

Variations in grizzly bear habitat selection in relation to the daily and seasonal availability of annual plant-food resources

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ABSTRACT

Determining how resource availability changes daily, seasonally and annually, and how wildlife react to these changes, is valuable for managing wildlife. For vegetative resources phenological information can be used to determine availability and model the distribution of available resources. This study develops a set of annually varying species distribution models using maximum entropy modeling for eight grizzly bear key plant-food species using 1635 food occurrences collected between 2001 and 2017. Seasonal availability (phenology) of plant-food species were then estimated daily at a 30 m resolution for the period 2000–2017 using ground data collected at 15 sites in 2015 and 2018 combined with newly created fine scale phenology product DRIVE (Daily Remote Inference of Vegetation). These food availability layers were then used to develop resource selection functions with grizzly bear GPS collar data to describe daily and seasonal habitat selection and to compare how this changes over a three-year period based on changes in mean annual precipitation. Results demonstrated that grizzly bears selected areas where key plant-food species were available and that habitat selection varied between wet and dry years dependant on season and species. In dry spring conditions, selection for root species was stronger and occurred earlier than for an average and wet year. In the wet summer, length of selection for forb species increased, while strength of selection for wet and dry years was species dependant. In the fall, strength of selection for berry species between wet and dry years was species dependant, but overall selection for berry species was prolonged in the dry fall year. This research aids in predicting how inter-annual differences in climate affect grizzly bear habitat selection and provides insights to managers regarding how changes in management practices that encourage growth of understory vegetation could be used to maximize food resources regionally for grizzly bears and other wildlife.

1. Introduction

Understanding and quantifying the spatial and temporal variation of food resources and their effect on wildlife is a persistent challenge in ecology (Gordon et al., 2004; Nijland et al., 2014). Under a changing climate, determining how resource availability changes daily, seasonally and annually, and how wildlife react to these changes, is important for informing management actions (Ciucci et al., 2014). Resource distribution across a landscape has been quantified through the use of species distribution models (SDMs), which model the probability of occurrence of individual species using environmental variables, such as

climate, land-cover and terrain variables combined with species presence/absence information (Elith and Leathwick, 2009). SDMs have been used extensively to estimate areas of conservation importance of threatened species, design habitat protected zones under future climates (Guisan and Thuiller, 2005; Roberts et al., 2014) and determine where suitable habitat for wildlife will occur (Elith et al., 2006). Studies that incorporate temporal aspects of vegetation distributions, as they relate to food resources for wildlife, are less common.

Several examples exist, that use SDMs to portray the distribution of wildlife plant-foods and habitat. On the Tibetan plateau, SDMs were used to map the distribution of important plant forage for ungulates and

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determine how their distribution varied under a changing climatic conditions (Wu et al., 2017). In Eastern Canada, SDMs were used to map the distribution of lichen important to critically endangered woodland caribou (*Rangifer tarandus caribou*) to determine suitable habitat (Silva et al., 2019). In Western Canada, this approach has been particularly important in assessing grizzly bear (*Ursus arctos*) habitat, which is challenging, given their diverse and seasonally variable omnivorous diet which consists of berries, roots, grasses/forbs, meat and insects (Nielsen et al., 2010; Nijland et al., 2014; Roberts et al., 2014). Nielsen et al. (2010) used logistic regression to model the distribution of key vegetative and non-vegetative grizzly bear food sources across the foothills of Alberta, Canada. They weighted the modeled important vegetative food species by bi-weekly importance (based on foraging seasons and diet) and evaluated bear use of the summed weighted species in each bi-weekly period using resource selection functions (RSFs). Using the combined SDMs and RSFs approach, Nielsen et al. (2010) demonstrated that knowledge of the seasonal distribution of food resources alone predicted the activity of grizzly bears, illustrating the connection between understanding bear resources and understanding their behavior. However, inter-annual changes in selection were not studied.

Changes in the timing of vegetative phenology events can be used to describe the timing of annually recurring events and provide insights into bottom up drivers of animal distribution (Nielsen et al., 2003; Sharma et al., 2009; Tattoni et al., 2019). For example, phenology has been used to understand and predict migration in many ungulate species, including red deer (*Cervus elaphus*) in Norway, who follow a green up wave ("surf" the green-wave) to maximize nutrition intake during spring (Bischof et al., 2012). While much of a grizzly bears diet depends on meat from species such as moose (*Alces alces*) and protein from insects such as ants (*Formicidae* spp.), vegetation foraging makes up a crucial portion of their diets (Munro et al., 2006; Nielsen et al., 2010). When foraging, grizzly bears do not necessarily follow a simple vegetation green up wave as their diet is diverse and season dependant, but they do capitalize on changes in available plant-food species as it relates to its nutritional quality. For example, alpine sweet-vetch (*Hedysarum alpinum*), a root species, is selected for prior to green-up, as this is when it contains the most nutrients (Coogan et al., 2012; Nijland et al., 2013). For forbs and grass species, such as clover (*Trifolium* spp.), horsetail (*Equisetum* spp.), cow parsnip (*Heracleum lanatum*) and dandelion (*Taraxacum officinale*), selection occurs in conjunction with green up, similar to selection by ungulates (Hebblewhite et al., 2008). In contrast, berry species, such as buffaloberry (*Shepherdia canadensis*) and blueberry species (*Vaccinium* spp.), are used in late summer through the start of senescence (Munro et al., 2006; Nielsen et al., 2004a; Pigeon et al., 2016). Krebs et al. (2009) quantified berry productivity over 10 years in the Canadian North and found that precipitation was a key driver in the phenology and productivity of berry crops. Tuell and Isaacs (2010) also found that early season precipitation had a direct influence on the timing of *Vaccinium corymbosum* (highbush blueberry) fruiting as higher than average precipitation deterred early season pollinators such as bees, leading to poor yield of berry crops. In addition to precipitation, snow pack has also been shown to affect production and thus availability of alpine sweet-vetch (Berman et al., 2019; Coogan et al., 2012), with less annual precipitation leading to a lower snow pack, resulting in an earlier melt and larger windows of availability.

At regional and global scales, vegetation spectral indices derived from satellite observations, such as normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI), can be used to describe the timing of vegetation phenology. Within the boreal forest, the start of the growing season has advanced between 0.23 and 0.28 days per year from 2000 to 2014 (Karkauskaite et al., 2017). Similarly, the start of growing season has advanced at a maximum rate of 0.78 days per year between 2000 and 2018 in the Yellowhead region of Western Canada, with advances occurring over multiple elevation and land-cover classes (McClelland et al., 2019). As regional phenology

shifts, so does the phenology of grizzly bear and other wildlife key plant-food species. For example, Laskin et al. (2019) determined that the phenology of buffaloberry is shifting earlier in Alberta, Canada, for both berry ripening (start of availability) and dispersal (end of availability). Shifting phenology under a changing climate coupled with increases in anthropogenic resources extractions, may be rapidly changing wildlife habitats locally and globally (Bisi et al., 2018; Laskin et al., 2019; Roberts et al., 2014), making knowledge on how habitats change between years important for risk assessment and management of important wildlife resources.

