portion of the MSH elk population that uses the high elevation areas within the Mount St. Helens National Monument, which in other areas appear to offer better DE.

Conclusions

My objective was to assess the spatial variation in summer habitat quality for elk across varying conditions at MSH using performance indices (IFBF and pregnancy) to provide a direct link between habitat and elk fitness. I was constrained in my efforts by a low (11%) return rate of samples from hunters, which indicates the need for long-term collection programs for similar habitat-performance studies based on harvested animals. Despite a limited sample I was able to show IFBF of adult elk provided a good index to pregnancy, but I was less successful in linking forage quality or quantity in the summer to IFBF. I found some evidence that high autumn IFBF in lactating elk was associated with areas of high DDE, elevation, and elk winter density. The effect sizes of the latter two variables were strongest. However, it is possible elevation and DDE are confounded because DDE is reported to be higher at high elevation sites in the PNW (Cook et al., in review). Also, there was lower spatial variation than expected for DDE at MSH at the scale that I measured it. Fine-scale analyses on animals with known movement trajectories may be needed to develop these relationships. Indeed, both DDE and elevation have been identified in recent, well-validated models for predicting summer elk use in several elk populations across the PNW (Rowland et al., in prep.).

My approach to relate habitat to nutritional condition followed Cook et al. (2013), who argued that non-lactating elk should not be used to monitor habitat performance because they have limited energetic demands and it is not possible to control for the portion of the summer that they have lactated. However, I found non-pregnant, not-lactating elk had the lowest IFBF in my limited sample. These results are potentially still consistent with Cook et al's (2013) description of seasonal and annual fat dynamics, where "step-down" declines in body condition occur with nutritional inadequacy, but declines are modified by the ability of elk to recover body fat during the summer (Cook et al., 2013). Elk in many environments can off-set winter decline in fat levels during spring and summer foraging such that negative effects from the previous winter and previous summer’s lactation can be eliminated. However, if forage is sufficiently low it is possible an animal’s annual equilibrium level of nutrition may lead to reproductive pause (Cook et al., 2013). I hypothesize that the non-lactating non-pregnant animals at MSH may reflect the poorest summer habitat conditions, and even with reproductive pause or when they lose a calf, they are unable to restore IFBF levels to where ovulation and conception will take place (Therrien et al., 2008). Although elk that enter the winter with low IFBF in autumn lose fat less rapidly during winter than individuals with higher autumn IFBF (Cook et al., 2013), body fat reserves in these low IFBF animals may be sufficiently low enough that they have the highest mortality risk when prolonged winters and delayed spring green-up occur. If this occurs at MSH, it may be these non-lactating and non-pregnant individuals that have died during pronounced mortality events that have occurred at MSH over the last decade (WDFW, 2006). My sample of non-lactating, non-pregnant elk was too small to discern nutritional patterns in their summer use areas, but focusing on these animals may be a key to understanding nutritional ecology of ungulates in Pacific Northwest environments.

Table 3.1. Descriptions of strata used to classify forage quality and availability around Mount St. Helens, Washington. Each strata was populated with forage availability (kg/ha) and DDE (kcal/g) from average values based on stratified randomly sampled vegetation plots in each strata during August 2010 and July-September 2011. See Appendix 13.

Strata name	Description
Volcanic ash	Sites comprised of more than 90% volcanic ash. Sites highly disturbed during the 1980 eruption and limited succession has occurred. Primarily located along the North Fork and South Fork Toutle river and high erosion areas of the pumice plains directly north of the Mount St. Helens crater.
MSH Wildlife Area (WA)	Located 6 km west of the MSH blast zone along the North Fork Toutle river. It is bounded by trees and escarpment to the north and the North Fork Toutle river to the south. The area is characterized by grassland and many non-native forbs which were periodically seeded in the area since the early 1980's because of the value as an important wintering location for elk around MSH.
Alder along the mudflow	Sites disturbed by the 1980 eruption with at least 75% alder. This community includes all stages of alder succession located directly adjacent to, or on the North Fork Toutle mudflow. This area is between the sediment retention dam in the west and the pumice plain in the east. Vegetation at these sites grows on volcanic ash substrate or volcanic hummocks and is characterized by less swordfern and more ruderal species compared with alder stands outside the blast zone.
Mesic and riparian pumice plain	High moisture areas on the pumice plain located along streams at higher elevations (1150-1330 m), and isolated wetland areas on flatter terrain below 1150 m. These areas are highly productive relative to other pumice plain communities and comprised of *Carex*, *Juncus*, *Salix*, and *Equisetum*.
Pumice plain upland grass	Low productivity communities located directly below the crater. Primarily found on stable slopes of the pumice plain between 1150-1700 m. Sites are characterized by low species diversity and primarily comprised of species unique to the blast zone including *Lupinus lepidus, Agrostis pallens*, and *Penstemon.*

Table 3.1. Continued.

Strata name	Description
Pumice plain lowland grass and forbs	Mixed grass and forb communities within the heavily disturbed blast zone but located farther from the crater than upland grass communities. Sites located between 700-1150 m and are generally more productive than upland grass sites. These communities do not have continuous shrubs or trees but have the occasional *Salix* or Douglas fir. Vegetation is less comprised of unique blast zone species and commonly includes *Hypochaeris radicata, Achillea millefolium*, and *Agrostis*.
Red alder	Sites not disturbed by the 1980 eruption with at least 75% alder. This stratum includes all stages of alder succession and all elevations, but usually occurs below 750 m. This community occurs on upland slopes with mesic well drained soils, or riparian features, but is also the result of natural succession after disturbance. Understory vegetation is dominated by swordfern, *Montia* spp., and the shrubs layer is frequently comprised of *Rubus spectabilis*.

Table 3.2. Habitat characteristics that were considered for *a priori* models to predict elk ingesta free body fat around Mount St. Helens, Washington. All covariates were mapped using a 30 m cell size unless otherwise specified. Type refers to sub category of covariates where (F) is forage, (H) is human disturbance, (D) is elk density, (W) is weather, and (E) refers to animal covariates.

Covariate	Type	Description
DDE	F	Dietary digestible energy (kcal/g) predicted using the Forest Service Westside elk habitat model (WEHM) in undisturbed conifer stands and predicted in hardwood stands and areas disturbed by the blast zone with a DDE model created in thesis Chapter 2.
AccpBio	F	Biomass of forage species readily accepted by elk. Forage species were classified using tame elk in grazing trials (Cook et al., in review) throughout western Washington and Oregon and related to percent canopy cover and proportion hardwood for modeling purposes. Accepted biomass was estimated in undisturbed conifer stands with the WEHM and was estimated in hardwood and novel areas by sampling vegetation biomass in 2011. See methods in Chapter 2 and Appendix 13.
Clearcuts	F	Forest stands less than 15 years of age. Clearcuts were identified using stand age layers, the Gradient Nearest Neighbor GIS layer from 2006, and was updated using orthographic photos from 2011. Pixels classified as a clearcut were given a value of 1 and were summed within the use buffer of each harvested elk.
SelecBio	F	Similar to accepted biomass but for forage species that are highly preferred by elk.
Dist_edge	F	Distance (m) to nearest forest/clearcut edge. This potentially indicates access to forage resources within a use buffer.
Canop_cov	F	Percent canopy cover of trees from the GNN layer. Cook et al. (in review) found a strong negative correlation between canopy cover and elk forage abundance.
Aug_prec	F	August precipitation (mm) in 4 by 4 km grid cells. Values were obtained from the Prism Climate Group. www.prism.oregonstate.edu. August was chosen because of its importance for late summer forage green-up (Johnson et al., 2013).
Elev	F	Elevation (m) from a 30 m DEM layer. Higher elevations are comprised of Pacific Silver Fir and Mountain Hemlock potential natural vegetation zones *sensu* Franklin and Dyrness (1988) and these ecotypes are commonly associated with higher quality forage (Cook et al., in review).

Table 3.2. Continued

Covariate	Type	Description
Dist_mudflow	F	Distance to WDFW Wildlife area along the North Fork Toutle River. The Wildlife Area has been seeded with legumes and high quality forage species in recent decades and annual forage enhancement projects might maintain a higher forage base during winter months.
Aspect	F	Categorical variable classified into cardinal directions (NE and SW). North facing slopes are commonly cooler and moister leading to variation in vegetation species, and temporal variability in senescence of forage species.
Rugged	F	Standard deviation in elevation (m) within a circular buffer. Ruggedness was calculated at various spatial scales including 100 m, 1 km, 5 km, and 10 km analysis windows.
Slope	F	Slope (%) for an individual cell within a 3 x 3 cell window.
Dist_all_road	F	Distance (m) to nearest road.
Dens_all_road	H	Density of all roads regardless of ownership or amount of use (roads/km^2).
Dist_pub_road	H	Distance (m) to nearest road freely accessible to the public. Roads were classified based on ownership and whether there was a locked gate.
Dens_pub_road	H	Density of roads freely accessible to the public (roads/km^2).
Dist_main_road	H	Distance (m) to nearest heavy-use roads. This included highways within the study area and arterial logging roads commonly used by logging operations and by hunters during the autumn. Roads on private logging lands were classified using Weyerhaeuser GIS road layers and during meetings with Weyco foresters.
Den_main_road	H	Density of all major roads (roads/km^2).
Num_hunter	H	Total number of hunters in the field throughout the hunting season for each game management unit. Data was accessed through the WDFW website and rasters were created for 2010 and 2011. http://wdfw.wa.gov/hunting/harvest/2011/elk_general.html
Hunter_days	H	Cumulative number of hunter days for each GMU calculated for 2010 and 2011 from WDFW hunter statistics. Hunter days was calculated as (number of hunters) x (average field days per hunter). http://wdfw.wa.gov/hunting/harvest/2011/elk_general.html
Len_season	H	Cumulative number of days with active hunting between 20 August and 15 January. Calculated for 2010 and 2011. http://wdfw.wa.gov/hunting/harvest/2011/elk_general.html

Table 3.2. Continued

Covariate	Type	Description
Elk_beta_kri	D	Summer elk pellet group abundance across the study area (groups/km^2). Data from pellet plots were corrected for detection based on observer experience and ground cover using beta regression and interpolated across the study area using Empirical Bayesian Kriging (EBK). EBK provides increased accuracy because it accounts for the error introduced by estimating the underlying semivariogram.
Elk_beta_idw	D	Similar to "Elk_beta_kri" but deterministically interpolated across the study area using inverse distance weighting (IDW).
Elk_idw	D	Raw summer pellet counts interpolated with inverse distance weighting. Counts were used to populate 1 x 1 km grid cells that contained the triangular pellet plot prior to interpolation. See Chapter 2.
Deer_beta_idw	D	Values of deer pellet groups were deterministically interpolated across the study area using (IDW).
Deer_grid	D	Raw deer pellet count values were used to populate the 1 x 1 km grid cell that contained the triangular pellet plots. See Chapter 2 methods.
Weight_aerial_d	D	Winter elk density (elk/km^2). Estimated from aerial helicopter counts of elk in March 2011. Visibility is restricted to open canopy forest stands. Counts were converted to density based on elk counted and area surveyed within a 9.9 km^2 grid cell. Density of elk in closed canopy forest was estimated based on clearcut density and ratio of GPS collared elk in clearcut versus closed canopy forest during aerial surveys. Density of clearcut and closed canopy was averaged using an area-weighted mean. See methods in Chapter 3.
Aerial_dens	D	Winter elk density (elk/km^2). Estimated from aerial helicopter counts of elk in March 2011. Visibility is restricted to open canopy forest stands. Counts were converted to density based on elk counted and area surveyed within a 9.9 km^2 grid cell but values were not adjusted for sightability.
WSI	W	Winter severity index. Calculated using the mean temperature lows and mean precipitation values (4 x 4 km cells) between December and March 2011 as (standardized precipitation) – (standardized temperature). A winter severity index was created for 2010 and 2011.

Table 3.2. Continued.

Covariate	Type	Description
Lac	E	Lactation status of elk. Assessed after inspection of the udder from each harvested elk and classified as (1) milk, (2) clear or semi-clear fluid, (3) dry, or (99) no data. But only category 1 and 3 were used during analysis to ensure accurate classifications.
Age	E	Age of elk estimated from counting cementum annuli of front incisors.
Harvest	E	Date of harvest for each elk. Calculated as number of days from 1 October 2011.

Table 3.3. Proportion of pregnant and lactating female elk and associated ingesta free body fat (IFBF) by age class at Mount St. Helens, Washington in autumn 2011.

Age Class	1 Yr	2-14 Yr
Autumn pregnancy rates (5 Nov - 12 Dec)	0 (n=4)	0.51 (n=35)
Late autumn pregnancy rates (22 Nov - 12 Dec)	-	0.64 (n=22)
Lactation (1 Oct - 15 Dec)	0 (n=10)	0.63 (n=67)
Percent IFBF (1 Oct - 15 Dec)	2.40^a (SD=2.17, n=10)	8.49^b (SD=5.64, n=67)

Different superscripts indicate a significant difference from other age groups at $P<0.05$.

Table 3.4. Models predicting ingesta free body fat of lactating elk harvested in autumn 2011 at Mount St. Helens, Washington. Included are the number of estimated parameters (*k*), AICc score, and AIC weight (w_i) for each model. Covariate descriptions are in Table 3.2.

Model	***k***	**AIC$_c$**	Δ_i	W_i
Date, Density, Elev	4	230.99	0.00	0.21
Date, Density	3	231.64	0.65	0.15
Date, Density, DDE, Elev	5	231.93	0.94	0.13
Date, Density, AccpBio, Elev	5	232.48	1.49	0.10
Date, Density, Road	4	232.99	2.00	0.08
Age, Date, Density, Elev	5	233.11	2.12	0.07
Age, Date, Density	4	233.73	2.74	0.05
Date, Density, Roads, AccpBio	5	234.24	3.25	0.04
Date, Density, Roads, DDE	5	234.28	3.29	0.04
Age, Date, Density, Roads	5	235.09	4.09	0.03
Density, Elev	3	235.11	4.11	0.03
Density	2	235.91	4.92	0.02
Density, DDE, Elev	4	236.53	5.54	0.01
Density, Roads	3	236.76	5.77	0.01
Age, Density, Roads	4	238.86	7.87	0.00
Age, Date	3	240.67	9.68	0.00
Age, Date, AccpBio	4	241.90	10.90	0.00
Elev	2	241.99	11.00	0.00
Age, Date, DDE	4	242.19	11.20	0.00
Null model	1	242.94	11.95	0.00
Roads	2	243.61	12.61	0.00
AccpBio	2	244.46	13.47	0.00
DDE	2	244.69	13.69	0.00
Age	2	340.93	109.93	0.00
Date	2	341.37	110.38	0.00

Table 3.5. Model parameters for predicting percent ingesta free body fat of lactating harvested elk in 2011 at Mount St. Helens, Washington. Table includes parameter values (B), *P*-value and standardized regression coefficients (SRC). Covariate descriptions are in Table 3.2.

Covariate	B	*P*	SRC
Intercept	1234.5	0.5671	0
Date	-0.0301	0.5680	-0.0980
Density	0.2971	0.0534	0.3282
Elev	0.0045	0.1251	0.1304

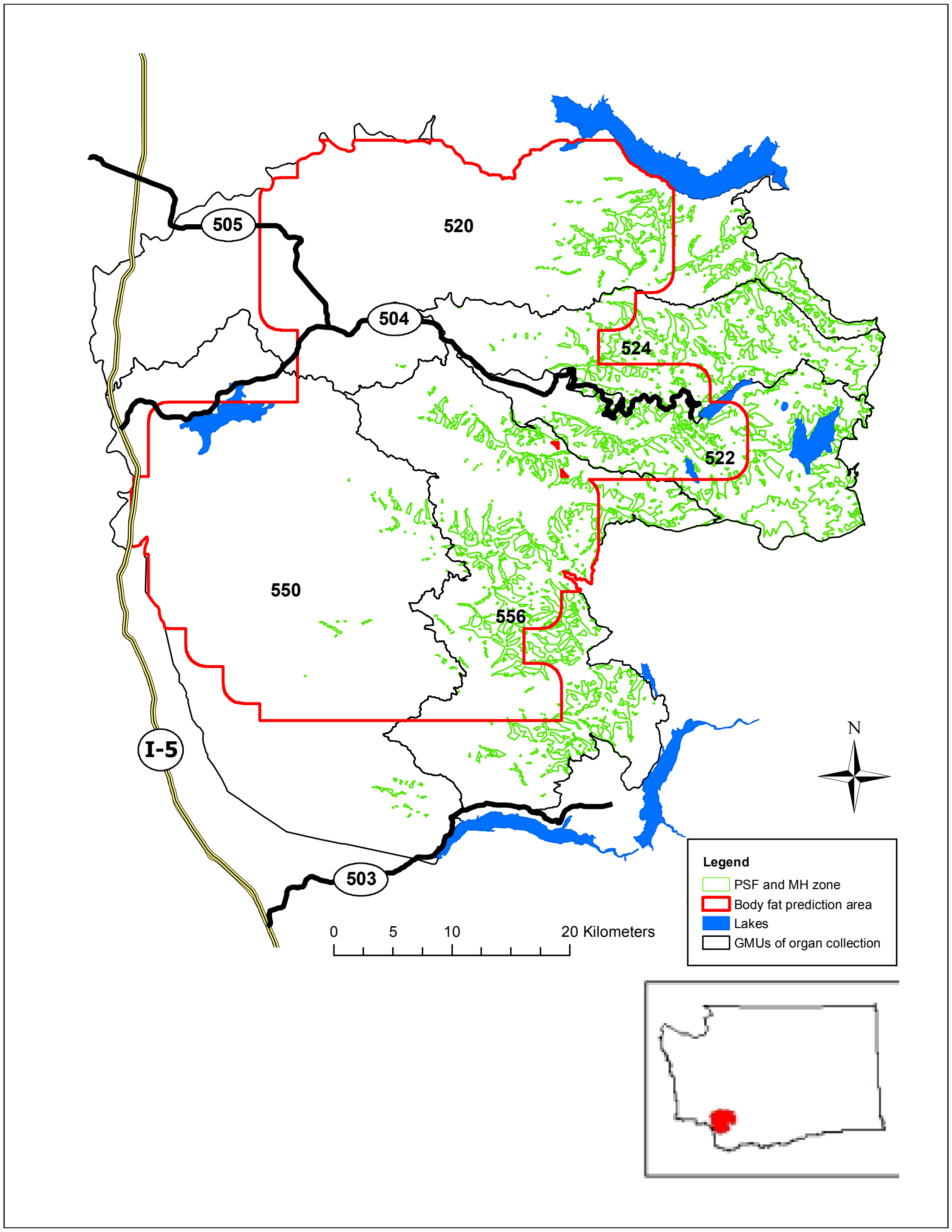

Figure 3.1. Study area for ingesta free body fat (IFBF) analysis at Mount St. Helens, Washington. Organs to assess IFBF were collected from 5 game management units (GMU) west of MSH. Ingesta free body fat was modeled and predicted for a smaller area (red outline) which was the spatial extent of the elk density covariate used during model selection.

