

VARYING NONLINEAR DEPENDENCIES IN HABITAT SELECTION:
ESTIMATING INSTEAD OF IMPOSING FUNCTIONAL FORMS

by

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ABSTRACT

Spatial heterogeneity of habitats and different foraging strategies can result in dissimilar patterns of habitat selection among individuals in a population. Studies have demonstrated that incorporating individual variation can influence model inferences. Thus, individual variation is increasingly being incorporated in habitat selection studies. Our objective was to advance the concept of individual variation in habitat selection by incorporating varying shapes (i.e., function forms) of responses among individuals. We used simulation modeling to develop a new analytical framework and introduce a new habitat selection metric, the Normalized Selection Ratio (NSR). Our results demonstrated the ability of the NSR to correctly estimate the strength and shape of complex simulated patterns of habitat selection, while simultaneously protecting against over-fitting. Using a simulated population of individuals, we showed how our approach can scale-up individual responses to facilitate population-level inference. We demonstrated how hierarchical clustering of individual-level response curves can identify and quantitatively describe different types of habitat selection within a population. When applied in a temporally dynamic framework, we showed that the NSR can detect ecological dynamics in habitat selection with quantitatively different inferences from analyses that pool data over time. We illustrated application of our approach using global positioning system (GPS) telemetry data for grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem (GYE). We investigated the direction (preference or avoidance) and shapes of grizzly bear selection for whitebark pine (*Pinus albicaulis*) habitat during fall from 2007 to 2014. Our general conclusions support previous findings that grizzly bears exhibit a high degree of individual variation in habitat selection. Our approach of hierarchically clustering response curves detected 4 groups of grizzly bears with distinctly different patterns of whitebark pine habitat selection. Based on the group-level mean responses, 77% of sampled bears selected for whitebark habitat and 23% selected for non-whitebark pine habitats. Among the hierarchical groups that selected for whitebark pine, we observed substantial variation in the strength and density of whitebark pine being used. These results demonstrated the ability of our approach to identify, quantify, and organize individual differences in habitat selection and improve our understanding of grizzly bear ecology in the GYE.

1. INTRODUCTION

Ecologists have long-recognized that individuals within the same population can differ substantially in how they acquire resources (Van Valen 1965). Despite this, researchers traditionally considered behavioral plasticity as having negligible impacts on ecological inferences: pooled data or population averages were believed sufficient for understanding ecological dynamics (Bolnick et al. 2003; Araujo et al. 2011). However, recent advances in Global Positioning System (GPS) telemetry are increasingly challenging this traditional viewpoint: large datasets, frequent locations, and near continuous activity data are now standard in animal tracking datasets. Accordingly, researchers are accounting for individual variation in habitat use and the results appear far from negligible: incorporating individual heterogeneity into analyses can reveal quantitatively different population-level inferences than “pooled” analyses of habitat selection (e.g., Nielsen et al. 2002; Aarts et al. 2008; Gillingham and Parker 2008; Moreau et al. 2012; Beyer et al. 2013).

Inter-individual variation in habitat selection is generally modeled by allowing parameter estimates to vary across individuals, either as random coefficients (particularly slopes) in mixed models or by fitting separate regression models to each individual (Gillies et al. 2006; Fieberg et al. 2010). Although these approaches account for differences between individuals, they do not represent a flexible framework in which selection can vary, in an unspecified way, as a function of habitat covariates (however, see Beyer et al. 2013 for a permutation approach). For example, the often-used exponential model in habitat selection studies (Johnson et al. 2006) specifies that the

response is exponentially changing (on the logit scale). Therefore, only the strength and direction of the response can vary across individuals. This implies homogeneity of functional forms in a population, and moreover, assumes we know a priori what that form should be. An alternative is to forego such assumptions and estimate the appropriate functional form, or nonlinear dependency, from the data itself (Aarts et al. 2008; Keele 2008). However, incorporating inter-individual variability in functional forms of habitat selection remains relatively rare (but see Aarts et al. 2008; Johnson et al. 2013, and Beyer et al. 2013). Even less common is the investigation of variation in functional forms over time. That habitat selection can vary seasonally is well understood, but exploration of temporal variation in functional forms is underrepresented in the literature (however, see Hooten et al. 2013). This is particularly important because observing temporal dynamics in habitat selection provides information about the variation of ecological processes underlying resource selection (McLoughlin et al. 2010).