In this study, we capitalize on recent advances in satellite data processing to model daily variation in grizzly bear key plant-food availability from 2000 to 2017. First, we developed dynamic SDMs for eight plant-food species which vary annually based on annual land-cover variables. Next we combine SDMs with a newly developed, daily, phenology data product (McClelland et al., 2019) and ground phenology data, to estimate availability for each food species. Availability layers are then combined with grizzly bear GPS collar data to evaluate how grizzly bears select for individual foods daily and seasonally. Results are then compared annually across a three-year period that exhibited large variations in mean annual precipitation. We hypothesize that daily and seasonal selection by grizzly bears for available key plant-food species will vary between wet and dry years. Specifically, we predict increased availability and selection of berry and root species in dry years, while greater availability and selection of forbs in wet years due to reductions in availability of preferred berries.

2. Study area

This research was conducted within the Yellowhead bear management area (BMA 3) in Alberta, Canada (Fig. 1). The Yellowhead BMA contains four natural sub regions as defined by Achuff (1994): alpine, subalpine and upper/lower foothills. Much of the alpine and subalpine area is contained within Jasper National Park, which is a minimally disturbed region in the western portion of our study area. Within the eastern alpine, subalpine and foothills region there is a large anthropogenic footprint created by historic and current oil and gas exploration and extraction, forestry activity and mining. Historic forest fires have been largely replaced by logging practices which serve to create natural openings that support multiple bear foods (Chavardès et al., 2018; Kearney et al., 2019; Nielsen et al., 2004b; Souliere et al., 2020; Stewart et al., 2012). Key bear plant-food species located in this region include, clover, cow parsnip, dandelion (forbs and graminoids), alpine sweet-vetch (root species) and velvetleaf blueberry (*Vaccinium myrtilloides*), huckleberry (*Vaccinium membranaceum*) and buffaloberry (berry species). Key meat food sources within this region include, bighorn sheep (*Ovis Canadensis*), elk (*Cervus Canadensis*), moose and deer species (*Cervidae* spp.) (Cristescu et al., 2016; Munro et al., 2006).

3. Methods

The methodological approach for this chapter is shown in Fig. 2. On the left of the flow diagram we begin with climate, terrain and annual land-cover variables. These variables are combined with individual food species presence locations and used in maximum entropy models to model the distribution of eight grizzly bear plant-food species. On the right hand side of the flow diagram we begin with MODIS and Landsat EVI data from 2000 to 2018 and fuse them through Dynamic Time Warping which produced a daily 30 m EVI product for all years from 2000 to 2018 entitled the Daily Remote Inference of VEgetation (DRIVE). Using DRIVE phenology data and ground derived species availability windows (when plant-food species are available for consumption) we extracted the start of availability (SOA) and end of availability (EOA) for each of the eight species. SOA and EOA layers were masked annually with an 80% probability mask derived from annual species distribution models where all pixels above this

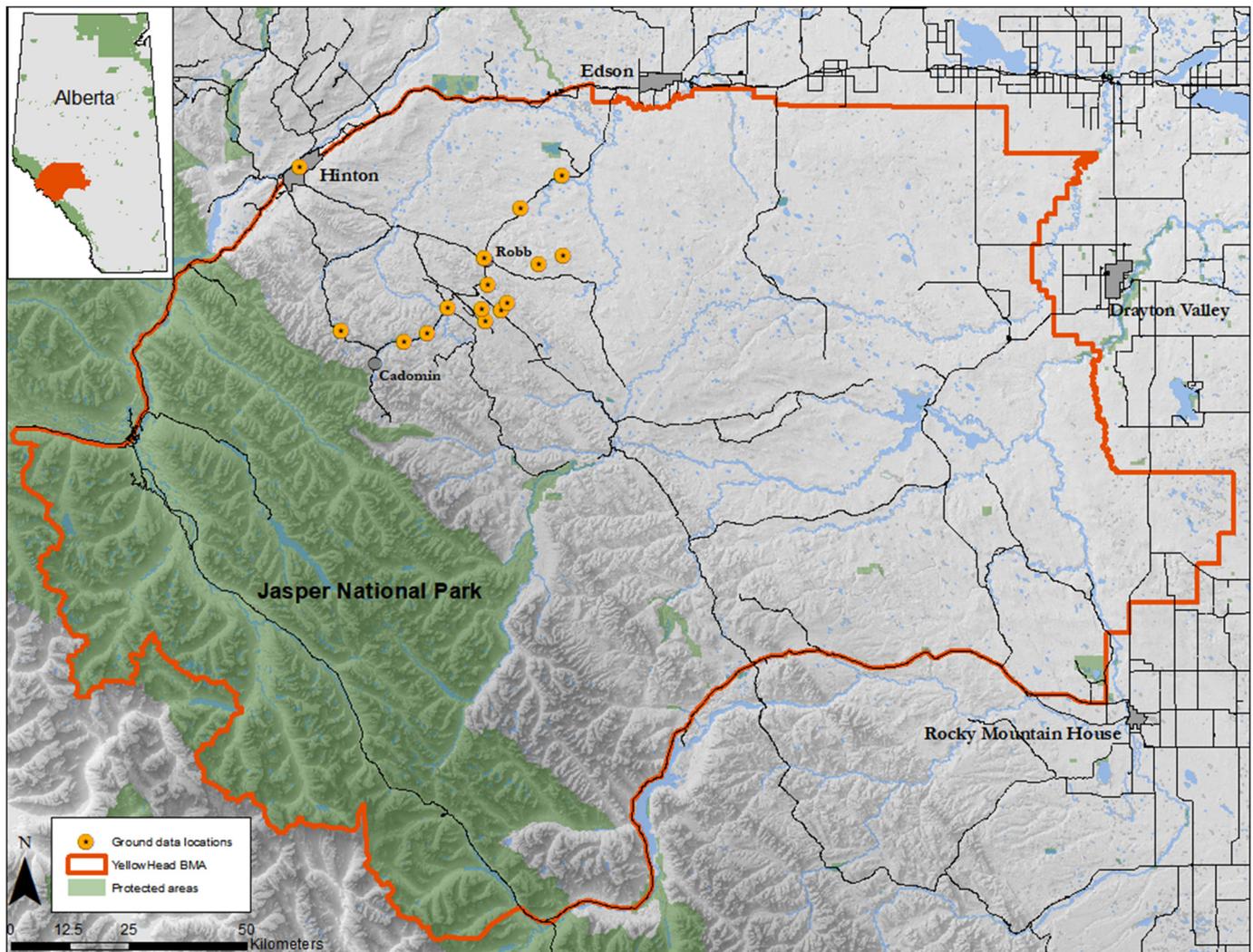


Fig. 1. Study area showing the Yellowhead Bear Management Area 3 border and location of ground data plots where species availability information was collected.

probability threshold were kept. The result is a SOA and EOA annual species availability window that shows where on the landscape species occur, and when they become available for consumption. Availability layers are then utilized in generalized linear mixed effect logistic regression models with annual land-cover variables, terrain variables daily EVI values and grizzly bear locations to create RSF functions capable of estimating daily, seasonal and annual habitat selection.