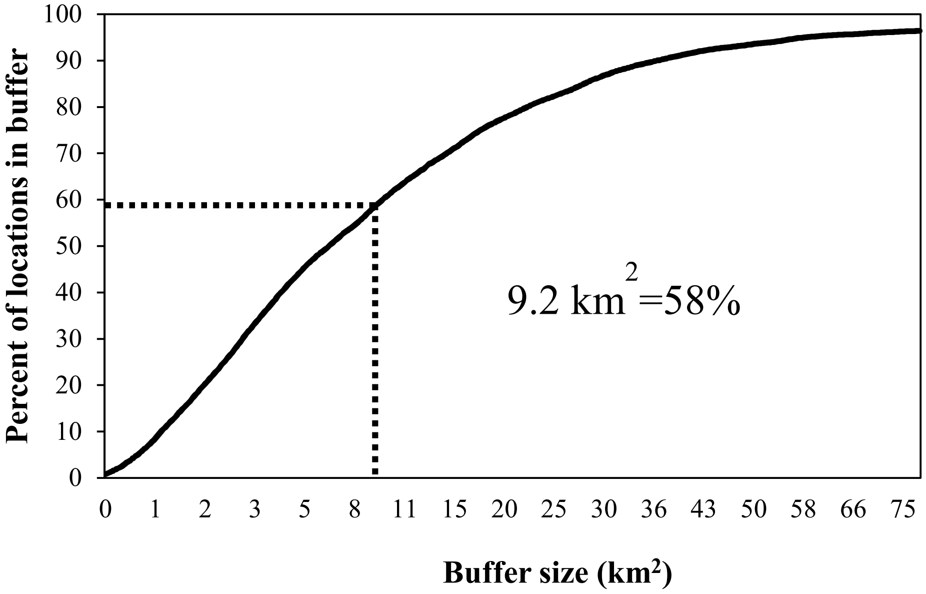

Figure 3.2. Approach used to identify the size of the average elk use buffer for the autumn period based on GPS movement data. This relationship is the percent of randomly selected autumn elk GPS locations inside a round buffer increasing in size. The buffer was centered on a randomly chosen location point prior to assessing location point inclusion. The buffer size chosen for analysis was 9.2 km^2.

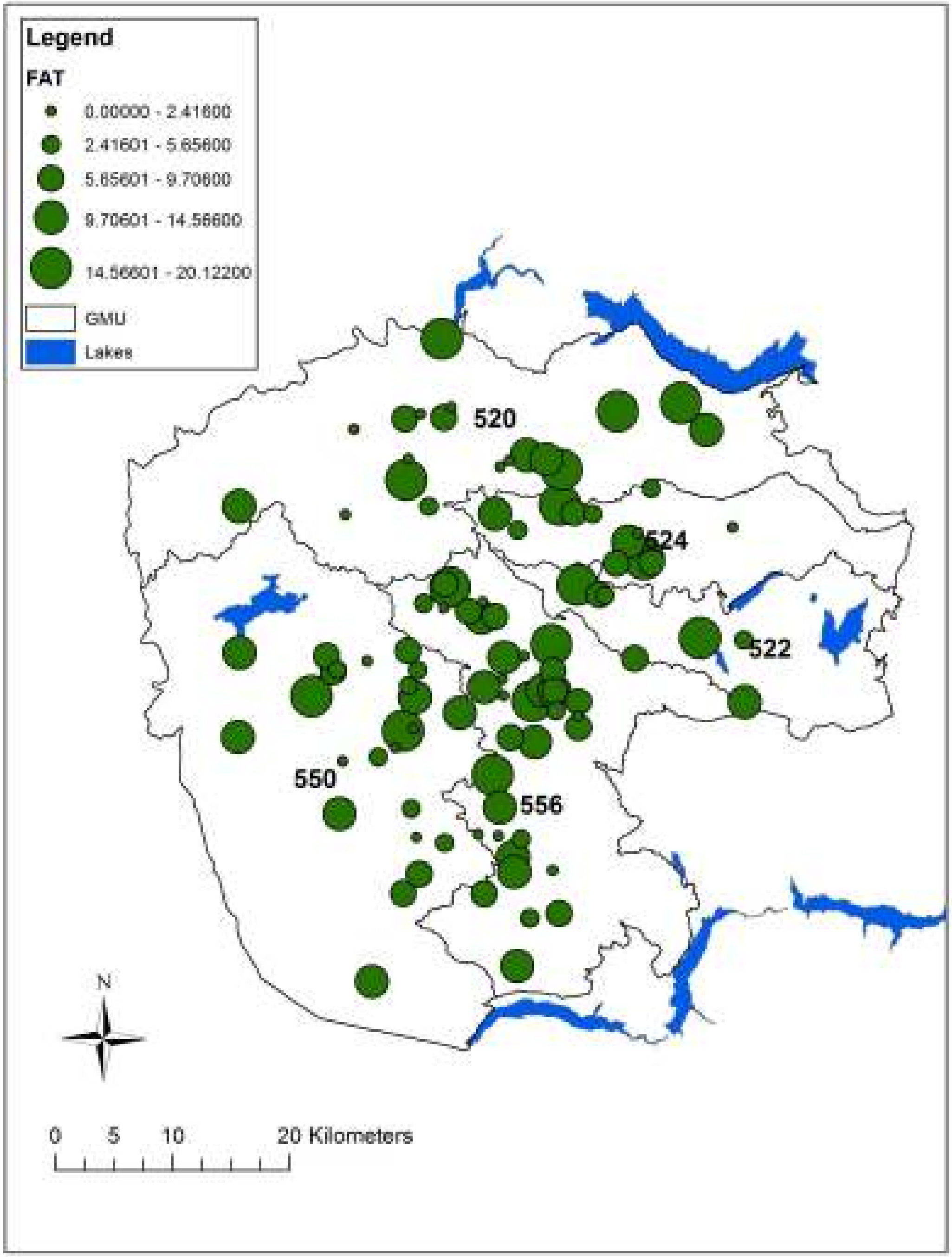

Figure 3.3. Location and percent ingesta free body fat of female elk around Mount St. Helens, Washington. Percent ingesta free body fat was estimated from organ samples submitted through hunter harvest between 1 October and 15 December 2011 using the Kistner subset score *sensu* Cook et al. (2001).

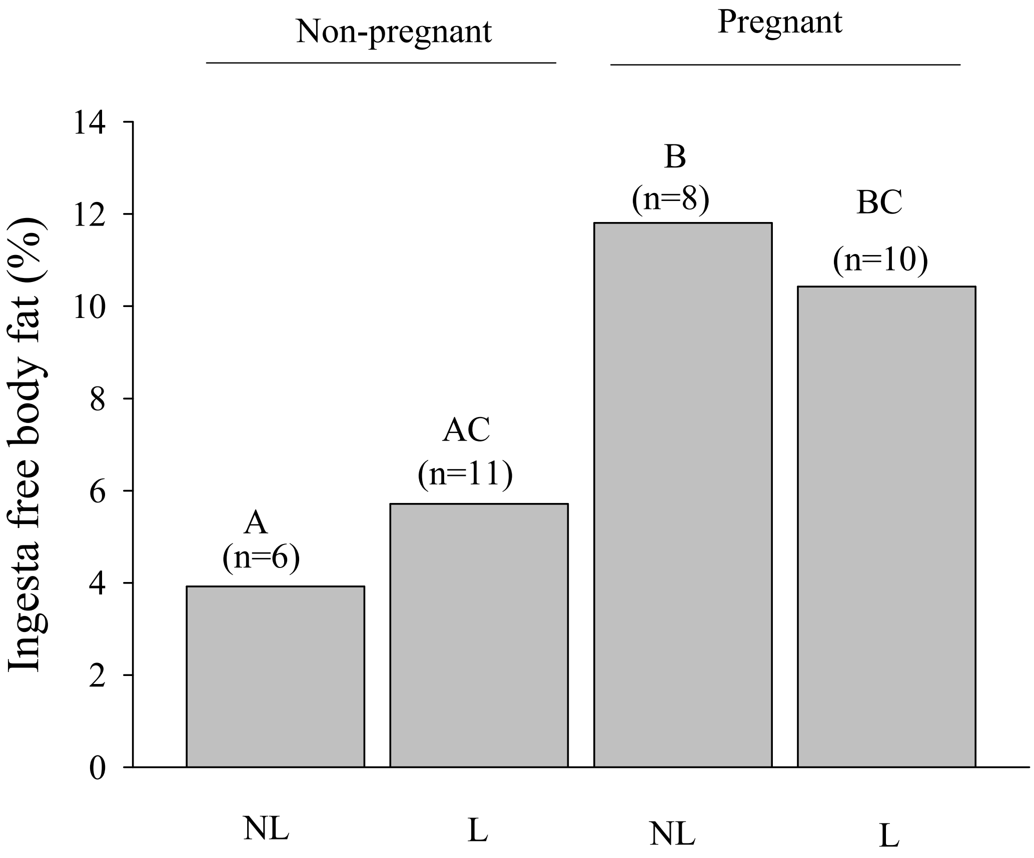

Figure 3.4. Percent ingesta free body fat of elk by lactation and pregnancy status at Mount St. Helens, Washington in autumn 2011. Ingesta free body fat was estimated using the Kistner subset score *sensu* Cook et al. (2001) using female elk organs collected from elk (2-14 yrs of age) harvested between 5 November and 15 December 2011. NL is non-lactating L is lactating. Significant difference is denoted by letters that are discrete (*P*<0.1).

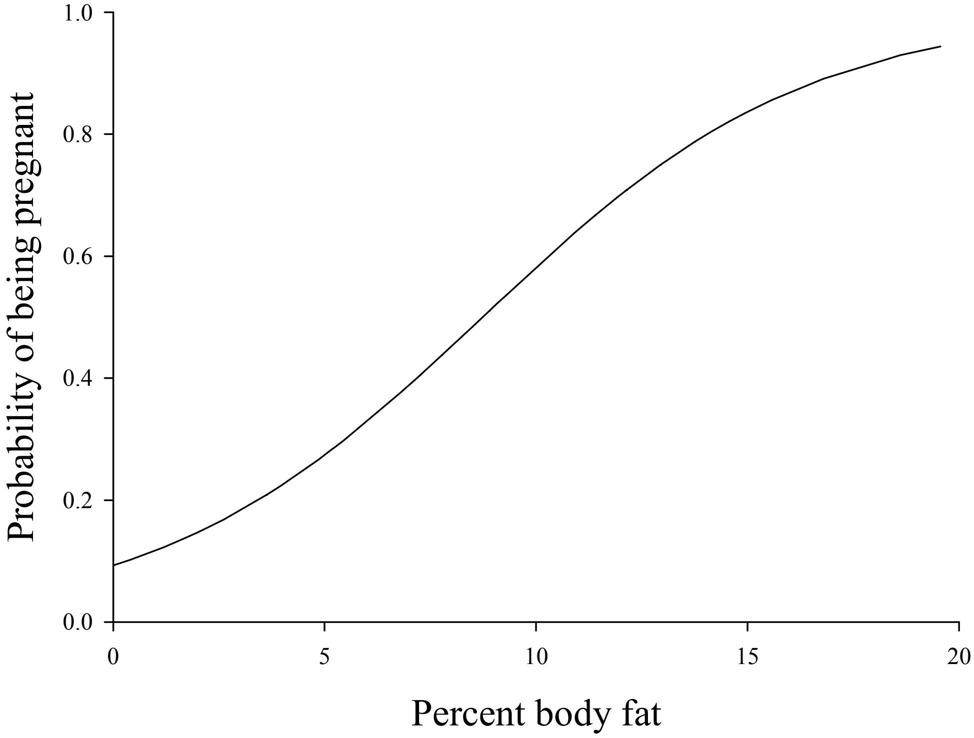

Figure 3.5. Probability of an elk being pregnant at Mount St. Helens according to percent ingesta free body fat estimated from the Kistner subset score *sensu* Cook et al. (2001) and based on organs submitted from hunter harvest in autumn 2011 (P<0.01). Probability of pregnancy = $(e^{(-2.28+0.261*x)}/(1+^{e(-2.28+0.261x)})$.

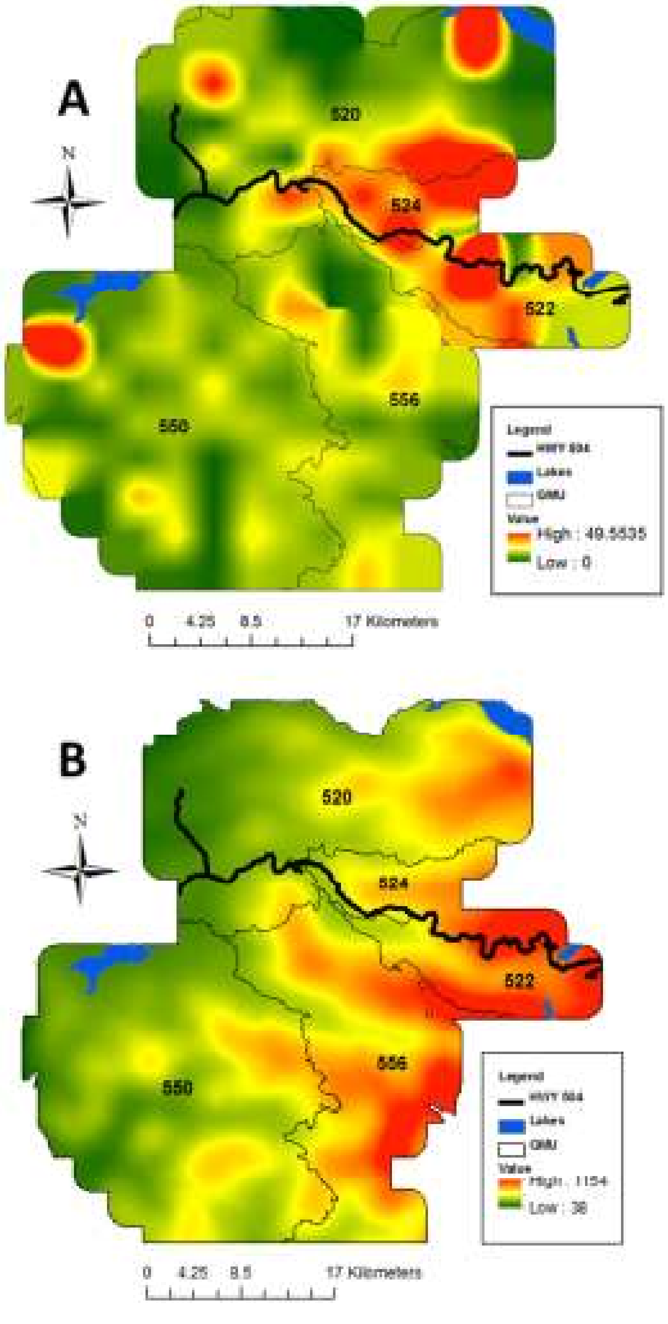

Figure 3.6. Habitat covariates used to predict percent ingesta free body fat at Mount St. Helens, Washington during autumn 2011. (A) Winter elk density (elk/km^2) based on aerial surveys in March 2011 and adjusted for visibility, (B) elevation (m) above sea level.

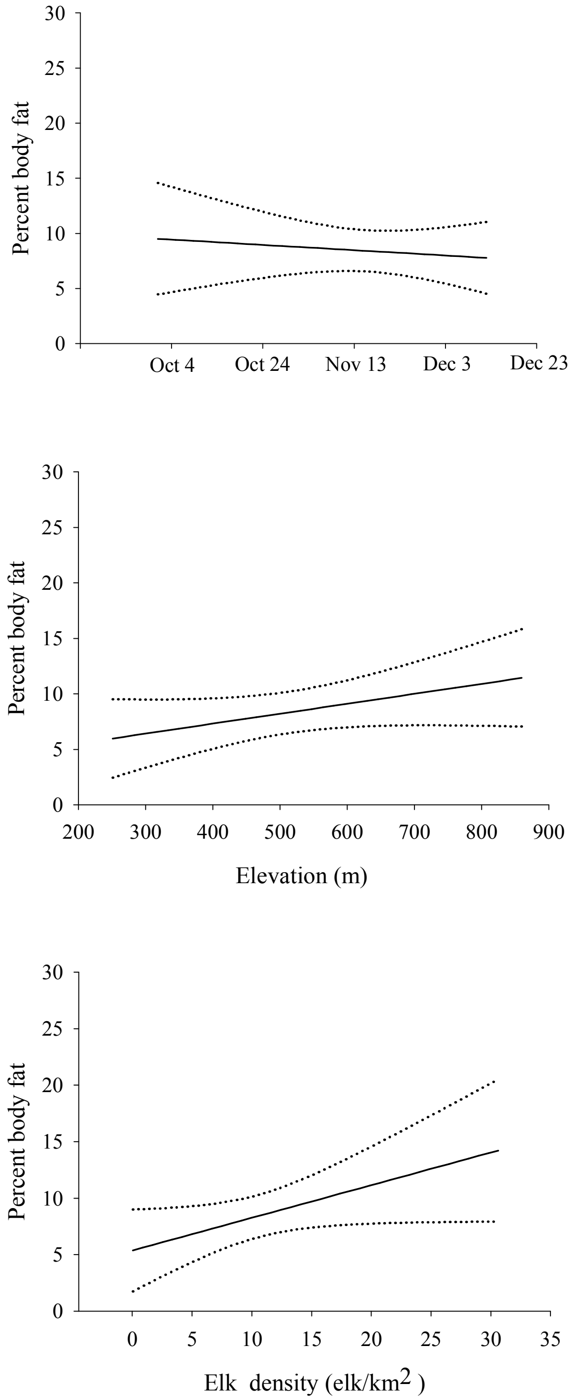

Figure 3.7. Effect of habitat covariates on ingesta free body fat of lactating cow elk harvested by hunters in autumn 2011 at Mount St. Helens, Washington. Covariate values were simulated across the range of observed habitat values while holding remaining covariates constant at their means. See Table 3.2 for descriptions of covariates.

