Using nutritional-landscape models to predict pregnancy rates of elk across broad spatial scales

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By
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Authorization to Submit Thesis

This thesis of Sierra L. Robatcek, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Using nutritional-landscape models to predict pregnancy rates of elk across broad spatial scales," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Understanding how the choices made by individual herbivores as they navigate heterogeneous landscapes scale up to influence population performance is critical for accurately forecasting population trajectories. Elk (*Cervus canadensis*) populations in Idaho have exhibited considerable variation in multiple vital rates, including pregnancy. Because elk populations that are not resource limited typically display high pregnancy rates (>80%), and several populations in Idaho regularly fall below this threshold, there is concern that habitat quality may be limiting the productivity of those populations. Nutritional condition is a primary driver of reproductive success in female herbivores, and thus poor habitat quality, suboptimal use of the nutritional landscape by elk, or a combination of both could cause depressed pregnancy rates. The goal of our research was to develop a series of linked dynamic models for predicting a) spatiotemporal variation in the nutritional landscapes available to elk in seven distinct populations in Idaho and b) interannual variation in pregnancy rates of those populations as a function of the overall quality and abundance of forage resources available to them and/or how they used those resources. Regression models for explaining spatiotemporal variation in usable forage biomass (biomass of forage that met or exceeded requirements for a female elk at peak lactation) generally performed well in each of our three study areas, with adjusted R^2 values ranging from 0.26 to 0.61. High-quality foraging habitat was most abundant during summer in the Teton and Diamond Creek elk zones, and was least abundant in the Beaverhead and Sawtooth elk zones. This trend was similar during the fall, with the Teton and South Fork of the Clearwater elk zones supporting the most high-quality habitat, and the Beaverhead and Sawtooth zones supporting the least high-quality habitat. Differing patterns of habitat use were observed among the four elk populations for which we had simultaneous GPS-collar and pregnancy data. Elk in the Diamond Creek and Sawtooth zones appeared to utilize the nutritional landscape sub-optimally (i.e., locations used by elk had less high-quality forage than random locations on the landscape), particularly during summer (June 1 – July 31), whereas elk in the South Fork of the Clearwater used high-quality foraging habitat in greater proportion than it was available. Our top model for relating pregnancy rates of elk to the nutritional landscape explained 60% of the variation in pregnancy rates among 18 elk-population-years. Our top model for relating pregnancy of elk to how they used the nutritional landscape explained 75% of the variation in pregnancy rates among 10 population-years. Variation in pregnancy rates was positively related to both the maximum value of usable forage biomass and the degree of heterogeneity in the nutritional landscape across elk management zones in Idaho. This supports our hypothesis that pregnancy is mediated by habitat quality, and provides additional empirical evidence of a fundamental link between the nutritional landscape in summer and fall and population performance of elk.

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Dedication

To the wild things of Idaho

Never does nature say one thing and wisdom another.

- Juvenal

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1: Introduction

Spatiotemporal heterogeneity in resource availability governs ecological processes at all levels of organization, from the individual to the ecosystem (Wiens 1989, Holling 1992, With and Crist 1995, Mueller and Fagan 2008). In terrestrial environments, heterogeneity at the landscape scale often is driven by vegetation communities that are "patchy" across time and space due to underlying variation in soil characteristics, topography, disturbance regimes, annual phenological cycles, or other factors. In patchy landscapes, the distribution and relative availability of high-quality foraging habitats plays a fundamental role in determining the potential of the landscape to support robust animal populations (Bjorneraas et al. 2012, Borowik et al. 2013, van Beest et al. 2010). Accordingly, understanding the mechanisms that underpin relationships among landscape heterogeneity, animal nutrition and individual fitness is critical for predicting variation in population performance (Parker et al. 2009, Cook et al. 2013, Long et al. 2016).

Abundance of high-quality forage is positively related to body condition, pregnancy and survival of adult herbivores (Merrill and Boyce 1991, Cook et al. 2004a Stewart et al. 2005, Bender et al. 2008), and to body mass and overwinter survival of offspring (Crête and Huot 1993, Parker et al. 2009). Conversely, forage of insufficient abundance or quality can amplify the negative effects of predation (FitzGibbon and Fanshawe 1988, Wirsing et al. 2002), environmental stochasticity (Saether 1997), and density dependence (Gaillard et al. 1998) on population performance. As habitat fragmentation and climate change increasingly result in shifting vegetation communities, loss of migration corridors, and unpredictable environmental conditions, dynamic models built on mechanistic relationships between nutrition and population performance will be invaluable for managing and monitoring wildlife population and their habitats.

The annual life cycles of temperate large herbivores closely parallel vegetation phenology, ostensibly to facilitate reproductive success by increasing access to high-quality forage when the energetic demands of reproduction are high (e.g., during late gestation and lactation; Albon and Langvatn 1992; Bischof et al. 2012). At northern latitudes, seasonal variation in resource availability imposes strong selective pressure on large herbivores to maximize energy and protein intake from foraging (Cook et al. 2004b; Monteith et al. 2013; Long et al. 2014, 2016). For example, during summer and fall, reproductive females must meet the demands of lactation while also replenishing reserves lost over winter (Therrien et al. 2007, Bårdsen 2009, Bårdsen and Tveraa 2012). A variety of behavioral strategies have been reported for accomplishing this objective in heterogeneous landscapes. For example, migration has been shown to improve fitness in some circumstances by reducing density-dependent feedbacks on life-history traits and improving vital rates, because mobile herbivores are able to exploit shifting patches of high-quality forage over a longer period of time (Gaillard 2013, Jesmer et al. 2018). "Surfing the green wave" (Merkle et al. 2016, Aikens et al. 2017) not only enhances current fitness, but also creates favorable foraging conditions later in the year by ensuring that some biomass is left on the landscape (in the absence of high herbivore densities). These residual resources can help to reduce mortality during episodic resource shortages in stochastic environments (Owen-Smith 2004).

In temperate environments forage quality typically peaks early in the growing season when cell soluble content is high (van Soest 1982). Capitalizing on this period is critical for ungulates, because even small increases in forage quality can have multiplier effects on condition and reproductive success (White 1983, Cook et al. 2004b). Accordingly, the behavioral strategies exhibited by ungulates often are driven by the need to increase access to high-quality forage. For example, female mule deer (*Odocoileus hemonius*) in poor condition (i.e., low levels of stored body fat) displayed a greater tendency to migrate than females in good condition occupying the same ranges in the Sierra Nevada of California (Monteith et al. 2011). Similarly, Hebbelwhite et al. (2008) reported that migratory elk in British Columbia enjoyed extended access to high-quality forage relative to resident elk, which translated into higher pregnancy rates and heavier calves.

Individual herbivores often exhibit diverse foraging and movement strategies as they attempt to maximize fitness in heterogeneous landscapes (Morales et al. 2005, van Beest and Milner 2013, Long et al. 2014). Such behavioral plasticity can sometimes serve to buffer individuals against negative affects of environmental variation (Huey et al. 2003, Kearney et al. 2009, Long et al. 2014). Nevertheless, the mechanisms by which individual behavior and resource heterogeneity interact to influence population performance are not fully understood. Wang et al. (2006) reported that spatial heterogeneity in vegetation greenness diluted the negative impacts of density dependence on elk and bison populations in Yellowstone, relative to more homogeneous landscapes. Similarly, Post et al. (2007, 2008) found that survival of caribou (*Rangifer tarandus*) calves was positively correlated with spatial variation in plant phenology, but negatively correlated with the magnitude of asynchrony between the timing of births and peak green-up of plants. These results suggest that resource heterogeneity can improve reproductive success of herbivores, but that spatial and temporal variation can influence populations in different ways. Thus, understanding how herbivores respond behaviorally to variation in resources across time and space is critical for establishing links between the nutritional landscape and population performance.

Although multiple vital rates and life-history traits can be affected by behavioral responses of herbivores to the nutritional landscape, pregnancy rates are a particularly useful metric for establishing links with population performance. Pregnancy rates closely reflect the overall nutritional status of a population (McCullough 1979). For example, female deer (*Odocoileus* spp.) that consume higher-quality diets produce twins more frequently, rarely fail to conceive, and reach sexual maturity sooner (McCullough 1979). Similarly, pregnancy rates in elk populations that are not nutritionally limited generally are high, with rates ≤80% indicative of resource limitation (Raedeke et al. 2002). Indeed, Cook et al. (2004b) reported that pregnancy rates of captive adult female elk fed diets low in digestible energy (DE) declined to <70%, and overwinter survival became unlikely when body fat levels dropped below 8%.

Females of long-lived iteroparous mammals typically favor their own survival and the expectation of future reproduction over current reproductive success (Therrien et al. 2007). In accordance with that strategy, abatement of reproductive effort can be exhibited by ungulates at various stages of the reproductive cycle. Cook et al. (2001) reported that inadequate nutrition during summer and autumn prevented estrus and ovulation in elk. In contrast, Milner et al. (2012) found evidence that female moose (*Alces alces*) adjusted investment levels during gestation or lactation in response to environmental variation.

Although pregnancy rates are useful for assessing the consequences of variation in the nutritional landscape and how that landscape is used by herbivores, data on pregnancy are difficult to obtain. Typically, assessing pregnancy rates requires capturing animals and drawing blood (for subsequent assay of pregnancy specific protein B) or using ultrasonography to detect a fetus. Helicopter captures are dangerous and costly, and inevitably cause stress to animals. Pregnancy status can also be determined through fecal sampling; however, this method is time consuming, and fecal assays are prone to error in the absence of validation data for the population being sampled. For these reasons, a dynamic model capable of predicting variation in pregnancy rates at broad spatial scales as a function of 1) spatiotemporal variation in the nutritional landscape, and/or 2) patterns of habitat use by herbivores would be of great value to wildlife managers.

The goals of our research were to develop a series of linked dynamic models for predicting: 1) spatiotemporal variation in the nutritional landscapes available to elk in seven distinct populations in Idaho; and 2) interannual variation in pregnancy rates of those populations as a function of the overall quality and abundance of forage resources available to them and/or how they used those resources. To accomplish this goal we intensively sampled forage quality and abundance in three study areas that spanned a wide range of variation in habitat, topography, and pregnancy rates of elk. We then upscaled those data to model nutritional landscapes in those and four additional study areas as a function of remotely sensed variables, quantified use of those landscapes by GPS-collared female elk, and modeled variation in pregnancy rates of elk populations across space and time based on differences in the respective nutritional landscapes and how they were utilized by elk (Fig. 1). We hypothesized that pregnancy rates of adult female elk would be influenced by variation (i.e., differences in overall quality and heterogeneity) in the nutritional landscapes available to them, in combination with how elk utilized those landscapes (herbivores may exhibit suboptimal patterns of use from a nutritional standpoint in the face of tradeoffs between forage and other factors such as predation risk [Middleton et al. 2013], anthropogenic disturbance, or thermoregulatory stressors [Long et al. 2014]). We predicted that pregnancy rates would be higher in populations where females had greater access to high-quality forage, and in populations where female elk consistently utilized high-quality foraging habitats.

2: Methods

Study areas

We conducted the field-based portion of our study in three elk management zones in Idaho that spanned a wide range of variation in habitat, topography, and pregnancy rates of elk (Fig. 2). The Diamond Creek elk zone was located in southeastern Idaho, the Sawtooth elk zone was located in central Idaho, and our third study area was located in northern Idaho (the South Fork of the Clearwater). Elevations in the Diamond Creek elk zone (42° 33' N; 111°12'W) range from 1,710 to 3,000 m. Average annual precipitation is 404 mm, most of which falls as snow between November and March. Diamond Creek is characterized by long, narrow mountain ranges separated by flat valley floors. The zone is bordered by Wyoming to the east and Utah to the south. The varied topography that characterizes the Diamond Creek zone creates a mosaic of habitat types including aspen (*Populus tremuloides*), sagebrush (*Artemisia* spp.), montane riparian, and mixed-conifer forests. Agricultural lands are concentrated along highway corridors around Grays Lake, along the Bear River, and in the Thomas Fork Valley. The large herbivore community includes moose, mule deer, white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), and elk. Mountain lions (*Puma concolor*) are the primary predator of adult elk, but black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) are also present. There are no known established wolf (*Canis lupus*) packs within the zone, although individuals are occasionally documented traveling through the area. Pregnancy rates in this zone are some of the highest in the state. In 2016 and 2018 all adult animals tested were pregnant (n = 29 and 21, respectively). This is above the state-wide average of 84.7%.

Elevations in the Sawtooth elk zone (44°, 15'N; 115°, 17'W) range from 856 to 3,400 m. Average annual precipitation is 724 mm, falling mostly as snow between November and

March. The western side of the zone is typically warmer and drier, and is characterized by ponderosa pine (*Pinus ponderosa*), montane grassland, and dry mixed conifer forests. The central and eastern portions of the zone are characterized by sagebrush and riparian valleys, Douglas fir (*Pseudotsuga menziesii*) intermediate zones, and alpine habitats above 2,500 m. Fire is a frequent form of disturbance in the Sawtooth zone, with fire return intervals ranging from 7-250 years depending on habitat type. Fires that occur in wilderness areas generally are allowed to burn, resulting in a mosaic of successional stages. This diverse landscape supports a rich herbivore community, including moose, mule and white-tailed deer, elk, pronghorn, bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Primary predators of adult elk include mountain lions and wolves, with black bear, coyotes, and bobcats also present. Pregnancy rates in this zone are typically around 74%, which is below the statewide average.

Our third study area was the South Fork of the Clearwater River (hereafter South Fork) in northern Idaho (45°, 53’N; 115° 47’W). Steep drainages and long ridgelines striate the South Fork basin, with elevations ranging from 467 to 2,200 m. Average annual precipitation is 610 mm, most of which accumulates as snow from January to March. Ponderosa pine forests and dry rangelands are found at lower elevations and along south-facing aspects, whereas western red cedar (*Thuja plicata*) and grand fir (*Abies grandis*) occupy cooler, moister aspects. Pockets of Douglas fir are scattered throughout the study area. White-tailed deer, elk, and moose inhabit the area, and mountain lions and wolves are the primary predators of adult elk. The South Fork elk herd is part of a larger population management unit (PMU); however, most of the animals within this herd summer in the same area and display highly variable pregnancy rates (52.9% in 2014 compared to 74.1% in 2017) that have consistently been below the statewide average since intensive pregnancy sampling began in 2013.

We used detailed data on forage quality and abundance from the Diamond Creek, Sawtooth, and South Fork elk zones to develop models of the nutritional landscape. We then applied those models to four additional zones that fell within the range of variation in habitat and topography encompassed by the three intensively sampled zones, and for which we had data on pregnancy rates of elk. The Beaverhead, Lemhi, and Salmon elk zones are comprised of vegetation types similar to the Sawtooth elk zone, with sagebrush and Ponderosa pine dominating at lower elevations and subalpine and Douglas fir occurring at higher elevations. The Teton elk zone is most similar to the Diamond Creek elk zone, with aspen communities interspersed with riparian areas and sagebrush steppe. Pregnancy rates in all four of these study areas are consistently near or above the statewide average (Table 1).

Modeling the nutritional landscape

During summer (June 1 – July 31) and fall (August 1 – September 15) 2016-2017, we conducted vegetation surveys to quantify quality and abundance of forage available to elk within each of our three primary study areas. We used the 30-m USDA Landfire biophysical settings Potential Vegetation Type (PVT) layer to stratify each study area into similar vegetation associations for sampling (LANDFIRE 2008; Table 2). In the Diamond Creek elk zone we sampled the following 7 PVTs, which made up 91.2% of the zone: 1) intermountain basins montane sagebrush steppe; 2) aspen forest and woodland; 3) montane Douglas-fir forest and woodland; 4) subalpine upper montane riparian; 5) subalpine dry-mesic spruce-fir forest and woodland; 6) subalpine mesic-wet spruce-fir forest and woodland; and 7) montane riparian. In the Sawtooth elk zone we sampled 9 PVTs that made up 98.9% of the zone: 1) subalpine fir woodland and parkland; 2) subalpine dry-mesic spruce-fir forest and woodland; 3) subalpine mesic-wet spruce-fir forest and woodland; 4) ponderosa pine woodland and savanna; 5) intermountain basins montane sagebrush steppe; 6) montane riparian; 7) lower montane foothill-valley-grassland; 8) dry-mesic mixed conifer ponderosa pine-Douglas-fir forest; and 9) dry-mesic montane mixed conifer-grand fir forest. In the South Fork we sampled 4 PVT zones that made up 94% of the study area: 1) Grand fir (*Abies grandis*); 2) western red cedar (*Thuja plicata*); 3) Douglas-fir; and 4) ponderosa pine. Sampling intensity within each PVT was proportional to the relative area of the PVT within each respective zone. To increase sampling efficiency over large areas we grouped sampling units (hereafter referred to as macroplots) into clusters of 3 to 6 macroplots each. We used a generalized random tessellation stratified (GRTS) survey design (Stevens and Olsen 2004) to distribute macroplots within clusters across the landscape subject to the following constraints: 1) to ensure spatial independence macroplots within a cluster were located ≥1.5 km apart in the same PVT and seral stage; 2) macroplots that were located in inaccessible terrain (private land with no access, >60% slope, or >12 km from the nearest road) or the wrong seral stage were either moved to the closest acceptable location or were removed and replaced with a new macroplot; and 3) all macroplots were ≥50 m from a neighboring PVT and 250 m from any road or designated motorized trail.

Each macroplot consisted of two 30-m transects placed 20 m apart, with five 0.75-m^2 quadrats positioned at even intervals along the transect line. We estimated percent tree canopy cover at each macroplot by calculating the proportion of total sampling points (sampling points were placed at 2-m intervals along each transect) at which live canopy intersected the crosshairs of a densitometer.

We used detailed data published by Cook (2002) on elk diets and foraging behavior in a diversity of habitats to identify key understory species to sample, and to group those species into “accepted” and “avoided” categories based on their level of preference by elk (Appendix A). We estimated biomass of key forage species at each macroplot using a double-sampling scheme (Bonham 1989). First, we visually estimated percent horizontal cover of each plant species within each of the 0.75-m^2 quadrats to the nearest 1%. We then selected the most species-rich quadrat in the macroplot for clipping. We clipped all plant species from 2 cm to 2.5 m in height (the approximate maximum foraging height of elk) and separated accepted species by plant part (leaves and inflorescences for forbs and graminoids, leaves and stems for shrubs, and current annual and last years’ growth for conifers); avoided species were not separated. Clipped samples were placed into paper bags and dried in a forced-air convection oven at 100° C for 24 hrs, typically within 2 d of collection. When samples could not be processed within this time frame we stored them loosely in a well-ventilated space until they could be dried. We weighed all dried samples using an Insten jewelry scale (0.1g). Any samples weighing <0.1 g were assigned a “trace” value of 0.01 g. Near the end of each season we inventoried the number of clipped biomass samples obtained for each plant species and conducted additional supplementary sampling when necessary to achieve adequate ($n \geq 10$) species-specific sample sizes for developing predictive equations to estimate biomass in unclipped quadrats.

We used multiple linear regression (Neter et al. 1996) to fit species-specific equations for estimating biomass in all unclipped quadrats (Appendix B). Candidate predictor variables included plant cover, tree canopy cover, and sample date, as well as interactions between plant cover and tree canopy cover, and plant cover and sample date. We log- and square-transformed each variable to test for non-linear relationships between the variable(s) and plant biomass. Log-transforming all variables consistently improved predictive power of regression models (based on adjusted R^2); therefore, we used log-transformed versions of all variables (and associated interactions) in subsequent model selection. We fit 7 models (Appendix B) for each plant species for which we had obtained ≥10 paired biomass and cover measurements (78 species in the Sawtooth and Diamond Creek zones, and 76 species in the South Fork zone). Species with <10 paired biomass and cover measurements were assigned to a life-form group (basal forbs, tall forbs, low shrubs, mid-tall shrubs, evergreen shrubs, graminoids, spruce-firs, or pines). We then fit the same 7 candidate models evaluated for individual species to the combined data for each life-form group. Similarly, when the intercept-only model was the best-fitting model for an individual species with $n \geq 10$, or the adjusted R^2 of the best model for a species was <0.2, we assigned the species to the appropriate life-form group. If inclusion of that species in the life-form model set dramatically reduced adjusted R^2 of the best model (>0.05 reduction in R^2), the species was kept separate. If inclusion of the species in the life-form model either improved or did not significantly reduce R^2 of the best model, it was retained, and the life-form model was used to predict biomass of that species in unclipped plots. We also developed separate regression models for plant parts whenever sample size was sufficient. Tall forbs, graminoids, low shrubs, and mid-tall shrubs were split into "high" and "low" quality parts. We classified upper stems and flowers of tall forbs, inflorescences of graminoids, and shrub leaves as high-quality parts, and lower stalks and stems of forbs and graminoids, and shrub stems as low-quality parts. We fit the same 7 models with log-transformed predictor variables to data that were partitioned by plant part.