3.1. Data

3.1.1. Grizzly GPS data

Grizzly bear location data were collected by the fRI Research Grizzly Bear Program from 2013 to 2017. Bears were captured using aerial darting and culvert traps. Collaring efforts adhered to protocols put forth by the Canadian Council on Animal Care for the safe handling of bears (Animal use Protocol Number 20010016). Captured bears were fitted with Followit GPS collars programmed to transmit locations hourly. Telemetry data were divided into three seasons corresponding to foraging seasons; spring defined as den emergence to June 15th, summer defined as June 16th to August 1st and fall defined as August 2nd to October 15th (Nielsen et al., 2004a; Roever et al., 2008a; Sorensen et al., 2015).

3.1.2. Environmental variables

We used climate, terrain and land-cover variables to model the

distribution of key plant-food species for the years 2000–2017 (Fig. 2). We acquired climate variables from ClimateNA, which utilizes historical climate records and PRISM down-sampling (Daly et al., 1994) to create 500 m resolution, normalized, climate layers from 1981 to 2010. Specifically, we used the variables mean annual temperature, precipitation, degree growing days (above 0 °C and 5 °C), May to September precipitation, frost free days and annual and summer heat moisture indices. (Table 1) (Wang et al., 2016). We used a 30 m resolution NASA Shuttle Radar Topography Mission digital elevation model (DEM) to develop terrain variables for slope, aspect, insolation (amount of energy distributed by the sun over varying terrain), Topographic Position Index (TPI, comparison of elevation of a central cell, to the elevation of surrounding pixels) and Topographic Wetness Index (TWI, quantifies surface water flows and accumulation). We created a “distance to road” variable using the Government of Alberta road data (<http://geodiscover.alberta.ca/>) to create a 30 m raster where each pixel recorded the distance to the nearest road. Distances greater than 1000 m were reclassified to 1000 m to account for the effect of roads diminishing at greater distances (Berman et al., 2019; Kite et al., 2016). Climate normals, terrain and road variables did not vary annually in the analysis.

Land-cover variables were derived using several methods. Six classes of land-cover at 30 m spatial resolution (bryoids, broadleaf, coniferous, herbs, mixed wood and shrubland) were available from Hermosilla et al. (2015). Distance to forest edge is based on land-cover

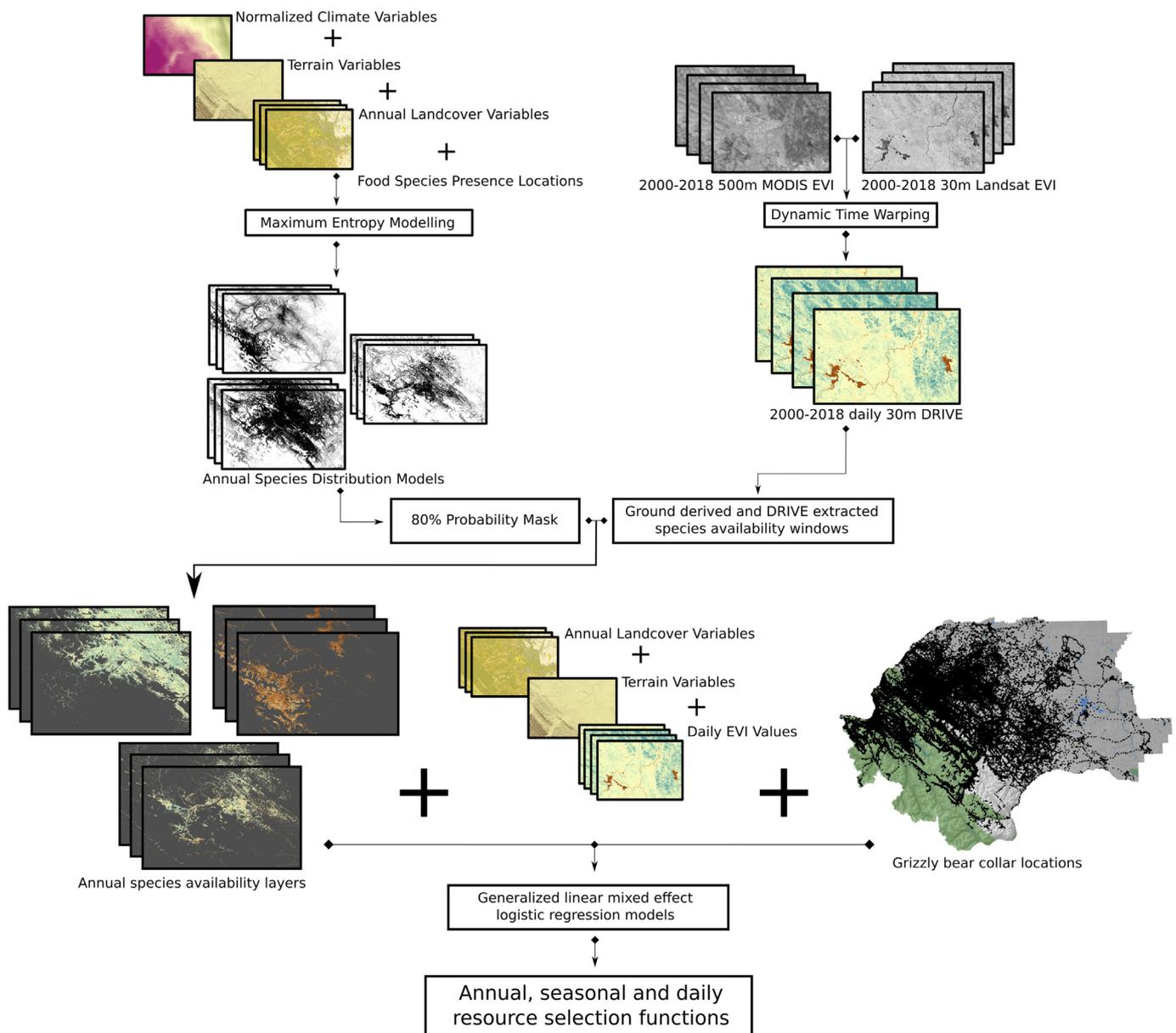


Fig. 2. Flow diagram of how annual availability layers and resource selection functions (RSFs) are created.

classes with edges characterized as any cell with a minimum of 3 adjacent cells classified as forest and 3 cells classified as non forest using 3×3 moving window (Kearney et al., 2019). Within a forest, the distance to forest edge is negative, while outside a forest the distance is positive to differentiate between the two states. Percent canopy cover for the region was quantified by Matasci et al. (2018), who combined Airborne laser Scanning data with Landsat spectral time series data to extrapolate and estimate canopy percent cover. All land-cover variables varied annually due to disturbances from wildfire, forestry and oil and gas activity within the region.