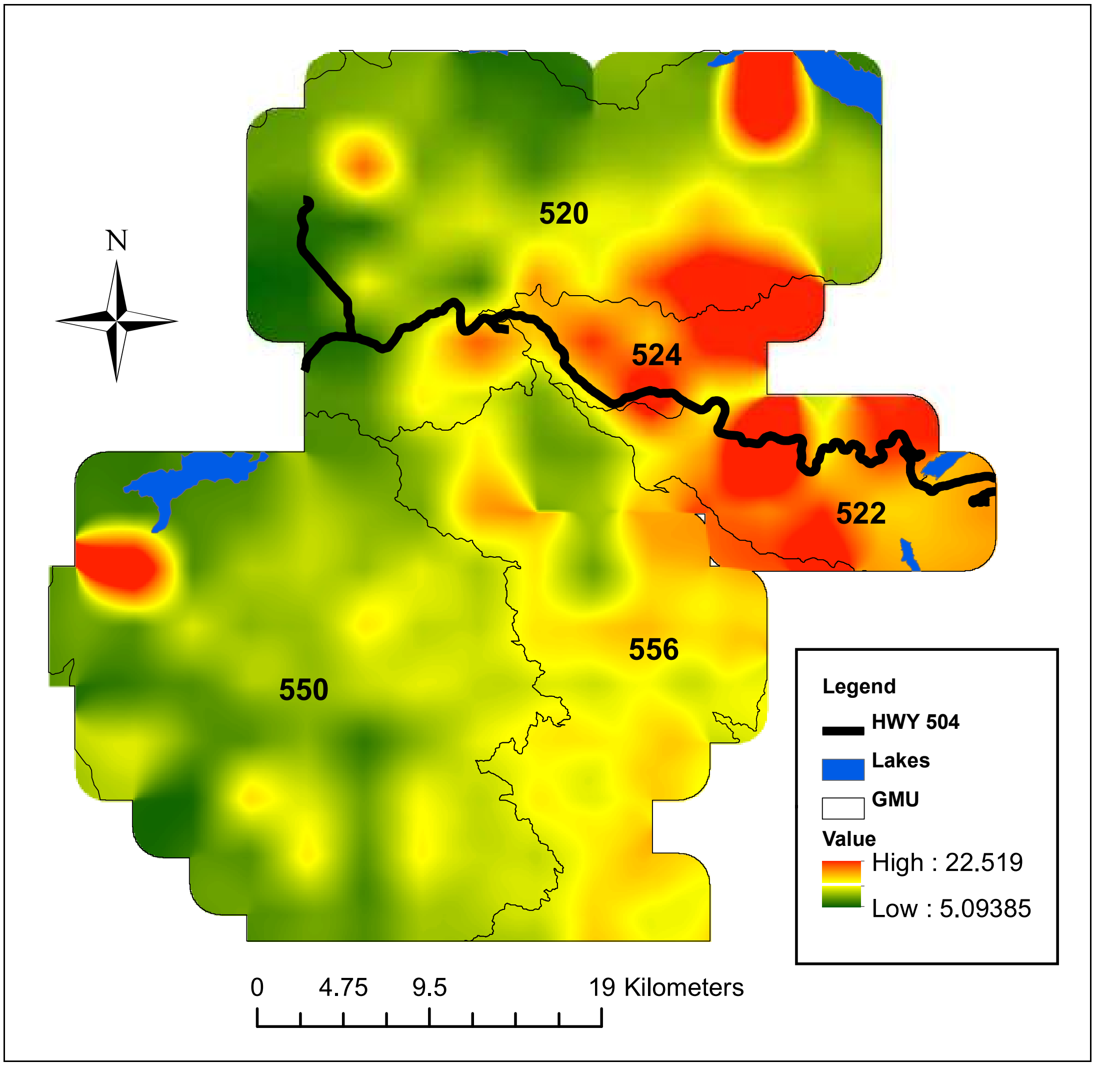

Figure 3.8. Predicted values of landscape ingesta free body fat (%) for lactating elk at Mount St. Helens on 15 November across 5 game management units (GMU) in autumn 2011.

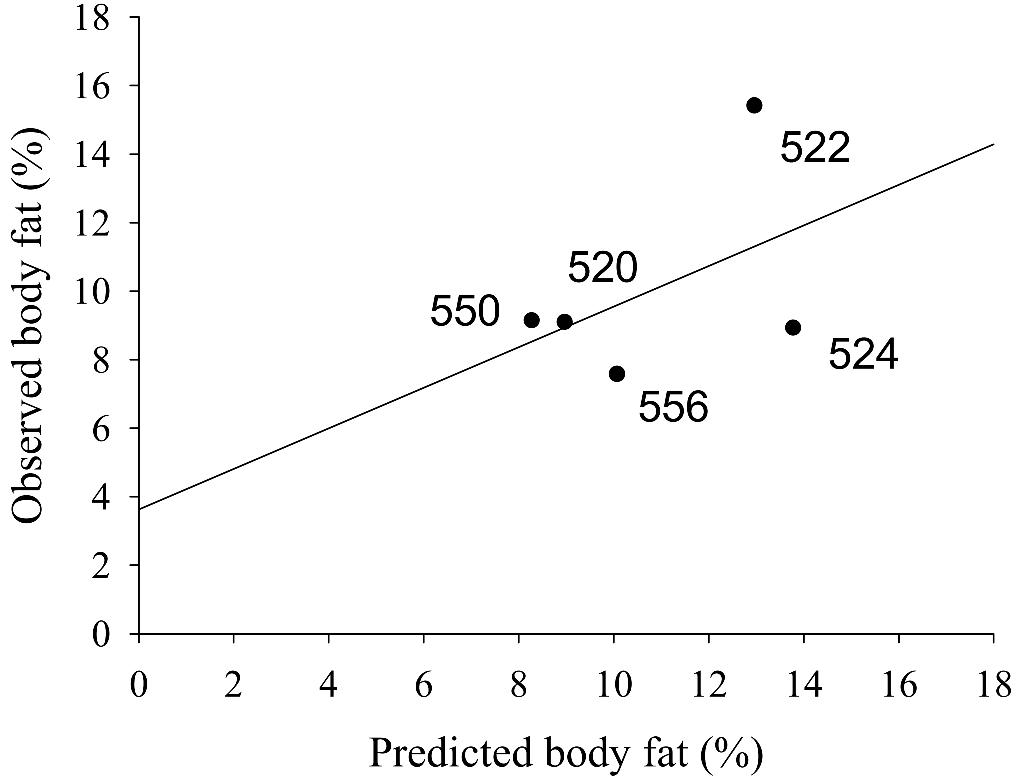

Figure 3.9. Relationship between predicted and observed ingesta free body fat. Mean predicted ingesta free body fat within each game management unit (GMU) on the x axis and mean observed ingesta free body fat values within each GMU for hunter-harvested lactating elk (n=55) in 2010 and 2011 at Mount St. Helens, Washington. Ingesta free body fat estimates for predicted and observed values are from Kistner subset scores *sensu* Cook et al. (2001) based on elk harvested by hunters at Mount St. Helens in autumn 2010 and 2011. Model fit was compared visually because of the small number of GMU data points.

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CHAPTER 4:

SYNTHESIS

The importance of early seral habitat for ungulates has been consistently reported in the literature (Witmer et al., 1985), which adds justification to recent concerns of wildlife managers (WDFW, 2006) regarding current forage conditions on early seral, heavily managed timberlands. Maintaining adequate forage for elk in the PNW is challenging because plant succession advances so quickly (Franklin and Dyrness, 1988). I found forage dynamics in the PNW were even more complex because vegetation is abundant (>4000 kg/ha), but mostly unpalatable to elk (Cook et al., in review). In recent decades elk management in the PNW has been further complicated by practices on United States Forest Service (USFS) lands promoting the development of late successional habitat, which potentially reduces elk forage conditions across the landscape. In contrast, the management of early seral stands on many private timberlands has intensified and silvicultural herbicide use has become common (Wagner et al., 2004). My personal communications with foresters in southwest Washington suggested operational herbicide use for silviculture became common around 1998. Until recently the implications of these types of changing land management regimes had not been adequately evaluated, in part because of a lack of regional studies, but also due to various limitations of methods used in previous research.

Results of past studies documenting change in understory biomass or composition (Vreeland et al., 1998; Rice et al., 1997; Blake and Hurst, 1987) have been limited because ungulates do not consume all plant species equally, nor are all plant species of the same nutritional quality (Cook, 2002; Jenkins and Starkey, 1991; Merrill, 1993). I studied how herbicide applications and herbivory may alter the availability of what a foraging elk is likely to eat, given it is available, and how total availability of nutritional resources (DE) change with these treatments. A somewhat similar approach focusing on preferred forage species was used in western Alberta (Strong and Gates, 2006) and Mississippi (Mixon et al., 2009), but preference was based either on expert opinion or on monitoring browsing/grazing intensity on plant species within plots. A limitation to such a plot-based approach is that browsing pressure can be confounded by multiple herbivore species, and use of a particular plant species may change based on composition of available forage (Lashly, 2009). In contrast, I used detailed information from Cook et al. (in review) on forage selection of elk across a range of feeding trials in PNW plant communities to identify elk “accepted” species. The value of my approach for evaluating herbicides was most evident in forest stands aged between 10-13 years. The recovery of total and accepted elk forages, as well as associated DE after herbicide treatment, was relatively rapid (~2 years after planting of crop seedlings), followed by a period of similar forage biomass across treatments between 3-9 years. However, after 10 years, total biomass declined in herbicide-treated sites but accepted biomass remained similar. In this case, evaluating herbicides in an elk specific framework led to a different conclusion than that of total biomass.

In contrast to herbicides, the influence of ungulate herbivory on forage resources was not evident until after ~3 years of exclosure, and by 6 years, differences in standing biomass of accepted forages for elk due to herbivory was approximately similar to the initial loss following herbicide application. Thus, a major difference between the herbicide and herbivory treatments I studied was the timing and the duration of the impact on vegetation. As such, while the major impact of herbicides was short-lived, the influence of herbivory on understory composition may be more constant than from herbicides and potentially has a greater long-term impact on the understory if herbivory remains high. For example, heavy browsing by moose on Isle Royal in northern Michigan has shifted the tree community towards predominantly spruce (McInnes et al., 1992).

At the landscape scale, the overall effect of operational herbicide treatments early in stand initiation on elk forage is likely of short duration and probably has less impact on nutritional resources for elk than effects from wide-spread declines in timber harvest in the PNW. However, more frequent use of herbicides or advances in herbicide technology may reduce forage development to a greater degree than observed in my data.

The elk herd at Mount St. Helens is currently in poor nutritional condition compared to other herds in Washington. Autumn estimates of IFBF from organs collected in 2011 as well as spring IFBF values collected by Cook et al. (2013) were some of the lowest recently recorded in the Cascades (Cook et al., 2013). Autumn estimates of pregnancy based on uteri collected in 2011 were very low. These pregnancy estimates are likely conservative because of detection bias and late conception, nevertheless, Cook et al. (2013) also observed low pregnancy rates in live elk captured at MSH between 2009 and 2012. Thus, there is strong support that current elk habitat conditions are different at Mount St. Helens than other elk herds in the Cascades.

My attempt to evaluate spatial and reproductive differences in body fat of lactating elk relative to small scale habitat changes at MSH was a first step to understanding how current land management more directly influences the performance of free ranging elk in the PNW. Recent advancements in habitat Resource Selection Function (RSF) models have been a significant improvement over past habitat models, but RSF's predict habitat use and do not predict reproduction or survival. For example, the recent Westside Elk Habitat Model (WEHM) allows users to successfully predict impacts of different land management decisions on elk habitat use (Rowland et al., in prep.) but does not necessarily inform managers about potential elk performance. I attempted to determine whether summer nutritional resources and elk density were related to autumn performance based on indices of body condition, but there were challenges associated with such an approach. An analysis using hunter harvested organs was difficult because it was challenging to collect enough samples. Additionally, samples varied in quality and observer bias was possible during the organ scoring process. Nevertheless, such an approach offered some interesting insights for habitat-performance relationships in the PNW.

I was unable to find strong evidence that higher DDE or accepted biomass in the habitats used by lactating elk at MSH improved body condition. My approach and sample size may have been unsuitable for observing a relationship between forage and body condition, and increasing body fat was better explained by increasing elk density and increasing elevation. Ungulate distributions have been used as an indicator of habitat quality for many years (Fretwell and Lucas, 1970; Suring and Vohs, 1979; Medcraft and Clark, 1986, Mereszczak et al., 1981) and higher elevation during summer has previously been recognized as a selected habitat feature by elk (Mysterud et al., 2001, Hebblewhite et al., 2006). However, increased elk performance associated with higher summer elevation has always been observed at a large or regional scale. To my knowledge, this study is one of the few studies to observe a small scale relationship between elevation and body condition. The sample size used for this model analysis was small, but if the observed patterns at MSH represent a real elevation relationship then this is a next step in understanding what habitat features affect elk performance at MSH.

Managers occasionally use regional divisions in habitat (i.e. GMUs) to bring structure to monitoring programs or management efforts. Spatially evaluating body condition at MSH indicates that it may also be important to consider natural or geographic divisions in habitat at the same time. Body condition remained similar across MSH GMUs (Appendix 12), but the reduced mean herd body fat and pregnancy at MSH relative to other Cascade elk herds (Cook et al., 2013; this study) suggests habitat differences exist. This may be partially explained by variation between the western and eastern regions of the MSH elk herd. The low elevation WHS zone in the western portion of the study area supported animals with significantly lower body fat than the higher elevation PSS and MHS zones in the east. Cook et al. (in review) observed a similar elevation trend in body condition of captive elk in the low elevation Willapa Hills versus the higher Nooksack area and attributed these differences to better forage at higher elevations.

Management Implications and Recommendations

The following are suggested management implications and recommendations based on the results from this study:

HERBICIDES AND HERBIVORY (Chapter 2)

- When high quality forage is the limiting factor for elk performance, focusing on elk accepted forage species when evaluating forest management strategies may provide a better assessment of habitat quality as well as link to demographic response of elk populations. This approach is particularly relevant when comparing treatment effects in areas of the PNW, where plant biomass can be high (~6208 kg/ha), yet as much as 99% of the available biomass is largely avoided by elk. Further, ratios of total to accepted biomass across treatments are not constant, so accounting for forage preference differences is important.
- The impact of herbicide-related forage reduction to local ungulate populations will depend on the extent of tree cutting within a management unit and the availability of preferred forage species in remaining forests. Because of the short period for recovery, only minor adjustments in harvest scheduling may be required if the objective is to maintain elk forage.

- With current herbicide regimes and reduced harvest rates of forests, it is important for the long-term management of ungulate populations to maintain a diversity of forest stand ages that provide adequate forages and forest cover across the landscape at the scale of the home range of deer and elk (Visscher and Merrill, 2009). This is important because, despite the relatively short-term effects of herbicides, where canopy closure leads to loss of plant understories over large areas because of past harvest schedules or natural disturbances, even a short-term reduction in forage availability may add to the nutritional stress of ungulates, especially in years coupled with severe winter conditions.
- Forage in early seral herbicide-treated stands at MSH was consistently better than in later seral stages, which suggests managers on federal or private lands concerned with elk productivity should attempt to maintain early seral habitats. Because of the challenges associated with landscape scale forage enhancement this objective can be better met when early seral habitat is maintained indirectly through other land objectives (i.e. timber harvest and forestry).

BODY CONDITION (Chapter 3)

- For management purposes, the performance of the MSH elk herd may be better evaluated relative to other herds by comparing western portions of the MSH region to some herds in the coastal hills (i.e. Willapa Hills) and the eastern portions of the herd to other Cascade elk herds. Comparing body condition of the MSH elk herd across its entire range relative to other Cascade elk herds may be misleading because large increases in elevation and resultant moisture occur from west to east within the MSH elk herds range, and this may be significant when assessing body condition.

- Based on my findings, IFBF estimates can provide an effective way of evaluating pregnancy rates at MSH (Trainer, 1971; Cook et al., 2004; Kohlman, 1999). However, in many cases body fat may be a more precise metric of habitat quality because pregnancy can occur in elk that are well below optimal nutrition (Cook et al., 2013). Nevertheless, adequate pregnancy rates are vital to the sustainability of an elk herd (Nelson and Peek, 1982) and the probability of pregnancy based on IFBF can be predicted at MSH using the logistic equation in Chapter 3.
- The best predictive model for body fat at MSH suggests that managers trying to reduce impacts on elk productivity should consider elevation when considering habitat management.
- Using the Kistner subset score can be an effective way for managers to evaluate elk body condition (Cook et al., 2001), however organ collection programs relying on hunter harvested samples will greatly benefit from multi-year data collection programs. Many options are available to increase organ submission (sportsman shows, project websites, flyers at hunting stores, incentive programs) but the most effective options include: 1) increasing mailing efforts of collection packages to prospective hunters, and 2) having technicians in the field to inform hunters and provide

assistance. I found the most effective approach was placing technicians at hunting access points (i.e. entrance to logging roads) as hunters were arriving (0400 – 0700) in the field each morning.

- Managers collecting organ samples that will be used to evaluate habitat conditions should put emphasis on obtaining accurate harvest locations where the animal lies in the field, and efforts to obtain the udder may help reduce hunter observer bias when assessing lactation status.

Future Directions

Evaluating the impacts of herbicide and herbivory using a retrospective study design provided a large sample size that was not spatially limited, and Lautenschlager and Sullivan (2004) suggest such an approach is highly relevant for depicting real-world treatment effects. However, future research can expand on my findings by using an experimental design that offers more control and provides the opportunity to evaluate novel herbicides and treatment regimes. Additionally, to further understand the interactive effects of herbicide and herbivory, future studies should use a case controlled approach that includes all combinations of herbicide and herbivory. Finally, studies have shown great potential when using radio-collared animals to evaluate home range quality and productivity (Mcloughlin et al., 2007; Bender et al., 2007), but using locations of harvested animals may not be an effective approach. Using GPS collared animals to evaluate movement paths in relation to individual performance may provide more insight into habitat-performance relationships.