To link forage biomass with forage quality across time, space, and species, we collected forage quality samples at each macroplot and pooled those samples within clusters based on life form (forbs, graminoids, or shrubs), plant part, and level of selection (aceepted or avoided). We summed cover estimates for each plant species across all macroplots within a cluster and identified the 5 most prevalent forb and shrub species and the 3 most prevalent grass species; those species were then sampled (clipped) for subsequent assays of nutritional quality. Remaining species were grouped into the following composite samples: 1) accepted forbs, shrub leaves, shrub stems, and grasses; 2) avoided forbs, shrub leaves, shrub stems, grasses; and 3) evergreens. Species that were partitioned into separate parts for biomass estimation also were divided similarly for forage quality analyses (flowers vs. stalks, stems vs. inflorescences, and leaves vs. stems for forbs, graminoids, and shrubs, respectively). Clipped forage quality samples were frozen within 6 hrs of clipping until they could be transferred to paper bags and dried at 40°C in a forced-air convection oven for 24 hrs. Dried samples were ground in a Wiley Mill (1-mm screen) and analyzed for neutral detergent fiber (NDF), acid detergent lignins (ADL) and ash (AIA; Dairy One Forage Lab, Ithaca, New York). We also obtained information on tannin content and gross energy of forage species common to our study areas from published (Wagoner 2011) and unpublished (R. Cook, personal communication) sources.

We estimated digestible energy (DE) content of each forage sample using the summative equations of Robbins et al. (1987), which integrated our data on NDF, ADL, AIA, gross energy, and tannins. We then combined species-specific data on forage biomass and forage quality to estimate usable forage biomass (i.e., biomass of forage that met or exceeded requirements for a female elk at peak lactation; Cook et al. 2002) at each macroplot using the FRESH-Deer model of Hanley et al. (2012). The FRESH-Deer model allowed us to integrate detailed information on both abundance and quality of forage into a single measurement of usable forage biomass at each sampled macroplot. Those spatiotemporally explicit estimates of usable biomass then served as the response variable in subsequent regression models of the nutritional landscape available to elk in each study area and season.

We modeled variation in usable biomass within study areas and seasons as a function of remotely sensed covariates known to influence or reflect vegetation dynamics at broad scales. Candidate predictor variables included the enhanced vegetation index (EVI, an index of vegetation greenness; U.S. Geological Survey, Earthdata), percent canopy cover (National Land Cover Database), PVT, monthly precipitation (PRISM Climate Group), snow water equivalent, snowmelt date, average temperature (Snowpack Telemetry Network), elevation, slope, aspect, soil depth, solar irradiance, and Julian day (Table 3). We extracted values of each of these variables to our macroplot locations using ArcGIS Spatial Analyst Tools. Temporally explicit variables were also matched to the macroplot sample date.

We used multiple linear regression to develop predictive models of usable biomass for each elk zone and season (Table 4). We began by checking for correlations between all pairs of our predictor variables; highly correlated ($|r| > 0.6$) variables were not included together in the same models. We then fit a series of univariate models, each of which included either the untransformed, log-transformed, or squared version of each of our predictor variables. We used those models to determine which version of each variable to bring forward to the next stage of the analysis (based on which version of the variable produced the lowest *p*-value). We also included interactions between canopy cover and PVT, and between EVI and PVT in the model-fitting process based on the premise that the influence of canopy cover and EVI on forage biomass might differ among PVTs. Next, we performed stepwise selection (Zuur et al. 2009) to identify variables and interactions with potential utility for predicting variation in usable forage biomass; variables with $p < 0.15$ were retained. We recorded the adjusted R^2 value as a measure of the predictive strength of the final model for each zone and season.

Our modeling analyses revealed that the riparian PVT in the Diamond Creek elk zone had a high degree of leverage, and the inclusion of that PVT resulted in inflated estimates of usable biomass. Although riparian habitats often are highly productive, riparian habitat in the Diamond Creek elk zone falls almost entirely within the Grays Lake National Wildlife Refuge, which is the largest hardstem bulrush (*Schnoenoplectus acutus*) nursery in North America. Elk rarely use this unpalatable species, and no GPS locations from collared elk in Diamond Creek occurred in the riparian PVT. Therefore, we chose to exclude this PVT from our analyses of the nutritional landscape in the Diamond Creek elk zone.

Animal capture and handling

To evaluate relationships between habitat use and pregnancy rates of elk, we collected data on space-use behavior of females during summer and fall, and population-level pregnancy rates during mid- to late-winter. From mid-December to early February, adult female elk ($n = 15$ to 28 per year in each zone) were captured either by net-gunning or chemical immobilization (3.5 mg of Carfentanil; Wildlife Pharmaceuticals, Fort Collins, CO) from a helicopter. Net-gunned animals were hobbled for safe handling and all animals were blindfolded to reduce stress. Chemically immobilized elk were reversed with an intramuscular injection of 350 mg Naltrexone HCL. At the time of capture, we fitted individuals with GPS radio collars (Lotek Lifecycle Pro500; Vectronic SURVEY Globalstar; Vectronic SURVEY Iridium) that were programmed to record locations every 13 or 23 hours. We extracted a blood sample from the jugular vein that was subsequently assayed for concentrations of pregnancy-specific protein B (PSPB) to determine pregnancy status, and we used tooth wear and gumline recession to assign animals to age classes (yearling, 2-9 years, 10-14 years, and >14 years).

Modeling spatiotemporal variation in pregnancy rates

The ultimate goal of our study was to relate interannual variation in pregnancy rates among elk populations to variation in the nutritional landscapes available to those populations and how they were utilized by elk. Thus, the effective sampling unit for analyses of pregnancy rates was the population-year. We obtained a minimum of 15 pregnancy samples (mean = 26, range = 15 to 47) within each population-year included in our analyses using several different methods. Blood samples obtained at the time of capture were the primary means of gathering data on pregnancy. However, capture efforts are expensive and time consuming, and obtaining an adequate sample across all study areas and years was challenging. Therefore, we also used blood samples collected from hunter-harvested cows (n=19), opportunistic mortalities (n = 1), and fecal samples (n = 184) to estimate pregnancy rates. Fecal samples were collected from February 20 – April 1, 2017-2018 in the South Fork, Sawtooth, Salmon, Beaverhead, and Diamond Creek elk zones, and were analyzed for concentrations of progesterone (P4) and pregnanediol-glucuronide (PdG; Smithsonian

Conservation Biology Institute; 1500 Remount Road, Front Royal, VA). Analysis of paired samples (i.e., female elk from which we obtained both blood and fecal samples) indicated that a progesterone threshold of 0.44 ug/g of dry weight resulted in assignment accuracy of 79%. Whenever possible, fecal samples were obtained from individuals known to be adult females (based on visual observation). When opportunistic fecal samples were collected without observation, samples were tested for sex identification to remove males (Laboratory for Ecological, Evolutionary and Conservation Genetics; University of Idaho, Moscow, ID). We avoided collecting blind samples as much as possible because we did not want to inadvertently include yearlings in our sample. When samples were obtained from unobserved animals, we collected only pellets that were most likely to come from an adult animal (based on pile, pellet, and bed size).

The Idaho Department of Fish and Game has collected data on pregnancy status of elk in several other populations over the past 4-5 years that fall within the range of variation in habitat and topography encompassed by our primary study areas. This provided an opportunity to extrapolate our nutritional landscape models beyond our three primary study areas and increase the number of population-years included in our analyses of variation in pregnancy rates. The Beaverhead elk population summers in both Idaho and Montana and crosses the Beaverhead mountain range during their annual migrations. We obtained annual pregnancy data for this population during 2014-2016 (n = 47, 23, and 16, respectively), and GPS collar data during 2015-2016 (n = 23 and 28, respectively). We also were able to obtain pregnancy data from the Lemhi elk population in 2017 (n = 29), the Salmon elk population in 2014 and 2017 (n = 15 and 28, respectively), and the Teton elk population in 2017 (n=26). The Lemhi and Salmon elk populations occupy similar habitats and overlap at the northern extent of their ranges. Based on the level of similarity in habitat we used seasonal models developed for the Sawtooth zone to predict variation in the nutritional landscapes available to elk in the Beaverhead, Lemhi, and Salmon populations. The Teton elk population occupies habitats similar to the Diamond Creek zone; therefore, we chose to use models developed for Diamond Creek to predict usable biomass within the Teton elk zone.

We used all available GPS collar data to delineate a Minimum Convex Polygon (MCP) boundary for each elk population. We then cast 1,000 random locations per PVT within each population MCP to quantify spatiotemporal variation in usable forage biomass and to facilitate a direct comparison of the nutritional landscapes available to elk across population-years. At each random location we used the appropriate zone- and season-specific model to estimate usable forage biomass at that location as a function of the environmental covariates identified as important predictors in the model-selection process. Because our models were both spatially and temporally explicit, the predicted values of usable biomass at random locations were calculated using the seasonal midpoints (June 28 and August 28 of each year) for time-dependent variables. We then calculated the mean, maximum, median, upper and lower quartiles, and the coefficient of variation (CV; used as a metric of heterogeneity in the nutritional landscape) of usable biomass at random locations within each PVT, zone, and year. Following this analysis we used the same approach to estimate usable biomass at each elk GPS location and each sample macroplot location, and to calculate the same set of descriptive statistics. Individual elk with <40 locations, or with three gaps of ≥3 days between fixes within a season, were excluded from our analyses. Additionally, locations that occurred in un-sampled PVTs (<13% of all locations) were removed.

We considered the mean, max, and CV of predicted usable biomass in summer and fall as candidate predictor variables in regression models of pregnancy rates. Because we had data on pregnancy rates of elk for more population-years ($n = 18$) than we had summer-fall GPS data ($n = 10$), we chose to construct two separate *a priori* model sets that represented: 1) effects of the nutritional landscape in general on pregnancy rates; and 2) effects of elk use of the nutritional landscape on pregnancy rates. Prior to modeling we used a correlation matrix to identify collinearity between variables ($|r| > 0.6$ considered to be correlated). In the first model set, max and CV of usable biomass in fall were positively correlated ($r = 0.77$); in the second model set, summer mean and max, summer mean and fall mean, and summer max and fall mean of usable biomass were positively correlated ($r = 0.95$, 0.77, and 0.81, respectively). Correlated variables were not included together in the same model. We standardized all variables to facilitate direct comparison of model coefficients. We ranked models using AIC corrected for small sample size (AIC_c) and calculated AIC model weights. We then used model averaging to produce parameter estimates for each variable within the 90% confidence set of models (Burnham and Anderson 2002). Model-averaged parameter estimates were weighted based on the Akaike weights (*wi*) associated with each model (Burnham and Anderson 2002; Gillies et al. 2006; Long et al. 2014). Positive parameter estimates indicated that pregnancy rates increased with increasing values of the variable, whereas negative parameter estimates indicated the opposite. Finally, we recorded the adjusted R^2 value of the best model in each set as a measure of the predictive power of that model.

3: Results

Usable forage biomass varied considerably among elk management zones, PVTs, and seasons (Fig. 3). Overall, usable biomass tended to be higher during summer and in more mesic PVTs across all three zones. Regression models for explaining spatiotemporal variation in usable biomass generally performed well in each of our three primary study areas (Fig. 4), with adjusted R^2 values ranging from 0.26 (Sawtooth summer model), to 0.61 (Diamond Creek fall model; Table 4). Top models for fall had greater predictive power than top models for summer in the Diamond Creek and Sawtooth zones, whereas seasonal models for the South Fork of the Clearwater zone performed similarly (Table 4). The relative availability of high-quality forage in each of our three intensively sampled elk management zones changed seasonally. In summer, the estimated proportion of each zone categorized as high-quality foraging habitat (i.e., the proportion of random locations within the zone that fell into the top 25% of the range of predicted usable biomass values across all zones and years) was highest in the Teton (90.7%) and Diamond Creek (31.47%) zones, lowest in the Beaverhead (8.8%), Salmon (13%), and Sawtooth (13.5%) zones, and intermediate in the South Fork zone (26.5%;) and the Lemhi zones (28.3% Fig. 5). The opposite trend was observed for the proportion of each zone categorized as low-quality foraging habitat (i.e., the lowest 25% of the range of predicted usable biomass values across all zones and years; Fig. 5). Similarly, during fall the greatest proportion of high-quality foraging habitat was observed in the Teton zone, followed by the South Fork, Lemhi, Diamond Creek, Salmon, Beaverhead, and Sawtooth zones (Fig. 5). In some zones, the majority of the landscape was classified as either high- or low-quality, with habitat of intermediate quality being relatively rare [e.g., Lemhi (summer) and Diamond Creek and Teton zones (fall)].

Use of the nutritional landscape by elk also differed markedly among populations in our three primary study areas. During summer, usable biomass of forage was lower at locations used by elk than at random locations in the Diamond Creek and Sawtooth zones (Fig. 6), suggesting that elk in those populations were not optimizing their use of the nutritional landscapes available to them during summer. In contrast, usable biomass was higher, on average, at locations used by elk than at random locations during summer in the South Fork of the Clearwater, suggesting that elk in that population selected habitats that increased their access to high-quality forage (Fig. 6). Moreover, the difference in usable biomass between used and random locations was most pronounced (i.e., evidence of selection for high-quality forage was strongest) in the South Fork population during 2017, when mean usable biomass at random locations reached the lowest point observed during our study (Fig. 6). During fall, mean usable biomass at locations used by elk tended to track usable biomass at random locations across study areas and years, suggesting that elk were not strongly selective of the nutritional landscape during that season (Fig. 6).

Our top model relating pregnancy of elk to the nutritional landscape explained 60% of the variation in pregnancy rates among 18 elk population-years in Idaho (adjusted R^2 = 0.60; Table 5), and included maximum usable biomass available to elk in summer and fall (Summer_max and Fall_max), as well as the coefficient of variation of usable biomass during summer (Summer_CV). Model-averaged parameter estimates were positive for all three predictor variables, indicating that pregnancy rates increased in population-years where the maximum usable biomass available was higher in summer and fall, and when there was more variation (heterogeneity) in the nutritional landscape during summer (Fig. 7).

Our top model for relating pregnancy of elk to how they used the nutrtional landscape explained 75% of the variation in pregnancy rates among 10 elk population-years in Idaho (adjusted $R^2 = 0.75$; Table 6), and included the coefficient of variation of usable biomass during summer and fall (Summer_CV and Fall_CV). Model-averaged parameter estimates were negative for Summer_CV and positive for the Fall_CV, indicating that greater consistency in use of the nutritional landscape by elk during summer was positively related to pregnancy rates, whereas the opposite was true during fall.

4: Discussion

Variation in pregnancy rates was positively related to both the maximum value of usable forage biomass and the degree of heterogeneity in the nutritional landscape across elk management zones in Idaho. This supports our hypothesis that pregnancy is mediated by habitat quality, and provides additional empirical evidence of a fundamental link between the nutritional landscape in summer and fall and population performance of elk. Our results also suggest, however, that the relationship between habitat quality and pregnancy rates of elk may be more nuanced than we anticipated. Mean usable biomass of available forage was not included in any of the top models for explaining variation in pregnancy rates. Instead, the combination of heteroegeneity and maximum quality of available forage was most influential. This suggests that elk need access to at least some patches of high-quality forage to achieve a sufficient level of condition to ensure conception, but that habitat diversity is also important. Previous research indicates that large herbivores like elk commonly face tradeoffs between forage and other factors such as risk of predation (Hebblewhite and Merrill 2009, Pierce et al. 2010), competition (Stewart et al. 2005), or costs of thermoregulation (Long et al. 2014). The influence of such tradeoffs on fitness, however, may attenuate in heterogeneous landscapes where herbivores have a greater array of choices available for simultaneously meeting demands for forage, security, and thermal cover.

The negative relationship between variation in usable forage biomass at locations used by elk during summer and pregnancy rates suggests that more consistent use of the nutritional landscape increases the probability of becoming pregnant. Variation in behavior among individuals can result from a variety of factors, and whether such variation is positively or negatively related to metrics of performance such as pregnancy rates depends on context. For example, animals often exhibit state-dependent responses to tradeoffs between factors that influence fitness (McNamara and Houston 1996, Long et al. 2014), and state dependence can produce a wide variety of foraging and movement strategies among individuals in a population (Morales et al. 2005, Forester et al. 2007, van Beest and Milner 2013). State-dependent strategies are adaptive (i.e., increases fitness) at the individual level, however, the variation they produce is unlikely to be negatively related to metrics of population performance. In contrast, even in the absence of complex tradeoffs, variation in behavior among individuals may still emerge when animals are unable to consistently optimize their foraging and movement patterns due to the complexity of the landscape (Belovsky 1984, Kie 1999). In such scenarios increased variation among individuals may reflect an increase in the prevalence of suboptimal patterns of behavior, thereby producing a negative relationship between variation in behavior and population performance.

Our results indicate that inconsistent use of the nutritional landscape by elk during summer negatively impacted the probability of becoming pregnant, even while variation in the nutritional landscape itself had a positive effect on pregnancy. This suggests that 1) within the ranges of variation included in our study, habitat complexity did not limit the ability of elk to optimize their use of the nutritional landscape, and 2) other factors such as predation risk or anthropogenic disturbance likely resulted in suboptimal use of the nutritional landscape and greater variation among individuals in some populations. We caution, however, that small sample size in our analysis of locations used by elk limits our ability to draw strong conclusions from those data. Moreover, it is difficult to explain why the effect of individual variation in behavior (i.e., use of the nutritional landscape) on pregnancy of elk changed direction between summer and fall. Thus, we suggest that this effect be considered a hypothesis worthy of additional testing.

Regardless of the cause, our results clearly demonstrate that elk in some management zones used locations where high-quality forage was less abundant than what was generally available in the landscape. In other words, elk in some populations appeared to avoid high-quality foraging habitats, especially during summer (e.g., the Diamond Creek and Sawtooth populations; Fig. 6), whereas the opposite was true in other populations (e.g., the South Fork population; Fig. 6). One potential explanation for this pattern is the need to avoid risky habitats, especially when offspring are young and vulnerable. Bjorneraas et al. (2012) reported that female moose in Norway with a calf at heel selected for both food and concealment cover when both were available, but tended to select more strongly for concealment cover when forced to make a tradeoff between the two. Similarly, Atkins et al. (in press) reported that bushbuck (a medium-sized browsing antelope) abandoned high-quality foraging habitats and entered dense cover when exposed to auditory or olfactory cues of predation risk. Dilution of this pattern of behavior in the fall during our study is consistent with an indirect effect of predators; by August, calves are larger and more mobile, potentially allowing females to utilize higher-quality habitats without posing undue risk to their offspring.

Similar to predation risk, human disturbance can impact habitat use by herbivores. Previous studies have documented displacement of elk (Paton et al. 2017), mule deer (Wisdom et al. 2004), and moose (Lykkja et al. 2009) from high-quality habitats by human activity. Although hunting pressure is typically the focus of such studies, increasing participation in non-consumptive use of the backcountry (e.g., hiking, camping, etc.) and a recent surge in off-road vehicle use in many areas could be altering habitat use by elk in the spring and summer months. For example, the Sawtooth elk herd is likely exposed to more recreational activity by humans than many elk population in the state, with extensive motorized and non-motorized trail systems radiating out from arterial roads. The Diamond Creek elk zone also is heavily roaded, and off-road vehicle use is increasing each year. Additionally, domestic livestock operations, particularly for sheep, are common in Diamond Creek. In contrast, the South Fork of the Clearwater is not as popular with recreationists outside of the hunting season, and although logging is still a common practice in the area, grazing is minimal, as is the existing trail system. Such variable levels of human disturbance could help to explain the differences we observed among seasons and populations in how elk used the nutritional landscape available to them.

Elk also expend large amounts of energy on thermoregulation during summer (Long et al. 2014), and thus optimal use of the nutritional landscape may sometimes be hindered by the need to reduce costs of thermoregulation and activity (Long et al. 2014, 2016). Those costs, especially in combination with the significant energetic demands and heat production associated with lactation (Loudon et al. 1987, Król and Speakman 2003, Monteith et al. 2014) could force female elk with calves to select habitats with greater thermal cover (i.e., more canopy cover). Canopy cover was negatively correlated with usable biomass ($r = -0.43$, -0.26, and -0.63 in Diamond Creek, the Sawtooths, and the South Fork respectively during summer, and $r = -0.28$ and -0.57 in the Sawtooths and South Fork during fall [canopy cover was not a significant predictor of usable biomass in Diamond Creek during fall]) in our study areas, suggesting that there was indeed a tradeoff between forage and thermal cover.