3.1.3. Plant-food availability data from ground observations

The availability of key plant species was defined using food availability windows determined from field observations and camera time-lapse images collected across 10 sites in 2018 and 5 sites in 2015 (Fig. 1). In 2018, field observations were collected at the beginning of May, the end of May and once a week in August over a 4×4 m quadrat. Sites were chosen based on an elevation gradient and for the presence of a minimum of two key species. Reconyx PC800 time-lapse

cameras were set at each site, 2 to 3 m above the ground, with a field of view encompassing each 4×4 m quadrat. Cameras captured 3–5 images daily between 11:00 h and 13:00 h. Food availability windows were derived for each species based on which day of the year (DOY) key phenological events occurred. Availability of alpine sweet-vetch was characterized from start of observations (snow free) until presence of flowers, as nutrition is poor post flowering (Coogan et al., 2012; Nijland et al., 2013). Availability of cow parsnip was determined to begin as celery-like shoots develop and ends as flowers begin to seed and stalks begin to appear woody. Availability of forb species horsetail and clover begins with greater than 50% leaf out and ends when yellowing or senescence occurred. Availability of dandelion was considered to begin with flowering and end when flowers went to seed. Lastly, Availability of berry species, buffaloberry, velvetleaf blueberry and huckleberry, began with the bearing of ripe fruit and ended with seed dispersal. Due to poor berry observations for buffaloberry in 2018, temporal windows were created using ground data and berry counts collected in 2015 at 5 ground sites. Between July 6th and August 10th, ripeness was determined at 6 intervals for each site. Day of the year (DOY) in which

Table 1
Description of variables used in maximum entropy species distribution models and grizzly bear resource selection functions, spatial resolution is in meters.

Description	Units	Median (range)	Spatial resolution
Terrain			
Elevation	meters	1350 (682–3689)	30 m
Aspect	degrees	162 (–1–360°)	30 m
Insolation	watt hours x 10 ⁵	1.01 (0.15–1.64)	30 m
Slope	degrees	6 (0–83°)	30 m
Topographic Position	index	3 (–344–347)	30 m
Terrain Wetness	index	6.8 (1.4–27.4)	30 m
Climate			
Mean annual temperature	°C	1.8 (–4.2–4.9)	500 m
Mean annual precipitation	millimeters	657 (285–2384)	500 m
May to September Precipitation	millimeters	425 (132–1104)	500 m
Degree days below 0 °C	days	1320 (681–2086)	500 m
Degree days above 5 °C	days	1018 (151–1450)	500 m
Annual heat-moisture	index	18.4 (3.0–43.6)	500 m
Summer heat-moisture	index	32.9 (7.4–114.0)	500 m
Frost free period	days	140 (116–170)	500 m
Annual land-cover			
Land cover class	class		30 m
Distance to forest edge	meters	0 (–2740, 7072)	30 m
Percent canopy cover	% x 10 ²	12 (0–69)	30 m
Distance to roads	meters	631 (0–1000)	30 m

availability began and ended for each species at each site was determined.

3.2. Annual species distribution and availability layers

3.2.1. Food species distribution models

We derived annual species distribution models to determine how species distribution changes under varying land-cover conditions using maximum entropy modeling (Maxent) (Fig. 2). Maxent is a machine learning approach where, probability distributions of target species are estimated by determining the probability distribution of maximum entropy (Phillips et al., 2006). Maxent is increasing in popularity due to its requirement of presence-only data combined with environmental information and its ability to infer distributions on incomplete data.

Maxent input variables consisted of presence data collected independently of ground camera data for the eight key plant-food species derived from 1635 sites measured from 2001 to 2017 by fRI Research (Table 2) (Nielsen et al., 2010; Roberts et al., 2014). Environmental variables were selected based on studies by Nielsen et al. (2010) and Nijland et al. (2013). Three variables (percent canopy cover, land-cover

Table 2

Includes species names, common names and food type as well as the number of presence locations per key plant-food species used in Maxent models.

Species	Common names	Food type	# Presence locations	Availability windows
* <i>Hedysarum alpinum</i>	Alpine sweet-vetch	Root	376	Available to 0.47
<i>Trifolium</i> spp.	Clover	Forb	192	0.63 to 1.74
<i>Equisetum</i> spp.	Horsetail	Forb	195	0.72 to 0.53
* <i>Taraxacum officinale</i>	Dandelion	Forb	111	0.56 to 0.96
* <i>Heracleum lanatum</i>	Cow parsnip	Forb	172	0.99 to 1.19
* <i>Shepherdia canadensis</i>	Buffaloberry	Berry	351	0.97 to 1.24
* <i>Vaccinium myrtilloides</i>	Velvetleaf blueberry	Berry	147	1.23 to 1.60
<i>Vaccinium membranaceum</i>	Huckleberry	Berry	91	1.24 to 1.54

Availability window portrays the percentage range of the satellite-derived phenology curves associated with the ground-observed day of the year at which availability begins and availability ends. Percentages 0–100% denote percentages prior to seasonal max. Percentages 100–200% denote percentages post seasonal max. * indicates species focused on in this study.

class, distance to forest edge) were selected to vary annually (Table 1). Maxent SDMs were created using the Maxnet package (Phillips et al., 2017) in the R statistical software (R Core Team, 2019) and validated using cross-validation where each species model was trained on 70% of locations and validated on the remaining 30%. We used bootstrapping to randomly sample training and validation datasets 100 times for each species. We assessed model performance using values of mean area under the curve (AUC) from all bootstrap iterations. AUC values between 0.5 and 0.75 indicate poor model performance, values between 0.75 and 0.9 indicate good model performance and values above 0.9 indicate high model performance (Manel et al., 2002). We then create binary presence-absence using an 80% threshold of probability of occurrence (Ramirez-Barahona et al., 2009). SDM pixels with probability values below 80% were set to 0 and values equal to or above 80% were set to 1. To compare annual SDMs to static SDMs, a 5-year average of presence-absence layer was created for each species by calculating the mean probability of occurrence from 2013 to 2017 for each pixel and, then again, creating a binary 5-year average variable as above.

3.2.2. Phenology data and availability layers

We added inter-annual variation to the annual species distribution models using daily phenology data derived from a recently developed approach known as DRIVE (Daily Remote Inference of VEgetation) (McClelland et al., 2019). DRIVE is a 30-m resolution daily phenology product, calculated using Dynamic Time Warping (DTW) to fuse Moderate Resolution Image Spectroradiometer (MODIS) imagery from Aqua and Terra satellites with and Thematic Mapper (ETM, ETM+ and OLI) imagery from Landsat 5, 7 and 8 satellite data. Annual 500 m resolution MODIS EVI values are fitted with a cubic spline and, using DTW, are warped to all other MODIS EVI years. Warping of MODIS allows the creation of a yearly rule set which is used to rearrange Landsat EVI values annually. Annual Landsat EVI values are then interpolated using a cubic spline creating a daily 30 m spatial resolution EVI product for the entire Yellowhead BMA from 2000 to 2018 (see McClelland et al., 2019 for further details).