In this paper we present an approach for incorporating variation of nonlinear functional forms in resource selection models. Statistics for quantifying resource selection have rapidly increased in complexity during the last decade (e.g., nested hierarchical generalized mixed models; Moreau et al. 2012). While these advancements are undeniably powerful, many are conceptually and mathematically complex; correct application generally requires expertise beyond the training of most ecologists and wildlife managers (Bolker et al. 2009). Consequently, and as suggest by others (e.g., Hooten et al. 2014), we believe the potential for adaptation, modification, and applied use of novel approaches for studying resource selection may be limited. Here, we attempt to

avoid this outcome by balancing statistical complexity with accessibility and, most importantly, ease of interpretability of ecological relationships. Using the Poisson point modeling (PPM) framework described by Warton and Shepherd (2010) and Aarts et al. (2012) and the flexible smoothing of generalized additive models (GAM), we develop an intuitive resource selection metric we refer to as the *Normalized Selection Ratio* (NSR). Our hope is that ecologists will adapt, refine, and improve upon our approach for use in their own ecological systems. We use static and temporally dynamic simulations of habitat use and graphical displays to present key concepts and main results. Finally, we illustrate an application of our technique in an applied conservation setting to empirical GPS telemetry data from grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem (GYE).

2. METHODS

Habitat Covariates, Availability, and Simulated Use

For simulations we modeled habitat selection as a function of a single continuous covariate, elevation, although our methods use standard model-fitting functions (GLM or GAM) and can easily incorporate multiple predictor variables. Using a 30-m digital elevation model (DEM; National Elevation Dataset, USGS 2009) and the *Focal Statistics* tool in the Geoprocessing Toolbox in ArcGIS 10.3.1 (ESRI 2015) we reclassified elevation as the mean of 30-m pixels within a 100-m radius ($elev_{100m}$) for each pixel. For the illustrative application to grizzly bear data we modeled selection as a function of whitebark pine (*Pinus albicaulis*; see *Application* section for details). The availability domain determining the spatial extent of pseudo-absence, or background, points for habitat selection models were defined at the individual, or third-order, level of selection (Johnson 1980). For simulations we used circles of two different sizes (5- and 10-km radii), whereby the large home range was 4 times the area of the small home range. These circles were placed subjectively over a DEM so that covariate ranges were similar, but the elevation probability density functions differed for the two domains. Thus, our simulated datasets present the practical challenge of comparing habitat selection among models that differ in area of overall availability (i.e., home-range size) and distribution of covariates values within that area (Beyer et al. 2010).

For each simulated dataset we constructed patterns of “known” selection using the *spatstat* package (Baddeley and Turner 2005) in Program R (R Core Team 2015). We first divided simulated home ranges into spatial sub-regions based on 50-m elevational

bins (e.g., >2000m to 2050m, >2050m to 2100m, etc.). To simulate presence, or “used,” locations that were proportional to availability, we determined the number of locations to allocate to each sub-region by multiplying the proportional area of each sub-region by the starting number of simulated locations ($n = 200$). We simulated selection and avoidance for particular elevation bands by increasing or decreasing the proportional-use sample size in the relevant sub-regions. Random locations from each sub-region were merged together to create a single “used” location dataset (Appendix A, Figure A.1).

Modeling Individual Heterogeneity

Two methods are generally suggested for modeling among-individual variation in presence-only resource selection studies (Fieberg et al. 2010): random intercepts and coefficients can be used in generalized linear, or additive, mixed models (GLMMs and GAMMs) to account for inter-individual differences. However, significant technical detail must be understood in order to use these models appropriately, and few ecologists are likely to be aware of the possible hazards (Murtough 2007; Bolker et al. 2009). An intuitive and simple alternative is to fit separate fixed-effect models to data from individual animals and perform secondary analyses of individual results to achieve population-level inferences (e.g., Nielsen et al. 2002; Sawyer et al. 2006; Murtough 2007; Fieberg et al. 2010). These so-called “two-stage” analyses provide an alternative to GLMMs and GAMMs and are more easily accessed by ecologists. Therefore, we followed the suggestions by Fieberg et al. (2010), and applied a two-stage framework for modeling individual responses in habitat selection. Application to the heterogeneity in the temporal domain follows the same approach except the unit of heterogeneity is

shifted from individual animals to the appropriate temporal unit (e.g., day, week, or month).

Variable Nonlinear Functional Forms

To allow flexibility in the shape of functional forms among individuals, or within individuals over time, we used a nonlinear regression framework. Although nonlinear transformations of covariates (e.g., including a quadratic term) is one strategy for modeling nonlinear dependencies, a priori knowledge of the correct transformation is usually not known (Keele 2008; Aarts et al. 2008). Alternatively, semi-parametric Generalized Additive Models (GAMs) allow for flexible specification of the response dependency through the use of smoothing functions rather than fixed parametric terms (Wood 2006).