It is also important to note that selection of higher-quality foraging habitat did not necessarily translate directly into higher pregnancy rates. For example, the South Fork elk population consistently used sites that provided more usable forage biomass than occurred at random in the landscape (Fig. 6), suggesting a high degree of selection. Yet, that population exhibited some of the lowest pregnancy rates observed in our study (Table 1). Strength of selection for a high-quality resource often varies as a function of its availability (Wam and Hjelhord 2010, Anderson et al. 2012), and thus in some instances measures of use alone (as opposed to selection, defined as used relative to availability) may provide a more direct link between animal behavior and fitness.

One caveat in interpreting our results is that we did not have data on lactation status for any of our collared elk, and we were therefore unable to account for the influence of lactation status on probability of pregnancy. Several studies have demonstrated the increased energy demands imposed on female herbivoes by lactation (e.g., Hamel and Côté 2007). Lactation can affect a female’s ability to garner sufficient energy reserves to facilitate conception in the fall (Festa-Bianchet et al. 1998) even when high-quality forage is available. As a result, variation in lactation status among females could decouple relationships between the nutritional landscape and pregnancy rates to some degree. Nevertheless, female herbivores can adjust their behavior to compensate for the additional demands of lactation (e.g., increase time spent foraging, bite rate, or habitat selection: Rachlow & Bowyer 1998; Ruckstuhl & Bianchet 1998; Hamel and Cote 2009). Moreover, we suggest that our inability to account for lactation status in models of pregnancy rates would, if anything, reduce our ability to detect relationships between the nutritional landscape and pregnancy, thus making our results conservative.

The ability to model variation in pregnancy rates as a function of landscape characteristics derived from remotely sensed data could be of great value to wildlife management agencies. Such models could reduce the cost and risks associated with capturing animals, which has become a high priority for management agencies throughout the country. Models such as those developed in our study provide a means of estimating a population parameter that is difficult to aquire, but that is important for larger population-level models (e.g., integrated population models; Arnold et al. 2017, Horne et al. 2018). Perhaps most importantly, using models that are grounded in principles of nutritional ecology to estimate pregnancy rates holds potential to shed light on the mechanisms underlying variation in this important vital rate. The modeling approach used in our study can be used by wildlife and land management agencies to assess habitat quality at a relatively fine spatial and temporal scale, as well as to map variation in the nutritional landscape across larger areas.

Spatiotemporally dynamic models are increasingly being used to track environmental changes and enable managers to take more proactive approaches to management of wildlife and their habitat. To ensure maximum accuracy of such models, however, it will continue to be important to update them frequently with ground-truthed data and updated GIS layers. Furthermore, predictive models should not be used as a standalone method for quantifying population parameters, but should be used in combination with other available datasets in order to achieve maximum accuracy.

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Tables

Table 1: Pregnancy rates of elk (*Cervus canadensis*) in each of seven elk management zones in Idaho, USA, estimated from blood samples, fecal samples, or both between 2013 and 2018.

Zone	Year	Pregnancy rate	Sample size (blood)	Sample size (fecal)
Diamond Creek	2015-16	1.00	n = 24	
	2016-17	0.84	n = 26	n = 30
	2017-18	1.00	n = 20	
Sawtooth	2014-15	0.86	n = 21	
	2015-16	0.67	n = 12	
	2016-17	0.68	n = 2	n = 25
	2017-18	0.75	n = 11	n = 19
South Fork	2013-14	0.53	n = 17	
	2014-15	0.80	n = 15	
	2015-16	0.73	n = 11	
	2016-17	0.75	n = 0	n = 28
	2017-18	0.66	n = 0	n = 32
Beaverhead	2014-15	0.87	n = 23	
	2015-16	0.93	n = 14	
	2016-17	0.89	n = 4	n = 43
	2017-18	0.85	n = 13	
Salmon	2014-15	0.93	n = 15	
	2017-18	0.82	n = 28	
Lemhi	2017-18	0.93	n = 27	
Teton	2017-18	0.90	n = 21	
Statewide Average	**2014 -18**	**0.88**	**n = 598**	**n = 177**

Table 2: Potential vegetation types (PVT) sampled in each of three elk management zones in Idaho, USA, and the percentage of each zone comprised by each PVT.

Zone	Potential vegetation type	PVT code	Percent of zone
Diamond Creek	Intermountain Basins Montane Sagebrush Steppe	ARTRW	34.8
	Rocky Mountain Aspen Forest and Woodland	POTR	18.3
	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland	PSME	12.5
	Rocky Mountain Subalpine Upper Montane Riparian Systems	Riparian	4.8
	Rocky Mountain Subalpine Dry-Mesic Spruce-fir Forest and Woodland	ABLA_dry	5.5
	Rocky Mountain Montane Riparian Systems	Riparian	5.6
	Rocky Mountain Subalpine Mesic-Wet Spruce-fir Forest and Woodland	ABLA_wet	9.7
Sawtooths	Northern Rocky Mountain Subalpine Woodland and Parkland	ABLA_parkland	18.6
	Rocky Mountain Subalpine Dry-Mesic Spruce-fir Forest and Woodland	ABLA_dry	22.8
	Rocky Mountain Subalpine Mesic-Wet Spruce-fir Forest and Woodland	ABLA_wet	7.3
	Northern Rocky Mountain Ponderosa Pine Woodland and Savanna	PIPO	12.9
	Intermountain Basins Montane Sagebrush Steppe	ARTRW	8.6
	Northern Rocky Mountain Riparian Systems	Riparian	2.1
	Northern Rocky Mountain Lower-Montane Foothill-Valley Grassland	FVG	1.6
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest - Ponderosa pine-Douglas-fir	Mixed_PIPO-PSME	8.0
	Middle Rocky Mountain Montane Douglas-fir Forest and Woodland	PSME	10.2
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest - Grand fir	Mixed_ABGR	7.8
South Fork	Grand fir	ABGR	77.5
	Douglas-fir	PSME	8.8
	Western Red Cedar	THPL	5.6
	Ponderosa pine	PIPO	2.4

Table 3: Sources of candidate predictor variables for modeling usable biomass.

Predictor variable layer	Source
April snow water equivalent (mm)	National Water and Climate Center, Snowpack Telemetry Network, https://www.wcc.nrcs.usda.gov/snow/
Sample month snow water equivalent (mm)	
Previous month snow water equivalent (mm)	
Snow melt date	
Average sample month temperature (C°)	
Sample month precipitation (mm)	PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu
Previous month precipitation (mm)	
Potential Vegetation Type	LANDFIRE. 2008. Biophysical Settings Layer, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey. http://landfire.cr.usgs.gov/viewer/.
Enhanced Vegetation Index	NASA LP DAAC MOD13Q1 MODIS/Terra Vegetation Indices 16-DAY l3 Global 250m SIN Grid V005. NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaac.usgs.gov)
Percent canopy cover	National Land Cover Database, https://catalog.data.gov/dataset/national-land-cover-database-nlcd-percent-tree-canopy-collection
Elevation (m)	Inside Idaho, http://insideidaho.org/popular_data.html
Soil Depth (mm)	Natural Resources Conservation Service, https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/

Table 4: Top models (based on adjusted R^2) for predicting spatial variation in usable forage biomass in the Diamond Creek (DC), Sawtooth (SAW), and South Fork of the Clearwater (FORK) elk management zones in Idaho, USA, during summer (June 1 – July 31) and fall (August 1 – September 15), 2016-2017. Predictor variables are defined as follows: 1) CanCov = percent canopy cover; 2) MnPrecip = average precipitation (mm) during the month in which forage sampling occurred; 3) AprilSWE = snow water equivalent in April (mm); 4) EVI = Enhanced Vegetation Index; 5) PVT = potential vegetation type; 6) SampleSWE = snow water equivalent (mm) during the month in which forage sampling occurred; 7) AvgTemp = average temperature (C°) during the month in which forage sampling occurred; 8) MeltDate = the first day snow levels equaled 0 cm and snow remained absent for the remainder of the sampling season; 9) PrevMnPrecip = average precipitation (mm) during the month prior to forage sampling; 10) Elevation = elevation (m); and 11) Slope = slope (degrees).

Zone_Season	Nutritional model	Adjusted R^2
DC_Summer	Usable Biomass = CanCov + AprilSWE + Elevation + MnPrecip + EVI + PVT	0.44
DC_Fall	Usable Biomass = EVI^2 + PVT + EVI^2 : PVT	0.61
SAW_Summer	Usable Biomass = CanCov + Elevation + log(Slope) + PVT + SampleSWE	0.26
SAW_Fall	Usable Biomass = PVT + log(CanCov) + AprilSWE + EVI	0.56
FORK_Summer	Usable Biomass = CanCov + EVI + AvgTemp + MeltDate + Elevation	0.47
FORK_Fall	Usable Biomass = CanCov + EVI + log(PrevMnPrecip)	0.44

Table 5: Candidate models for explaining interannual variation in pregnancy rates of elk (*Cervus canadensis*) in seven elk-management zones in Idaho, USA (*n* = 18 population-years; see Table 1 for detailed data on sampling units) as a function of the nutritional landscape. Descriptive statistics used to represent the nutritional landscape included the mean, max, and coefficient of variation (CV) in usable forage biomass available to elk in each population-year during summer (June 1 – July 31) and fall (August 1 – September 15); details on the calculation of those statistics are provided in the main text. We report relative (AIC_c) and absolute (adjusted R^2) measures of fit for each model, as well as the Akaike weight (w_i).

Model	**AICc**	**ΔAICc**	**w_i**	**Adjusted R^2**
Pregnancy = Summer_max + Summer_CV + Fall_max	137.61	0.00	0.36	0.60
Pregnancy = Summer_CV + Fall_CV	137.79	0.18	0.33	0.53
Pregnancy = Summer_max + Fall_max	139.34	1.73	0.15	0.49
Pregnancy = Summer_max + Summer_CV + Fall_CV	140.01	2.40	0.11	0.54
Pregnancy = Summer_Max	144.33	6.72	0.01	0.24
Pregnancy = Fall_max	145.21	7.60	0.01	0.20
Pregnancy = Fall_CV	145.93	8.32	0.01	0.17
Pregnancy = Summer_max + Summer_CV	146.96	9.35	0.00	0.22
Pregnancy = Summer_CV	147.05	9.44	0.00	0.11
Pregnancy = Summer_mean + Summer_max	147.58	9.97	0.00	0.19
Pregnancy = Fall_mean + Fall_max	148.19	10.58	0.00	0.16
Pregnancy = Fall_mean + Fall_CV	149.29	11.68	0.00	0.11
Pregnancy = Summer_mean + Summer_CV	149.45	11.84	0.00	0.10
Pregnancy = Fall_mean	150.01	12.40	0.00	-0.04
Pregnancy = Summer_mean + Summer_max + Summer_CV	150.13	12.52	0.00	0.20
Pregnancy = Summer_mean	150.32	12.71	0.00	-0.06

Table 6: Candidate models for explaining interannual variation in pregnancy rates of elk (*Cervus canadensis*) in seven elk-management zones in Idaho, USA (*n* = 10 population-years; see Table 1 for detailed data on sampling units) as a function of how elk used the nutritional landscape (i.e., estimates of usable forage biomass at locations used by GPS-collared elk). Descriptive statistics used to represent the nutritional landscape included the mean, max, and coefficient of variation (CV) in usable forage biomass available to elk in each population-year during summer (June 1 – July 31) and fall (August 1 – September 15); details on the calculation of those statistics are provided in the main text). We report relative (AIC_c) and absolute (adjusted R^2) measures of fit for each model, as well as the Akaike weight (w_i)

Model	**AICc**	**ΔAICc**	**w_i**	**Adjusted R^2**
Pregnancy = Summer_CV + Fall_CV	76.23	0.00	0.57	0.75
Pregnancy = Fall_CV	78.10	1.88	0.22	0.52
Pregnancy = Summer_max + Fall_max	80.35	4.12	0.07	0.62
Pregnancy = Summer_max	82.54	6.31	0.02	0.25
Pregnancy = Summer_max + Summer_CV + Fall_CV	82.68	6.45	0.02	0.77
Pregnancy = Summer_mean	82.69	6.46	0.02	0.24
Pregnancy = Fall_max	83.56	7.33	0.01	0.17
Pregnancy = Summer_max + Summer_CV + Fall_max	83.60	7.37	0.01	0.75
Pregnancy = Fall_mean + Fall_max	83.89	7.66	0.01	0.46
Pregnancy = Fall_mean + Fall_CV	84.10	7.88	0.01	0.45
Pregnancy = Summer_CV	84.44	8.21	0.01	0.09
Pregnancy = Fall_mean	86.08	9.85	0.00	-0.07
Pregnancy = Summer_max + Summer_CV	86.26	10.03	0.00	0.32
Pregnancy = Summer_mean + Summer_CV	87.75	11.52	0.00	0.21

Figures

Figure 1: Conceptual model illustrating our approach to relating pregnancy rates of elk (*Cervus canadensis*) to spatiotemporal variation in the nutritional landscape and how that landscape is used by elk. We first combined detailed data on biomass and quality of forage plants consumed by elk with data on nutritional requirements for supporting lactation to estimate "usable" forage biomass at each sampled location. We then used regression models to explain spatiotemporal variation in usable biomass as a function of key enviormental covariates, and used the resulting models to map the nutritional landscape available to elk in each population-year included in our study. Finally, we related metrics of the nutritional landscape and how it was used by elk to pregnancy rates in a second regression analysis.

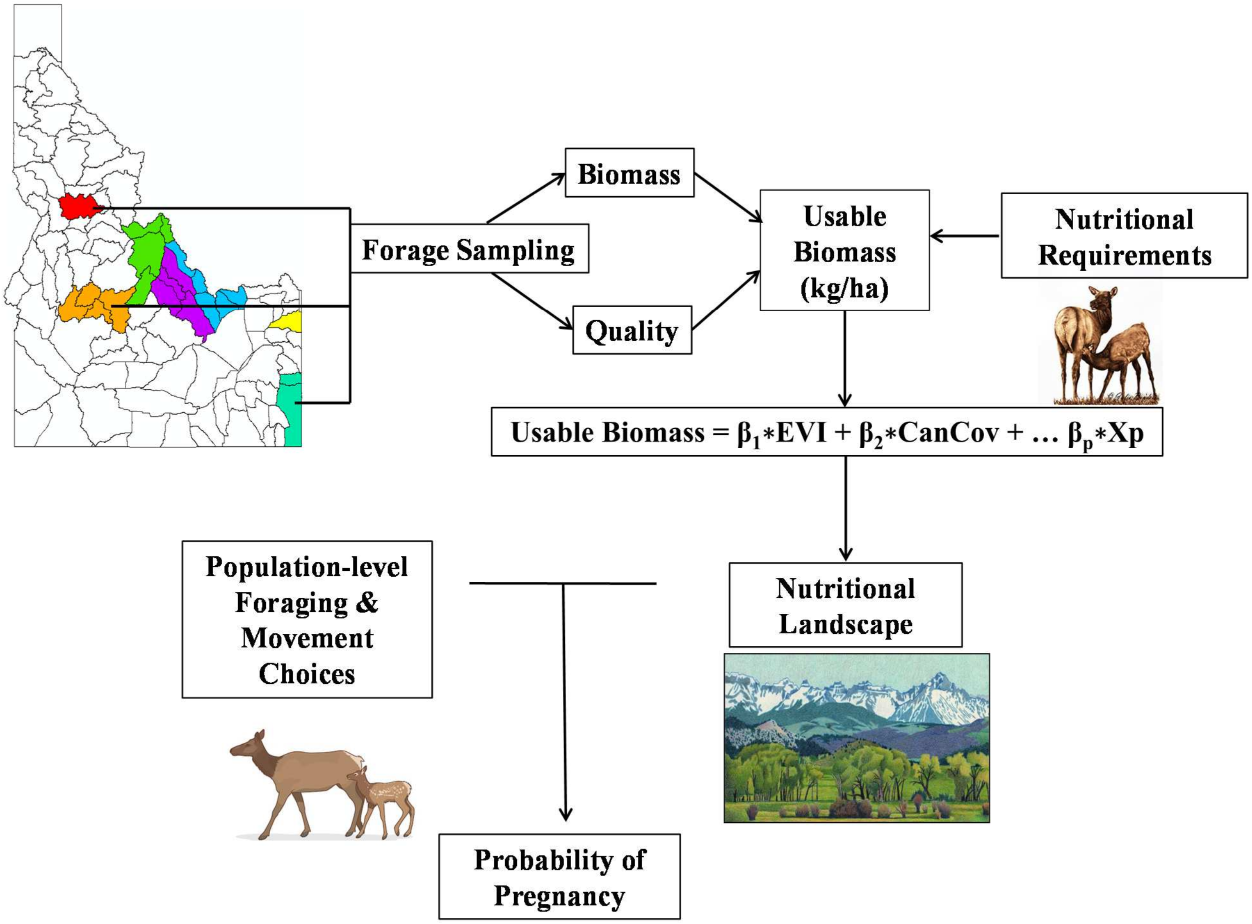


Figure 2: Study area locations in Idaho, USA. Intensive vegetation sampling was conducted in the South Fork of the Clearwater River drainage and the Sawtooth and Diamond Creek elk zones.

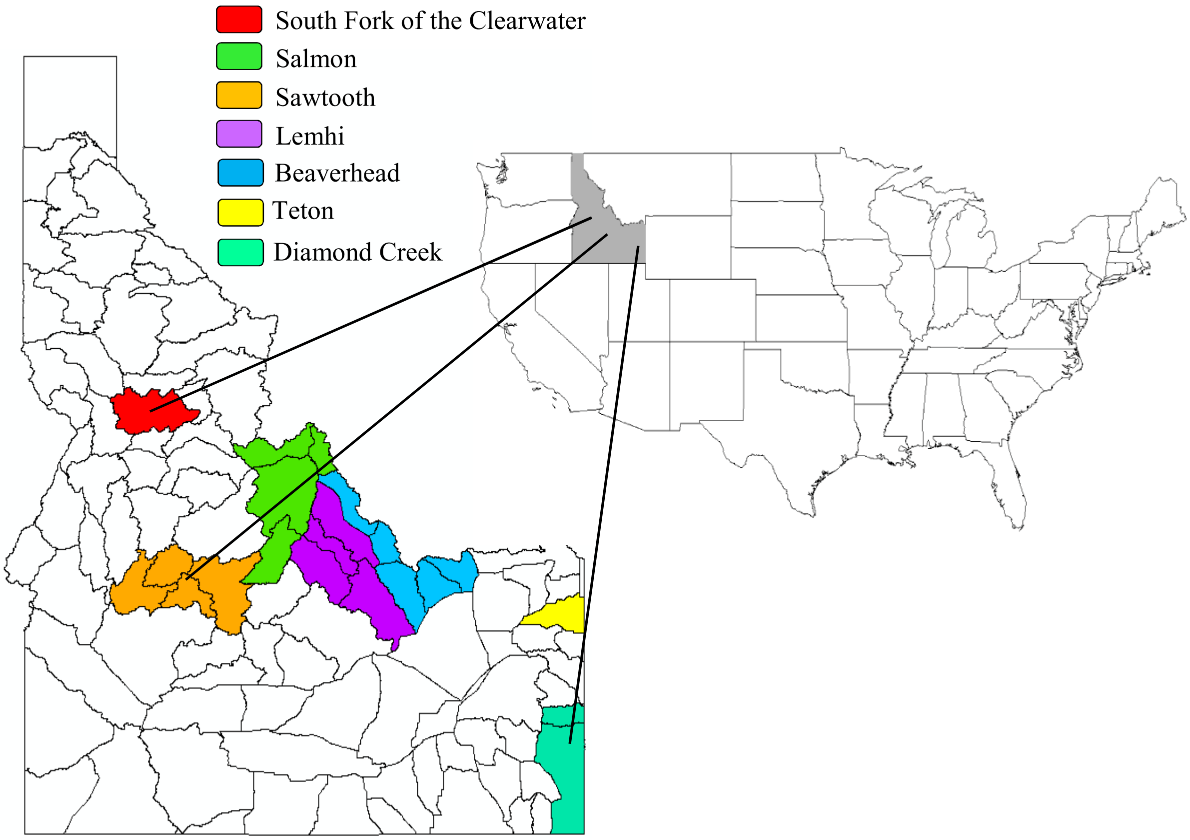


Figure 3: Mean (±90% CI) usable biomass of forage (kg/ha) in potential vegetation types comprising >90% of each of three elk management zones in Idaho, USA during summer (May 25–July 1) and fall (August 1–September 15) of 2016 and 2017. Acronyms for each potential vegetation type are described in Table 2.