In order to translate ground-derived food availability windows to DRIVE, and calculate regional plant-food availability, we first extracted DRIVE phenology curves at each ground observation site, for the year in which the ground data was collected. Extracted DRIVE curves were split into two sections, green up and senescence, with the center occurring at the maximum EVI value (seasonal maximum) (Fig. 3). Minimum values were then calculated for green up and senescence. Percentages along the DRIVE curve (0–100% referring to the green up portion of the curve and 100–200% referring to the senescence portion of the curve) (Fig. 3) were then extracted for the DOY of start and end of availability that were derived from plant-food ground site observations. Percentages along the curve we used as they allow start and end of availability to vary with different curve shapes as they relate to differing elevation, land-cover and vegetation classes. To obtain a single percent value for start of availability and end of availability percentages along the DRIVE

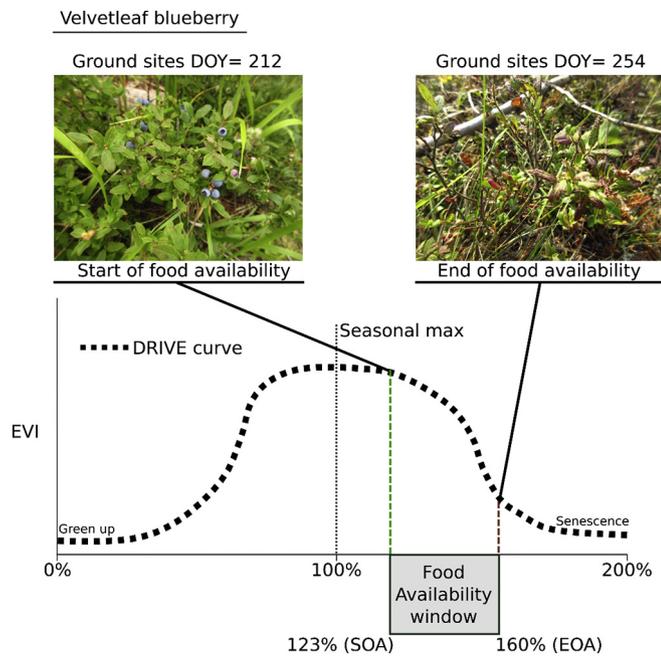


Fig. 3. Process for deriving food availability windows from ground sites and DRIVE. Images represent start of availability (SOA) and end of availability (EOA) at ground sites. DRIVE curves are extracted for each ground site and percent values along the curve are extracted for corresponding day of year (DOY). SOA and EOS percentages are then used to extract SOA and EOA for every pixel over the entire Yellowhead BMA.

curve were averaged across all sites for each species creating final start and end of availability percentages (Table 2). These start and end of availability percentages were then used to calculate start and end of availability for each DRIVE pixel for the entire study area for each bear plant-food species. For all species except clover and horsetail, pixels where length of availability was less than 10 days were excluded. For clover and horsetail, pixels with length of availability less than 30 days were excluded as they have larger availability windows (Table 2). Derived start and end of availability layers were then masked using 80% presence-absence SDMs.

3.3. Grizzly bear habitat selection

We compared used and available locations of collared bears using a GLMM (Generalized Linear Mixed Effects Model) to estimate grizzly bear habitat selection. We compared five models of varying complexity to determine whether plant-food species availability covariates are useful in determining grizzly bear habitat selection.

3.3.1. Grizzly bear used and random locations

Grizzly bear GPS locations were resampled to 6 h intervals for all individuals of all age/sex classes in a season, which has been shown to minimize autocorrelation (Boyce et al., 2010; Nielsen et al., 2002). Any individual bear with less than 60 observations and a range of

observations less than 30 days were removed from the data set. Individual home ranges were calculated with the “adehabitatHR” package (Calenge, 2006) in R statistical software using minimum convex polygons. To account for outliers, only 95% of location were used. We then defined available locations (hereby defined as random locations) by calculating the area for each seasonal individual home range and, for each individual bear, generating 5 random locations per km² (Nielsen et al., 2004b). In this analysis, we used a total of 48 bear-years in spring, 56 bear-years in summer and 53 bear-years in fall.

3.3.2. Habitat covariates

To determine how grizzly bears utilized the key plant-food species, we extracted binary covariates from the generated food availability layers, indicating a) if a grizzly bear was within 100 m of a pixel with a seasonal food source (food presence variable), and, b) if a grizzly bear was within 100 m of a pixel with a seasonal food source at a date when each food source was available (food availability variable). To account for interactions between presence and available variables we created a combined presence-availability variable. This was achieved by combining presence and availability variables create a tertiary variable with three values representing a) plant-foods being neither present nor available, b) plant-foods being present and unavailable and c) plant-foods being present and available with all variables pertaining to within 100 m of a grizzly bear.

3.3.3. Grizzly bear RSF models

We developed RSF models to quantify annual grizzly bear habitat selection from 2013 to 2017. RSFs were developed by fitting generalized linear mixed effects logistic regression models to the sample of used and random bear locations of bears. The fixed effects were satellite-derived environmental variables describing available habitat (Table 1). We used a random intercept to account for non-independence within relocations of individual bears of different age and sex classes and allow a varying response within different reproductive classes and individual bears as this has been consistently observed in many habitat selection studies (Kearney et al., 2019; Nielsen et al., 2004a; Roever et al., 2008b; Stewart et al., 2013). Models were built seasonally for spring, summer and fall, using all using plant-food species important during that season.

We used AIC (Akaike Information Criterion) to compare among five candidate models for each foraging season (Table 3) beginning with a Core model and increasing in complexity (Berman et al., 2019; Kearney et al., 2019; Nielsen et al., 2004a). We further validated models by determining predictive accuracy with bin correlations and bin proportions using area-adjusted frequencies (see supplementary materials) as AIC is known to choose the most complex models. We compared multiple models within this study to ensure the efficacy of Annual Availability models in comparison to other candidate models. The Core model consisted of land-cover and terrain variables (Table 1), with quadratic terms included for insolation, TWI, distance to roads and distance to forest edge, given previous evidence for they have been show non-linear relationships with grizzly bear use (Berman et al., 2019; Kearney et al., 2019; Nielsen et al., 2010; Roever et al., 2008b) (Table 3, Core). We then created a Greenness model, consisting of the Core model and daily EVI values (derived from DRIVE), to test whether

Table 3

Overview of the 5 models created for each season. Polynomial variables are indicated with “²” and interactions between variables are indicated using “:”.