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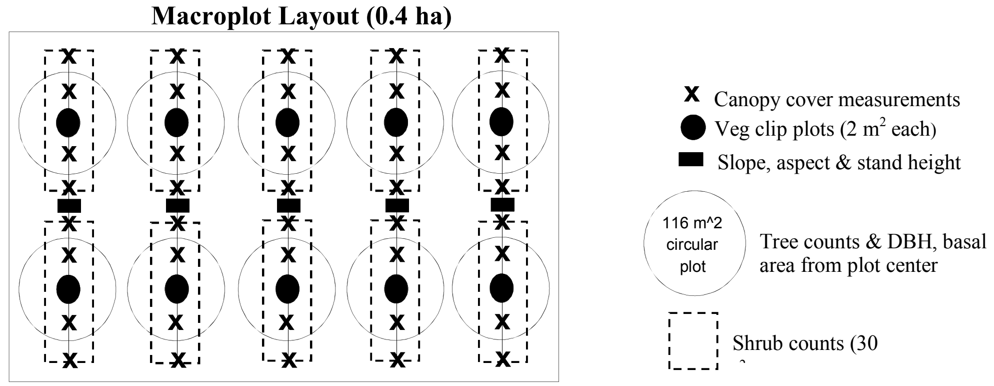
Appendices



Appendix 1. Layout of vegetation sampling transects and plots within a macroplot at herbicide and exclosure study sites. Note: canopy cover measurements were also taken at each clip plot.

Appendix 2. Herbicide-treated and untreated plot locations and site attributes for plots sampled in southwest, Washington in 2010 and 2011.

ID[a]	Treat[b]	Year	Age (yrs)	X (UTM)	Y (UTM)	Elev (m)	Asp (deg)	Slope (deg)	Loc[b]	Type[c]
1N	N	2010	2	520359	5116284	545	111	26	U	flat
1Y	Y	2010	2	520603	5116331	550	120	17	U	flat
2N	N	2010	2	533462	5146176	433	243	12	U	flat
2Y	Y	2010	2	533039	5146085	396	231	12	M	flat
3N	N	2010	3	540107	5126370	753	15	37	M	flat
3Y	Y	2010	3	527298	5123614	309	210	9	F	flat
4N	N	2010	4	531769	5123882	390	152	27	M	cave
4Y	Y	2010	4	531445	5123952	396	160	35	M	cave
5N	N	2010	4	540268	5120310	422	191	5	M	vex
5Y	Y	2010	4	524798	5118622	419	33	16	M	vex
6N	N	2010	4	540605	5120637	548	232	14	M	cave
6Y	Y	2010	4	524551	5121707	497	215	17	L	flat
7N	N	2010	4	539275	5121090	474	235	31	U	flat
7Y	Y	2010	4	524563	5121793	505	250	27	M	cave
8N	N	2010	6	548167	5143332	721	310	53	M	flat
8Y	Y	2010	6	524206	5118387	432	24	2	F	flat
9N	N	2010	7	545231	5142804	554	18	9	M	flat
9Y	Y	2010	7	523735	5122747	450	266	6	B	cave
10N	N	2010	7	537041	5124790	833	18	27	U	flat
10Y	Y	2010	7	521051	5119492	376	253	12	H	flat
11N	N	2010	10	544146	5141762	629	30	11	U	flat
11Y	Y	2010	10	522706	5120600	267	342	9	M	flat
12N	N	2010	12	537461	5139619	429	35	11	U	flat
12Y	Y	2010	12	521818	5119825	398	244	30	L	cave
13N	N	2011	1	538307	5120427	344	28	23	L	flat
13Y	Y	2011	1	538199	5120539	337	32	31	L	flat
14N	N	2011	1	545863	5139791	764	234	36	M	flat
14Y	Y	2011	1	549975	5139361	704	205	16	H	flat
15N	N	2011	2	524987	5097036	238	69	34	U	flat
15Y	Y	2011	2	524840	5096962	273	149	37	U	flat
16N	N	2011	6	527090	5126600	285	158	20	F	flat
16Y	Y	2011	6	527410	5127020	260	26	4	U	flat
17N	N	2011	11	535392	5140511	523	173	28	M	flat
17Y	Y	2011	11	536009	5138797	503	255	9	H	flat
18N	N	2011	5	552060	5100740	463	93	24	M	vex

Appendix 2. Continued

ID[a]	Treat[b]	Year	Age (yrs)	X (UTM)	Y (UTM)	Elev (m)	Asp (deg)	Slope (deg)	Loc[b]	Type[c]
18Y	Y	2011	5	548516	5107720	465	127	8	F	flat
19N	N	2011	5	552302	5100445	364	78	46	M	cave
19Y	Y	2011	5	546926	5105803	367	240	16	M	flat
20N	N	2011	4	549066	5098016	614	113	27	M	vex
20Y	Y	2011	4	549056	5108626	580	126	23	U	flat
21N	N	2011	9	547369	5067414	425	316	5	F	flat
21Y	Y	2011	9	549809	5078491	397	276	21	M	flat
22N	N	2011	6	554701	5077387	786	222	34	M	flat
22Y	Y	2011	6	554794	5077238	779	210	43	M	flat
23N	N	2011	11	539083	5141533	619	229	22	U	cave
23Y	Y	2011	11	544955	5140641	678	180	33	F	flat
24N	N	2011	13	539190	5140418	466	191	23	M	flat
24Y	Y	2011	13	539691	5140226	458	167	10	U	flat
25N	N	2011	5	550104	5098913	556	155	46	M	vex
25Y	Y	2011	5	535989	5105650	619	135	40	M	vex
26N	N	2011	5	539775	5183236	206	-	0	F	flat
26Y	Y	2011	5	540067	5182869	207	-	0	F	flat
27N	N	2011	3	523535	5172474	525	225	29	H	vex
27Y	Y	2011	3	523679	5172472	532	182	25	H	vex

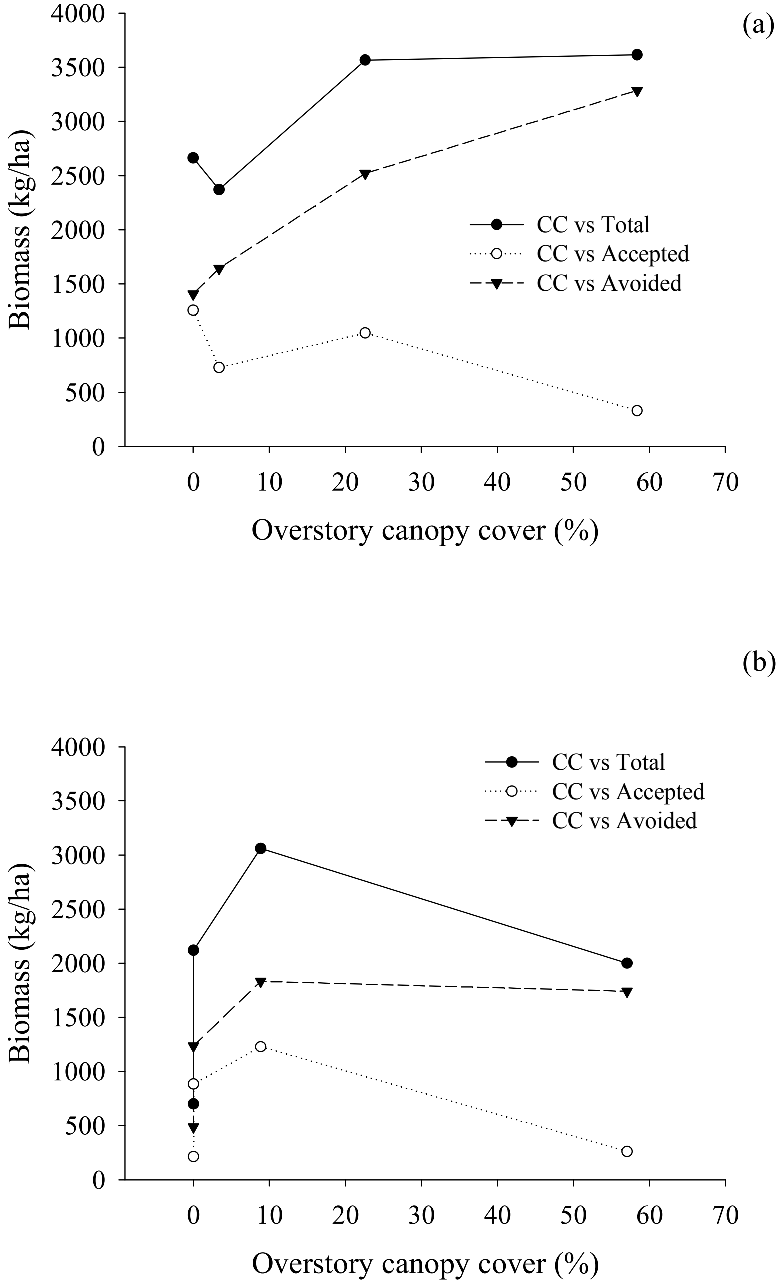
[a] ID corresponds to study area maps and denotes paired sites and treatment.

[b] Loc is location of plot on dominant slope and is classified into flat (F), bottom (B), lower (L), middle (M), upper (U), and hilltop (H).

[c] Type refers to geometry of slope in plot and is classified as flat (flat), concave (cave), and convex (vex) *sensu* Cook et al. (in review).

Appendix 3. Distance (m) between paired herbicide-treated and untreated sites sampled in 2010 and 2011 at Mount St. Helens, WA. See figure 2.1 for plot locations.

Untreated site	Treated site	Distance (m)
1N	1Y	248.49
2N	2Y	432.68
3N	3Y	13102.14
4N	4Y	331.48
5N	5Y	15561.82
6N	6Y	16089.62
7N	7Y	14728.79
8N	8Y	34588.76
9N	9Y	29400.02
10N	10Y	16844.85
11N	11Y	30124.80
12N	12Y	25229.07
13N	13Y	155.59
14N	14Y	4134.42
15N	15Y	164.58
16N	16Y	528.02
17N	17Y	1821.67
18N	18Y	7828.18
19N	19Y	7590.09
20N	20Y	10610.00
21N	21Y	11342.55
22N	22Y	175.64
23N	23Y	5939.36
24N	24Y	536.53
25N	25Y	15640.35
26N	26Y	468.99
27N	27Y	144.01
Average		9768.98



Appendix 4. Biomass of forage preference groups in relation to percent overstory canopy cover in (a) herbicide-untreated and (b) herbicide-treated sites at Mount St. Helens, Washington. Sites were sampled during the summer of 2010 and 2011 and canopy cover was measured using a moosehorn. See Chapter 2 methods for more details.

Appendix 5. Location and site attributes of Weyerhaeuser exclosures sampled in 2011.

ID[a]	Road access	X (UTM)	Y (UTM)	Age (yrs)	Size (ha)	Elev (m)	Asp (deg)	Slope (deg)	Loc[b]	Type[c]
E1	1003A	539862	5135729	6	0.023	369	80	18	B	flat
E2	1003D	539783	5135496	6	0.023	392	252	18	U	flat
E3	1003	538554	5135262	6	0.023	436	43	12	M	flat
E4	200A	525490	5119012	6	0.023	489	164	22	M	cave
E6	200A	525596	5119095	6	0.023	512	180	16	U	cave
E6	1460	538730	5104134	6	0.023	486	241	10	M	flat
E7	219	528807	5119218	3	0.046	624	350	6	U	flat
E8	4770	525369	5121310	4	2.813	554	291	7	F	flat
E9	521D	535965	5139608	4	1.034	518	243	16	U	flat
E10	23	515933	5120439	4	1.152	336	301	7	B	flat
E11	1400	538749	5103214	3	0.033	469	175	10	U	flat
E12	8700	549508	5076875	0	0.036	368	100	6	U	flat
E13	8652	552880	5079002	0	0.033	679	-	0	H	flat
E14	6500	535726	5101581	0	0.134	412	218	9	U	flat
E15	1550	520917	5136756	2	0.093	113	-	0	M	flat
E16	012C	514557	5115897	2	0.059	350	124	10	U	flat

[a] Each site represents a macroplot sampled inside and outside the exclosure

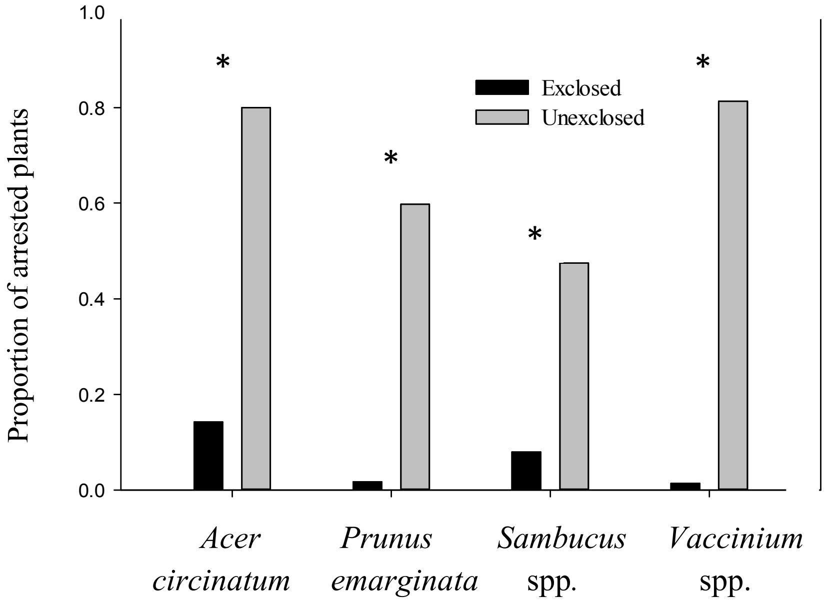
[b] Loc is location of plot on dominant slope and is classified into flat (F), bottom (B), lower (L), middle (M), upper (U), and hilltop (H).

[c] Type refers to geometry of slope at plot and is classified as flat (flat), concave (cave), and convex (vex) *sensu* Cook et al. (in review).

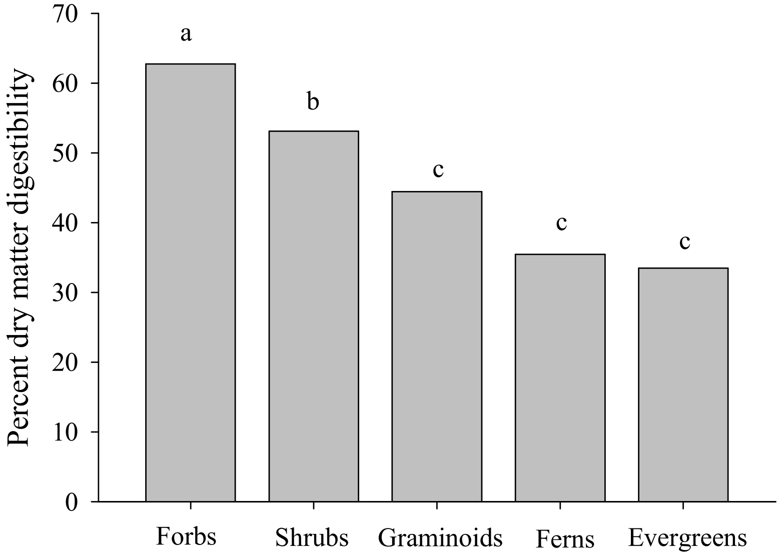
Appendix 6. Regression equations from Merrill (1985) used to predict leaf weight (g DM) and twig weight (g DM) from plant volume (height x diameter, cm^2) with the y intercept forced through zero.

		Leaf Weight			Twig Weight		
Species	N	b	S.E.	r^2	B	S.E.	r^2
Acer circinatum	22	0.006	0.001	0.86	0.002	0	0.77
Alnus rubra	22	0.007	0.001	0.78	0.005	0.001	0.83
Berberis nervosa	25	0.018	0.001	0.86	0.002	0.001	0.73
Gaultheria shallon	23	0.011	0.001	0.88	0.002	0.001	0.3
Populus trichocarpa	18	0.007	0.001	0.7	0.005	0.001	0.82
Salix spp.	22	0.007	0.001	0.83	0.004	0.001	0.71
Sambucus racemosa	25	0.008	0.001	0.81	0.009	0.001	0.76
Vaccinium parvifolium	10	0.008	0.001	0.92	0.006	0.001	0.86
Prunus emarginata[a]	-	0.007	-	-	0.005	-	-
Rhamnus purshiana[b]	-	0.007	-	-	0.004	-	-

[a,b] Model average used for beta coefficient



Appendix 7. Percent of shrub species arrested by herbivory inside versus outside exclosures *sensu* Keigley and Frisina (1998). * indicates a significant difference in distribution between exclosure treatments at $\alpha \leq 0.05$.



Appendix 8. Mean dry matter digestibility values of 142 plants by vegetation class analyzed in this study or compiled from the literature for this region in late summer (see Appendix 10). Different letters represent significant difference in mean DMD values (at $\alpha \leq 0.05$).

Appendix 9.A. Understory diversity after herbicide application and herbivory

Methods

I calculated species richness (S), diversity, and evenness for accepted and avoided forage preference classes. The Shannon-Wiener index (H') was calculated for each plot based on the proportional biomass of each species (Magurran, 1988). Comparing Shannon index values across treatments can produce inaccurate results (Jost, 2006; Chao, 2008; Hill, 1973), so values were converted to 'effective number of species' as D_1=EXP(H'), which represents the number of species if all were equally common (Jost 2006). Evenness was calculated as J'=H'/(ln S) based on Pielou (1966). I tested for significant (α=0.05) main effects (age, treatment) and their interaction for species richness, evenness and diversity using ANOVA based on a split-plot design because plots were paired within sites. All references to age and years refer to time since crop trees were planted, and crop trees were always planted within 1 year of the preceding harvest. Post-hoc tests of treatment differences were based on paired T-tests within stand ages. Diversity indices were calculated in PC-ORD 6 and data were transformed using log or square root transformation when necessary.