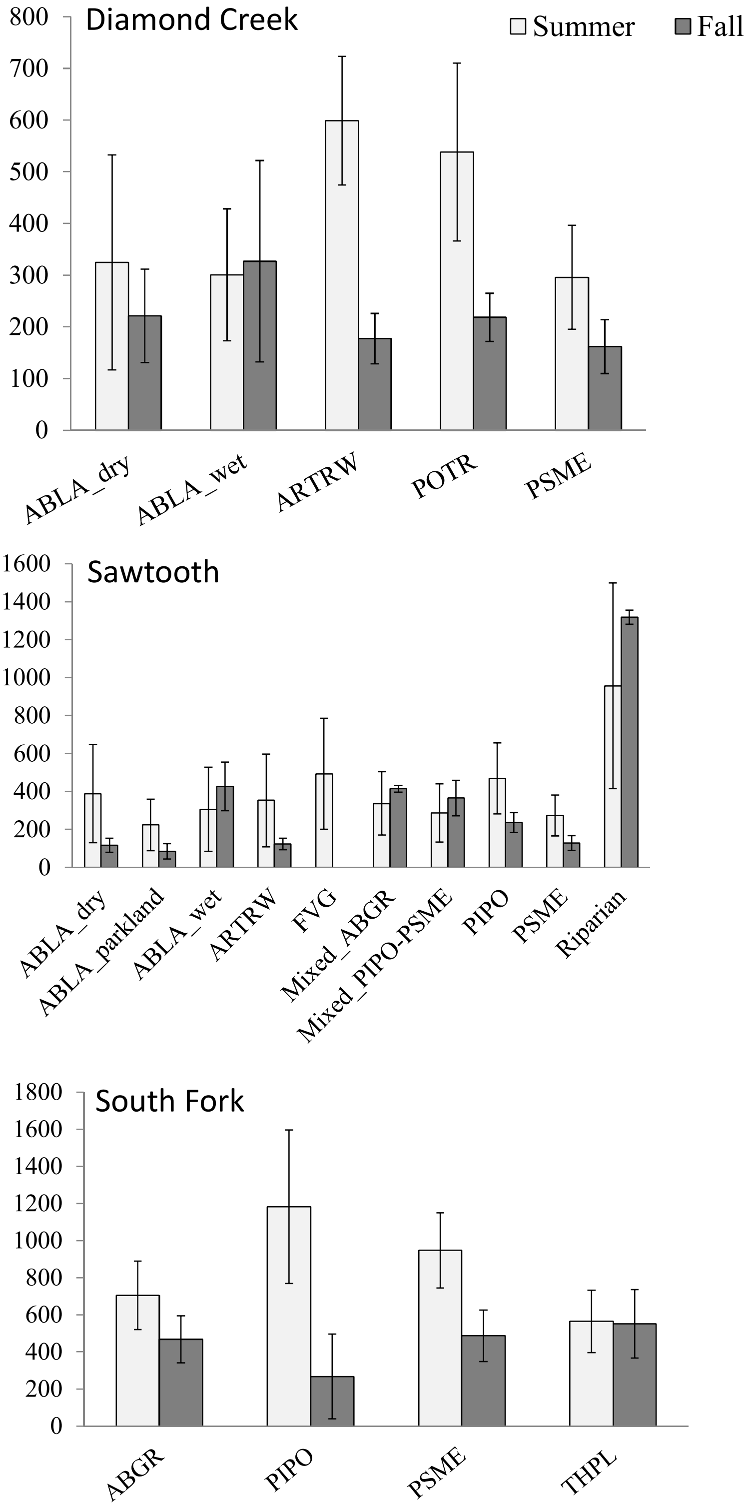


Figure 4: Relationship between measured and model-predicted (models presented in Table 4) values of usable forage biomass at macroplot locations sampled in three elk management zones in Idaho, USA during summer (June 1 – July 31) and fall (August 1- September 15) of 2016 and 2017.

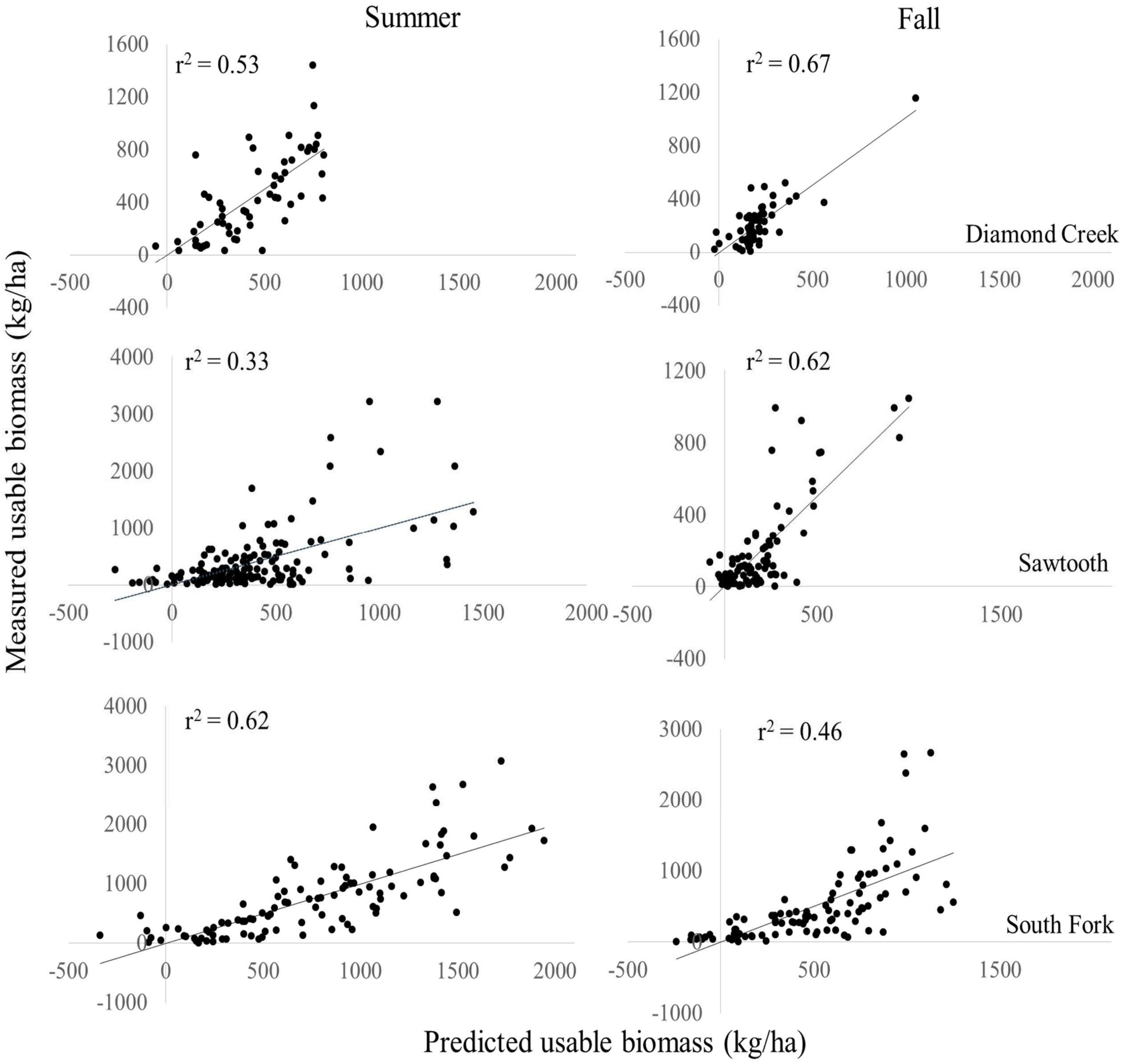


Figure 5: Percent of randomly sampled locations in each zone during summer (June 1 – July 31) and fall (August 1 – September 15) that fell into each of four quartiles of usable forage biomass (low = <245 kg/ha, mid-low = 245-423 kg/ha, mid-high = 423-705 kg/ha, and high = >705 kg/ha).

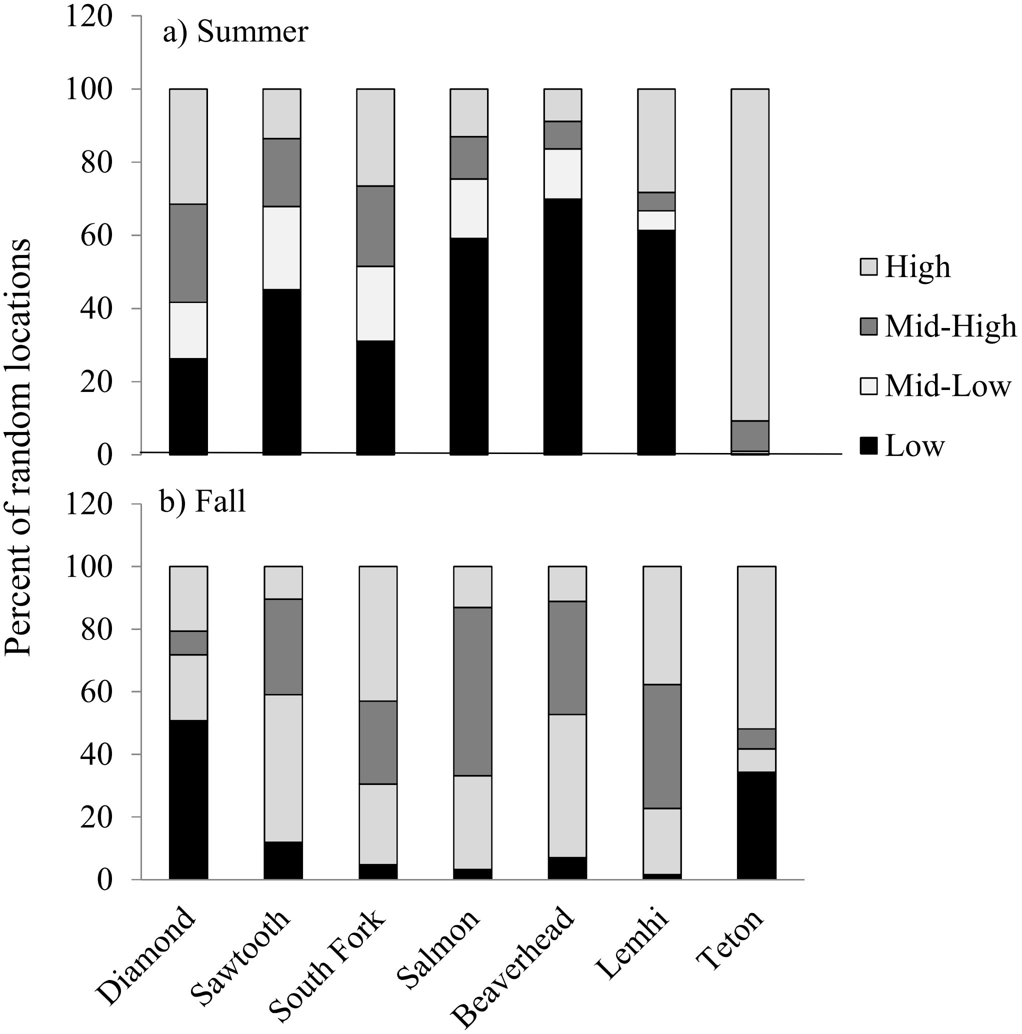


Figure 6: Boxplots of predicted usable biomass of forage at random locations (R; 1,000 locations per potential vegetation type) and locations used by elk (*Cervus canadensis*: U; derived from GPS-collar data)in each of four elk management zones in Idaho, USA for which we obtained GPS-collar data during summer (June 1 – July 31) and fall (August 1 – September 15).

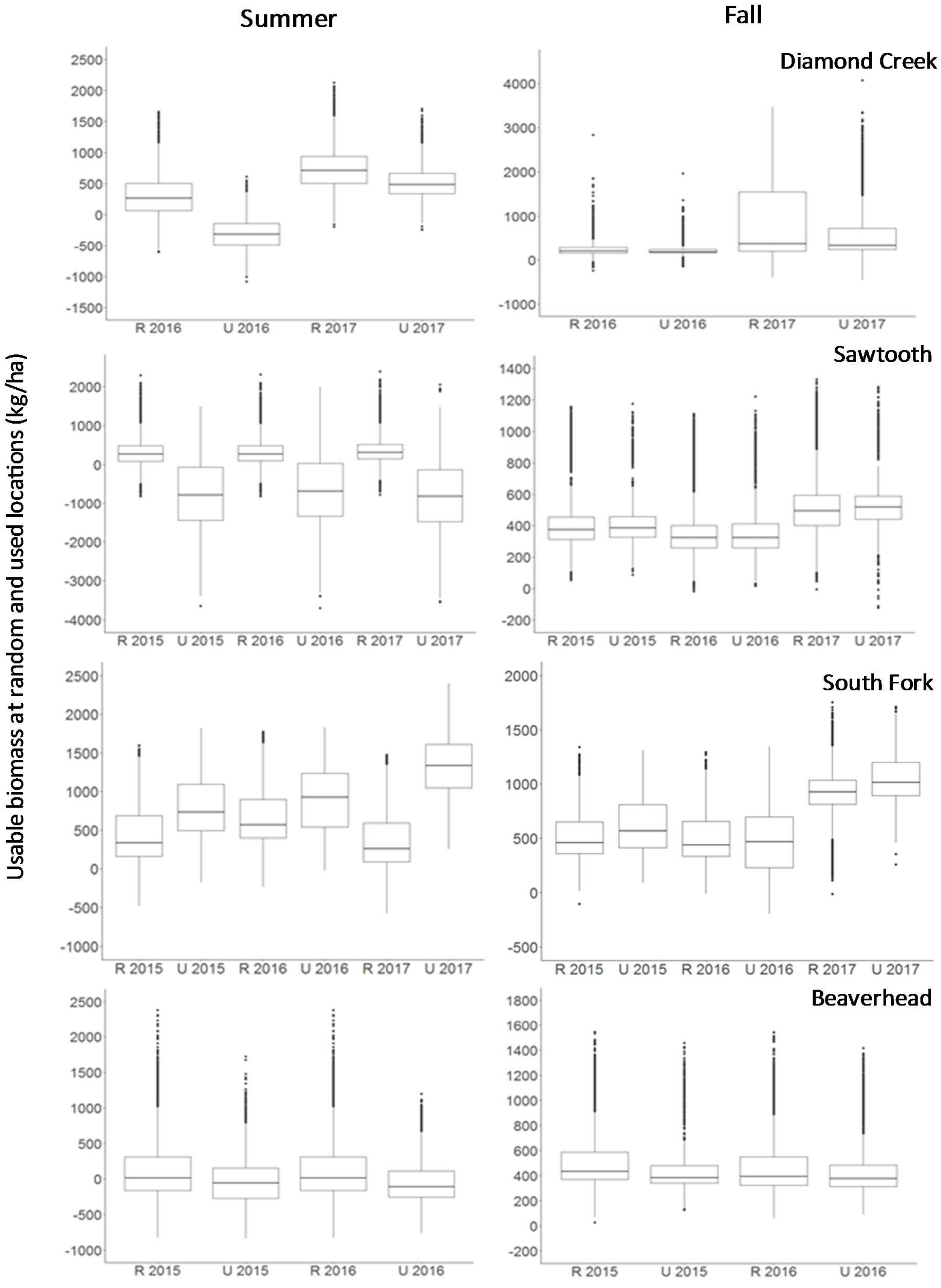
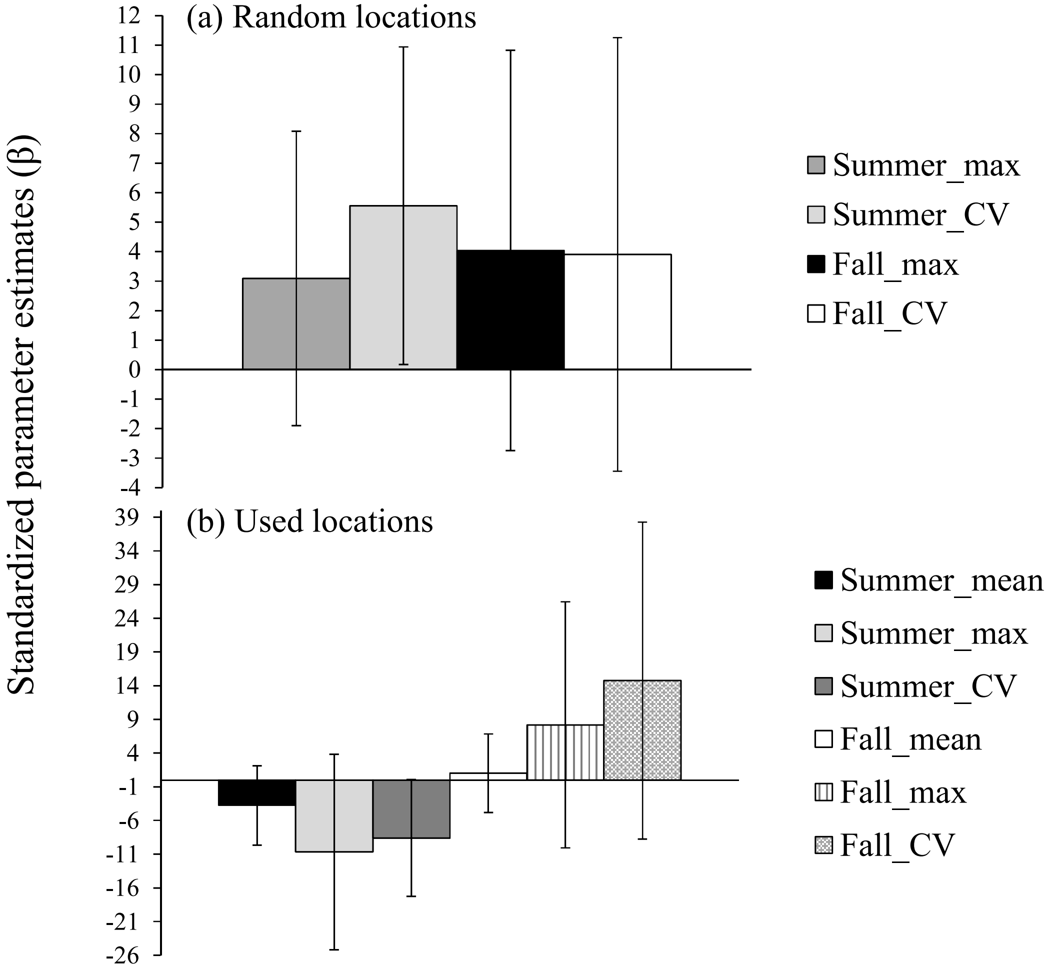


Figure 7: Model-averaged, standardized parameter estimates (with 90% confidence intervals) obtained from multiple regression models of elk (*Cervus canadensis*) pregnancy rates in Idaho, USA. Predictor variables were descriptive statistics (mean, max, and coefficient of variation) derived from model-predicted estimates of usable forage biomass at (a) random locations (*n* = 1,000 locations per PVT) that served as an index of the available nutritional landscape in each of seven elk management zones, and (b) locations used by elk in each managmenet zone (determined from GPS-collared females).



Appendices

Appendix A: List of plant species sampled during our study and the associated level of selection by elk. Level of selection by elk (*Cervus canadensis*) was based on published and unpublished data provided by R. Cook. Taxonomy: The PLANTS Database, USDA, NRCS, 2016 (http://plants.usda.gov, accessed 4/1/2016).