Regardless of the approach used, nonlinear dependencies of a response on a predictor cannot be represented by a single term, such as a parameter estimate. Therefore, the general approach of drawing inferences about habitat selection based on model parameter estimates (e.g., Boyce et al. 2002; Hebblewhite and Merrill 2008; Beyer et al. 2010; Moreau et al. 2012) is not applicable. This is unfortunate, as parameter estimates provide an intuitive framework for understanding disproportionality between habitat usage and availability: positive values demonstrate selection for, negative values selection against, and zero represents use proportional to availability. In this paper we demonstrate how to interpret habitat selection metrics on the response scale such that nonlinear dynamics can be interpreted in the same manner as parameter estimates: the magnitude and direction of selection relative to a baseline-level of no selection.

Habitat Selection Function

Among the methods available for assessing animal-habitat relationships from presence-only telemetry data, the Resource Selection Function (RSF) has arguably surfaced as the most popular (McLoughlin et al. 2010; Aarts et al. 2012; Northrup et al. 2013). Aarts et al. (2008) point out that the “resources” in RSFs may actually represent ecological quantities that are non-depletable, and elevation as used in this paper is a prime example. Thus, the word “habitat” rather than “resource” is more reflective of the ecological processes being modeled, and we hereafter refer to these functions as *Habitat Selection Functions* (HSFs; Aarts et al. 2008).” HSFs quantify the disproportionality between habitat usage and availability. Such non-random use is the defining characteristic of habitat selection and considered to be biologically insightful under the assumption that it reflects importance of habitat types, or something about how an organism perceives and responds to its environment (Manly et al. 2002; Beyer et al. 2010; Aarts et al. 2012).

Several papers have highlighted the connections between the three most common approaches of estimating Habitat Selection Functions (HSFs): logistic regression, maximum entropy, and inhomogeneous Poisson process (IPP) models (Warton and Shepherd 2010; Aarts et al. 2012; Fathian and Hastie 2013; Renner and Warton 2013). Although the long history and widespread use of logistic regression in ecology likely make it the most widely accessible and understood approach, here we use the IPP framework for two key reasons: First, the response being modeled, intensity

$\left(\frac{\text{number of points}}{\text{unit area}}\right)$, is unambiguous and easily understood in terms of animal location data

(Renner et al. 2015). This greatly improves interpretability, transparency, and use of HSFs over more traditional measures such as RSF scores or relative probability. For telemetered animals, it should be noted that intensity (λ), is not an estimate of actual intensity of occupancy per unit area, but rather the expected density of GPS locations per spatial unit (e.g., km^2), had the point generating process resulted in the total number of GPS locations (presence points) within the specified spatial domain. Second, the role and assignment (number and location) of pseudo-absence points is clearly defined for IPP models; thus the focus is taken away from how to select these and shifted toward selecting and interpreting plausible models (Warton and Shepherd 2010; Renner et al. 2015). IPP models can be performed in a variety of standard statistical packages and the spatstat package (Baddeley et al. 2015) in Program R is well-documented and provides access for ecologist without advanced statistical expertise.

Inhomogeneous Poisson Process (IPP) Model

For a presence-only dataset represented by a spatial point pattern $u = \{u_{x_1, y_1}, \dots, u_{x_n, y_n}\}$ located within the availability domain $\mathcal{A}_k$, we modeled the intensity (λ) of the point process as a function of elevation ($elev_{100m}$):

$$\lambda(u) = \exp(B_0 + f(elev_{100m}) + \varepsilon \tag{eqn 1}$$

where:

u_n = the spatial location of n “used” locations

B_0 = intercept term

$f(elev_{100m})$ = the best-fit adaptive smoothing function for $elev_{100m}$ using penalized cubic regression splines (Wood 2006). See smoothing function section below for details.

Models were fit using the technique of Baddeley and Turner (2005) to approximate maximum likelihood estimates based on the numerical quadrature device originated by Berman and Turner (1992; Baddeley et al. 2015). Based on exploratory analyses of simulated and empirical grizzly bear GPS data, we modified the default quadrature scheme generated by the spatstat program by fixing the distance between dummy points at 90 m. This ensured that all HSF were estimated at the same spatial resolution (grain) regardless of the sample size of used points or the size of the availability domain (extent). Increasing the resolution of dummy points beyond this scale resulted in insignificant differences in fitted result but large increases in computation time. For each point j in the quadrature, response values (y_j ; [0 or 1]), covariate values (z_j), and weights (w_j) were assigned following the procedures of Baddeley et al. (2015; page 347). We fit IPP models following *equation 1* using Generalized Additive Models (GAM) in the mgcv package (Wood, 2004; 2011) in Program R, specifying the model as a loglinear Poisson model fitted to the response of y_j and the covariate values of z_j with weights w_j (Baddeley et al. 2015).