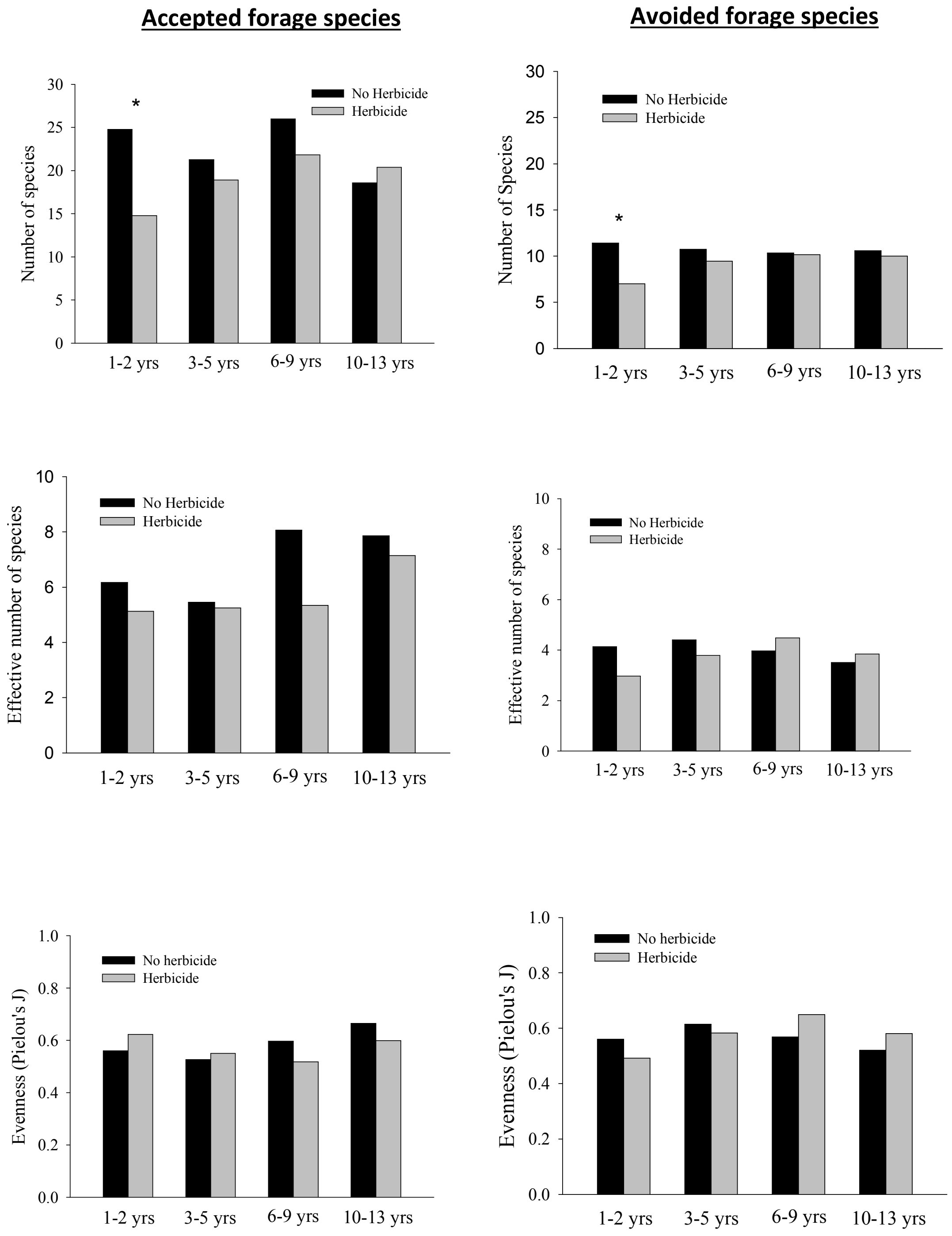
Results

HERBICIDES

Avoided and accepted understory species richness decreased with herbicide application ($P<0.05$). Species richness was reduced for 2 years after application with accepted species richness declining from 24.8 species to 14.8 species ($P<0.05$), and avoided species declined from 11.4 to 7 species ($P<0.05$). The decline was primarily related to uncommon species, which lead to minimal difference in Shannon entropy or true diversity. Evenness of accepted and avoided species was similar, but highly variable between sites (Appendix 7.B).

EXCLOSURES

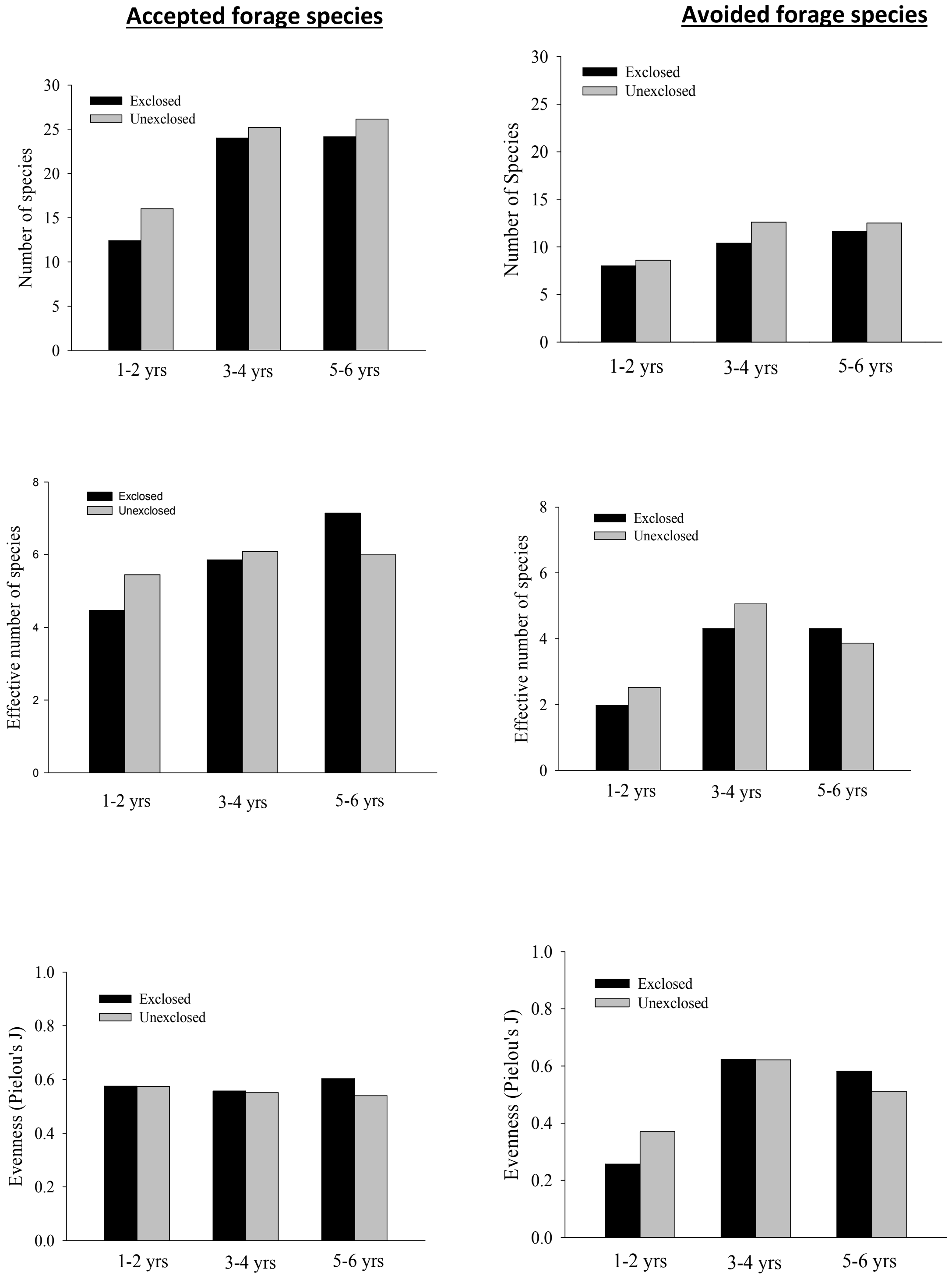
Species richness increased with age for both avoided and accepted species ($P<0.01$) with a main treatment effect for herbivory ($P<0.05$) resulting from a marginally higher number of species outside exclosures. Accepted species had similar diversity and evenness across treatments and age, whereas avoided species diversity and evenness increased with age but greater increases occurred inside exclosures (54%) versus unexclosed areas (27%) (Appendix 7.C).



Accepted forage species

Avoided forage species

Appendix 9.B. Elk accepted and avoided species richness, diversity, and evenness in herbicide-treated and untreated sites sampled at Mount St. Helens, Washington in 2011.



Appendix 9.C. Elk accepted and avoided species richness, diversity, and evenness in exclosed and unexclosed sites sampled at Mount St. Helens, Washington in 2011.

Appendix 10. Names of each plant, project code, vegetation class, elk forage preference, digestibility (DMD), and plant selection ratio for each species sampled in 2010 and 2011. Column description at end of table.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Abies amabilis	ABAM	CT	A	33.37	C	1,2	0.00	-
Abies grandis	ABGR	CT	A	33.37	C	1,2	0.00	-
Abies procera	ABPR	CT	A	33.37	C	1,2	0.00	-
Acer circinatum	ACCI	S	S	53.07	S	2	119.45	-
Acer macrophyllum	ACMA	DT	S	50.1	S	2	76.51	-
Achillea millefolium	ACMI	F	N	59.47	S	2	27.00	4
Achlys triphylla	ACTR	F	N	66.68	S	1	11.00	-
Adenocaulon bicolor	ADBI	F	N	64.07	C	1,2	38.21	-
Adiantum pedatum	ADPE	FE	N	64.08	S	1	0.91	-
Agoseris grandiflora	AGGR	G	N	35.9	G	2	11.02	3
Agrostis exarata	AGEX	G	N	35.9	G	2	23.81	-
Agrostis spp.	AGRO	G	N	35.9	S	2	23.81	-
Aira caryophyllea	AICA	G	A	46.84	C	1,2	0.71	2
Alnus rubra	ALRU	DT	S	49.7	S	2	3.12	-
Anaphalis margaritacea	ANMA	F	S	46.1	S	2	16.63	-
Anemone oregana	ANOR	F	N	64.07	C	1,2	27.00	4
Anemone spp.	ANEM	F	N	64.07	C	1,2	27.00	4
Antennaria spp.	ANTE	F	N	64.07	C	1,2	0.63	-
Arenaria macrophylla	ARMA	F	N	64.07	C	1,2	27.00	4
Asarum caudatum	ASCA	F	N	64.07	C	1,2	0.68	-
Aster spp.	ASTE	F	N	64.07	C	1,2	27.00	4
Astragalas spp.	ASTR	F	N	64.07	C	1,2	0.40	-
Athyrium filix-femina	ATFI	FE	A	35.43	C	1,2	0.91	-
Avena spp.	AVEN	G	A	46.84	C	1,2	0.71	2
Berberis nervosa	BENE	ES	A	45.44	S	2	0.17	-

Appendix 10. Continued.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Blechnum spicant	BLSP	FE	A	31.8	S	2	0.09	-
Borage spp.	BORA	F	A	64.07	C	1,2	0.82	1
Bromus carinatus	BRCA	G	N	59	S	7	11.02	3
Bromus sitchensis	BRSI	G	N	42.43	G	2	11.02	3
Bromus spp.	BROM	G	N	42.43	S	2	11.02	3
Bromus vulgaris	BRVU	G	N	42.43	G	2	13.12	-
Campanula scouleri	CASC	F	N	59.25	S	1	27.00	4
Carex obnupta	CAOB	CA	S	30.7	G	2	11.02	3
Carex spp.	CARE	CA	S	30.7	S	2	53.52	-
Castilleja hispida	CAHI	F	N	64.07	C	1,2	27.00	4
Catabrosa aquatica	CAAQ	G	N	46.84	C	1,2	11.02	3
Cerastium fontanum	CEFO	F	N	64.07	C	1,2	27.00	4
Cerastium nutans	CENU	F	N	64.07	C	1,2	27.00	4
Cerastium pumilum	CEPU	F	N	64.07	C	1,2	27.00	4
Cerastium spp.	CERA	F	N	64.07	C	1,2	27.00	4
C. leucanthemum	CHLE	F	N	65.51	S	1	0.85	-
Cirsium spp.	CIRS	F	N	75.9	S	3	4.74	-
Collomia heterophylla	COHE	F	A	64.07	C	1,2	0.81	-
Coptis laciniata	COLA	F	N	64.07	C	1,2	27.00	4
Cornus canadensis	COCA	F	N	67.96	S	1	49.12	-
Corylus cornuta	COCO	S	S	56.59	C	1,2	17.77	-
Crepis capillaris	CRCA	F	N	60.34	S	1	1.67	-
Crepis spp.	CREP	F	N	60.34	S	1	1.67	-
Cytisus scoperius	CYSC	S	N	56.59	C	1,2	79.70	-
Dactylis glomerata	DAGL	G	N	41.6	S	2	47.06	-

Appendix 10. Continued.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Deschampsia elongata	DEEL	G	A	36.1	S	2	0.71	2
Deschampsia spp.	DESC	G	A	36.1	G	2	0.03	-
Dicentra formosa	DIFO	F	N	59.47	S	2	51.92	-
Digitalis purpurea	DIPU	F	A	64.06	S	3	0.38	-
Disporum hookeri	DIHO	F	N	64.07	C	1,2	4.35	-
Disporum smithii	DISM	F	N	62.53	S	1	27.00	4
Disporum spp.	DISP	F	N	62.53	G	1	27.00	4
Elymus glaucus	ELGL	G	N	46.9	G	2	9.86	-
Elymus spp.	ELYM	G	N	46.9	S	2	9.86	-
Epilobium angustifolium	EPAN	F	N	60	S	2	10.62	-
Epilobium watsonii	EPWA	F	A	61.79	S	1	1.14	-
Equisetum spp.	EQUI	G	N	50.7	S	2	1.05	-
Erodium circinatum	ERCI	F	A	64.07	C	1,2	0.82	1
Festuca occidentalis	FEOC	G	N	47	S	7	0.89	-
Festuca spp.	FEST	G	N	44.54	G	2	11.02	3
Fragaria vesca	FRVE	F	N	56.2	G	7	27.00	4
Fragaria virginiana	FRVI	F	N	56.2	G	7	0.52	-
Galium aparium	GAAP	F	N	59.47	S	2	4.22	-
Galium oreganum	GAOR	F	N	59.47	G	2	2.26	-
Galium spp.	GALI	F	N	59.47	G	2	27.00	4
Galium triflorum	GATR	F	N	59.4	S	3	4.22	-
Gaultheria shallon	GASH	S	A	21.8	S	2	0.19	-
Geranium columbinum	GECO	F	A	62.81	G	1	0.82	1

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Appendix 10. Continued.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Geranium robertianum	GERO	F	A	62.81	G	1	0.82	1
Geranium spp.	GERA	F	N	62.81	S	1	27.00	4
Geum macrophyllum	GEMA	F	N	65.16	S	1	0.03	-
Gnaphalium spp.	GNAP	F	A	64.07	C	1,2	0.82	1
Gymnocarpium dryopteris	GYDR	FE	N	35.43	C	1,2	5.78	-
Hieracium albiflorum	HIAL	F	N	64	S	7	31.93	-
Hieracium scouleri	HISC	F	N	59.47	G	2	27.00	4
Hieracium spp.	HIER	F	N	59.47	S	2	27.00	4
Holcus lanatus	HOLA	G	N	53.7	S	2	5.62	-
Holodiscus discolor	HODI	S	N	56.59	C	1,2	5.42	-
Hordeum spp.	HORD	G	N	46.84	C	1,2	11.02	3
Hydrophyllum tenuipes	HYTE	F	N	64.07	C	1,2	27.00	4
Hypericum perforatum	HYPE	F	S	61	S	1	3.85	-
Hypochaeris radicata	HYRA	F	S	63.9	S	2	30.27	-
Hypochaeris spp.	HYPO	F	S	63.9	G	2	27.00	4
Ilex aquifolium	ILAQ	S	A	33.62	C	1,2	1.38	-
Iris spp.	IRIS	F	N	64.07	C	1,2	27.00	4
Iris tenax	IRTE	F	S	64.07	C	1,2	17.26	-
Juncus effusus	JUEF	R	N	42.43	G	2	11.02	3
Juncus spp.	JUNC	R	N	42.43	S	2	0.88	-
Lactuca ludoviciana	LALU	F	N	59.59	G	1	27.00	4
Lactuca muralis	LAMU	F	N	59.59	S	1	27.00	4
Lactuca serriola	LASE	F	N	65.9	S	8	27.00	4
Lactuca spp.	LACT	F	N	59.59	G	1	9.79	-
Lapsana communis	LACO	F	A	64.07	C	1,2	0.82	1
Lathyrus latifolius	LALA	F	N	61.55	G	1	27.00	4

Appendix 10. Continued.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Lathyrus spp.	LATH	F	N	61.55	S	1	2.15	-
Lotus crassifolius	LOCR	F	N	59.47	G	2	27.00	4
Lotus mircanthus	LOMI	F	N	67.3	S	1	27.00	4
Lupinus latifolius	LULA	F	N	73.8	G	2	27.00	4
Lupinus spp.	LUPI	F	N	73.8	S	2	27.00	4
Luzula spp.	LUZU	G	S	39.8	S	2	4.41	-
Maianthemum canadensis	MACA	F	S	59.47	G	2	27.00	4
Maianthemum dilatatum	MADI	F	S	59.47	S	2	10.99	-
Melica bulbosa	MEBU	G	N	46.84	C	1,2	0.08	-
Mentha spp.	MENT	F	N	64.07	C	1,2	27.00	4
Mitella spp.	MITE	F	N	64.07	C	1,2	27.00	4
Montia sibirica	MOSI	F	N	59.47	S	2	1.56	-
Oemleria cerasiformis	OECE	S	N	78.6	S	3	37.71	5
Osmoriza chilensis	OSCH	F	A	64.07	C	1,2	0.82	1
Oxalis oregana	OXOR	F	S	59.47	S	2	2.69	-
Parentucellia viscosa	PAVI	F	A	64.07	C	1,2	0.82	1
Phacelia hastata	PHHA	F	N	64.07	C	1,2	27.00	4
Plantago lanceolata	PLLA	F	N	59.47	G	2	27.00	4
Plantago major	PLMA	F	N	59.47	G	2	0.42	-
Plantago spp.	PLAN	F	N	59.47	S	2	27.00	4
Poa compressa	POCO	G	N	53.2	G	2	0.30	-
Poa pratensis	POPR	G	A	54	S	7	0.09	-
Poa spp.	POAS	G	A	53.2	S	2	2.02	-
Polystichum munitum	POMU	FE	A	20	S	2	0.02	-
Populus trichocarpa	POTR	DT	N	56.1	S	2	9.90	-
Prunella spp.	PRUN	F	A	67	S	1	2.17	-
Prunella vulgaris	PRVU	F	A	67	G	1	0.82	1

Appendix 10. Continued.