Model	Variables
Core	(Distance to roads) ² + TWI ² + (Distance to forest edge) ² + Land-cover + Elevation + Insolation ² + Random Intercept(Age sex class / Individual bear year)
Greenness	Core + (Daily EVI) ²
Average Presence	Core + (Daily EVI) ² + 5 Year average food presence
Annual Presence	Core + (Daily EVI) ² + Food presence:Year
Annual Availability	Core + (Daily EVI) ² + Food presence:Food availability:Year

Table 4

Seasonal validation metrics for all five tested models. AIC indicates the Akaike Information Criterion score for each model, correlation is the average spearman rank correlation coefficient between area-adjusted frequency of occurrence and the 10 probability bins created for each RSF model. Proportion refers to proportion of bins with an area adjusted frequency significantly different than 0.

Models	AIC	Delta AIC	Correlation coefficient	Proportion
Spring				
Core	56,473	763	0.40	0.4
Greenness	56,401	691	0.41	0.4
Average Presence	55,903	192	0.86	0.9
Annual Presence	55,789	78	0.90	0.9
Annual Availability	55,710	0	0.89	0.9
Summer				
Core	61,517	1165	0.61	0.5
Greenness	60,936	584	0.65	0.6
Average Presence	60,575	222	0.94	1.0
Annual Presence	60,522	170	0.83	0.8
Annual Availability	60,352	0	0.95	1.0
Fall				
Core	79,782	1474	0.76	0.8
Greenness	79,126	818	0.82	0.8
Average Presence	78,546	238	0.94	1.0
Annual Presence	78,322	14	0.80	0.8
Annual Availability	78,308	0	0.93	1.0

EVI improved upon the core model. EVI was input as a 2nd order polynomial due to an expected non-linear reaction to EVI by grizzly bears (Table 3, Greenness). Next, to simulate seasonal models with no inter-annual variation and to determine whether annual models better captured variation in grizzly bear habitat selection, we created an Average Presence model by adding our 5-year average food presence-absence variables to EVI Models (Table 3, Average Presence). We then created an Annual Presence model to determine how seasonal selection changed annually. For the Annual Presence model we added presence of plant-food species with fixed effect interactions between food presence and year (Table 3, Annual Presence). Lastly, Annual Availability models were developed to observe how annual, seasonal and daily food availability affected selection of key plant-food species. We added annual food availability, which is capable of characterising daily food availability, to annual food presence, by using the combined presence-availability variable. In this model, fixed effect interactions were specified between annual food presence-availability variables and year to determine how selection changed due to variations in annual food availability and to determine whether annual selection for present and available foods was greater than simply present foods (Table 4, Annual Availability). All models were fit using the glmer function in the lme4 package (Bates et al., 2015) within R statistical software (R Core Team, 2019).

Odds of selection for available foods versus present and unavailable foods were calculated and compared over the 3-year period representing years of dry (2016), average (2015) and wet (2017) mean annual precipitation to test whether selection for available food resources improved over present food sources. Daily probability of use was also calculated and compared for available foods and contrasted of the three years.

4. Results

For simplification of results we focus on two plant-food species per season, five plant-food species in total.

4.1. Grizzly bear RSF model comparison

In all seasons, Annual Availability models showed the lowest AIC score indicating that they were the strongest model. Based on spearman

rank coefficients we see that the best model alternates dependant on the season. Spring correlation over all models was the lowest with Annual Presence models showing the highest correlation (0.90) and Annual Availability Models being the second most correlated (0.89). For summer models, the Annual Availability model had the highest correlation (0.95) and the Average Availability model showed the second highest correlation (0.94). In fall, the Average Presence model was the most strongly correlated (0.94) and Annual Availability models was second strongest (0.93). Across all seasons, Annual Availability models were the most consistent model and contained the highest or tied for highest proportion of bins with an area-adjusted frequency significantly different from 0 thus we determined it a suitable model on which to continue the analysis.

4.2. Comparing odds of selection for available vs. present and unavailable plant-foods

In the dry year the trend for all species was for stronger selection when available compared to present but unavailable, especially for alpine sweet-vetch. However, in average and wet years, the selection for the majority of plant-food species was more variable. For the majority of species we found that there was similar or stronger selection for when a food species was perceived as available compared to when it was present but unavailable (Fig. 5). The two species where this did not occur was in spring for alpine sweet-vetch and in fall for buffaloberry where selection for present and unavailable was stronger than when available for both wet years, and in the case of buffaloberry, this also occurred in the average year. (Fig. 5).

4.3. Seasonal and daily selection for available food species

Seasonal selection of key plant-food species by bears varied between wet (2017), dry (2016) average precipitation (2015) years. Similar daily trends were exhibited by species across years; however, there were differences in the day when plant-food species became available, length of availability (Fig. 4) and the day when they were selected for by grizzly bears (Fig. 5).

In spring, strongest selection for alpine sweet-vetch occurred in the dry year with selection also occurring in the wet and average years. Daily selection of habitat where alpine sweet-vetch is available follows similar trends throughout all three years with selection occurring in early to mid spring. During the dry year, we observe selection occurring earlier than in an average and wet year (Fig. 5).

In spring, there was strong selection for dandelion during the wet year, with slight selection during the average year and avoidance during the dry year. Daily selection, in spring, of habitat where dandelion was available followed similar trends across all three years with selection occurring mid to late spring. During the dry year, daily selection occurred earlier than in the wet year, and daily selection in both dry and wet years occurred earlier than in our average year. In summer, the strongest selection for dandelion occurred in the wet year followed by the average year. Slight selection for dandelion was observed during the dry year. Daily selection of habitat where dandelion was available followed similar trends throughout all three years with selection occurring at the start of summer and ending before the middle of summer. Daily selection in the wet year occurred slightly later and lasted longer than in average and dry years (Fig. 5).

In summer, selection for cow parsnip occurred in the dry year with neither seasonal selection nor avoidance in wet and average years. Daily selection of habitat where cow parsnip was available followed similar trends in all three years with selection occurring mid to late summer. Daily selection during the wet year occurred earlier than in the average and dry year and selection in the average year occurred earlier than in the dry year (Fig. 5).