Smoothing Function

We used an adaptive penalized smoother and cubic regression splines for the smoothing and penalty basis, which helps to protect against over- or under-smoothing. The adaptive structure allowed the amount of smoothing to vary as a function of the data

(Wood 2006; Liu and Guo 2010). This is an advantage when estimating functions that are very smooth in some areas, but have sharp peaks or abrupt changes in other regions (Storlie et al. 2008). Such patterns can be expected in HSFs when there is strong selection in a relatively narrow region of the parameter space (e.g., Aarts et al. 2008; Buckley et al. 2011) or when animals exhibit thresholds rather than continuous gradients in selection across the covariate space. Additionally, the penalty per degree of freedom (γ) in the smoothing penalty criterion was increased from 1.0 to 1.4, which aids in reducing overfitting with minimal degradation in prediction error performance (Wood, 2006).

To avoid forcing a fixed smoothing penalty across models, we allowed the penalty structure to vary across different individuals or time periods. For each model we selected the optimal penalty structure using the AIC equivalent UnBiased Risk Estimator (UBRE; Wood 2000; Wahaba 1990) criterion within an information-theoretic framework. The irregular parameter specifying the dimension of the smoothing basis (k) was fixed at a constant value of 21. Wood (2006) demonstrated that the exact value of k is not critical, provided it is larger than is believed to be necessary to approximate the smooth function, and not too large as to be overly-costly in computational time. We controlled the effective degrees of freedom (edf; Janson et al. 2013) of the smooth by varying the dimension of the smoothing penalty basis (m) from 5 (the default minimum) to $k - 3$, selecting the value of m that minimized the UBRE score among competing models (Figure 1). Exploratory analyses of simulated and empirical data showed that values of m less than 5 were virtually never selected but dramatically increased computational time.

Model Interpretation

Although derived from parameter estimates, response-level metrics from HSFs (e.g., intensity $[\lambda]$, relative probability, RSF score, true probability) articulate little about disproportionality between use and availability. For example, two parameter estimates (β) equal to zero for two different animals have the same meaning - use proportional to availability. However, when converted to the response scale, the predicted values derived from the β estimates will almost certainly be different because they are conditional on each individual's home-range size and covariate distribution (see Beyer et al. 2010). To overcome this challenge and be able to interpret nonlinear functional forms of habitat selection, we developed a response-scale index that is unaffected by these conditional dependencies and thus comparable across different individuals, models, and datasets. We refer to this as the *Normalized Selection Ratio* (NSR) and describe it in detail below. Although we use the IPP response metric, intensity, the conceptual approach is applicable to any of the various HSF response metrics (e.g., intensity $[\lambda]$, relative probability, RSF score, true probability).

Normalized Selection Ratio (NSR)

To understand an estimate of intensity as a measure of habitat selection requires comparison with a reference intensity reflecting neutral selection, or habitat use proportional to availability. By definition, intensity of use proportional to availability will be equal to the mean intensity of the spatial point process (u) in the availability window ($\mathcal{A}$), such that:

$$\lambda_{Ref} = \frac{\# \text{ GPS locations}}{\text{home range area}} = \frac{n_{total}}{\mathcal{A}} \quad \text{eqn 2}$$

For example, given a home range area $\mathcal{A} = 50 \text{ km}^2$ and used sample $n_{total} = 200$, $\lambda_{Ref} = 4 \text{ locations/km}^2$; an estimate of intensity above or below 4 reflects selection or avoidance, respectively. Note that λ_{Ref} does not require information about the distribution of covariate values, and therefore is invariant to the proportional composition of the habitat types within $\mathcal{A}$.

To convert an intensity estimate (λ_{Est} ; eqn 1) to a NSR we divide by the reference intensity:

$$NSR = \frac{\lambda_{Est}}{\lambda_{Ref}} \quad \text{eqn 3}$$

This normalizes λ_{Est} by rescaling it to a dimensionless quantity where use proportional to availability is equal to 1. Values greater than 1 represents selection for a particular habitat type and values less than 1 represent selection against a habitat type. By representing intensity as a ratio we have a very intuitive and straightforward way to quantify the magnitude and direction of selection on the response-level. For example, a $NSR = 1.5$ is an estimated intensity of use 50% greater than when use is proportional to availability. Similarly, a NSR of 0.5 is an estimate intensity of use 50% less than when use is proportional to availability.

Single-Stage Simulations: Inter-Individual Inference

We used simulated availability domains (5- and 10-km radii circles) to generate the same patterns of selection in regions of different size and covariate distribution in order to illustrate two key points: first, the ability of the unsupervised smoothing penalty optimization routine to identify a variety of nonlinear functional forms. Second, we

demonstrate how the NSR accounts for response-level dependencies across individuals and allows for comparison of HSF across fundamentally different availability domains (5- and 10-km radii) and relative distributions.