Plant code	Family	Scientific name	Common name	Level of selection
ABCO	Pinaceae	*Abies concolor*	White fir	Avoided
ABGR	Pinaceae	*Abies grandis*	Grand fir	Avoided
ABLA	Pinaceae	*Abies lasiocarpa*	Subalpine fir	Avoided
ACCO4	Ranunculaceae	*Aconitum columbianum*	Columbian monkshood	Avoided
ACGL	Aceraceae	*Acer glabrum*	Rocky mountain maple	Selected
ACHY	Poaceae	*Achnatherum hymenoides*	Indian ricegrass	Selected
ACMI2	Asteraceae	*Achillea millefolium*	Common yarrow	Selected
ACNEN2	Poaceae	*Achnatherum nelsonii*	Columbia needlegrass	Avoided
ACPH	Polygonaceae	*Aconogonon phytolaccifolium*	Poke knotweed	Avoided
ACRUA8	Ranunculaceae	*Actaea rubra arguta*	Red baneberry	Selected
ADBI	Asteraceae	*Adenocaulon bicolor*	Pathfinder	Selected
AGCR	Poaceae	*Agropyron cristatum*	Crested wheatgrass	Selected
AGGL	Asteraceae	*Agoseris glauca*	False dandelion	Selected
AGOC	Asteraceae	*Ageratina occidentalis*	Western snakeroot	Avoided
AGOS	Asteraceae	*Agoseris spp.*	Dandelion spp.	Selected
AGROP	Poaceae	*Agropyron spp.*	Wheatgrass spp.	Selected
AGROS	Poaceae	*Agrostis spp.*	Bentgrass spp.	Selected
AGSC5	Poaceae	*Agrostis scabra*	Rough bentgrass	Selected
AGUR	Lamiaceae	*Agastache urticifolia*	Horsemint	Avoided
ALBR	Liliaceae	*Allium brandegeei*	Brandegee's onion	Avoided
ALGE2	Poaceae	*Alopecurus geniculatus*	Water foxtail	Avoided
ALLI	Liliaceae	*Allium spp.*	Onion spp.	Avoided
ALNUS	Betulaceae	*Alnus spp.*	Alder spp.	Selected
ALRO3	Malvaceae	*Alcea rosea*	Hollyhock	Avoided
ALRU2	Betulaceae	*Alnus rubra*	Red alder	Selected
ALSI	Betulaceae	*Alnus sinuata*	Sitka alder	Selected
ALVIC	Betulaceae	*Alnus viridis*	Green alder	Selected
AMAL2	Rosaceae	*Amelanchier alnifolia*	Saskatoon serviceberry	Selected
AMSIN	Boraginaceae	*Amsinckia spp.*	Fiddleneck	Avoided
ANAL4	Asteraceae	*Antennaria alpina*	Alpine pussytoes	Avoided
ANAN2	Asteraceae	*Antennaria anaphaloides*	Pearly pussytoes	Avoided

ANAPHspp	Asteraceae	*Anaphalis spp.*	Pearly everlasting spp.	Avoided
ANCA14	Apiaceae	*Anthriscus caucalis*	Bur chervil	Selected
ANDRO3	Primulaceae	*Androsace spp.*	Rock jasmine	Avoided
ANEN	Ranunculaceae	*Anemone spp.*	Anemone spp.	Avoided
ANGEL	Apiaceae	*Angelica spp.*	White angelica	Avoided
ANMA	Asteraceae	*Anaphalis margaritacea*	Western pearly everlasting	Avoided
ANNE	Asteraceae	*Antennaria neglecta*	Field pussytoes	Avoided
ANPA	Ranunculaceae	*Anemone parviflora*	Smallflowered anemone	Avoided
ANPI	Ranunculaceae	*Anemone piperi*	Piper's anemone	Avoided
ANPU	Asteraceae	*Antennaria pulcherrima*	Showy pussytoes	Avoided
ANRA	Asteraceae	*Antennaria racemosa*	Raceme pussytoes	Avoided
ANRO2	Asteraceae	*Antennaria rosea*	Rosy pussytoes	Avoided
ANTE	Asteraceae	*Antennaria spp.*	Pussytoes spp.	Avoided
APAN2	Apocynaceae	*Apocynum androsaemifolium*	Spreading dogbane	Selected
APIA	Apiaceae	*Apiaceae spp.*	Parsley spp.	Avoided
AQCA	Ranunculaceae	*Aquilegia canadensis*	Red columbine	Selected
AQCO	Ranunculaceae	*Aquilegia coerulea*	Colorado blue columbine	Selected
AQFL	Ranunculaceae	*Aquilegia flavescens*	Yellow columbine	Selected
AQFO	Ranunculaceae	*Aquilegia formosa*	Western columbine	Selected
ARAB	Brassicaceae	*Arabidopsis spp.*	Rockcress spp.	Avoided
ARAC2	Caryophyllaceae	*Arenaria aculeata*	Prickly sandwort	Avoided
ARAL	Arecaceae	*Arnica angustifolia*	Alpine arnica	Selected
ARAL2	Ericaceae	*Arctostaphylos uva-ursi*	Bearberry	Selected
ARAN7	Rosaceae	*Argentina anserina*	Silverweed cinquefoil	Selected
ARAR8	Asteraceae	*Artemisia arbuscula*	Little sagebrush	Avoided
ARCA13	Asteraceae	*Artemisia cana*	Silver sagebrush	Avoided
ARCAA	Caryophyllaceae	*Arenaria capillaris americana*	Fescue sandwort	Avoided
ARCH3	Asteraceae	*Arnica chamissonis*	Leafy arnica	Selected
ARCO5	Caryophyllaceae	*Arenaria congesta*	Ballhead sandwort	Avoided
ARCO9	Asteraceae	*Arnica cordifolia*	Heart-leaved arnica	Selected
ARCTI	Asteraceae	*Arctium spp.*	Burdock	Selected
ARDI2	Brassicaceae	*Arabis divaricarpa*	Spreading-pod rockcress	Avoided
ARDR	Brassicaceae	*Arabis drummondii*	Drummond's rockcress	Avoided
AREN	Caryophyllaceae	*Arenaria spp.*	Sandwort spp.	Avoided
ARFE3	Caryophyllaceae	*Arenaria fendleri*	Fendler's sandwort	Avoided
ARFR4	Asteraceae	*Artemisia frigida*	Prairie sage	Avoided
ARHO	Brassicaceae	*Arabis hoffmannii*	Reflexed rockcress	Avoided
ARLA8	Asteraceae	*Arnica latifolia*	Broadleaf arnica	Selected
ARLU	Asteraceae	*Artemisia ludoviciana*	White sagebrush	Selected
ARMA	Caryophyllaceae	*Arenaria macrophylla*	Largeleaf sandwort	Avoided
ARMO	Brassicaceae	*Arabis modesta*	Rocky mountain sandwort	Avoided

ARMO4	Asteraceae	*Arnica mollis*	Hairy arnica	Selected
ARMO8	Asteraceae	*Arnica montana*	Meadow arnica	Selected
ARNICA	Asteraceae	*Arnica spp.*	Arnica spp.	Selected
ARNO4	Asteraceae	*Artemisia nova*	Black sagebrush	Avoided
ARRI	Asteraceae	*Artemisia rigida*	Scabland sagebrush	Avoided
ARSC	Asteraceae	*Artemisia scopulorum*	Alpine sage	Selected
ARSE2	Caryophyllaceae	*Arenaria serpyllifolia*	Thymeleaf sandwort	Avoided
ARSO	Asteraceae	*Arnica sororia*	Twin arnica	Selected
ARTR4	Asteraceae	*Artemisia tripartita*	Three-tip sagebrush	Avoided
ARTRW8	Asteraceae	*Artemisia tridentata wyomingensis*	Wyoming big sagebrush	Avoided
ASAT1	Fabaceae	*Astragalus atratus*	Field milkvetch	Selected
ASCAN	Fabaceae	*Astragalus canadensis*	Canadian milkvetch	Selected
ASCAU	Aristolochiaceae	*Asarum caudatum*	British Columbia wildginger	Avoided
ASCO	Asteraceae	*Eurybia conspicua*	Western showy aster	Selected
ASFO	Asteraceae	*Argyroxiphium forbesii*	Leafy aster	Selected
ASTER	Asteraceae	*Aster spp.*	Aster spp.	Selected
ASTRAG	Fabaceae	*Astragalus spp.*	Vetch spp.	Selected
ATFI	Dryopteridaceae	*Athyrium filix-femina*	Common ladyfern	Avoided
ATRIP	Chenopodiaceae	*Atriplex spp.*	Saltbush	Avoided
BAMA4	Asteraceae	*Balsamorhiza macrophylla*	Cutleaf balsamroot	Selected
BASA3	Asteraceae	*Balsamorhiza sagittata*	Arrowleaf balsamroot	Selected
BERU	Scrophulariaceae	*Besseya rubra*	Red besseya	Selected
BOGR2	Poaceae	*Bouteloua gracilis*	Blue grama grass	Selected
BOMA	Saxifragaceae	*Boykinia major*	Mountain boykinia	Selected
BORA	Boraginaceae	*Myosotis spp.*	Forget-Me-Not spp.	Selected
BOTRY	Ophioglossaceae	*Botrychium spp.*	Grape fern	Avoided
BRAN	Poaceae	*Bromus anomalus*	Nodding brome	Selected
BRCA	Poaceae	*Bromus carinatus*	California brome	Selected
BRCI2	Poaceae	*Bromus ciliatus*	Fringed brome	Selected
BRIN2	Poaceae	*Bromus inermis*	Smooth brome	Selected
BRINP5	Poaceae	*Bromus inermis pumpellianus*	Northern brome	Selected
BRMA4	Poaceae	*Bromus marginatus*	Mountain brome	Selected
BROMUS	Poaceae	*Bromus spp.*	Bromus spp.	Selected
BRTE	Poaceae	*Bromus tectorum*	Cheatgrass	Avoided
BRVU	Poaceae	*Bromus vulgaris*	Columbia brome	Selected
CAAQ	Cyperaceae	*Carex aquatilis*	Water sedge	Selected
CABRB	Brassicaceae	*Carbamine breweri breweri*	Brewer's bittercress	Avoided
CABU	Orchidaceae	*Calypso bulbosa*	Fairy slipper	Selected
CACA4	Poaceae	*Calamagrostis canadensis*	Marsh reedgrass	Selected
CACO36	Scrophulariaceae	*Castilleja covilleana*	Rocky mountain paintbrush	Selected
CAGE	Cyperaceae	*Carex geyeri*	Geyer's sedge	Selected

CALE4	Ranunculaceae	*Caltha leptosepala*	White marsh marigold	Selected
CALI4	Scrophulariaceae	*Castillega linariifolia*	Narrow-leaf paintbrush	Selected
CAMI12	Scrophulariaceae	*Castillega miniata*	Giant red paintbrush	Selected
CANU3	Liliaceae	*Calochortus nuttallii*	Sego lily	Avoided
CANU4	Asteraceae	*Carduus nutans*	Musk thistle	Avoided
CAOC4	Scrophulariaceae	*Castilleja occidentalis*	Yellow paintbrush	Selected
CAPA5	Ranunculaceae	*Caltha palustris*	Marsh marigold	Selected
CAQUB2	Liliaceae	*Camassia quamash breviflora*	Small camas	Selected
CAREX	Cyperaceae	*Carex spp.*	Carex spp.	Selected
CARO2	Campanulaceae	*Campanula rotundifolia*	Bluebell of Scotland	Selected
CARU	Poaceae	*Calamagrostis rubescens*	Pinegrass	Selected
CARY	Caryophyllaceae	*Dianthus spp.*	Carnation spp.	Avoided
CAST	Scrophulariaceae	*Castilleja spp.*	Paintbrush spp.	Selected
CATA2	Onagraceae	*Camissonia tanacetifolia*	Tansy-leaf suncup	Selected
CEAL12	Caryophyllaceae	*Cerastium alpinum*	Alpine chickweed	Selected
CEAR4	Caryophyllaceae	*Cerastium arvense*	Field chickweed	Selected
CEGL2	Caryophyllaceae	*Cerastium glomeratum*	Sticky chickweed	Selected
CERA	Caryophyllaceae	*Cerastium spp.*	Chickweed spp.	Selected
CESA	Rhamnaceae	*Ceanothus sanguineus*	Redstem ceanothus	Selected
CESO	Asteraceae	*Centauria solstitialis*	Yellow starthistle	Avoided
CEST	Asteraceae	*Centauria stoebe*	Spotted knapweed	Avoided
CEVE	Rhamnaceae	*Ceanothus velutinus*	Ceanothus	Avoided
CHEV	Asteraceae	*Chaenactis evermannii*	Evermann's chaenactis	Selected
CHJU	Asteraceae	*Chondrilla juncea*	Rush skeletonweed	Avoided
CHLA13	Onagraceae	*Chamerion latifolium*	Dwarf fireweed	Selected
CHLE	Asteraceae	*Chrysanthemum leucanthemum*	Oxeye daisy	Selected
CHME	Pyrolaceae	*Chimaphila menziesii*	Menzie's pipsessewa	Avoided
CHRY	Asteraceae	*Chrysothamnus spp.*	Rabbitbrush spp.	Avoided
CHTW	Scrophulariaceae	*Chionophila tweedyi*	Tweedy's snowlover	Selected
CHUM	Pyrolaceae	*Chimaphila umbellata*	Prince's pine	Avoided
CHVI8	Asteraceae	*Chrysothamnus viscidiflorus*	Yellow rabbitbrush	Avoided
CIAL	Onagraceae	*Circaea alpina*	Small enchanter's nightshade	Selected
CIAR4	Asteraceae	*Cirsium arvense*	Canada thistle	Avoided
CIFO	Asteraceae	*Cirsium foliosum*	Elk thistle	Selected
CIIN	Asteraceae	*Cichorium intybus*	Chicory	Selected
CIRS	Asteraceae	*Cirsium spp.*	Thistle spp.	Avoided
CLAYT	Portulacaceae	*Claytonia spp.*	Springbeauty	Selected
CLCO	Ranunculaceae	*Clematis columbiana*	Rock clematis	Selected
CLCOR	Portulacaceae	*Claytonia cordifolia*	Heartleaf springbeauty	Selected
CLFL3	Portulacaceae	*Claytonia lanceolata*	Lanceleaf springbeauty	Selected
CLHI	Ranunculaceae	*Clematis hirsutissima*	Hairy clematis	Selected

CLLI	Ranunculaceae	*Clematis ligusticifolia*	Western white clematis	Selected
CLME	Portulacaceae	*Claytonia megarhiza*	Alpine springbeauty	Selected
CLOC2	Ranunculaceae	*Clematis occidentalis*	Blue clematis	Selected
CLPE	Portulacaceae	*Claytonia perfoliata*	Miner's lettuce	Selected
CLPU	Onagraceae	*Clarkia pulchella*	Pink fairies	Selected
CLRU2	Portulacaceae	*Claytonia rubra*	Redstem springbeauty	Selected
CLSI	Portulacaceae	*Claytonia sibirica*	Siberian springbeauty	Selected
CLUN	Liliaceae	*Clintonia uniflora*	Bride's bonnet	Avoided
COAR	Convolvulaceae	*Convolvulus arvensis*	Field bindweed	Avoided
COCA	Cornaceae	*Cornus canadensis*	Bunchberry dogwood	Selected
COGR4	Polemoniaceae	*Collomia grandiflora*	Grand collomia	Avoided
COLI2	Polemoniaceae	*Collomia linearis*	Narrow-leaved collomia	Avoided
COLL	Polemoniaceae	*Collomia spp.*	Collomia spp.	Avoided
COMA25	Orchidaceae	*Corallorhiza maculata*	Coralroot	Avoided
CONU	Cornaceae	*Cornus nuttalii*	Pacific dogwood	Selected
COOC	Ranunculaceae	*Coptis occidentalis*	Idaho goldthread	Selected
COPA28	Rosaceae	*Comarum palustre*	Marsh cinquefoil	Selected
COPA3	Scrophulariaceae	*Collinsia parviflora*	Blue-eyed Mary	Avoided
COSE16	Cornaceae	*Cornus sericea*	Redosier dogwood	Selected
COSE5	Fumariaceae	*Corydalis sempervirens*	Pink corydalis	Selected
COST	Cornaceae	*Cornus stolonifera*	Red stem dogwood	Selected
COUM	Santalaceae	*Comandra umbellata*	Bastard toadflax	Avoided
CRAC2	Asteraceae	*Crepis acuminata*	Longleaf hawksbeard	Selected
CRAT	Asteraceae	*Crepis atribarba*	Slender hawksbeard	Selected
CRDO2	Rosaceae	*Crataegus douglasii*	Black hawthorn	Selected
CREPIS	Asteraceae	*Crepis spp.*	Hawksbeard spp.	Selected
CROC	Asteraceae	*Crepis occidentalis*	Gray hawksbeard	Selected
CRTO4	Boraginaceae	*Cryptantha torreyana*	Torrey's cryptantha	Avoided
CRYP	Boraginaceae	*Cryptantha spp.*	Cryptanthia spp.	Avoided
CYFR	Dryopteridaceae	*Crystopteris fragilis*	Brittle bladderfern	Avoided
CYOF	Boraginaceae	*Cynoglossum officinale*	Houndstongue	Avoided
DACA3	Poaceae	*Danthonia californica*	California oatgrass	Selected
DACT	Poaceae	*Dactylis spp.*	Orchardgrass spp	Selected
DAFR6	Rosaceae	*Dasiphora fruticosa*	Shrubby cinquefoil	Selected
DAGL	Poaceae	*Dactylis glomerata*	Orchardgrass	Selected
DAIN	Poaceae	*Danthonia intermedia*	Timber oatgrass	Selected
DANT	Poaceae	*Danthonia spp.*	Danthonia spp.	Selected
DANTspp	Poaceae	*Danthonian spp.*	Oatgrass spp	Selected
DAPA2	Poaceae	*Danthonia parryi*	Parry's oatgrass	Selected
DAUN	Poaceae	*Danthonia unispicata*	Onespike danthonia	Selected
DECEA5	Poaceae	*Deschampsia alpina*	Tufted hairgrass	Avoided

DELPH	Ranunculaceae	*Delphinium spp.*	Larkspur spp.	Avoided
DENU2	Ranunculaceae	*Delphinium nuttallianum*	Nelson's larkspur	Avoided
DEPI	Brassicaceae	*Descurainia pinnata*	Western tanseymustard	Avoided
DEPIN	Brassicaceae	*Descurainia pinnata nelsonii*	Nelson's tanseymustard	Avoided
DESCH	Poaceae	*Deschampsia spp.*	Hairgrass spp	Avoided
DIDE	Caryophyllaceae	*Dianthus deltoides*	Maiden pink	Avoided
DIHO	Liliaceae	*Disporum hookeri*	Drops-of-gold	Avoided
DOPU	Primulaceae	*Dodecatheon pulchellum*	Pretty shootingstar	Selected
DRYOP	Dryopteridaceae	*Dryopteris spp.*	Woodfern spp.	Avoided
ELCA4	Poaceae	*Elymus canadensis*	Canada wildrye	Selected
ELCO4	Poaceae	*Leymus condensatus*	Giant wildrye	Selected
ELEL5	Poaceae	*Elymus elymoides*	Squirreltail	Avoided
ELGL	Poaceae	*Elymus glaucus*	Smooth wildrye	Selected
ELLA3	Poaceae	*Elymus lanceolatus*	Thickspike wheatgrass	Selected
ELRE4	Poaceae	*Elymus repens*	Quackgrass	Avoided
ELTR7	Poaceae	*Elymus trachycaulus*	Slender wheatgrass	Selected
ELYLE	Poaceae	*Elymus spp.*	Rye spp.	Selected
EPAN2	Onagraceae	*Epilobium angustifolium*	Fireweed	Selected
EPBR3	Onagraceae	*Epilobium brachycarpum*	Tall Annual willowherb	Avoided
EPCI	Onagraceae	*Epilobium cilatum*	Purple-leaved willowherb	Avoided
EPIL	Onagraceae	*Epilobium spp.*	Willowherb spp.	Avoided
EPLA3	Onagraceae	*Epilobium lactiflorum*	Milkflower willowherb	Avoided
EQHY	Equisetaceae	*Equisetum hyemale*	Horsetail	Avoided
ERAN	Asteraceae	*Erigeron annuus*	Eastern daisy fleabane	Selected
ERAN5	Polygonaceae	*Eriogonum androsaceum*	Rockjasmine buckwheat	Selected
ERBL	Asteraceae	*Erigeron bloomeri*	Scabland fleabane	Selected
ERCI6	Geraniaceae	*Erodium cicutarium*	Redstem stork's bill	Avoided
ERGL	Poaceae	*Eragrostis glomerata*	Smooth fleabane	Selected
ERGR9	Liliaceae	*Erythronium grandiflorum*	Yellow avalanche lily	Selected
ERHE2	Polygonaceae	*Eriogonum heracleoides*	Parsnipflower buckwheat	Selected
ERIC	Ericaceae	*Pyrola spp.*	Wintergreen spp.	Avoided
ERIG	Asteraceae	*Erigeron spp.*	Fleabane spp.	Selected
ERIO	Polygonaceae	*Erigonum spp.*	Buckwheat spp.	Selected
ERLA6	Asteraceae	*Eriophyllum lanatum*	Oregon sunshine	Selected
ERNA10	Asteraceae	*Ericameria nauseosa*	Rubber rabbitbrush	Avoided
EROV	Polygonaceae	*Eriogonum ovalifolium*	Cushion buckwheat	Selected
ERPA30	Asteraceae	*Ericameria parryi*	Parry's rabbitbrush	Avoided
ERPE3	Asteraceae	*Erigeron peregrinus*	Subalpine fleabane	Selected
ERSP4	Asteraceae	*Erigeron speciosus*	Aspen fleabane	Selected
ERST3	Asteraceae	*Erigeron strigosus*	Fleabane daisy	Selected
ERST4	Polygonaceae	*Eriogonum strictum*	Strict desert buckwehat	Selected