In fall, bears selected for buffaloberry in the dry and wet year and avoidance was observed in the average year. Daily trends in selection of

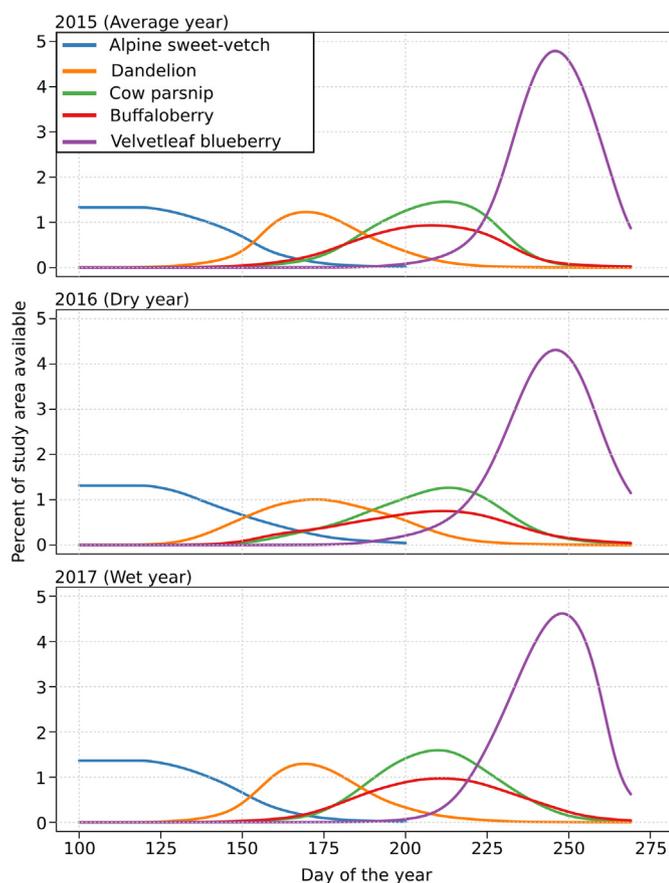


Fig. 4. Percent of the landscape that is considered available for each plant-food species over each year.

habitat where buffaloberry was available varied over the three years, however, selection generally occurred at the start of fall. Daily selection occurred earliest during the wet year. Daily selection occurred at similar times during the dry and average years and was more sustained than in the wet year with selection lasting longest in the dry year (Fig. 5).

In fall, selection of velvetleaf blueberry occurred in the wet year with weaker seasonal selection during the dry year. In the average year neither seasonal selection nor avoidance was observed. Daily selection of habitat where velvetleaf blueberry was available followed similar trends in all three years with selection occurring mid to late fall. In the wet and average years, a peak of daily selection was observed prior to mid fall. After mid fall, daily selection occurs earliest in the dry year followed by the average and then wet year (Fig. 5).

5. Discussion

Through this research we take conventional species distribution models using terrain and climate variables and add annual disturbance creating annually varying SDMs. We then combine annual SDMs with the DRIVE output, creating new daily plant-food availability layers. These innovative availability layers offer researchers flexible habitat information at an unprecedented scale. By creating layers representing the daily availability of eight key grizzly bear plant-food species from 2000 to 2017, we demonstrated that the annual and daily variations in distribution and availability of food species changed grizzly bear habitat selection, providing key insights into how the landscape is used by bears on a daily basis, highlighting the importance of fine scale plant-food availability layers. Through these methods we show that day of selection varies on an annual basis over years of differing mean annual precipitation demonstrating that mean annual precipitation may affect

the timing in which grizzly bears forage for different plant-foods. We also found that bears showed seasonal habitat selection, which varied between years. In addition, our results showed that over three years of differing average annual precipitation levels, key bear food resources varied in seasonal importance between root, forb and berry species.

5.1. Model performance

Annual availability models out performed all other models based on AIC values and performed most consistently well across all seasons when considering correlation and proportion values. We see slightly worse performance in correlation than Annual Presence models in spring, which may indicate grizzly bears, are moving to areas of known presence first and awaiting plant-food availability or that availability windows are not capturing the full extent of plant-food availability. We also observe slightly poorer correlation than Average Presence models in fall, which may indicate that annual SDMs are over estimating variations in the distribution of berry shrubs. Comparing when grizzly bears select for available plant-foods vs. present and unavailable plant-foods results suggest bears generally select for foods when they are perceived as available by Annual Availability models, especially in dry years. This may be due to the majority of species being available longer in dry years (Fig. 4). In the wet year, while selection for available alpine sweet-vetch in the spring and buffaloberry in the fall occurs, there is stronger selection for when these food species are predicted to be present, but unavailable. This signifies that either the food availability windows are not as accurate estimating the availability of those two species in wet years, or there is something else that is available in these areas that grizzly bears are selecting for, such as meat in the spring or meat, ants and other forage in the fall.

5.2. Grizzly bear habitat selection

In the dry year, higher seasonal selection in alpine sweet-vetch and earlier selection than in wet (2017) and average (2016) years may be due to lower mean annual precipitation, indicating less winter precipitation leading to a smaller snow pack allowing snow to melt faster and grizzly bears to begin foraging for alpine sweet-vetch earlier (Berman et al., 2019). We may see highest selection for alpine sweet-vetch during this time as it is the only available plant-food and thus the primary food source while grizzly bears wait for green up. (Coogan et al., 2012). Grizzly bear seasonal selection of dandelion and cow parsnip alternate between wet and dry years indicating higher production of cow parsnip and lower dandelion production during years of less precipitation (Molina-Montenegro et al., 2010), or that cow parsnip come available later in dry years and less overlap occurs with other forb species making it the most desirable food source available. Selection for buffalo berry is strongest in dry years, which may be due to higher berry production during dry years as less precipitation occurs during flowering and berry ripening (Benedict, 2007; Tuell and Isaacs, 2010).

Selection in the wet year when compared to the dry year had an opposite trend for almost all plant-foods, however velvetleaf blueberry did not appear to follow a discernable pattern in relation to mean annual precipitation. It appears that selection increases throughout all three years indicating berry production may increase as well. We do observe a trend in timing of selection, with selection during the dry year occurring earliest followed by the average year and then the wet year. Remberg et al. (2014) showed that antioxidants increase in blueberry species under years of heavy rainfall, which may increase periods of blueberry consumption. We also note that the area where velvetleaf blueberry is present is larger than for other food species within this study (Supplemental Fig. 2) and it is possible that velvetleaf blueberry may have higher berry production in different regions during different years creating a sustained availability. Alternatively, error is being introduced due to a larger area of occurrence not accurately representing velvetleaf blueberry distribution. To create more accurate species