We simulated five selection scenarios based on different elevation ($elev_{100m}$) regions, relative availabilities (i.e., relative covariate densities), functional forms, and strengths of selection. Scenario 1 created positive selection for elevations of 2900-3100m, a region where relative availabilities were approximately equivalent between the two availability domains. Scenario 2 simulated positive selection for elevations of 3100-3300m, where the relative availability of the 5-km domain was 1.75 times greater than the 10-km domain. Scenario 3 simulated bivariate selection by combining Scenario B with an additional zone of positive selection for elevations 2500-2700m. Scenario 4 simulated positive selection across a larger section of covariate space by combining the zones from scenarios 1 and 2 (i.e., 2900-3300m). For scenarios 1-4 the strength of selection was simulated to be 2x the intensity of use proportional to availability. Finally, scenario 5 created selection in the same elevation zone as 1, 2900-3100m, but with the strength of selection 3x the expected intensity of use proportional to availability (see Table 1 for summary of simulation scenarios). The number of locations used to increase the selection strength in the focal zones was subtracted from non-focal areas proportional to their availability (rounding to the nearest integer), which approximately maintained the original sample size ($n = 200$). Because the spatial distribution of the simulated points within each 50-m elevation bin was a systematic random process, we replicated the

simulation process 10 times for each scenario to capture this variation. We fit models using *equation 1* to each replication and present the mean results for each scenario.

We evaluated goodness-of-fit using 10 independent (simulated) datasets and the methods of Boyce et al. (2002) and Johnson et al. (2006). Fitted models were predicted spatially and NSR values were appended to the independent test datasets. Using 8 equally-spaced bins spanning the range of the predicted NSR within the availability domain, the area-adjusted midpoint value of each bin was used to calculate the expected proportional contributions. Simple linear regression between expected and observed bin proportions (Johnson et al. 2006) and Spearman rank correlations (Boyce et al. 2002) were used to assess out-of-sample model performance.

Two-Stage Simulation: Inter-Individual Heterogeneity

To demonstrate the NSR in a two-stage analysis, we considered population-level inferences in the presence of inter-individual heterogeneity in functional forms. We simulated use ($n \approx 200$) following the methods and selection scenarios described in the *Single stage simulations* section to generate spatial points for 16 hypothetical individuals. At the population-level we simulated a non-uniform selection pattern by assigning 50% the individuals to scenario 3, 25% of the individuals to scenario 1, and 25% of the individuals as use proportional to availability (see Table 1 for scenario definitions).

We fit individual stage-1 habitat selection models for elevation ($elev_{100m}$) following the previously describes methods using equation 1, and calculated individual NSRs following equations 2 and 3. We selected the 5-km² domain as the smaller quadrature scheme allowed for faster computational times. Goodness-of-fit of

these models were evaluated in the previous section, therefore we do not address goodness of fit during this exercise.

As a baseline population-level metric, we used the standard approach of averaging individual stage-1 responses, weighted by the inverse of their standard errors (Sawyer et al. 2006; Murtough 2007; Fieberg et al. 2010). To account for the non-uniformity at the population-level, we used hierarchical cluster analysis to classify NSR curves into similar groups and calculated the mean and variance of the NSR for each group. Metrics used to quantify dissimilarity in most conventional clustering methods (e.g., means) are not suitable for NSR response curves because they ignore the interdependence among values. To overcome this we performed a discrete wavelet transform (DWT) using the “TSclust” package in program R. This replaced the original NSR curves with their wavelet approximation coefficients and then quantified dissimilarity using the wavelet approximations (Montero and Vilar, 2014). We performed a hierarchical clustering analysis (method = complete linkage) in the “cluster” package in program R on the matrix of DWT dissimilarities for the 16 simulated individuals. We used the conventional graphical approach based on the dendrogram output from the hierarchical clustering algorithm to determine the number of clusters and cluster membership. Means of the group-level NSR curves, weighted by the inverse of their standard error, provide quantitative descriptions of the different types, or classes, of selection within the population. Relative group sizes quantify the proportional contribution of unique selection patterns to the overall population-level pattern of habitat selection.

Two-Stage Simulation: Intra-Individual Heterogeneity

To simulate temporal dynamics we combined scenarios 1, 3, and 4 from the *Single-stage simulations* with periods of use proportional to availability. Using a 10-day rolling window and approximately 20 “used” locations per day, we simulated use ($n \approx 200$) following the methods from single stage simulations to generate spatial points for each day. To fill in moving windows between scenarios, 9 1-day steps and linear interpolation determined the allocation of used locations relative to availability of elevation. In total, we simulated 41 10-day windows, spanning a total of 50 days, following the temporal progression of: use proportional to availability, Scenario 3, Scenario 5, use proportional to availability, scenario 4 (Appendix A, Figure A.2).