Species	Code	Class[a]	Prefb	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Prunus emarginata	PREM	S	N	61.82	S	1	3.36	-
Pseudotsuga menziesii	PSME	CT	A	34.2	S	2	0.15	-
Pteridium aquilinum	PTAQ	FE	A	25.85	S	2	2.62	-
Ranunculus repens	RARE	F	N	59.47	G	2	27.00	4
Ranunculus spp.	RANU	F	N	59.47	S	2	27.00	4
Rhamnus purshiana	RHPU	S	S	58.57	S	1	46.12	-
Ribes acerifolium	RIAC	S	N	45.44	G	2	37.71	5
Ribes sanquineum	RISA	S	S	45.44	G	2	8.24	-
Ribes spp.	RIBE	S	N	45.44	S	2	8.24	-
Rosa gymnocarpa	ROGY	S	N	67.5	S	7	37.71	5
Rosa nutkana	RONU	S	N	65.85	S	8	37.71	5
Rosa spp.	ROSA	S	N	45.44	S	2	0.82	-
Rubus discolor	RUDI	RU	A	40.7	S	3	0.87	-
Rubus laciniatus	RULA	RU	A	54.25	S	1	0.65	6
Rubus leucodermis	RULE	RU	A	54.02	S	1	0.26	-
Rubus parviflorus	RUPA	RU	S	49.4	S	2	7.91	-
Rubus spectabilis	RUSP	RU	N	35.2	S	2	3.47	-
Rubus ursinus	RUUR	RU	A	45.44	S	2	0.69	-
Rumex spp.	RUME	F	N	58.67	S	1	0.67	-
Salix spp.	SALI	S	S	34.1	S	2	28.89	-
Sambucus racemosa	SARA	S	N	68.6	S	2	65.41	-
Sambucus spp.	SAMB	S	N	68.6	S	2	37.71	5
Scrophularia californica	SCCA	F	N	68	S	9	27.00	4
Senecio spp.	SENE	F	A	66.16	S	1	1.15	-
Senecio sylvaticus	SESY	F	A	60.3	S	3	1.15	-
Senecio triangularis	SETR	F	N	66.16	G	2	27.00	4
Smilacina spp.	SMIL	F	S	66.02	S	1	1.08	-

Appendix 10. Continued.

Species	Code	Class[a]	Pref[b]	DMD[c]	Cat	Source[e]	U/A[f]	S-ID[f]
Smilacina stellata	SMST	F	S	66.02	S	1	27.00	4
Sonchus asper	SOAS	F	N	64.07	C	1,2	0.52	-
Sorbus sitchensis	SOSI	S	S	56.59	C	1,2	193.2	-
Stachys cooleyea	STCO	F	N	65	S	2	5.81	-
Stellaria borealis	STBO	F	N	64.03	G	1	27.00	4
Stellaria crispa	STCR	F	N	64.03	G	1	3.31	-
Stellaria spp.	STEL	F	N	64.03	S	1	27.00	4
Symphoricarpos spp.	SYMP	S	S	63.8	S	3	45.32	-
Taraxacum offcinale	TAOF	F	N	72.2	S	8	27.00	4
Taraxacum spp.	TARA	F	N	72.2	G	8	27.00	4
Tellima grandiflora	TEGR	F	A	64.07	C	1,2	0.00	-
Thuja plicata	THPL	CT	A	33	S	6	0.00	-
Tiarella trifoliata	TITR	F	N	43	S	4	0.05	-
Tolmiea menziesii	TOME	F	N	64.07	C	1,2	1.67	-
Tragopogon dubius	TRDU	F	N	58.4	S	7	27.00	4
Trientalis latifolia	TRLA	F	A	64.07	C	1,2	2.63	-
Trifolium repens	TRRE	F	S	73.7	S	3	413.4	-
Trillium spp.	TRIL	F	A	64.07	C	1,2	0.51	-
Tsuga heterophylla	TSHE	CT	A	32.9	S	2	0.00	-
Unknown forb	UNKF	F	N	64.07	C	1,2	27.00	4
Unknown grass	UNKG	G	N	46.84	C	1,2	11.02	3
Unknown shrub	UNKS	S	N	56.59	C	1,2	37.71	5
Urtica dioica	URDI	F	A	64.07	C	1,2	0.82	1
Vaccinium alaskaense	VALO	S	N	34.15	S	10	7.76	-
Vaccinium membranaceum	VAME	S	A	58.3	S	7	0.65	6
Vaccinium ovatum	VACO	S	A	37	G	5	0.03	-
Vaccinium parvifolium	VAPA	S	S	58.7	S	5	83.87	-
Vaccinium spp.	VACC	S	N	37	S	5	83.87	-
Vancouveria hexandra	VAHE	F	N	61.49	S	1	14.35	-

Appendix 10. Continued.

Species	Code	Class[a]	Pref[b]	DMD[c]	Cat[d]	Source[e]	U/A[f]	S-ID[f]
Veronica americana	VEAM	F	A	59.47	G	2	1.38	-
V. beccabunga americana	VEBE	F	N	59.47	G	2	1.22	-
Veronica officinalis	VEOF	F	N	59.47	S	2	27.00	4
Vicia americana	VIAM	F	N	58.5	G	1	27.00	4
Vicia spp.	VICI	F	N	58.5	S	1	27.00	4
Vicia tetrasperma	VITE	F	N	58.5	G	1	27.00	4
Viola spp.	VIOL	F	N	66.17	S	1	6.50	-
Vulpia myuros	VUMY	G	A	46.84	C	1,2	0.71	2
Vulpia spp.	VULP	G	N	46.84	C	1,2	11.02	3

[a] Vegetation class includes: carex (CA) coniferous trees (CT), deciduous trees (DT), forbs (F), fern (FE), graminoids (G), *Rubus* spp. (RU), and shrubs (S).

[b] Pref refers to forage preference of elk classified into Avoided (A), Selected (S), and Neutral species. Forage preference was based on grazing trials of elk on silvicultural lands through Washington and Oregon (Cook et al., in review)

[c] DMD based on specimens collected in late summer and early autumn.

[d] Value refers to how DMD value was assigned. DMD Value for each row assigned as species (S), genus (G), or vegetation class (C).

[e] Cat denotes where DMD value was found: (1) Collected in August 2011 and analysed at WSU Habitat Nutrition Lab; (2) Merrill et al., 1995; (3) Perez, 2006; (4) Leslie et al., 1984; (5) Jenkins et al., 1996; (6) Kirchoff et al., 1998; (7) Damiran et al., 2002; (8) Canon et al., 1987; (9) Rhodes and Sharrow, 1990; (10) Hanley and McKendrick, 1983.

[f] Elk selection ratios of plant species in the PNW. Values derived from Cook et al. (in review). Calculated as proportion of bites used divided by proportion of available biomass. Plant species with no selection ratio were given an average value from a combined vegetation class and preference category (S-ID). Categories were (1) avoided Forb, (2) avoided grass, (3) accepted grass, (4) accepted forbs, (5) accepted Shrub, (6) avoided shrub. A dash (-) denotes a species specific value.

Dear Antlerless Elk Permit Holder,

You have been selected for an antlerless elk permit hunt in GMU 550. As part of a new study within the Mt. St. Helen's elk herd designed to better estimate population and body condition, WDFW biologists are assessing cow elk body condition in this area. Body condition in elk can be evaluated by the amount of fat surrounding the heart and kidneys. To assess cow elk body condition in GMU 550, **you are being asked to collect the needed samples detailed below** from any cow elk (yearling or older) you harvest and provide them for examination. WDFW will be looking at a variety of factors in evaluating condition: organ assessment, age analysis (via tooth sample), prior nursing status, etc. Your assistance is important to the success of this study.

Because fat levels on the heart and kidneys are essential to this assessment, these organs must be collected with **all** attached fat. For example, a kidney that has had the fat removed cannot be used to evaluate body condition. Please see the enclosed diagrams for details regarding the sample collection described below.

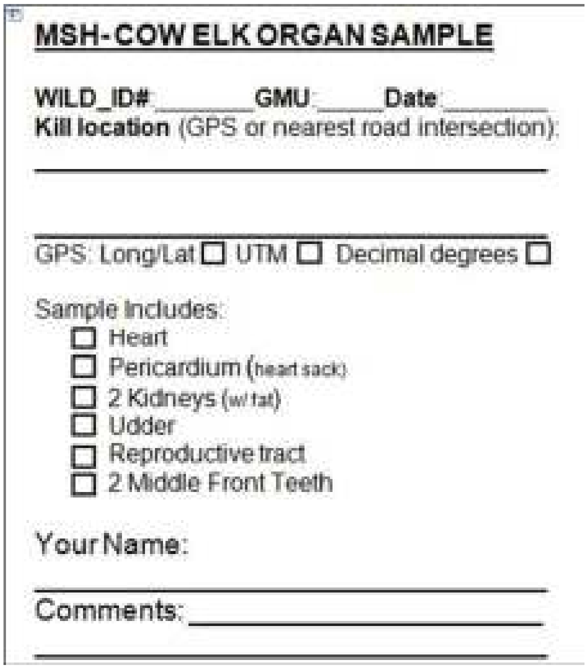
Please remove the **heart with the pericardium** (membrane bag covering the heart) still attached. **Both** the heart and the pericardium are needed for the assessment. Remove **both kidneys**, which are typically found near and behind the large liver (as in people, they are positioned near the back of the body cavity). The kidneys are often obscured by a considerable fat capsule, making them difficult to see. However, they can be located fairly easily by finding the liver and feeling all large fatty deposits near the liver. The kidneys are relatively firm, oblong organs about 5-9 inches long that are easily felt through the soft fat tissue. Remove the kidneys **with all attached fat** (include about a 3-4" flap of fat around the margin of each kidney to be sure). An instructional video on collecting the kidneys can be found at http://www.dfw.state.or.us/resources/hunting/ See attached diagram for help.

Please collect the **2 middle incisor teeth** so your cow elk can be aged. These are the 2 center teeth in the middle of the lower front jaw (in front of the tongue). Also, **we need to know** whether your cow nursed a calf this summer. Note whether the **udder** is dry or whether you can produce clear fluid or true milk by pulling firmly on the teats. Lastly, we are asking you to collect a large thumb size **piece of the liver** for trace mineral analysis. Please fill out the enclosed data form with all the information pertaining to the samples you have collected. Please place the data form in the small bag and put with all of your samples (heart, kidneys, teeth, liver) in the large plastic bag included with this letter. Samples can be deposited at drop off sites identified on the back of this letter OR if available, leave samples with a volunteer from the St. Helens Land Access Program that will be at certain gates on Weyerhaeuser St. Helens Tree Farm property. Extra sample labels, bags, and directions will also be available at these locations and with access volunteers. Samples can also be placed in a plastic garbage bag, large Ziploc, etc. Please double check that you have included the data form with your samples. Your assistance is greatly appreciated on behalf of the St. Helen's elk resource. Please call if you have further questions.

Sincerely,

Encl: Organ Diagram & Tooth Diagram
Pictures of heart and kidneys
Plastic bag for organs
Plastic bag for data form
Data Form

Appendix 11.A. Letter mailed to hunters requesting submission of their cow organs. This was mailed out by WDFW two weeks before each special permit cow hunt at Mount St. Helens, Washington in autumn 2011.



MSH- COW ELK ORGAN SAMPLE

WILD_ID#________**GMU**:_____**Date**:________
Kill location (GPS or nearest road intersection):

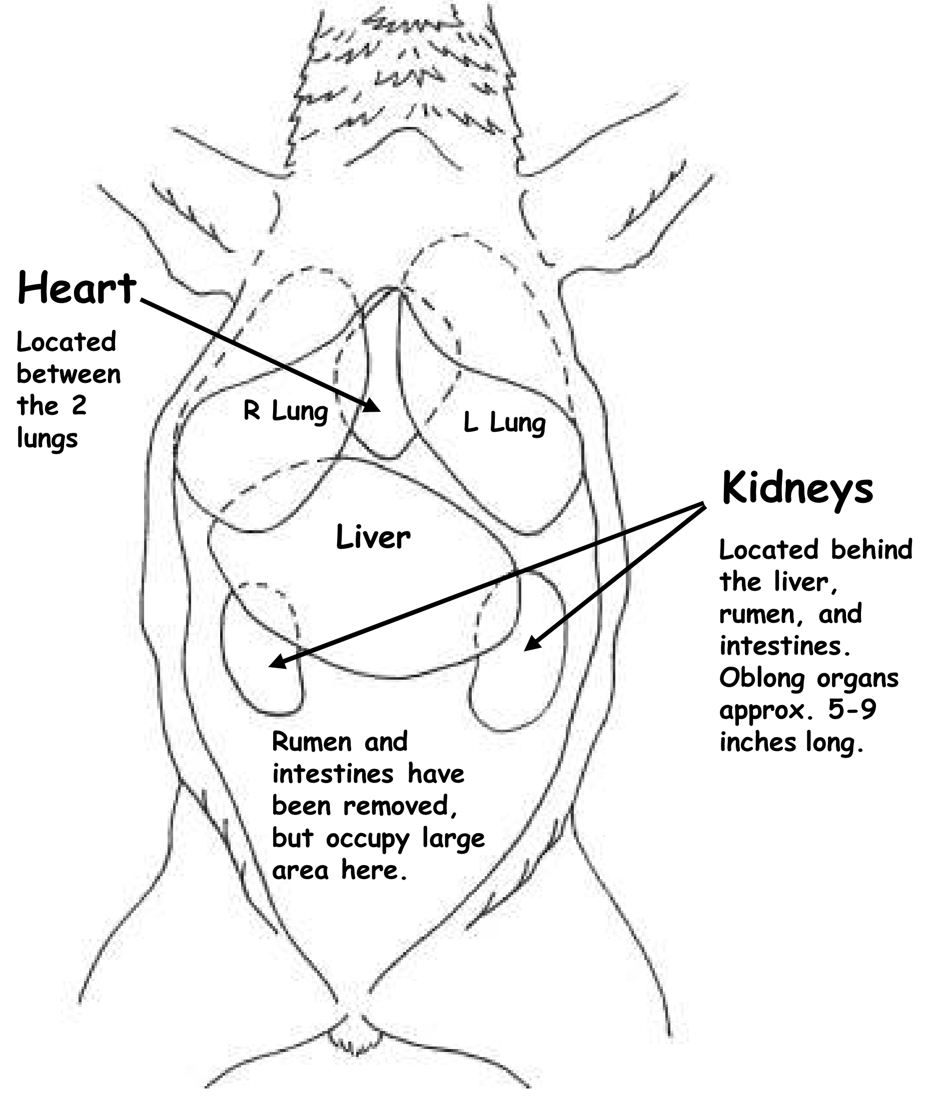
____

____
GPS: Long/Lat ☐ UTM ☐ Decimal degrees ☐

Sample Includes:
- ☐ Heart
- ☐ Pericardium (heart sack)
- ☐ 2 Kidneys (w/ fat)
- ☐ Udder
- ☐ Reproductive tract
- ☐ 2 Middle Front Teeth

Your Name:
____
Comments: __________________________
____

Appendix 11.B. Data card sent to hunters for elk organ collection at Mount St. Helens, Washington in autumn 2011.



Located between the 2 lungs

Located behind the liver, rumen, and intestines. Oblong organs approx. 5-9 inches long.

Rumen and intestines have been removed, but occupy large area here.

Please bring samples to a drop off location, to the Vancouver Office of WDFW (2108 Grand Blvd) or leave w/ a WDFW land access volunteer. Ice/freeze samples if not dropped off within 24hrs. Call (xxx) xxx-xxxx w/ questions. Thank you.

Appendix 11.C. Diagram of organ locations in female elk. Document sent to hunters at Mount St. Helens, Washington in autumn 2011 during organ collection efforts.

Heart Removal

There is fat associated both with the **heart and the pericardium** (membrane around the heart). **Both** of these fat deposits are important for assessing body condition. Remove the heart (with intact pericardium) by cutting the large vessels near the top of the heart. **Do not separate the pericardium from the heart or remove any of the associated fat from the heart**. Hearts damaged during harvest can often still provide useful information.

Heart with pericardium

Please bring samples to a drop off location, to the Vancouver Office of WDFW (2108 Grand Blvd) or leave w/ a WDFW land access volunteer. Ice/freeze samples if not dropped off within 24hrs. Call (xxx) xxx-xxxx w/ questions. Thank you.

Appendix 11.D. Instruction sheet for removing elk heart. Sent to hunters in autumn 2010 around Mount St. Helens, Washington.

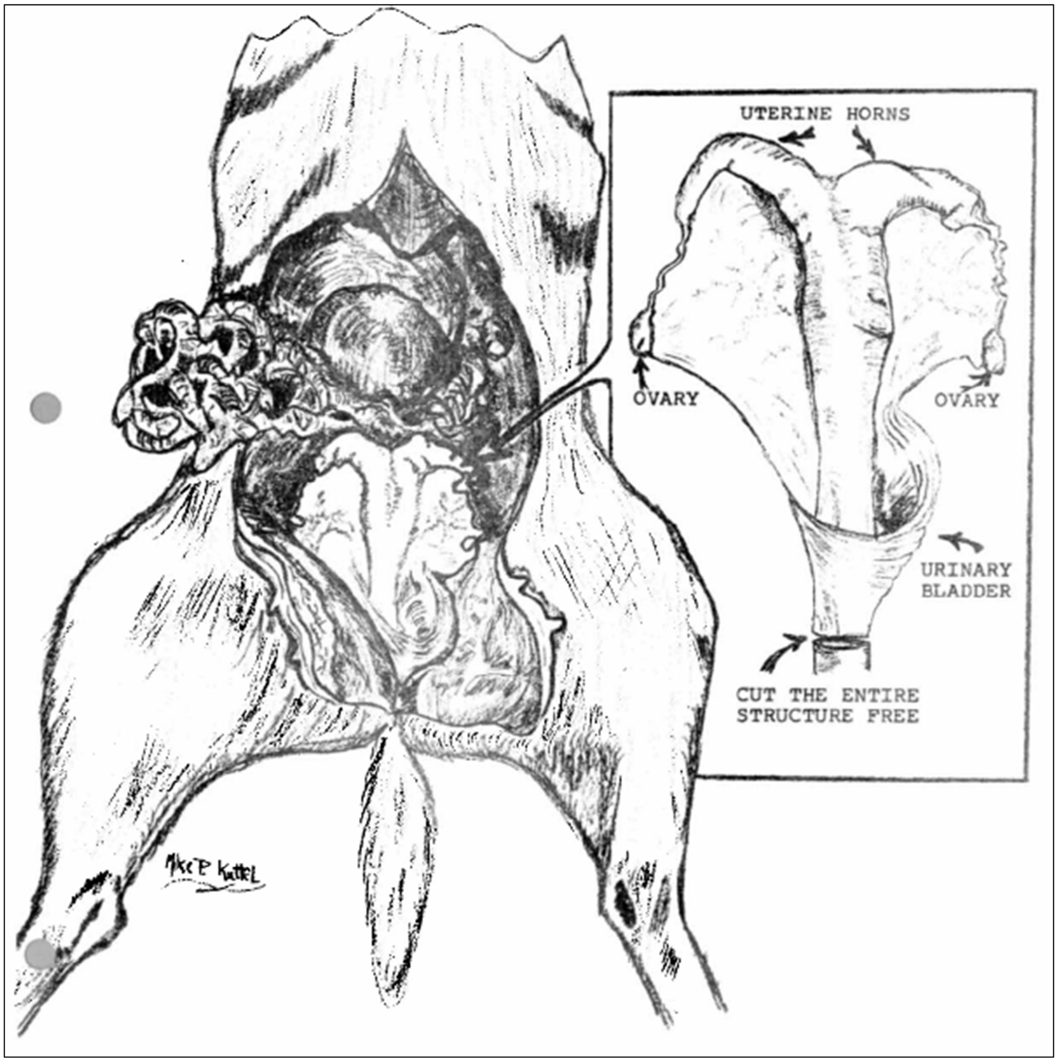
Kidney Removal

An elk has 2 kidneys, which are relatively firm, oblong organs approximately 5-9" in length and often covered with globular fat deposits. The amount of fat covering the kidney is extremely useful to interpreting body condition in elk. The kidneys are located in the back of the body cavity, behind the liver, rumen, and intestines. Remove **both** kidneys. To avoid losing any of the fatty tissue, lift the kidney slightly and cut the membranous tissue surrounding it several inches beyond the actual border of the kidney. **Do not clean the kidneys of any of the fatty covering surrounding them; this fat is essential**.