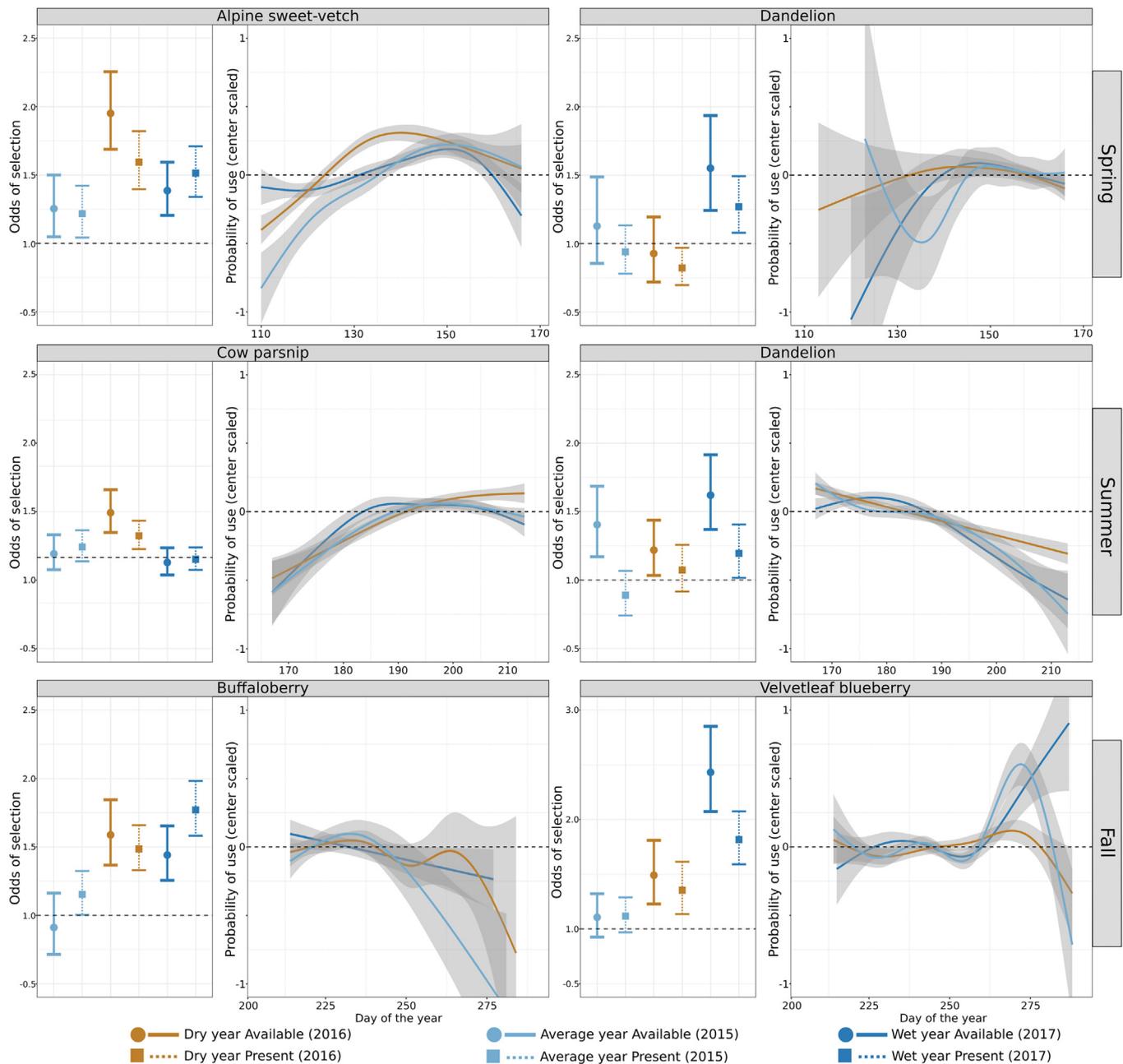


Fig. 5. For each focus species in each season, we show first the seasonal odds of selection for present and available food species compared present but unavailable food species with error bars representing a 95% confidence interval and second, the daily probability of use shown with a line plot. Rows represent seasons.

distribution layers, a higher number of vegetation plots that are more widely distributed may be needed.

Observations of how grizzly bear habitat selection varies in years with different average annual precipitation provide insight into how grizzly bears may react in future years with changing climatic conditions. Roberts et al. (2014) modeled grizzly bears food distribution into the future using SDMs. They showed that under rising temperatures, grizzly bear foods will remain largely unaffected and, in some cases, the distribution of food species is predicted to increase. While the distribution of food species may increase, our results inferred that different precipitation regimes affect availability, of individual food resources for grizzly bears. If the climate consistently becomes drier, grizzly bears may shift from forbs that rely on wet years for production to other food sources such as cow parsnip during the summer season (Roberts et al., 2014). If the climate becomes wetter we may see alpine sweet-vetch

production being impacted and bears having to search elsewhere for food while velvetleaf blueberry becomes available longer providing an important food source late into the season which may delay den entry (Pigeon et al., 2016). Lower snowpack during dry years may result in an earlier start of the growing season allowing roots and forbs to become available for consumption earlier in the season, which may mean earlier den emergence for grizzly bears (Coogan et al., 2012) and may translate into better body condition of bears (Boulanger et al., 2013; Nielsen et al., 2013). Varying food availability associated with wet and dry years may also affect hunting and insect foraging activities in the future and determine years in which carnivorous activities may become more prevalent. All these shifts in food availability for bears may also affect bear-human interactions as bears may increase utilization of anthropogenic food resources and available livestock on a shared landscape (Linnell et al., 1999).

5.3. Management implications

In using new techniques to combine complex datasets we have developed a novel approach to describe the intricacies of vegetation and plant food availability at a fine spatial and temporal scale, ushering in a new age in biodiversity assessment. Our results contain important management implications that should be considered under increasingly variable climatic conditions. The ability to predict the timing of food resources will lead to a better ability to predict spatially and temporally where grizzly bears will occur on the landscape and in which years early or late den emergence or denning may happen. With our spatially explicit food availability layers, we provide a tool which may be used to evaluate the effect of industry practices on important food resources under varying environmental factors. This combined with knowledge of understory revegetation may allow managers to create a sustained food supply for not only grizzly bears but other wildlife species as well, and allow the creation of higher quality habitats into the future.

5.4. Limitations

While this study successfully provides a new methodology, monitoring techniques and insights into the annual, seasonal and daily availability of key plant-food species for grizzly bears, there were some limitations. Improvements can be made in the creation of food availability windows, as ground data sites consisted of a small sample size and the majority occurred under open canopy conditions. To further the development of these methods adding additional ground verification sites under differing forest stand and crown closure conditions would be beneficial. Continued observations over multiple years would also allow for more accurate food availability windows. Availability windows could then be tailored to different land-cover classes that may alter the overall phenology observation for that site. This would help strengthen and refine models for habitat selection on a heterogeneous landscape. Furthermore, this study focuses on plant-food species. While much of a grizzly bear's diet and habitat selection is driven by availability of plant-foods, grizzly bears also consume meat depending seasonal and annual availability. Future models may look at including a meat component.

5.5. Conclusion

Here we provide new methodologies for monitoring the complex food systems of grizzly bears using fine-scale remote sensing techniques that combine daily/annual phenology data with species distribution layers. With this research we have created unprecedented annual, seasonal and daily food species availability layers with which we were able to model grizzly bear habitat selection over an identical time scale and show how habitat use changes under years of different annual precipitation. While this paper focuses on grizzly bears, these novel techniques could perceivably be used to monitor the key plant-food species for a variety of wildlife species and be used to determine future plant-food trends under changing climate regimes and provide ecologists and managers a like a valuable tool for plant-food monitoring.

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Author contributions

All authors contributed to the design and implementation of the research, to the analysis of the results and to the writing of the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2020.101116>.

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