ERUM	Polygonaceae	*Eriogonum umbellatum*	Sulfur buckwheat	Selected
EUCO36	Asteraceae	*Eurybia conspicua*	Showy aster	Selected
EUEN	Asteraceae	*Eucephalus engelmannii*	Engelmann's aster	Selected
EUES	Euphorbiaceae	*Euphorbia esula*	Leafy spurge	Avoided
EUGL18	Asteraceae	*Eucephalus glabratus*	Smooth aster	Selected
EUIN9	Asteraceae	*Eurybia integrifolia*	Thickstem aster	Selected
FECA4	Poaceae	*Festuca campestris*	Mountain rough fescue	Selected
FEID	Poaceae	*Festuca idahoensis*	Idaho fescue	Selected
FEOV	Poaceae	*Festuca ovina*	Sheep fescue	Selected
FESCUE	Poaceae	*Festuca spp.*	Fescue spp.	Selected
FRFA	Gentianaceae	*Frasera fastigiata*	Clustered green gentian	Selected
FRSP	Gentianaceae	*Frasera speciosa*	Monument plant	Selected
FRVE	Rosaceae	*Fragaria vesca*	Woodland strawberry	Selected
FRVI	Rosaceae	*Fragaria virginiana*	Wild strawberry	Selected
GAAR	Asteraceae	*Gaillardia aristata*	Blanketflower	Avoided
GABO2	Rubiaceae	*Galium boreale*	Northern bedstraw	Avoided
GADE2	Orchidaceae	*Galeandra bicarinata*	Deceptive groundsmoke	Avoided
GAHU	Ericaceae	*Gaultheria humifusa*	Alpine spicywintergreen	Avoided
GAHU2	Onagraceae	*Gayophytum humile*	Dwarf groundsmoke	Avoided
GALLI	Rubiaceae	*Galium spp.*	Bedstraw spp.	Selected
GAOV	Ericaceae	*Gaultheria ovatifolia*	Western teaberry	Selected
GATR3	Rubiaceae	*Galium triflorum*	Sweet-scented bedstraw	Selected
GEAF	Gentianaceae	*Gentiana affinis*	Pleated gentian	Selected
GEMA4	Rosaceae	*Geum macrophyllum*	Large-leaved avens	Selected
GERA	Geraniaceae	*Geranium spp.*	Geranium spp.	Selected
GETR	Rosaceae	*Geum triflorum*	Prairie smoke	Selected
GEVI	Gentianaceae	*Geranium viscosissimum*	Sticky purple geranium	Selected
GEVI2	Gentianaceae	*Gentiana newberryi tiogana*	Sticky geranium	Selected
GLLE3	Fabaceae	*Glycyrrhiza lepidota*	Wild licorice	Selected
GLMA	Primulaceae	*Glaux maritima*	Sea milkwort	Selected
GOOB2	Orchidaceae	*Goodyera oblongifolia*	Rattlesnake plantain	Selected
GOOD	Orchidaceae	*Goodyera spp.*	Plantain spp.	Selected
GROU	Asteraceae	*Packera spp.*	Groundsel spp.	Selected
GRSQ	Asteraceae	*Grindelia squarrosa*	Curlycip gumweed	Avoided
GYDR	Dryopteridaceae	*Gymnocarpium dryopteris*	Western oakfern	Avoided
HAFL2	Boraginaceae	*Hackelia floribunda*	Many-flowered stickseed	Avoided
HECO26	Poaceae	*Hesperostipa comata*	Needle-&-thread	Avoided
HECY2	Saxifragaceae	*Heuchera cylindrica*	Roundleaf alumroot	Selected
HEDY	Fabaceae	*Hedysarum*	Sweetvetch	Selected
HEGR8	Saxifragaceae	*Heuchera grossulariifolia*	Currantleaf alumroot	Selected
HEMA80	Apiaceae	*Heracleum maximum*	Common cowparsnip	Avoided

HEMU3	Asteraceae	*Heliomeris multiflora*	Showy goldeneye	Selected
HENU	Asteraceae	*Helianthus nuttallii*	Nuttall's sunflower	Selected
HEPA	Asteraceae	*Helianthella parryi*	Common alumroot	Selected
HEUC	Saxifragaceae	*Heuchera spp.*	Alumroot spp.	Selected
HEUN	Asteraceae	*Helianthella uniflora*	Oneflower helianthella	Selected
HIAL2	Asteraceae	*Hieracium albiflorum*	White hawkweed	Selected
HIAU	Asteraceae	*Hieracium aurantiacum*	Orange hawkweed	Selected
HICA10	Asteraceae	*Hieracium caespitosum*	Meadow hawkweed	Selected
HICY	Asteraceae	*Hieracium cynoglossoides*	Houndstongue hawkweed	Selected
HIER	Asteraceae	*Hieracium spp.*	Hawkweed spp.	Selected
HIERO	Poaceae	*Hierochloe spp.*	Bison grass	Selected
HIGR	Asteraceae	*Hieracium gracile*	Slender hawkweed	Selected
HISC2	Asteraceae	*Hieracium scouleri*	Scouler's woollyweed	Selected
HIUM	Asteraceae	*Hieracium umbellatum*	Narrow-leaved hawkweed	Selected
HODI	Rosaceae	*Holodiscus discolor*	Oceanspray	Selected
HOJU	Poaceae	*Hordeum jubatum*	Foxtail barley	Selected
HYAN2	Clusiaceae	*Hypericum anagalloides*	Bog St. John's wort	Avoided
HYCA4	Hydrophyllaceae	*Hydrophyllum capitatum*	Ballhead waterleaf	Selected
HYHO	Asteraceae	*Hymenoxys hoopesii*	Owl's claws	Selected
ILRI	Malvaceae	*Iliamna rivularis*	Streambank globemallow	Selected
IOAL	Asteraceae	*Ionactis alpina*	Lava aster	Selected
IOST	Asteraceae	*Ionactis stenomeres*	Rocky mountain aster	Selected
IPAG	Polemoniaceae	*Ipomopsis aggregata*	Scarlet gilia	Selected
IRMI	Iridaceae	*Iris missouriensis*	Western blue flag iris	Avoided
ISAR	Cleomaceae	*Isomeris arborea*	Bladderpod	Avoided
JUCO	Juncaceae	*Juncus compressus*	Common juniper	Avoided
JUNC	Juncaceae	*Juncus spp.*	Rush spp.	Selected
JUOC	Juncaceae	*Juniperus occidentalis*	Western juniper	Avoided
JUSC2	Cupressaceae	*Juniperus scopulorum*	Rocky mountain juniper	Avoided
KOCR	Poaceae	*Koleria cristata*	Prairie junegrass	Selected
KRLA2	Chenopodiaceae	*Krascheninnikovia lanata*	Winterfat	Selected
LACTU	Asteraceae	*Lactuca spp.*	Lettuce spp.	Selected
LAOC	Pinaceae	*Larix occidentalis*	Western larch	Avoided
LAPU2	Lamiaceae	*Lamium purpureum*	Purple nettle	Avoided
LASE	Asteraceae	*Lactuca serriola*	Prickly lettuce	Selected
LATA	Asteraceae	*Lactuca tatarica*	Blue lettuce	Selected
LATH	Fabaceae	*Lathyrus spp.*	Pea spp.	Selected
LEDE	Brassicaceae	*Lepidium densiflorum*	Common pepperweed	Avoided
LENU8	Polemoniaceae	*Leptosiphon nuttallii*	Nuttall's liananthus	Avoided
LEVI3	Brassicaceae	*Lepidium virginicum*	Peppergrass	Avoided
LIBO3	Caprifoliaceae	*Linnaea borealis*	Twinflower	Avoided

LICA2	Apiaceae	*Ligusticum canbyi*	Canaby's licoriceroot	Avoided
LICO6	Orchidaceae	*Listera cordata*	Heart-leaved twayblade	Selected
LIGL2	Saxifragaceae	*Lithophragma glabrum*	Bulbous woodland-star	Selected
LIGUST	Apiaceae	*Ligusticum spp.*	Licorice-root	Selected
LILE3	Linaceae	*Linum lewisii*	Western blue flax	Selected
LILI	Asteraceae	*Liatris ligulistylis*	Rocky mountain blazing star	Selected
LILIA	Liliales	*Liliaceae spp.*	Liliaceae spp.	Avoided
LIPA5	Saxifragaceae	*Lithophragma parviflorum*	Smallflower woodland-star	Selected
LIPE2	Linaceae	*Linum perenne*	Western blue flax	Selected
LIRU4	Boraginaceae	*Lithospermum ruderale*	Yellow puccoon	Selected
LOAM	Apiaceae	*Lomatium ambiguum*	Wyeth's biscuitroot	Selected
LOCA4	Apiaceae	*Lomatium canbyi*	Canby's biscuitroot	Selected
LOCI	Caprifoliaceae	*Lonicera ciliosa*	Orange honeysuckle	Selected
LOCU	Apiaceae	*Lomatium cusickii*	Cusick's biscuitroot	Selected
LODI	Apiaceae	*Lomatium dissectum*	Fern-leaved biscuitroot	Selected
LOMA	Apiaceae	*Lomatium spp.*	Lomatium spp.	Selected
LONI	Caprifoliaceae	*Lonicera spp.*	Honeysuckle spp.	Selected
LOTR2	Apiaceae	*Lomatium triternatum*	9-leaved desert parsley	Avoided
LOUT2	Caprifoliaceae	*Lonicera utahensis*	Utah honeysuckle	Selected
LULE	Fabaceae	*Lupinus lemmonii*	Prairie lupine	Selected
LUPA4	Juncaceae	*Luzula parviflora*	Small-flowered woodrush	Selected
LUPI	Fabaceae	*Lupinus spp.*	Lupine spp.	Selected
LUSEM3	Fabaceae	*Lupinus sericeus marianus*	Silky lupine	Selected
LUWY	Fabaceae	*Lupinus wyethii*	Wyethii larkspur	Avoided
LUZU	Juncaceae	*Luzula spp.*	Woodrush	Selected
MACA2	Asteraceae	*Machaeranthera canescens*	Hoary tanseyaster	Selected
MAGL2	Asteraceae	*Madia glomerata*	Mountain tarweed	Avoided
MARA7	Liliaceae	*Maianthemum racemosum*	Feathery false lily of the valley	Avoided
MARE11	Berberidaceae	*Mahonia repens*	Oregon grape	Selected
MAST4	Lilaceae	*Maianthemum stellatum*	False Solomon's seal	Avoided
MEAR4	Lamiaceae	*Mentha arvensis*	Wild mint	Avoided
MEBU	Poaceae	*Melica bulbosa*	Oniongrass	Selected
MEFE	Ericaceae	*Menziesii ferruginae*	Rusty menziesia	Avoided
MELO4	Boraginaceae	*Mertensia longiflora*	Long-flowered bluebells	Selected
MEOB	Boraginaceae	*Mertensia oblongifolia*	Oblongleaf bluebells	Selected
MERT	Boraginaceae	*Mertensia spp.*	Bluebells spp.	Selected
MESA	Fabaceae	*Medicago sativa*	Alfalfa	Selected
MICR	Asteraceae	*Microseris spp.*	Microseris spp.	Selected
MIGR	Polemoniaceae	*Microsteris gracilis*	Slender phlox	Avoided
MIGU	Scorphulariaceae	*Mimulus guttatus*	Yellow monkeyflower	Avoided
MINU	Asteraceae	*Microseris nutans*	Nodding microceris	Selected

MIOB2	Caryophyllaceae	*Minuartia obtusiloba*	Alpine sandwort	Avoided
MITELLA	Saxifragaceae	*Mitella spp.*	Miterwort	Avoided
MIVI2	Scorphulariaceae	*Mimulus viscidus*	Sticky monkeyflower	Avoided
MOLA6	Caryophyllaceae	*Moehringia lateriflora*	Blunt-leaved sandwort	Avoided
MUMO	Poaceae	*Muhlenbergia montana*	Mountain muhly	Selected
MYSY	Boraginaceae	*Myosotis sylvatica*	Woodland forget-me-not	Selected
NEBR	Hydrophyllaceae	*Nemophila breviflora*	Great Basin nemophile	Avoided
NOFEG	Brassicaceae	*Noccaea fendleri glauca*	Alpine pennycress	Avoided
OPHO	Araliaceae	*Oplopanax horridus*	Club leaf	Avoided
OPPO	Cactaceae	*Opuntia polyacantha*	Plains pricklypear	Selected
ORAL4	Asteraceae	*Oreostemma alpigenum*	Tundra aster	Selected
ORAS	Poaceae	*Oryzopsis asperifolia*	White-grained mountain ricegrass	Selected
ORLU2	Scorphulariaceae	*Orthocarpus luteus*	Yellow owl's clover	Selected
ORSE	Pyrolaceae	*Orthilia secunda*	Sidebells wintergreen	Avoided
OSBE	Apiaceae	*Osmorhiza berteroi*	Mountain sweetcicily	Selected
OSMO	Apiaceae	*Osmorhiza spp.*	Sweetcicily spp.	Selected
OSOC	Apiaceae	*Osmorhiza occidentalis*	Western sweetcicily	Selected
OXDI	Oxalidaceae	*Oxalis dichondrifolia*	Mountain sorrel	Selected
OXVI	Oxalidaceae	*Oxalis violacea*	Sticky locoweed	Avoided
PACA15	Asteraceae	*Packera cana*	Woolly groundsel	Selected
PAMU11	Asteraceae	*Packera multilobata*	Lobeleaf groundsel	Selected
PAMY	Celastraceae	*Paxistima myrsinites*	Falsebox	Selected
PAPA19	Asteraceae	*Packera pauciflora*	Rayless alpine groundsel	Selected
PASA2	Apiaceae	*Pastinaca sativa*	Wild parsnip	Selected
PASM	Poaceae	*Pascopyrum smithii*	Western wheatgrass	Selected
PAST10	Asteraceae	*Packera streptanthifolia*	Rocky mountain groundsel	Selected
PAWE4	Asteraceae	*Packera werneriifolia*	Hoary groundsel	Selected
PEAL11	Scorphulariaceae	*Penstemon albertinus*	Alberta penstemon	Selected
PEBR	Scorphulariaceae	*Pedicularis bracteosa*	Bracted lousewort	Avoided
PEDE4	Scorphulariaceae	*Penstemon deustus*	Hotrock penstemon	Selected
PEDIC	Scorphulariaceae	*Pedicularis spp.*	Lousewort spp.	Selected
PEFR	Asteraceae	*Petasites frigidus*	Arctic sweet coltsfoot	Selected
PEFR3	Scorphulariaceae	*Penstemon fruticosus*	Shrubby penstemon	Selected
PEGA3	Apiaceae	*Perideridia gairdneri*	Yampa	Selected
PEGL5	Scorphulariaceae	*Penstemon globosus*	Globe penstemon	Selected
PEGR2	Scorphulariaceae	*Pedicularis groenlandica*	Elephanthead	Selected
PENS	Scorphulariaceae	*Penstemon spp.*	Penstemon spp.	Selected
PEPR2	Scorphulariaceae	*Penstemon procerus*	Slender blue penstemon	Selected
PERA	Scorphulariaceae	*Pedicularis racemosa*	Parrot's beak	Selected
PERY	Scorphulariaceae	*Penstemon rydbergii*	Rydberg's penstemon	Selected

PESE11	Scorphulariaceae	*Penstemon secundiflorus*	Sidebells penstemon	Selected
PEVI3	Scorphulariaceae	*Penstemon virens*	Blue Mist penstemon	Selected
PHAL2	Poaceae	*Phleum alpinum*	Alpine timothy	Selected
PHAR3	Poaceae	*Phalaris arundinacea*	Reed canarygrass	Selected
PHAU3	Polemoniaceae	*Phlox austromontana*	Mountain phlox	Avoided
PHEM	Ericaceae	*Phyllodoce empetriformis*	Pink mountain heather	Avoided
PHGL	Ericaceae	*Phyllodoce glanduliflora*	Yellow mountainheath	Avoided
PHHA	Hydrophyllaceae	*Phacelia hastata*	Silverleaf scorpionweed	Selected
PHHE	Hydrophyllaceae	*Phacelia heterophylla*	Varileaf phacelia	Avoided
PHHO	Polemoniaceae	*Phlox hoodii*	Spiny phlox	Avoided
PHLE4	Hydrangeaceae	*Philadelphus lewisii*	Syringa	Selected
PHLI	Hydrophyllaceae	*Phacelia linearis*	Thread-leaved phacelia	Avoided
PHLO2	Polemoniaceae	*Phlox longifolia*	Longleaf phlox	Avoided
PHLOX	Polemoniaceae	*Phlox spp.*	Phlox spp.	Avoided
PHMA5	Rosaceae	*Physocarpus malvaceus*	Mallow ninebark	Selected
PHMUD	Polemoniaceae	*Phlox multiflora depressa*	Rocky mountain phlox	Avoided
PHPR3	Poaceae	*Phleum pratensis*	Timothy	Selected
PHPU5	Polemoniaceae	*Phlox pulvinata*	Cushion phlox	Avoided
PHSU3	Polemoniaceae	*Phlox subulata*	Moss phlox	Avoided
PIAL	Pinaceae	*Pinus albicaulis*	Whitebark pine	Avoided
PICEA	Pinaceae	*Picea spp.*	Spruce spp.	Avoided
PICO	Pinaceae	*Pinus contorta*	Lodgepole pine	Avoided
PIEN	Pinaceae	*Picea engelmannii*	Engelmann spruce	Avoided
PIFL	Ericaceae	*Pieris floribunda*	Limber pine	Avoided
PIMO	Pinaceae	*Pinus monticola*	Western white pine	Avoided
PIPO	Pinaceae	*Pinus ponderosa*	Ponderosa pine	Avoided
PIPU	Pinaceae	*Picea pungens*	Colorado blue spruce	Avoided
PLAN	Plantaginaceae	*Plantago spp.*	Plantain spp.	Avoided
PLAT	Orchidaceae	*Platanthera spp.*	Fringed orchid	Avoided
PLMA2	Plantaginaceae	*Plantago major*	Common plantain	Avoided
PLOR4	Orchidaceae	*Platanthera orbiculata*	Round-leaved orchid	Avoided
POAC	Poaceae	*Poa spp.*	Poa spp.	Selected
POAL2	Poaceae	*Poa alpina*	Alpine bluegrass	Selected
POAL26	Rosaceae	*Potentilla alba*	White cinquefoil	Selected
POARC	Rosaceae	*Potentilla arguta convallaria*	Cream cinquefoil	Selected
POAVA	Polygonaceae	*Polygonum aviculare arenastrum*	Prostrate knotweed	Selected
POBI6	Polygonaceae	*Polygonum bistortoides*	American bistort	Selected
POBU	Poaceae	*Poa bulbosa*	Bulbous bluegrass	Selected
PODI2	Rosaceae	*Potentilla diversifolia*	Diverse-leaved cinquefoil	Selected
PODO4	Polygonaceae	*Polygonum douglasii*	Douglas' knotweed	Avoided
POFL3	Rosaceae	*Potentilla flabellifolia*	Fanleaf cinquefoil	Selected