Kidneys with fat and tissue

Please bring samples to a drop off location, to the Vancouver Office of WDFW (2108 Grand Blvd) or leave w/ a WDFW land access volunteer. Ice/freeze samples if not dropped off within 24hrs. Call (xxx) xxx-xxxx w/ questions. Thank you.

Appendix 11.E. Instructions for removing the elk kidneys. Form sent to hunters in autumn 2011 around Mount St. Helens, Washington.



Appendix 11.F. Diagram of reproductive tract sent to hunters in autumn 2011 around Mount St. Helens, Washington.

Appendix 12.A. Spatial differences across game management units in ingesta free body fat (IFBF) around Mount St. Helens, Washington between 2009 and 2011.

Methods

Organs required to estimate the Kistner subset score (heart, pericardium, kidneys) were collected by WDFW from 2009-2011 in 5 GMUs (520, 522, 524, 550, 556). For the first two years samples were only collected during the modern firearm hunt in November. In 2011, samples were collected from 1 October to 15 December. Organs were analyzed in the same way each year using the same technicians (see Chapter 3 methods for details). In this analysis, only November samples were used from 2011, so that sampling dates were roughly equal across years. Samples were compared with ANOVA and a BONFERONI post hoc test. GMU and year comparisons were done for lactating, non-lactating, and both groups combined, which is collectively referred to as “all females”.

Results

Estimates of IFBF for all females averaged across all GMUs at MSH in November 2011 were similar to IFBF estimates averaged across all GMUs at MSH in November 2009 and 2010. Between 2009, 2010, and 2011 body fat was similar between individual GMUs for all females and also for each individual GMU averaged across all years. Similarly, there were no differences for lactating or non-lactating groups across years or GMUs. However, in 2009 and 2010 non-lactating females were consistently higher in IFBF than lactating females, but data from 2011 suggests that the lactating female group generally had higher estimates of IFBF. In particular, the IFBF estimates for non-lactating females in GMUs 524 and 556 from 2011, although not significantly different, were notably low and the most inconsistent when compared to 2009 and 2010 data.

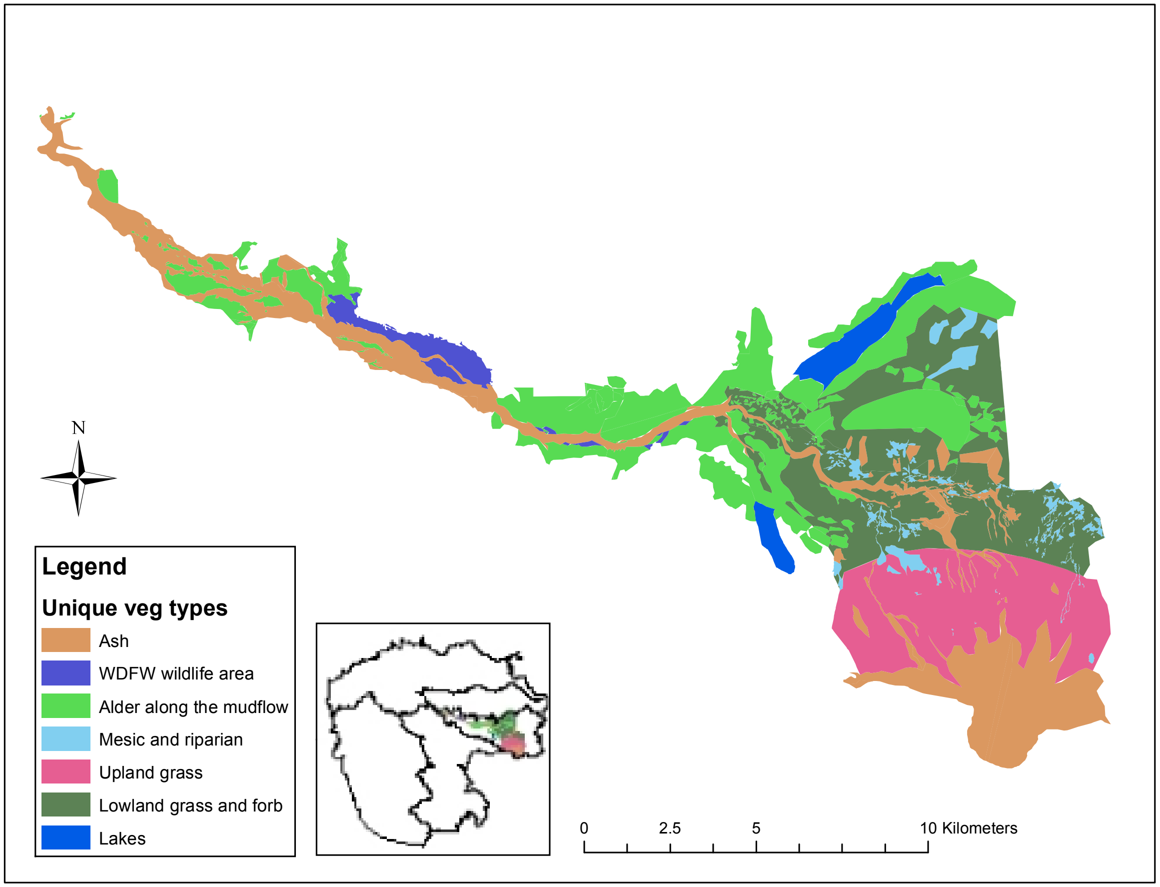
Discussion

IFBF estimates from female elk in GMU 524 and 556 in 2011 were not consistent with previous years. Some variation in IFBF may be explained by unseasonably low levels of precipitation between June and October 2011, which was one of the 15 driest summers since 1949 (Prism, 2013), or perhaps some variation is related to increased hunting pressure as WDFW has increased hunting permits in GMU 524 and 556 to reduce the MSH elk herd (WDFW, 2006). However, it remains unclear (but see Chapter 3 discussion) why it was primarily non-lactating individuals that had inconsistently low IFBF in 2011, and additionally, IFBF levels that were generally lower than lactating females.

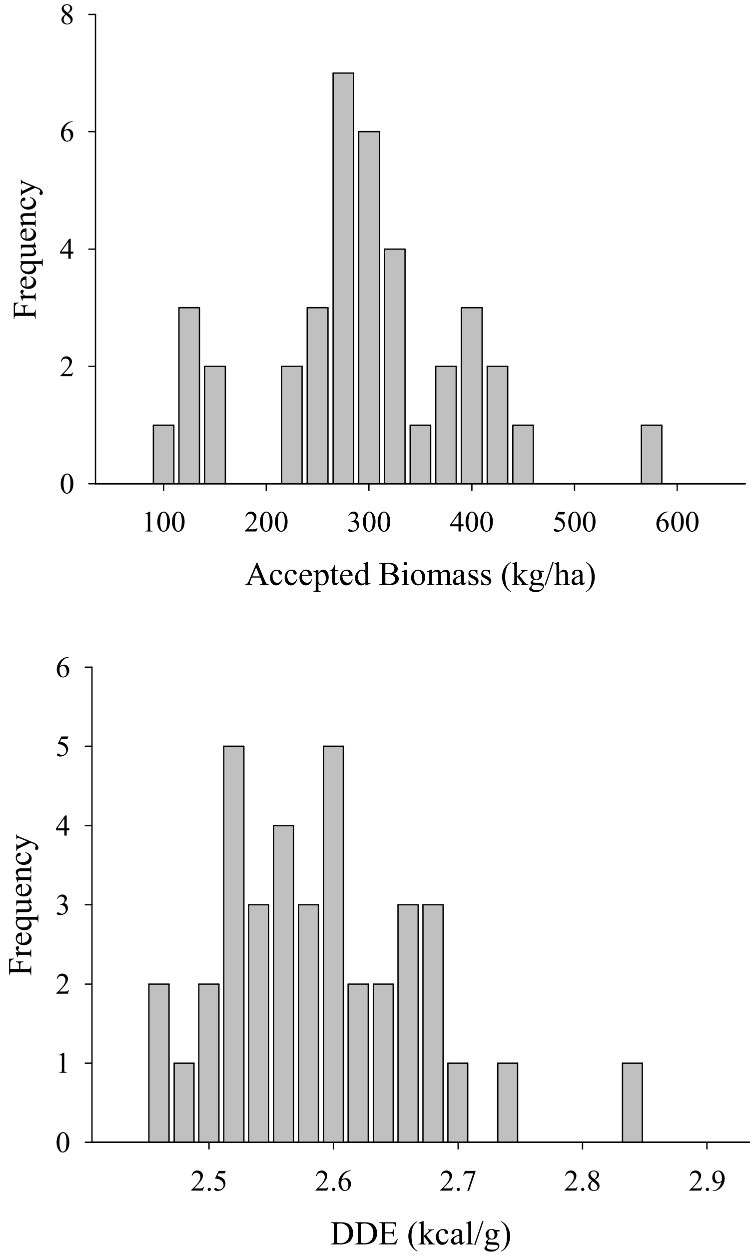
Some of the lowest autumn IFBF values recorded at MSH (5%), but also low relative to the PNW, came from female elk on an isolated section of the North Fork Toutle River mudflow during 2003 (Cook et al., 2013). IFBF estimates from organ data collected between 2009 and 2011 suggest IFBF from elk harvested within these disturbed areas of the national monument are highly variable (IFBF=10.71 ± 5.66) but still consistently higher than the 5% reported by Cook et al. (2013). These findings support the conclusion of Cook et al. (2013) that their low body fat measurements obtained from corral trapping females along the North Fork Toutle River likely represents a distinct group of elk from a very specific area.

Appendix 12.B. November Body fat (IFBF) for lactation status, year, and GMU at Mount St. Helens, Washington for November 2009 through 2011. Ingesta free body fat was estimated from the Kistner subset score *sensu* Cook et al. (2001). Values are: mean and (SD). Values with the same superscript are different: *a*=0.05.

	Lactating				Non-lactating				All females			
	2009	2010	2011	All YRS	2009	2010	2011	All YRS	2009	2010	2011	All YRS
All GMU	7.09	8.36	8.64	7.91	10.01	9.65	7.32	9.17	8.44	8.99	8.01	8.52
	(4.5)	(4.3)	(5.5)	(4.7)	(4.8)	(5.7)	(5.7)	(5.5)	(4.8)	(5.0)	(5.6)	(5.1)
520	7.03	8.69	7.13	7.56	8.83	5.79	12.19	8.94	8.02	7.11	9.47	8.27
	(4.4)	(4.9)	(6.3)	(5.2)	(6.6)	(5.6)	(6.9)	(6.6)	(5.5)	(5.3)	(6.9)	(5.9)
522	6.26	12.36		7.78	13.56			13.56	9.18	12.36		9.71
	(4.4)	-	-	(4.7)	(6.0)	-	-	(6.0)	(5.9)	-	-	(5.4)
524	6.88	8.93	16.33	8.64	11.12	11.09	6.07	9.85	9.27	10.18	8.12	9.38
	(6.0)	(4.6)	(4.6)	(5.8)	(5.0)	(5.6)	(5.0)	(5.5)	(5.7)	(5.2)	(6.4)	(5.6)
550	7.3	10.19	9.05	8.57	8.06	10.98	8.19	8.91	7.58	10.49	8.77	8.69
	(4.5)	(3.5)	(5.3)	(4.6)	(3.2)	(6.6)	(5.0)	(4.7)	(4.0)	(4.7)	(5.1)	(4.6)
556	7.17	7.06	8.06	7.38	10.09^a	9.69	5.37^a	8.70	8.47	8.34	6.87	7.99
	(4.0)	(4.3)	(5.0)	(4.3)	(4.7)	(5.5)	(4.8)	(5.3)	(4.5)	(5.0)	(5.0)	(4.8)



Appendix 13. Unique vegetation communities within the blast zone that were sampled to estimate forage resources at Mount St. Helens, Washington in autumn 2011. See descriptions in Table 3.1.



Appendix 14. Histograms of mean accepted biomass and DDE from all elk harvest sites used in the ingesta free body fat model for lactating elk at Mount St. Helens, Washington in 2011 (n=38). Mean values at each harvest site were calculated within a 9.2 km^2 circular buffer.

Appendix 15. Proportion of GPS collared female elk in clearcuts versus closed canopy forest in March and April of 2009-2012 at Mount St. Helens, Washington. Proportions are based on GPS movement data from late winter and are specific to regions of the study area and time of day. Proportions were used to estimate elk density in closed canopy forest for each region and time period based on density estimates in clearcuts from aerial survey data collected in March and April 2011 at Mount St. Helens, Washington.

Region and time period of survey	Proportion
South - 7:00 to 12:59	0.533
South - 13:00 to 14:59	0.520
South - 15:00 to 17:00	0.577
North - 7:00 to 12:59	0.483
North - 13:00 to 14:59	0.483
North - 15:00 to 17:00	0.562
Mudflow - 7:00 to 12:59	0.538
Mudflow - 13:00 to 14:59	0.595
Mudflow - 15:00 to 17:00	0.686

Appendix 16. Variation of ingesta free body fat and habitat covariates for harvest sites of lactating elk that were used to model ingesta free body fat at Mount St. Helens in 2011 (n=38). Mean, median, minimum value, maximum values, range, standard deviation and, coefficient of variation are presented for IFBF and each covariate. See Table 3.2. for descriptions of covariates.

	IFBF	Harvest	Age	DDE	AccpBio	Clearcuts	Canopy_cov	Density[a]	Elev	Roads[b]
Mean	8.25	16/11/11	6.66	2.60	309.20	29236.66	55.11	10.49	520.29	1.44
Median	8.09	25/11/11	7.00	2.59	308.67	28454.50	53.98	9.01	489.50	1.46
Min	0.00	1/10/11	2.00	2.46	99.26	0.00	20.82	0.04	251.00	0.30
Max	19.56	12/12/11	12.00	2.87	607.88	60057.00	80.93	30.63	860.00	2.30
Range	19.56	-	10.00	0.41	508.62	60057.00	60.12	30.59	609.00	2.00
SD	5.69	-	2.74	0.08	104.80	17393.41	13.82	6.37	166.45	0.48
CV	0.69	-	0.41	0.03	0.34	0.59	0.25	0.61	0.32	0.33

[a] Covariate name is Weight_aerial_d

[b] Covariate name is Den_main_road

Appendix 17.A. Influence of habitat on ingesta free body fat of all elk (lactating and non-lactating) at Mount St. Helens, Washington in 2011.

Methods

To relate habitat features to ingesta free body fat (IFBF) of all female elk at MSH I used the same approach as outlined in Chapter 3. In brief, organs from harvested animals were evaluated for fat content and used to predict IFBF, and then I characterized habitat conditions within a use buffer at the harvest location of each elk. Habitat covariates were checked for correlation using Pearson product-moment correlation ($r \geq 0.60$, $P<0.05$). I selected between covariates that were similar by evaluating the AIC values for each covariate independently. Covariates were related to IFBF in a model selection framework using AICc and models were validated using samples from 2010. For more details see Chapter 3 methods. Note that the models presented in this appendix include lactating and non-lactating females because both groups had similar IFBF, and such an approach allowed for a larger sample size. However, results must be interpreted with caution because previous research has shown lactating and non-lactating elk are under different energetic constraints. Non- lactating females potentially won't be highly influenced by habitat conditions because of their low energetic demands (Cook et al., 2004).

Results

I used 55 of 102 available samples for modeling habitat influence on IFBF because these samples had information on harvest location, lactation status, and they were from elk that were at least 2 years old. I excluded 4 habitat covariates (terrain ruggedness, slope, clearcuts, and public roads) from being included in the models because they were highly correlated with other covariates. After model selection, I evaluated their effect in the top model by substitution and found little support for the inclusion of any of the 4 covariates (Appendix 17.D).

The top 5 models explained from 16 to 8% of the total variation in IFBF (Appendix 17.B) and the confidence limits of β coefficients of Age, Date and DDE overlapped with zero (Appendix 17.C). The top 6 equally supported models were model averaged resulting in elk age, date of harvest, and roads having a negative effect on elk IFBF in autumn while density in the previous winter and forage covariates had a positive effect on IFBF (Appendix 17.E).

I was able to use 16 lactating elk samples collected in 2010 with known harvest locations to evaluate the model predictions at the scale of the 9.2 km^2 buffer. Predicted IFBF values (Appendix 17.F) based on the model predictions from habitat conditions were not closely correlated (r=0.2, P=0.61). I also used the model to predict the mean IFBF for 4 GMUs in the study unit (Appendix 17.G) and compared the mean values of IFBF of 37 elk collected across each GMU. I found that at the scale of the GMU, model predicted and observed values were still not closely correlated (r=0.70, P=0.30).

Discussion

The best IFBF model using samples from lactating and non-lactating females (All females) differed from the lactating model because DDE was in the top model that included all females, and elevation in the lactating model was replaced by a main road density covariate when the model included all females. Reviewing the top models indicates there is slightly more evidence (ΔAIC_c =0.90) that DDE was more influential on IFBF than AccpBio. Although AccpBio and DDE are correlated, Cook et al. (in review) documented IFBF and DDE were linearly related, whereas the relationship between AccpBio and IFBF was nonlinear. This may explain why DDE instead of AccpBio appeared in the top model.