Using equations 1-3, stage-1 models were fitted and NSR curves generated for each 10-day moving window ($n = 41$) allowing the data to determine the best-fitting nonlinear functional form for each model. We merged the 41 NSR datasets together and added the mean day of the moving window as a temporal covariate. The stage-2 analysis allowed us to assess ecological dynamics by creating a NSR surface as a function of elevation and time. Here we extended our use of GAMs to 2-dimensions (elevation and time) in order to describe a nonlinear NSR surface:

$$\log(NSR + 1) = f(elev_{100m}, mean\ day\ of\ moving\ window) + \varepsilon,$$

where NSR = normalized selection ratio, $f(elev_{100m}, mean\ day\ of\ moving\ window)$ = tensor product 2D smoothing function.

We used a non-isotropic smoothing penalty (i.e., tensor product) to account for the different units of the time and elevation dimensions (Wood 2006) and incorporated

the uncertainty of the stage-1 estimates using the inverse of the stage-1 NSRs standard errors as a weighting covariate. The penalty per degree of freedom (γ) in the smoothing penalty criterion was increased from 1.0 to 1.4 to protect against over-fitting (Wood 2006). Multiple models with different basis penalty combinations (elevation and time) were competed in an information theoretic framework and we selected the penalty combination that minimized the Generalized Cross-Validation score (GCV; Craven and Wahaba, 1979). When the scale estimate (ϕ) is unknown, as is the case for the stage-2 GAM, GCV is reported instead of UBRE as in the case of stage-1 Poisson models ($\phi = 1$).

We evaluated goodness-of-fit at the seasonal level using 10 replications of 4-fold cross validation of the entire dataset. To minimize the impacts of autocorrelation, we assessed temporal dynamics stratifying folds by day rather than random folds of all locations. We assessed model performance at the moving window scale using withheld and training data within the temporal domain. For both approaches we evaluated Spearman rank correlations using 8 area-adjusted bins following the methods of Boyce et al. (2002).

Application: Inter-Individual Grizzly Bear Habitat Selection

Background

In the Greater Yellowstone Ecosystem, the calorie-rich seeds of whitebark pine (*Pinus albicaulis*) have been long considered a staple fall resource for grizzly bears with home ranges containing whitebark pine habitat (Mattson et al. 1992; Schwartz et al. 2003). Whitebark pine primarily occurs at high elevations (>2500m; Mattson and

Reinhardt 1990) and is a mast seeding conifer. Mast seeding is a phenomenon whereby individual trees produce seeds synchronously at super-annual intervals, resulting in wide fluctuations in seed production at the population level (Rapp et al. 2013). Annual variation in whitebark pine seed production has been correlated with grizzly bear movements (Blanchard and Knight 1991; Haroldson and Gunther 2013), survival (Mattson et al. 1992; Haroldson et al. 2006), human-bear conflicts and management actions (Mattson et al. 1992; Gunther et al. 2004). The causative mechanisms implicit in these findings is the search for alternative fall-foods occurring at lower elevation habitats where the risk of bear-human conflicts can be greater if such areas have anthropogenic influences (Schwartz et al. 2010). These findings have raised concern among conservation stakeholders and resource managers due to the recent ecosystem-level decline in whitebark pine populations within the GYE from the combination of mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*) (Gibson et al. 2008; Macfarlane et al. 2013). For example, in 2009 a United States federal court overturned the 2007 delisting rule, in part because the U.S. Fish and Wildlife Service had not adequately considered the impacts of potential loss of whitebark pine seeds (United State Fish and Wildlife Service 2010; see Interagency Grizzly Bear Study Team 2013 section 1.1 for comprehensive legal background and section 3 for detailed background on the relationship between grizzly bears and whitebark pine).

Here we illustrate application of the NSR in the applied context of grizzly bear habitat selection for whitebark pine habitat in the GYE from 2007 to 2014. This time period represents approximately 7 years of sustained mortality of mature whitebark pine

and a substantially diminished whitebark pine resource at the ecosystem level (Bjornlie et al. 2014; Greater Yellowstone Whitebark Pine Monitoring Group 2014). We intentionally avoid the “fishing expedition” approach of trying to sort out a large number of explanatory variables (Bolker 2008) and focus on the hypothesis at the crux of conservation and management concerns: given the substantial ecosystem-level decline in whitebark pine, do grizzly bears in the GYE select for habitats other than whitebark pine during fall?