POGL9	Rosaceae	*Potentilla glandulosa*	Sticky cinquefoil	Selected
POGLR2	Poaceae	*Poa glauca rupicola*	Timberline bluegrass	Selected
POGR9	Rosaceae	*Potentilla gracilis*	Graceful cinquefoil	Selected
POMU	Dryopteridaceae	*Polystichum munitum*	Western swordfern	Avoided
PONEI2	Poaceae	*Poa nemoralis interior*	Inland bluegrass	Selected
PONO	Poaceae	*Poa norbergii*	Rough cinquefoil	Selected
POPR	Poaceae	*Poa pratensis*	Kentucky bluegrass	Selected
POPU3	Polemoniaceae	*Polemonium pulcherrimum*	Jacob's ladder	Avoided
PORE5	Rosaceae	*Potentilla recta*	Sulfur cinquefoil	Selected
POSE	Poaceae	*Poa secunda*	Steppe bluegrass	Selected
POTE	Rosaceae	*Potentilla spp.*	Cinquefoil spp.	Selected
POTR5	Salicaceae	*Populus tremuloides*	Quaking aspen	Selected
POVI3	Polygonaceae	*Polygonum viviparum*	Alpine bistort	Selected
POWH	Poaceae	*Poa wheeleri/nervosa*	Wheeler's bluegrass	Selected
PREM	Rosaceae	*Prunus emarginata*	Bitter cherry	Selected
PRHO2	Liliaceae	*Prosartes hookeri*	Hooker's fairybell	Avoided
PRTR4	Liliaceae	*Prosartes trachycarpa*	Roughfruited fairybells	Avoided
PRUNUS	Rosaceae	*Prunus spp.*	Cherry spp.	Selected
PRVI	Rosaceae	*Prunus virginiana*	Chokecherry	Selected
PRVU	Lamiaceae	*Prunella vulgaris*	Common selfheal	Selected
PSME	Pinaceae	*Pseudostuga menziesii*	Douglas-fir	Avoided
PSSP6	Poaceae	*Pseudoroegneria spicata*	Bluebunch wheatgrass	Selected
PTAN	Monotropaceae	*Pterospora andromedea*	Woodland pinedrops	Avoided
PTAQ	Dennstaedtiaceae	*Pteridium aquilinum*	Bracken fern	Avoided
PUTR2	Rosaceae	*Purshia tridentata*	Antelope bitterbrush	Selected
PYCH	Pyrolaceae	*Pyrola chlorantha*	Greenish-flower wintergreen	Avoided
PYROLA	Pyrolaceae	*Pyrola spp.*	Wintergreen spp.	Avoided
PYUN2	Asteraceae	*Pyrrocoma uniflora*	Plantain goldenweed	Selected
RAAC2	Ranunculaceae	*Ranunculus acriformis*	Sharpleaf buttercup	Avoided
RACO3	Asteraceae	*Ratibida columnifera*	Prairie coneflower	Selected
RANU	Ranunculaceae	*Ranunculus spp.*	Buttercup spp.	Avoided
RHAL	Ericaceae	*Rhododendron albiflorum*	Cascade azalea	Avoided
RHGL	Anacardiaceae	*Rhus glabra*	Smooth sumac	Avoided
RHPU	Rhamnaceae	*Rhamnus purshiana*	Cascara buckthorn	Avoided
RIAU	Grossulariaceae	*Ribes aureum*	Golden currant	Selected
RIBES	Grossulariaceae	*Ribes spp.*	Currant spp.	Selected
RICE	Grossulariaceae	*Ribes cereum*	Squaw currant	Selected
RIHU	Grossulariaceae	*Ribes hudsonianum*	Northern black currant	Selected
RILA	Grossulariaceae	*Ribes lacustre*	Prickly currant	Selected
RIVI3	Grossulariaceae	*Ribes viscosissium*	Sticky currant	Selected
ROAC	Rosaceae	*Rosa acicularis*	Prickly rose	Selected

RONU	Rosaceae	*Rosa nutkana*	Nootka rose	Selected
ROSA	Rosaceae	*Rosa spp.*	Rose spp.	Selected
ROSI	Hydrophyllaceae	*Romanzoffia sitchensis*	Mistmaiden	Selected
ROWO	Rosaceae	*Rosa woodsii*	Wood's rose	Selected
RUAC3	Polygonaceae	*Rumex acetosella*	Common sheep sorrel	Avoided
RUARA2	Rosaceae	*Rubus arcticus acaulis*	Dwarf Raspberry	Selected
RUBUS	Rosaceae	*Rubus spp.*	Blackberry spp.	Selected
RUDB	Asteraceae	*Rudbeckia spp.*	Coneflower	Selected
RUHI2	Asteraceae	*Rudbeckia hirta*	Black-eyed susan	Selected
RUID	Rosaceae	*Rubus idaeus*	American red raspberry	Selected
RULA	Rosaceae	*Rubus laciniatus*	Cutleaf blackberry	Selected
RULE	Rosaceae	*Rubus leucodermis*	Whitebark raspberry	Selected
RUMEX	Polygonaceae	*Rumex spp.*	Sorrel spp.	Selected
RUNI	Rosaceae	*Rubus nivalis*	Snow raspberry	Selected
RUOC2	Asteraceae	*Rudbeckia occidentalis*	Western coneflower	Selected
RUOCA	Asteraceae	*Rudbeckia alpicola*	Western rayless coneflower	Selected
RUPA	Rosaceae	*Rubus parviflorus*	Thimbleberry	Selected
RUPA6	Polygonaceae	*Rumex paucifolius*	Alpine sorrel	Selected
RUPU	Rosaceae	*Rubus pubescens*	Dwarf red blackberry	Selected
RUUR	Rosaceae	*Rubus ursinus*	California blackberry	Selected
SABA4	Salicaceae	*Salix barrattiana*	Barrett's willow	Selected
SABE2	Salicaceae	*Salix bebbiana*	Bebb willow	Selected
SADO	Lamiaceae	*Satureja douglassii*	Yerba buena	Selected
SAGE2	Salicaceae	*Salix geyeriana*	Geyer willow	Selected
SALIX	Salicaceae	*Salix spp.*	Salix spp.	Selected
SAMB	Caprifoliaceae	*Sambucus sp*	Elderberry spp.	Selected
SAOR2	Saxifragaceae	*Saxifraga oregana*	Bog saxifrage	Selected
SAPL2	Salicaceae	*Salix planifolia*	Flat-leaved willow	Selected
SASC	Salicaceae	*Salix scouleriana*	Scouler's willow	Selected
SAXI	Saxifragaceae	*Saxifraga spp.*	Saxifrage spp.	Avoided
SCAL	Scrophulariaceae	*Scrophularia lanceolata*	Lanceleaf figwort	Avoided
SCRO	Scrophulariaceae	*Scrophularia spp.*	Figwort spp.	Avoided
SCUTE	Lamiaceae	*Scutellaria spp.*	Skullcap	Avoided
SECR	Asteraceae	*Senecio crassulus*	Thick-leaved groundsel	Selected
SEHY2	Asteraceae	*Senecio hydrophilus*	Water ragwort	Selected
SEIN2	Asteraceae	*Senecio integerrimus*	Lambstongue ragwort	Selected
SELA	Crassulaceae	*Sedum lanceolatum*	Lanceleaf stonecrop	Selected
SENE	Asteraceae	*Senecio spp.*	Ragwort spp.	Selected
SESE2	Asteraceae	*Senecio serra*	Tall ragwort	Selected
SESP4	Asteraceae	*Senecio sphaerocephalus*	Marsh groundsel	Selected
SETR	Asteraceae	*Senecio trangularis*	Arrowleaf groundsel	Selected

SEVU	Asteraceae	*Senecio vulgaris*	Canada groundsel	Selected
SHCA	Elaeagnaceae	*Shepherdia canadensis*	Buffaloberry	Selected
SIHY	Poaceae	*Sitanion hystrix*	Squirreltail	Avoided
SILE	Caryophyllaceae	*Silene spp.*	Campion spp.	Avoided
SIME	Caryophyllaceae	*Silene menziesii*	Menzie's campion	Avoided
SIMO2	Indaceae	*Sisyrinchium montanum*	Rocky mountain blue-eyed grass	Avoided
SIPA4	Caryophyllaceae	*Silene parryi*	Parry's catchfly	Avoided
SMST	Liliaceae	*Smilicina stellata*	Starry false lily of the valley	Selected
SOCA6	Asteraceae	*Solidago canadensis*	Canada goldenrod	Selected
SOLI	Asteraceae	*Solidago spp.*	Goldenrod spp.	Selected
SOMU	Asteraceae	*Solidago multiradiata*	Rocky mountain goldenrod	Selected
SOOL	Asteraceae	*Sonchus oleraceus*	Sow thistle	Selected
SOSC	Rosaceae	*Sorbus scopulina*	Green's mountain ash	Selected
SOSI2	Rosaceae	*Sorbus sitchensis*	Western mountain ash	Selected
SPBE2	Rosaceae	*Spiraea betulifolia*	Birch-leaved spirea	Selected
SPCR	Rosaceae	*Sporobolus cryptandrus*	Sand dropseed	Selected
SPPL	Rosaceae	*Spiraea splendens*	Rose meadowsweet	Selected
STAM2	Liliaceae	*Streptopus amplexifolius*	Claspleaf twisted stalk	Selected
STCA	Caryophyllaceae	*Stellaria calycantha*	Northern starwort	Avoided
STELL	Caryophyllaceae	*Stellaria spp.*	Starwort spp.	Avoided
STIPA	Poaceae	*Stipa spp*	Ricegrass spp.	Selected
STLA7	Asteraceae	*Stenotus lanuginosus*	Woolly mock goldenweed	Selected
STLO	Caryophyllaceae	*Stellaria longifolia*	Long-leaved starwort	Avoided
STLO2	Caryophyllaceae	*Stellaria longipes*	Long-stalked starwort	Avoided
STPA	Lamiaceae	*Stachys palustris*	Swamp nettle	Avoided
SYAL	Caprifoliaceae	*Symphoricarpos albus*	Common snowberry	Selected
SYAS3	Asteraceae	*Symphyotrichum ascendens*	Western aster	Selected
SYEA2	Asteraceae	*Symphyotrichum eatonii*	Eaton's aster	Selected
SYOC	Asteraceae	*Symphoricarpos occidentalis*	Snowberry	Selected
SYPL	Scrophulariaceae	*Syntheris platycarpa*	Idaho kittentails	Avoided
SYRO3	Asteraceae	*Symphoricarpos robynsianum*	Longleaf aster	Selected
TABR	Taxaceae	*Taxus brevifolia*	Pacific yew	Avoided
TAOF	Asteraceae	*Taraxacum officinale*	Common dandelion	Selected
TAVU	Asteraceae	*Tanacetum vulgare*	Common tansey	Selected
TETR	Asteraceae	*Tetradymia spp.*	Tetradymia spp.	Avoided
THALI2	Ranunculaceae	*Thalictrum spp.*	Meadow-rue	Avoided
THAR5	Brassicaceae	*Thalaspi arvense*	Field pennycress	Avoided
THIN6	Poaceae	*Thinopyrum intermedium*	Intermediate wheatgrass	Selected
THMO6	Fabaceae	*Thermopsis montana*	Mountain goldenbean	Avoided
THOC	Ranunculaceae	*Thalictrum occidentale*	Western meadow-rue	Avoided
THPL	Cupressaceae	*Thuja plicata*	Western redcedar	Avoided

THSP	Ranunculaceae	*Thalictrum sparsiflorum*	Fewflower meadow-rue	Avoided
TITR	Saxifragaceae	*Tiarella trifoliate*	Threeleaf foamflower	Avoided
TOAR	Apiaceae	*Torilis arvensis*	Spreading hedgeparsley	Selected
TOLY	Asteraceae	*Tonestus lyallii*	Lyall's goldenweed	Selected
TRAC	Sapindaceae	*Tristiropsis acutangula*	Northern fleabane	Selected
TRCA	Poaceae	*Trisetum canescens*	Tall trisetum	Selected
TRCAR	Ranunculaceae	*Trautvetteria caroliniensis*	Carolina bugbane	Avoided
TRDU	Asteraceae	*Tragopogon dubius*	Yellow salsify	Selected
TRGR4	Liliaceae	*Trillium grandiflorum*	Large-flowered trillium	Avoided
TRGR7	Liliaceae	*Triteleia grandiflora*	Wild hyacinth	Avoided
TRIF	Fabaceae	*Trifolium spp.*	Clover spp.	Selected
TRIL	Liliaceae	*Trillium spp.*	Trillium spp.	Avoided
TRLA	Primulaceae	*Trientalis latifolia*	Broadleaf starflower	Avoided
TROV	Liliaceae	*Trillium ovatum*	Pacific trillium	Selected
TRRE3	Fabaceae	*Trifolium repens*	White clover	Selected
TRSP2	Poaceae	*Trisetum spicatum*	Spike trisedum	Selected
TRTE	Zygophyllaceae	*Tribulus terrestris*	Puncturevine	Avoided
TSME	Pinaceae	*Tsuga mertensiana*	Mountain hemlock	Avoided
TYLA	Typhaceae	*Typha latifolia*	Broad-leaf cattail	Avoided
URDI	Urticaceae	*Urtica dioica*	Stinging nettle	Avoided
URTIC	Urticaceae	*Urtica spp.*	Bladderwort	Avoided
VACA	Ericaceae	*Vaccinium caespitosum*	Dwarf bilberry	Selected
VACC	Ericaceae	*Vaccinium spp.*	Vaccinium spp.	Selected
VACE	Ericaceae	*Vaccinium cespitosum*	Dwarf blueberry	Selected
VAED	Valerianaceae	*Valeriana edulis*	Edible valerian	Selected
VALER	Valerianaceae	*Valeriana spp.*	Valerian spp.	Selected
VAME	Ericaceae	*Vaccinium membranaceum*	Huckleberry	Selected
VAOC2	Valerianaceae	*Valeriana occidentalis*	Western valerian	Selected
VASC	Ericaceae	*Vaccinium scoparium*	Grouse whortleberry	Avoided
VASI	Valerianaceae	*Valeriana sitchensis*	Sitka valerian	Selected
VAVI	Ericaceae	*Vaccinium vitis-idaea*	Ligonberry	Avoided
VEAL80	Scorphulariaceae	*Veronica alpina*	Alpine speedwell	Avoided
VEBI2	Scorphulariaceae	*Veronica biloba*	Bilobed speedwell	Avoided
VECAC2	Liliaceae	*Veratrum californicum*	False hellebore	Avoided
VEDU	Poaceae	*Ventenata dubia*	North Africa grass	Avoided
VEHA2	Verbenaceae	*Verbena hastata*	Vervain	Selected
VERON	Scrophulariaceae	*Veronica spp.*	Speedwell spp.	Avoided
VESE	Scorphulariaceae	*Veronica serpyllifolia*	Thymeleaf speedwell	Avoided
VEST	Verbenaceae	*Verbena stricta*	Hoary verbena	Selected
VETH	Scorphulariaceae	*Verbascum thapsus*	Common mullein	Avoided
VIAM	Fabaceae	*Vicia americana*	American vetch	Selected

VICA4	Violaceae	*Viola canadensis*	Canadian violet	Selected
VINU2	Violaceae	*Viola nuttalli*	Nuttall's violet	Selected
VIOL	Violaceae	*Viola spp.*	Violet spp.	Selected
VIPU4	Violaceae	*Viola purpurea*	Goosefoot violet	Selected
VISO	Violaceae	*Viola novae-angliae*	Blue violet	Selected
VITR	Violaceae	*Viola arvensis*	Sage violet	Selected
WYAM	Asteraceae	*Wyethia amplexicaulis*	Yellow mule's ear	Selected
WYHE2	Asteraceae	*Wyethia helianthoides*	White mule's ear	Selected
XETE	Liliaceae	*Xerophyllum tenax*	Common beargrass	Selected
XYGL	Asteraceae	*Xylorhiza glabriuscula*	Woody aster	Selected
ZIVE	Liliaceae	*Zigadenus venenosus*	Deathcamus	Avoided

Appendix B: Species-specific linear regressions of p1ant biomass against plant cover (%), tree canopy cover (%), sample date, and interactions between plant cover and tree canopy cover and/or plant cover and sample date. Coefficients are shown for variables included in the best model for each species or lifeform group, along with the adjusted R^2 value of the model. We used these models to estimate biomass of forage in all unclipped quadrats in the Sawtooth and Dimaond Creek elk zones (Central), and the South Fork of the Clearwater drainage (Fork), Idaho, USA.

Study area	Plant code	No. of samples	Adj. R^2	Intercept	Plant cover	Canopy cover	Sample date	Plant cover: Canopy cover	Plant cover: Sample date
Central	ABLA	31	0.80	0.24	2.60	-0.02		-0.38	
Central	ACGL	10	0.66	-1.30	2.45	-0.79			
Central	ACMI2	94	0.60	-1.73	1.90	-0.33		0.36	
Central	AMAL2 Leaves	47	0.62	-1.51	1.34				
Central	AMAL2 Stems	47	0.45	-2.77	1.35				
Central	AMAL2	47	0.60	-1.10	1.33				
Central	ANAL	15	0.40	-2.09	1.92	-0.29		-0.60	
Central	ANMA	10	0.87	-3.77	3.25	0.76		-0.51	
Central	ANRO2	13	0.48	-9.92	36.38		3.94		-17.75
Central	ANTENRIA	11	0.79	24.93	-13.65		-13.48		7.60
Central	ARCO9	69	0.55	-1.33	1.64	-0.23			
Central	ARTR Leaves	38	0.86	0.67	0.91				
Central	ARTR Stems	38	0.67	2.61	0.90		-1.57		
Central	ARTRW8	38	0.85	0.94	0.93				
Central	ASTER Flowers	28	0.63	-1.01	1.62	-0.71		0.25	
Central	ASTER Stalks	28	0.15	-4.95	1.07				
Central	ASTER	28	0.67	-0.98	1.75	-0.74		0.29	
Central	ASTRA Flowers	12	0.82	-0.14	-0.64	-0.59		0.62	
Central	ASTRA	12	0.82	-0.14	-0.64	-0.59		0.62	
Central	BASA3	17	0.97	0.61	-1.74		-0.52		1.69
Central	BROMUS Flowers	65	0.59	-1.46	2.19	-0.12			

Central	BROMUS Stalks	65	0.28	-1.23	-23.13		-1.58		12.25
Central	BROMUS	65	0.61	-3.95	-5.20		1.08		4.00
Central	BRTE	12	0.61	31.16	1.89	0.36	-18.18		
Central	CANU3	12	0.64	-1.75	2.33	-0.43			
Central	CAREX Flowers	166	0.57	-9.66	6.45		4.21		-2.33
Central	CAREX	166	0.57	-9.66	6.45		4.21		-2.33
Central	CARU Flowers	83	0.54	-7.01	1.76		2.76		
Central	CARU Stalks	83	0.22	-5.03	1.02	0.10		-0.25	
Central	CARU	83	0.57	-7.92	1.82		3.18		
Central	CASTspp. Flowers	20	0.40	9.08	1.72		-5.34		
Central	CASTspp. Stalks	20	0.22	-21.10	0.38		8.78		
Central	CAST	20	0.48	9.04	1.48	0.29	-5.39		
Central	CERA spp.	14	0.28	-2.07	1.83				
Central	CEVE	20	0.77	-21.46	9.16		9.85		-3.56
Central	CHVI8 Leaves	15	0.33	5.95	1.06		-2.91		
Central	CHVI8 Stems	15	0.33	9.04	1.03		-4.61		
Central	CHVI8	15	0.49	9.59	1.05		-4.38		
Central	COPA3	26	0.45	-1.67	1.97	-0.32			
Central	DOPU	10	0.67	-0.89	1.22				
Central	EPAN2 Flowers	57	0.59	-1.65	1.73				
Central	EPAN2 Stalks	57	0.39	-3.36	-11.04		-0.91		6.44
Central	EPAN2	57	0.70	-6.33	2.10		2.27		
Central	ERHE2	14	0.85	-20.03	12.63		9.52		-5.51
Central	ERUM	12	0.81	45.27	-15.83		-22.45		8.36
Central	FEID Flowers	11	0.92	-4.57	5.98		1.67		-2.19
Central	FEID	11	0.82	-6.21	6.61		2.61		-2.56
Central	FRVI	59	0.61	-2.42	1.82				
Central	GABO2 Flowers	16	0.73	-11.30	14.91		4.24		-6.22
Central	GABO2 Stalks	16	0.21	-4.66	-14.46		0.06		7.89
Central	GABO2	16	0.79	-2.96	2.96				