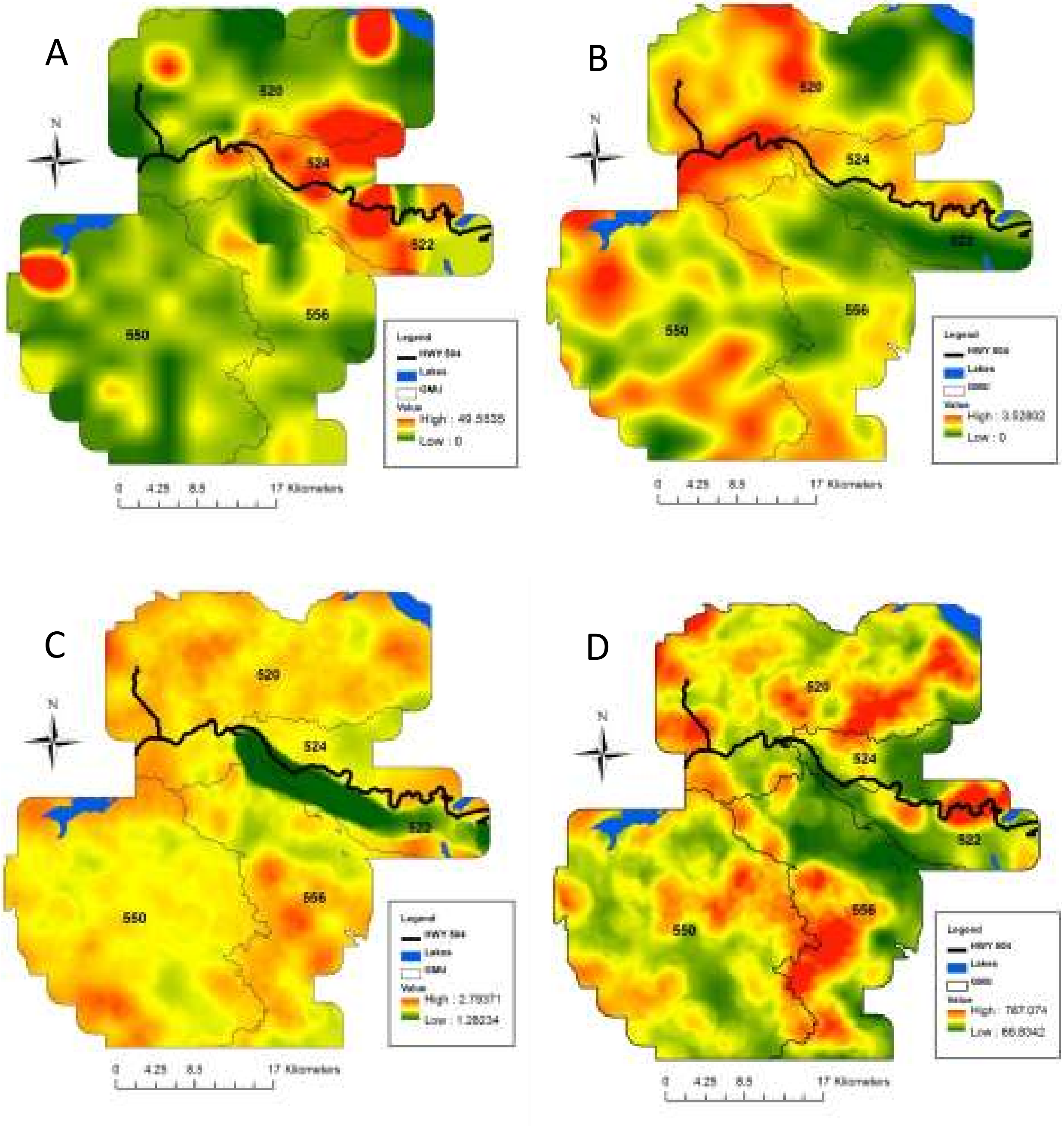
Roads have long been recognized as an avoided habitat feature by elk (Rowland et al., 2000; Wisdom and Cook, 2000; Rowland et al., 2005). However, the decline in elk performance because of roads has always been indirectly inferred through research that monitors elk heart rates or glucocorticoids stress hormones (Millspaugh et al., 2001; Ward and Cupal, 1979). To my knowledge, this study is one of the first to potentially observe a more direct relationship between major roads and declining body condition in female elk, and this may be a next step in understanding what habitat features affect elk performance. This study also provides validation for current elk habitat models (i.e. WEHM) that account for the negative impact of roads.

Appendix 17.B. Models predicting ingesta free body fat of cow elk harvested in autumn 2011 at Mount St. Helens, Washington. Included are the number of estimated parameters (*k*), AICc score, and AIC weight (w_i) for each model. Covariate descriptions are provided in Table 3.2.

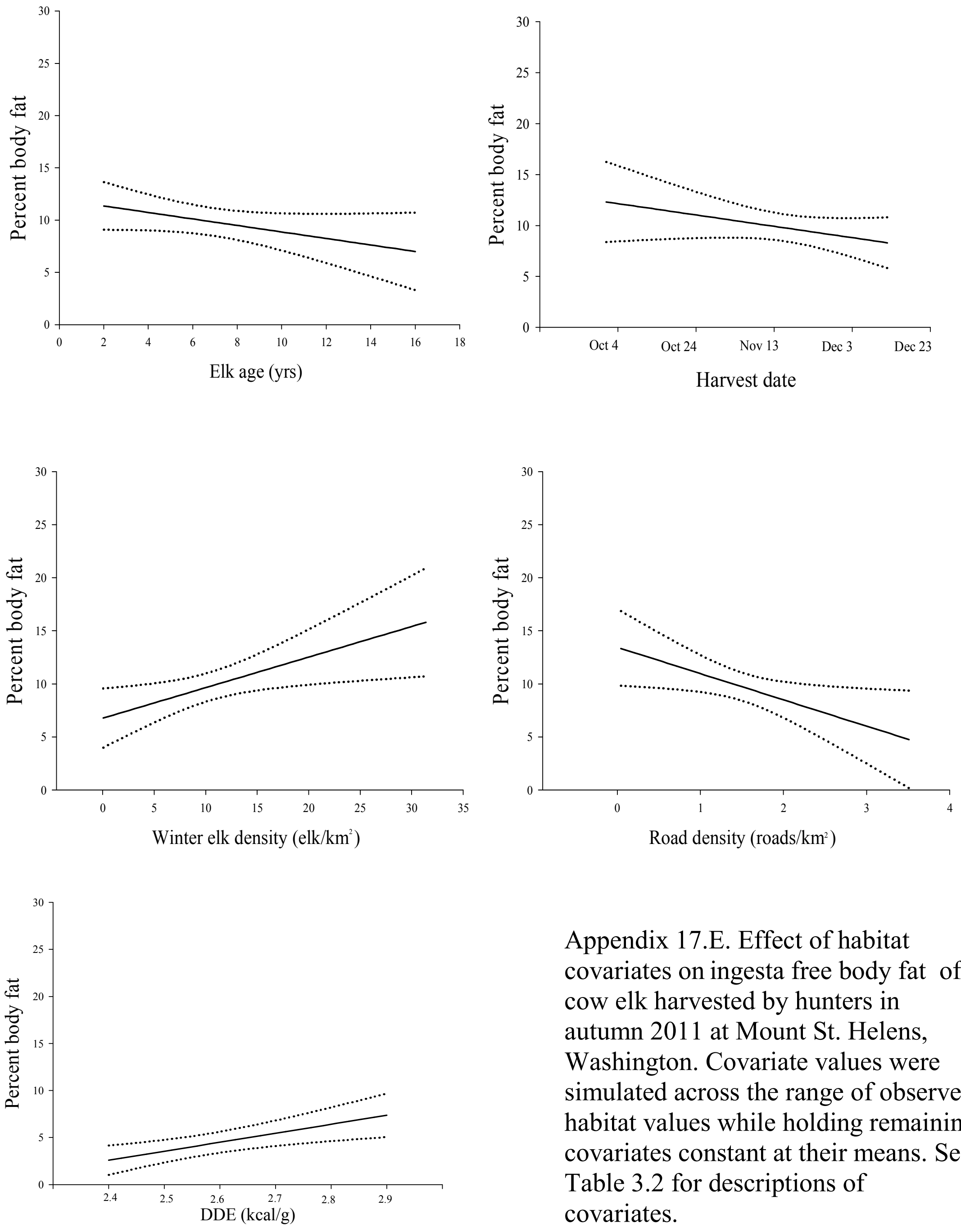
Model	***k***	**AIC$_c$**	Δ_i	W_i
Age, Date, Density, Roads	4	336.89	0.00	0.16
Age, Density, Roads	5	336.95	0.05	0.16
Date, Density, Road	4	337.74	0.85	0.11
Age, Date, Density, Roads, Lac	6	337.91	1.01	0.10
Date, Density, Roads, DDE	5	338.04	1.15	0.09
Age, Date, Density, Roads, DDE	6	338.37	1.48	0.08
Age, Density, Roads, DDE	5	338.42	1.52	0.08
Date, Density, Roads, AccpBio	5	338.94	2.04	0.06
Age, Date, Density, Elev	5	339.72	2.82	0.04
Age, Date, Density, Lac	5	339.75	2.85	0.04
Age, Date, Density	4	340.13	3.23	0.03
Age, Roads, DDE	4	341.07	4.18	0.02
Null model	1	341.91	5.02	0.01
Age, Date, Lac	4	343.14	6.24	0.01
Age, Date, DDE	4	343.73	6.83	0.01
Age, Date, AccpBio	4	344.87	7.98	0.00

Appendix 17.C. Body fat model parameters for predicting percent ingesta free body fat of an adult harvested cow elk in 2011 at Mount St. Helens, Washington. This table includes parameter values (B), confidence intervals (CI), *P*-value and standardized regression coefficients (SRC). Covariate descriptions are provided in Table 3.2.

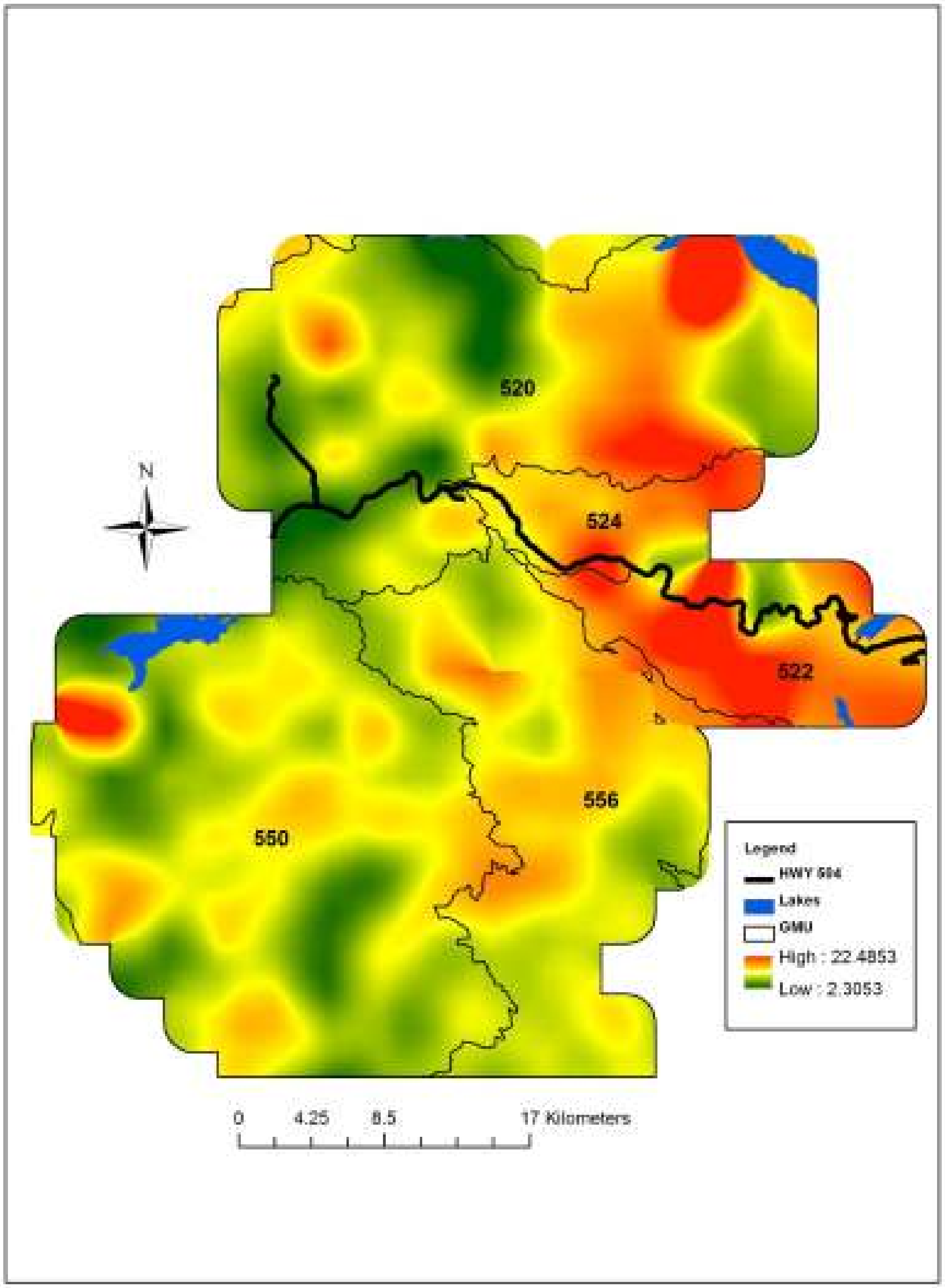
Covariate	B	*P*	SRC
Intercept	1535.11752	0.4029	0
Age	-0.229378	0.0774	-0.1589
Date	-0.037417	0.1193	-0.1291
Density	0.264372	0.0285	0.3038
Roads	-2.437664	0.0352	-0.2853
DDE	2.276211	0.34	0.0330



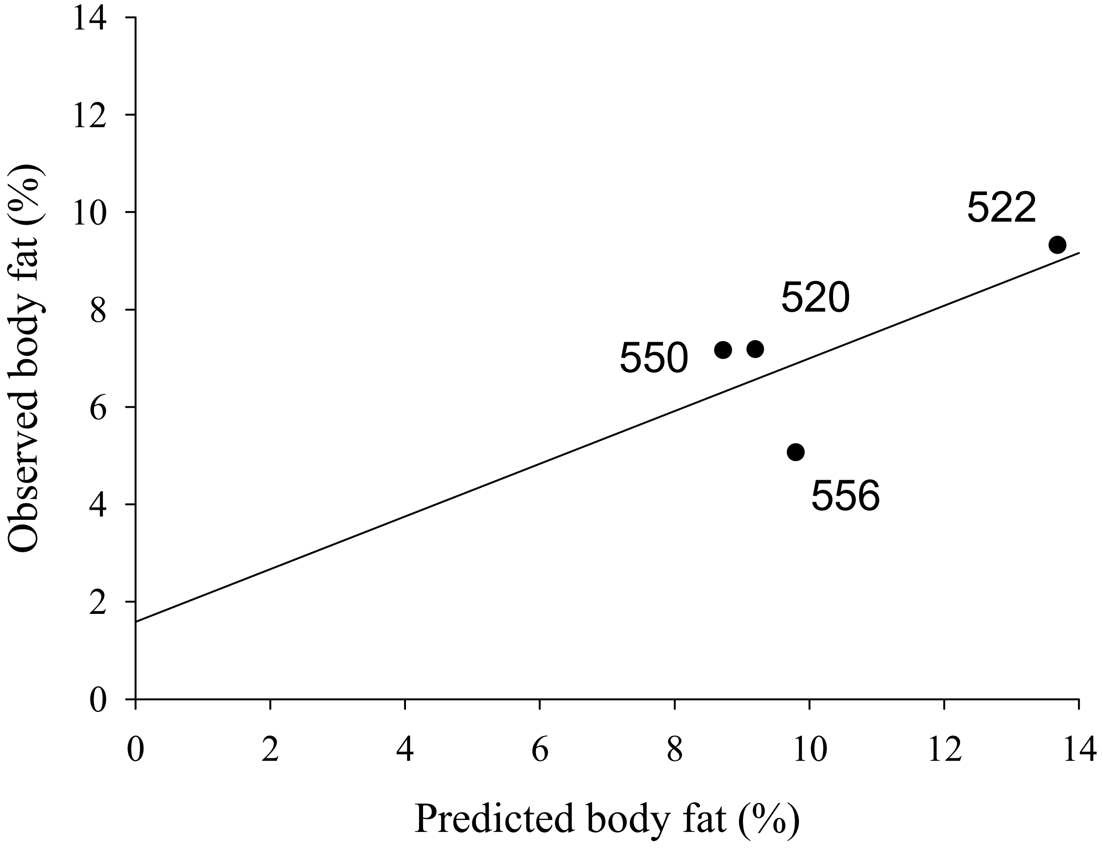
Appendix 17.D. Habitat covariates used to predict percent ingesta free body fat at Mount St. Helens, Washington during autumn 2011. (A) Winter elk density (elk/km^2) based on aerial surveys in March 2011 and adjusted for visibility, (B) Road density (roads/km^2) of major, high use logging roads and highways, (C) DDE (kcal/g) predicted from the Westside Elk Habitat Model and field sampling in volcanic areas, and (D) accepted biomass (kg/ha) *sensu* Cook et al. (in review).



Appendix 17.E. Effect of habitat covariates on ingesta free body fat of cow elk harvested by hunters in autumn 2011 at Mount St. Helens, Washington. Covariate values were simulated across the range of observed habitat values while holding remaining covariates constant at their means. See Table 3.2 for descriptions of covariates.



Appendix 17.F. Predicted values of landscape ingesta free body fat (%) for elk at Mount St. Helens on 15 November across 5 game management units (GMU).



Appendix 17.G. Relationship between predicted landscape ingesta free body fat averaged by game management unit (GMU) on the x axis and observed ingesta free body fat values of hunter-harvested elk (n=46) in autumn 2011 averaged for 4 game management units (520, 522, 550, and 556) at Mount St. Helens, Washington. Ingesta free body fat estimates for predicted and observed values are from Kistner subset scores *sensu* Cook et al. (2001) based on elk harvested by hunters at Mount St. Helens.