Study Area

The study area extent covered more than 50,000 km² of occupied grizzly bear range in the GYE (Bjornlie et al. 2014). The GYE is one of the largest intact temperate-zone ecosystems in the world and extends approximately 450 km north to south and 250 km west to east, and is primarily composed of elevations above 1500 m (Newman and Watson 2009). Yellowstone and Grand Teton National Parks and portions of 5 national forests make up the majority of the GYE. The central Yellowstone Plateau and the surrounding mountains are covered with forests of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (Pierce et al. 2007). The GYE contains the headwaters of 25 large rivers and drainages and is traversed by the continental divide (detailed descriptions of the study area can be found in Schwartz et al. 2006).

Bear Capture and GPS Telemetry

Member agencies of the Interagency Grizzly Bear Study Team captured grizzly bears in the GYE for research and monitoring purposes and fitted selected individuals

with GPS transmitters. Grizzly bear and handling procedures used for this study were reviewed and approved by the Animal Care and Use Committee (ACUC #201201) of the U.S. Geological Survey; procedures conformed to the Animal Welfare Act and to U.S. Government principles for the utilization and care of vertebrate animals used in testing, research, and training. Captures were conducted under U.S. Fish and Wildlife Service Endangered Species Permit [Section (i) C and D of the grizzly bear 4(d) rule, 50 CFR17.40 (b)], with additional state research permits for Wyoming, Montana, and Idaho, and National Park Service research permits for Yellowstone and Grand Teton National Parks. Grizzly bears were captured using culvert traps or Aldrich leg-hold snares (Blanchard 1985). With the exception of dependent offspring, captured grizzly bears were fitted with GENIV (Telonics, Inc., Mesa, Arizona) GPS collars, with on-board data storage and integrated activity sensors.

Whitebark pine seeds do not typically mature and become available for grizzly bear consumption until early August, but can be fed on throughout the fall season (Mattson et al. 1991). Pre-denning behavior is associated with reduced movements and lethargy before entering the den (Servheen & Klaver 1983; Manchi & Swenson 2005) and can begin as early as late September/early October for some individuals (Haroldson et al. 2002). Similarly, in order to recover expended collars before winter, many collars were scheduled to drop off animals in early October. Thus, to reduce the potential bias of pre-hibernation behavior and collar loss on habitat selection we restricted our analysis to the months of August and September, when bears are hyperphagic and actively acquiring calories on the landscape. Although this may not capture the entire season of whitebark

pine use for all individuals, we assumed that it included the peak of the whitebark pine foraging season (Mattson et al. 1992; Costello et al. 2014) and is suitable for detecting the selection for whitebark pine habitat had it occurred.

Grizzly bear bedding and resting sites may occur in areas separate from foraging (Munero et al. 2006; Nielsen et al. 2010) and we restricted our analysis to active GPS locations to (1) better reflect the behavioral processes related to foraging (see Appendix B) and (2) reduce the potential bias in intensity estimates that may occur from clusters of resting locations. To protect against potential habitat-related bias from missed GPS locations (Frair et al. 2004), we restricted our analysis to collars with $\geq 85\%$ acquisition success during “active” periods in August and September. This resulted in a dataset of 32 individual bear years, 19 females, 13 males, ranging from 3 to 24 years in age. The interval between scheduled GPS attempts varied from 30 minutes to 2 hours, resulting in a variable number of total locations per individual. However, differences in sample size are accounted for by the NSR by the reference intensity term (λ_{Ref} ; eqn. 2).

The Point Process modeling framework used in this analysis clearly defines the role of pseudo-absence points as simply a device for approximating an integral (Baddeley et al. 2015). This shifts the focus away from defining availability, because ratios of used to pseudo-absence points and sampling far from used points are no longer relevant (Renner et al. 2015). Therefore, we selected a simple and consistent availability domain at the third-order scale of selection (Johnson 1983), using the outer perimeter of dissolved 1-km buffers around all GPS locations for each individual bear-year. Although the

ecological concept of a home range may be different than that of an availability domain, we use the two terms interchangeably.

Whitebark Pine Covariates

The narrow scope of this applied management question provides the opportunity to contextualize the selection process using the single covariate of whitebark pine, although we consider this to be a proxy for a suite of unmeasured quantities that occur within whitebark pine habitat. We quantified whitebark pine as a density-based covariate based on the distribution of whitebark pine in the GYE (Macfarlane et al. 2013). We rasterized the Macfarlane et al. (2013) polygon geospatial layer at a 30-m pixel resolution and used the Focal Statistics tool in the Geoprocessing Toolbox in ArcGIS 10.3.1 (ESRI 2015) to calculate the relative density [range: 0-1] of 30-m whitebark pine pixels within a 500-m radius of each pixel in the raster layer. The radius term in the focal density calculation acts as a smoothing parameter and we selected 500m as the local neighborhood based on the distance grizzly bears are capable of moving between GPS intervals and a transition zone between densities of 0 and 1. Our intention was not to find the spatial scale (i.e., grain) at which bears respond to whitebark pine, but to create a covariate that can distinguish different types of whitebark pine stands (e.g., contiguous vs. patchy), stand edges, regions close to whitebark pine, and areas absent of whitebark pine (i.e., density of 0).