Central	GATR3 Flowers	15	0.67	-3.11	1.62				
Central	GATR3	15	0.67	-3.11	1.62				
Central	GEVI2 Flowers	77	0.62	-6.42	1.88		1.99		
Central	GEVI2 Stalks	77	0.21	-4.52	2.59	-0.07		-0.50	
Central	GEVI2	77	0.65	-6.14	2.00		1.83		
Central	HECO26 Flowers	20	0.47	-0.23	1.45	-0.25			
Central	HECO26 Stalks	20	0.78	-4.62	-0.01	-0.04		0.79	
Central	HECO26	20	0.71	-16.77	14.25		7.47		-5.69
Central	HIAL2	10	0.70	12.25	1.31		-6.64		
Central	HIERACIUM	16	0.19	-1.88	1.26				
Central	HISC2	12	0.90	-11.60	22.17		5.21		-10.18
Central	HYCA4	11	0.73	-1.03	-4.42	-0.75		1.79	
Central	JUNC Flowers	23	0.55	-8.71	1.26		4.05		
Central	JUNC	23	0.62	-7.66	1.29		3.66		
Central	LENU8	19	0.71	-12.47	2.23		4.97		
Central	LILIA	17	0.77	-0.74	0.49	-0.81		0.87	
Central	LOUT2 Leaves	11	0.85	-36.80	14.47		17.57		-6.55
Central	LOUT2 Stems	11	0.59	-4.24	1.83				
Central	LOUT2	11	0.83	-35.22	14.13		16.88		-6.37
Central	LUPINE Flowers	37	0.53	-1.75	1.43				
Central	LUPINE Stalks	37	0.43	-5.49	2.04				
Central	LUPINE	37	0.70	-1.88	1.84				
Central	LUSEM3 Flowers	45	0.62	-6.13	1.51		2.36		
Central	LUSEM3 Stalks	45	0.17	-4.61	1.21				
Central	LUSEM3	45	0.81	-0.71	1.47	-0.31		0.13	
Central	MARE11 Leaves	32	0.52	-0.95	1.29				
Central	MARE11 Stems	32	0.53	-29.75	13.68		12.74		-5.83
Central	MARE11	32	0.51	-0.86	1.32				
Central	MOLA6	12	0.69	-4.87	5.41	0.28		-0.66	
Central	MidSH Leaves	371	0.66	-1.30	1.51	-0.17			

Central	TFORB Flowers	798	0.55	-4.37	1.69	-0.12	1.29		
Central	RHIZO Flowers	298	0.49	-1.30	1.57				
Central	BUNCH Flowers	312	0.52	-3.61	1.71		1.16		
Central	LowSH Leaves	93	0.33	-1.53	1.23				
Central	SAGE Leaves	53	0.81	0.60	0.92	-0.21			
Central	MidSH Stems	371	0.51	-3.66	1.36	-0.17	0.79		
Central	TFORB Stalks	798	0.18	-7.81	1.03	-0.13	1.73		
Central	RHIZO Stalks	298	0.12	-1.84	-5.53		-1.32		3.04
Central	LowSH Stems	93	0.43	-20.93	7.88		8.68		-3.07
Central	SAGE Stems	53	0.66	-0.81	1.02	0.04		-1.64	
Central	BASAL	1055	0.56	-4.41	2.01	-0.12	1.15		
Central	MidSHRUB	371	0.66	-0.77	1.44	-0.17			
Central	TFORB	849	0.62	-4.44	1.90	-0.16	1.39		
Central	RHIZO	311	0.56	1.18	-1.97		-1.20		1.84
Central	BUNCH	312	0.53	-3.73	1.73		1.23		
Central	LowSHRUB	93	0.61	-0.77	1.47	-0.14			
Central	SAGE	53	0.83	0.85	0.95	0.09		-0.85	
Central	SPRUCE-FIR	52	0.67	1.13	1.46	-0.47			
Central	PINE	43	0.74	4.10	1.63		-2.29		
Central	EVERGREEN	24	0.77	-8.61	1.90		3.44		
Central	ORAS Flowers	12	0.55	-3.36	3.01				
Central	ORAS	12	0.55	-3.36	3.01				
Central	OSBE Flowers	36	0.52	0.10	-6.87	-0.56		1.91	
Central	OSBE Stalks	36	0.21	-4.66	-6.34		-0.12		3.51
Central	OSBE	36	0.57	2.24	-8.67		-2.24		5.12
Central	OSOC Flowers	35	0.59	-3.89	2.48				
Central	OSOC	35	0.59	-3.89	2.48				
Central	PAPA19	11	0.65	19.22	-34.49		-10.59		18.17
Central	PENS spp. Flowers	45	0.13	-0.88	0.73				
Central	PENS spp. Stalks	45	0.15	-4.56	1.40				

Central	PENS spp.	45	0.47	-0.73	1.17				
Central	PHPR3 Flowers	17	0.38	0.18	0.61				
Central	PHPR3 Stalks	17	0.54	-52.47	2.01		23.77		
Central	PHPR3	17	0.93	0.04	1.17	0.17			
Central	PICO	28	0.72	5.70	1.60		-3.05		
Central	POA Flowers	70	0.44	-1.96	2.15				
Central	POA spp.	70	0.44	-1.85	2.17				
Central	POAL26	12	0.87	8.14	2.94	-0.62	-4.67		
Central	POARC	12	0.52	-2.33	2.28				
Central	PODI2	10	0.82	-1.46	1.66				
Central	POPR Flowers	18	0.47	-4.18	0.90		2.15		
Central	POPR	18	0.49	-4.03	0.91		2.07		
Central	POSE Flowers	25	0.45	20.39	-10.00		-10.57		5.60
Central	POSE Stalks	25	0.27	-4.56	-0.06	-0.27		0.36	
Central	POSE	25	0.52	19.42	-8.93		-10.13		5.13
Central	POTR5 Leaves	26	0.92	-19.80	12.14		9.09		-5.18
Central	POTR5 Stems	26	0.36	-2.53	1.20				
Central	POTR5	26	0.89	-21.36	13.39		10.10		-5.84
Central	PRVI Leaves	18	0.83	-1.30	1.86	-0.27			
Central	PRVI Stems	18	0.67	-2.23	1.66	-0.28			
Central	PRVI	18	0.83	-0.89	1.80	-0.27			
Central	PSME	13	0.71	-29.08	14.75		13.96		-6.53
Central	PSSP6 Flowers	14	0.56	-8.97	1.43		4.38		
Central	PSSP6 Stalks	14	0.72	-4.77	0.06	0.80		0.42	
Central	PSSP6	14	0.52	-8.40	1.38	0.28	4.12		
Central	PUTR2	10	0.79	0.32	1.00				
Central	ROAC Leaves	15	0.72	-0.96	1.77	-0.42			
Central	ROAC Stems	15	0.88	0.12	0.01	-1.05		0.53	
Central	ROAC	15	0.84	1.00	0.36	-0.84		0.37	
Central	ROSAspp. Leaves	16	0.81	-19.29	2.78	0.39	7.11		

Central	ROSAspp. Stems	16	0.25	-3.31	1.35			
Central	ROSAspp.	16	0.90	-14.87	2.69	0.42	5.13	
Central	SENECIO Flowers	15	0.37	-0.60	1.31			
Central	SENECIO	15	0.37	-0.60	1.31			
Central	SPBE2 Leaves	24	0.41	-0.59	1.04			
Central	SPBE2 Stems	24	0.35	-2.12	1.25			
Central	SPBE2	24	0.47	-0.28	1.09			
Central	STCA	19	0.59	-3.45	3.51			
Central	STLO	11	0.79	-4.20	5.78			
Central	SYOC Leaves	75	0.69	-3.45	2.43	0.41		-0.28
Central	SYOC Stems	75	0.60	-4.05	2.16	0.48		-0.26
Central	SYOC	75	0.77	-2.85	2.31	0.48		-0.29
Central	TAOF	49	0.48	-2.34	1.39	-0.22		0.37
Central	THOC Flowers	46	0.71	0.20	1.74	-0.67		
Central	THOC Stems	46	0.03	-4.76	0.20			
Central	THOC	46	0.71	0.20	1.75	-0.67		
Central	TRDU	10	0.73	-3.45	4.01	0.79		-0.81
Central	VAME Leaves	13	0.68	0.47	0.85	-0.17		
Central	VAME Stems	13	0.62	3.30	0.73		-1.96	
Central	VAME	13	0.68	0.84	0.83	-0.15		
Central	VAOC2 Flowers	23	0.72	-2.84	1.84			
Central	VAOC2 Stalks	23	0.10	-4.73	0.86			
Central	VAOC2	23	0.87	0.63	0.88	-0.87		0.31
Central	VASC Leaves	26	0.51	10.75	0.93		-5.88	
Central	VASC Stems	26	0.37	-3.16	3.09	0.66		-0.56
Central	VASC	26	0.70	4.01	1.02		-2.03	
Central	VINU2	17	0.82	-1.22	1.43	-0.37		0.23
Central	VIOL spp.	45	0.28	-4.71	1.86	0.29		
Fork	ABGR	53	0.77	0.20	2.13	-0.82		
Fork	ABLA	22	0.83	2.48	0.34	-1.10		0.35

Fork	ACGL	24	0.74	-2.33	1.90	-0.32			
Fork	ACGL Leaves	24	0.73	-2.45	1.83	-0.35			
Fork	ACGL Stems	24	0.66	-10.77	1.60		3.08		
Fork	ACMI	39	0.70	-13.88	7.93		5.97		-2.96
Fork	ADBI	35	0.59	-2.75	1.71				
Fork	AMAL	20	0.85	-6.24	1.18	-0.61	3.70		
Fork	AMAL Leaves	20	0.87	-5.51	1.24	-0.65	3.26		
Fork	AMAL Stems	20	0.38	-17.75	0.77	-1.39	9.83		
Fork	ANMA	11	0.78	44.13	1.84	0.34	-21.83		
Fork	ANMA Flowers	11	0.74	47.93	1.74	0.31	-23.59		
Fork	ANNUAL	79	0.47	-6.15	1.60	-0.20	2.30		
Fork	ANPI	116	0.27	-3.01	1.72				
Fork	ARLA	22	0.81	-1.62	1.10				
Fork	ARMA	67	0.44	-5.46	1.48	-0.26	2.14		
Fork	ARNCO	33	0.68	-1.18	1.00				
Fork	ASCAU	21	0.82	-1.16	1.99	-0.37			
Fork	BERE	20	0.66	5.90	1.54		-3.30		
Fork	BERE Leaves	20	0.48	-1.16	1.38				
Fork	BERE Stems	20	0.69	-2.77	2.70	-0.58			
Fork	BROMUS	14	0.25	-1.42	1.31				
Fork	BROMUS	14	0.42	-2.38	1.76				
Fork	BRVU Flowers	47	0.12	-2.78	1.39				
Fork	BRVU Stalks	47	0.13	-8.76	-13.09		2.68		7.24
Fork	CAGE Flowers	40	0.71	-0.77	1.31				
Fork	CAGE Stalks	40	0.55	-0.89	1.27				
Fork	CAGE	40	0.48	-4.75	1.26	0.34			
Fork	CARE	98	0.53	-1.30	1.71	-0.15			
Fork	CARE Flowers	98	0.51	-1.71	1.73				
Fork	CARE Stalks	98	0.43	-4.79	1.75	0.05		-0.31	
Fork	CARU	38	0.44	0.79	-6.38		-1.12		3.85

Fork	CARU Flowers	38	0.39	-2.97	-6.24		0.42		3.82
Fork	CARU Stems	38	0.42	-2.86	-6.56		-0.01		3.93
Fork	CESA	14	0.44	-7.83	1.35		3.40		
Fork	CHUM	37	0.56	-1.36	1.86				
Fork	CIRS-AC	24	0.79	-9.91	2.01	-0.50	4.28		
Fork	CLUN	66	0.62	-3.66	1.86	-0.51	1.37		
Fork	COCA	29	0.49	-1.11	1.48	-0.27			
Fork	COOC	83	0.57	-0.76	1.42	-0.31			
Fork	DAGL	19	0.56	-0.44	1.43				
Fork	DAGL Flowers	19	0.56	-0.80	1.39				
Fork	DAGL Stems	19	0.44	-2.58	1.76				
Fork	DIHO	34	0.61	-1.13	1.37	-0.32			
Fork	DIHO Flowers	34	0.51	-2.83	1.27				
Fork	DIHO Stems	34	0.56	-3.91	1.40				
Fork	ELYM	44	0.45	-0.74	1.42				
Fork	ELYM Flowers	44	0.26	-2.30	0.65	0.10		0.28	
Fork	ELYM Stalks	44	0.37	-6.55	1.50		2.51		
Fork	EPAN	60	0.79	-5.80	1.47	-0.25	2.59		
Fork	EPAN Flowers	60	0.64	-5.50	1.46	-0.18	1.90		
Fork	EPAN Stalks	60	0.75	-7.51	1.62	-0.31	3.06		
Fork	ERIG spp.	18	0.60	-8.03	1.81		2.86		
Fork	ERIGspp. Flowers	18	0.64	-7.11	1.79		2.33		
Fork	ERIGspp. Stalks	18	0.46	-16.24	1.93		5.56		
Fork	FEID	12	0.85	-1.91	1.72				
Fork	FEID Flowers	12	0.81	-2.29	1.81				
Fork	FEID Stalks	12	0.45	24.00	-21.49		-12.93		10.48
Fork	FEOC	11	0.53	-2.24	2.56				
Fork	FEOC Flowers	11	0.49	-2.45	2.48				
Fork	FEOC Stalks	11	0.65	-3.68	2.47				
Fork	FESTU	17	0.58	-2.04	2.15				

Fork	FESTU Flowers	17	0.60	-2.74	2.32				
Fork	FESTU Stalks	17	0.46	24.95	-31.73		-13.39		16.14
Fork	FRVE	76	0.60	3.88	-3.95		-2.80		2.68
Fork	GATR	43	0.25	-3.10	1.88				
Fork	HIERsp	42	0.68	-8.62	2.28	-0.28	3.15		
Fork	HODI	19	0.80	-2.35	2.16	0.42		-0.31	
Fork	HODI Leaves	19	0.77	-2.48	2.13	0.38		-0.29	
Fork	HODI Stems	19	0.53	-3.45	1.22				
Fork	HYPE	20	0.78	-12.52	2.53		5.49		
Fork	LIBO	45	0.73	-2.15	2.94	0.07		-0.41	
Fork	LOUT	25	0.81	-1.23	1.23				
Fork	LOUT Leaves	25	0.29	-1.26	0.92				
Fork	LOUT Stems	25	0.78	-11.40	1.47		3.74		
Fork	LUPI	13	0.80	16.51	-5.78		-8.60		3.58
Fork	LUZU	26	0.48	-14.09	1.27		6.02		
Fork	LUZU Flowers	26	0.48	-13.87	1.30		5.85		
Fork	LUZU Stalks	26	0.04	-15.08	11.57		5.60		-5.64
Fork	MEFE	27	0.70	-0.72	0.82				
Fork	MITELLA	39	0.58	-7.95	1.71	-0.20	3.21		
Fork	OSCH	24	0.55	-3.83	2.57				
Fork	OSCH Flowers	24	0.55	-3.83	2.57				
Fork	PAMY	21	0.57	-0.85	2.22	-0.47			
Fork	PAMY Leaves	21	0.46	-1.50	2.10	-0.52			
Fork	PAMY Stems	21	0.33	-2.91	1.97				
Fork	PENS	41	0.70	-0.21	1.52	-0.55			
Fork	PENS Flowers	41	0.72	-0.73	1.59	-0.44			
Fork	PENS Stalks	41	0.21	-2.25	0.65	-0.65			
Fork	PHMA	29	0.80	1.49	0.53	-0.50		0.15	
Fork	PHMA Leaves	29	0.82	0.55	0.71	-0.37		0.11	
Fork	PHMA Stems	29	0.25	-1.63	0.93				

Fork	PHPR	17	0.44	-20.12	26.39		9.28		-11.57
Fork	PHPR Flowers	17	0.77	-34.55	45.71		15.44		-20.67
Fork	PHPR Stems	17	0.36	-1.53	2.26	0.43			
Fork	PICO	20	0.61	2.83	0.11	-1.02		0.42	
Fork	POA	23	0.43	-0.55	1.37				
Fork	POA Flowers	23	0.29	-1.62	1.41	0.27		-0.76	
Fork	POA Stalks	23	0.35	-2.92	1.75	0.41			
Fork	POGR	10	0.92	-8.75	5.19		3.98		-1.90
Fork	POMU	11	0.71	-20.84	1.38	4.37			
Fork	PSME	19	0.78	-14.45	1.99		5.60		
Fork	PTAQ	24	0.55	0.54	1.08	-0.31			
Fork	PYROLA	24	0.46	-8.02	1.34		2.93		
Fork	RIVI	12	0.68	-1.20	1.58				
Fork	RIVI Flowers	12	0.65	-1.44	1.58				
Fork	RIVI Stems	12	0.47	-3.98	1.58	0.60			
Fork	ROSA	45	0.66	-3.37	1.31	-0.40	1.39		
Fork	ROSA Flowers	45	0.51	-1.29	1.38	-0.33			
Fork	ROSA Stems	45	0.50	-8.11	1.49	-0.46	2.79		
Fork	RUPA	41	0.56	-0.35	1.08	-0.24			
Fork	RUPA Leaves	41	0.51	-0.35	0.99	-0.25			
Fork	RUPA Stems	41	0.41	-10.62	1.58		3.07		
Fork	SASC	10	0.92	-0.98	1.36				
Fork	SMST	72	0.58	-0.88	1.38	-0.36			
Fork	SMST Flowers	72	0.48	-1.44	1.47	-0.36			
Fork	SMST Stems	72	0.15	-0.29	-7.92		-1.98		4.39
Fork	SOLID spp.	15	0.59	-12.88	2.02		5.68		
Fork	SOLIDspp. Flowers	15	0.46	-18.31	2.02		7.64		
Fork	SOLIDspp. Stalks	15	0.53	-1.69	2.10				
Fork	SPBE	62	0.45	-0.32	1.21	-0.30			
Fork	SPBE Leaves	62	0.43	-0.89	1.27	-0.24			

Fork	SPBE Stems	62	0.38	-7.00	1.28	-0.33	2.41		
Fork	SYAL	105	0.68	0.51	0.92	-0.61		0.13	
Fork	SYAL Leaves	105	0.65	0.21	0.90	-0.68		0.15	
Fork	SYAL Stems	105	0.50	-5.36	1.32	-0.32	1.70		
Fork	THMO	15	0.40	1.16	0.68	-0.18			
Fork	THOC	29	0.40	-7.46	1.58	-0.70	3.45		
Fork	THPL	14	0.69	-17.36	10.17		7.89		-4.27
Fork	TITR	29	0.48	-0.48	1.72	-0.62			
Fork	TRIF	33	0.67	-1.33	1.10	-0.49		0.22	
Fork	TROV	21	0.42	-4.43	2.37				
Fork	TSHE	12	0.82	-2.69	2.40	-0.39			
Fork	TSME	14	0.60	-1.13	1.37				
Fork	VAME spp.	121	0.77	-0.38	1.40	-0.37			
Fork	VAMEspp. Leaves	121	0.73	-0.82	1.42	-0.34			
Fork	VAMEspp. Stems	121	0.71	-8.31	1.42	-0.38	3.09		
Fork	VASC	56	0.72	-0.96	1.61	-0.38			
Fork	VIOL	116	0.33	-2.83	1.53				
Fork	XETE	89	0.71	10.22	-1.94		-4.93		1.61
Fork	MidSHRUB	559	0.72	-1.96	1.36	-0.30	0.65		
Fork	BUNCH	382	0.53	-3.52	1.51	-0.16	1.27		
Fork	LowSHRUB	190	0.61	-0.70	1.43	-0.24			
Fork	TFORB	810	0.68	-5.71	1.88	-0.35	2.21		
Fork	BASAL	929	0.56	-4.21	1.62	-0.29	1.41		
Fork	RHIZO	86	0.48	-8.05	1.50		3.10		
Fork	EVERGREEN	70	0.71	-0.52	1.49	-0.36			
Fork	FERN	49	0.63	-0.98	1.59	-0.19			
Fork	SPRUCE-FIR	89	0.79	1.45	1.04	-1.04		0.23	
Fork	PINE	72	0.72	-8.15	1.70	-0.61	3.87		
Fork	MidSHRUB Leaves	559	0.36	-1.22	1.46	-0.17		-0.12	
Fork	MidSHRUB Stems	559	0.40	-6.97	1.20	-0.35	2.35		

Fork	BUNCH Flowers	382	0.48	-4.18	1.61		1.06	
Fork	BUNCH Stalks	382	0.21	-2.46	-4.36		-0.23	2.59
Fork	LowSHRUB Leaves	190	0.08	4.31	0.43	-0.33	-3.10	
Fork	LowSRHUB Stems	190	0.08	1.65	0.37	-0.25	-2.28	
Fork	TFORB Flowers	810	0.09	-6.07	3.42		1.15	-1.34
Fork	TFORB Stalks	810	0.10	-3.57	0.49	-0.21		
Fork	RHIZO Flowers	86	0.38	-5.38	-5.98		1.49	3.67
Fork	RHIZO Stalks	86	0.18	-3.47	0.99			