We quantified the mortality-level of whitebark pine at the home range level based on the Landscape Assessment System Index (LAS; Macfarlane et al. 2013). LAS rankings were based on aerial surveys and ranged from 0 to 6, with rankings >4 generally

indicating no live overstory remaining. For each bear-year we quantified an overall mortality estimates as the area-weighted mean of LAS scores for mapped whitebark pine polygons.

We used annual whitebark pine cone counts from long-term monitoring transects to classify annual production as a binary response at the ecosystem-level. Years above the long-term mean were classified as “good” whereas those below the median were classified as “poor” (Haroldson et al. 2004; Haroldson 2015).

Statistical Analyses

We followed the previously described two-stage methods for modeling inter-individual heterogeneity including construction of quadrature schemes, IPP model structure (equation 1), optimal smoothing-penalty selection, NSR calculations (equations 2 & 3), hierarchical clustering of individual NSR curves, and quantification and description of unique group-level selection patterns.

3. RESULTS

Single-Stage Simulations: Inter-Individual Inference

The NSR index adjusted the raw estimates of intensity, $\lambda(u)$, for the conditional dependency of the area of the availability domain, $\mathcal{A}$, regardless of functional form, strength of selection, and relative distribution of elevation values (Figure 2; Appendix A, Figure A.3). Estimated NSR curves closely matched the simulated regions of selection as well as the simulated magnitudes of selection. Similarities between NSR values in the focal regions of positive selection ($\text{NSR} > 1$), but differences in the non-focal regions ($\text{NSR} < 1$) were a result of maintaining original sample sizes by removing used locations, proportional to availability, from the non-focal elevation bins (see methods).

Out-of-sample model evaluation, based on 10 independent simulated “use” datasets for each scenario, displayed positive rank correlations across area-adjusted NSR bins ($\bar{\rho}_{5\text{ km}} = 0.88$; $SE_{5\text{ km}} = 0.06$; $\bar{\rho}_{10\text{ km}} = 0.86$; $SE_{10\text{ km}} = 0.07$). Similarly, linear regression of expected versus observed NSR bin frequencies consistently resulted in high r^2 values, slopes not differing from 1, and intercepts not differing from 0 across simulations (Table 2). Thus, there was little evidence of poor model performance (Wiens et al. 2008; Johnson et al. 2006) and quantitative support that the adaptive splines, optimized smoothing penalties, and over-fitting protection measures adequately balanced bias-variance tradeoffs. Scenarios with simulated use spanning 400 meters of elevation (scenarios 3 and 4) had the lowest Spearman rank correlations ($\rho_{\text{scenario } 3} = 0.81$; $\rho_{\text{scenario } 4} = 0.77$). This was likely a function of NSR binning and the use of rank correlations for model evaluating (Boyce et al. 2002), rather than poor model

performance. For example, simulations of use proportional to availability that are correctly estimated will have near linear NSR curves with intercepts near 1 and slopes near zero but highly variable Spearman rank correlations with means close to 0.

Two-Stage Simulation: Inter-Individual Heterogeneity

Population-level inference based on the mean NSR ($n = 16$) shows a complex pattern of nonlinear selection for elevation (Figure 3.A). The out-of-phase regions of positive and negative selection between scenarios 1 (univariate; $n = 4$) and 3 (bivariate; $n = 8$), combined with the proportional-use scenarios ($n = 4$) had strong biasing, or attenuating, effects on the individual selection patterns. For example, in the mid-elevation zone between 2900 and 3100m, the population-level mean showed use approximately proportional to availability, yet 75% percent of the individuals (scenarios 1 and 3) show strong selection or avoidance in this region.

The hierarchical clustering of the individual NSR curves provided strong support for classifying the hypothetical population into three distinct groups, or selection strategies. Relative to the three simulation scenarios, group size and membership within clusters was assigned with 100% accuracy (Figure 3.B). Group-level mean NSR curves using the 3-group solution provided quantitative descriptions of the unique selection strategies within the hypothetical population that closely matched scenario definitions (Figure 3.C; see Table 1 for scenario definitions). The estimated population-level variance (0.1302) based on the pooled mean was approximately 9.5 times higher than the variance estimate calculated using the appropriate group-level means (0.0137).

There was modest evidence of clustering beyond the 3-group level which can be seen in the dendrogram at heights less than 4. For example, individuals 1, 7, and 8 in group 1, individual 3 in group 2, and individual 3 in group 3, can be visually identified as being different than the remaining individuals in their respective groups (Appendix A, Figure A.4).

Two-Stage Simulation: Intra-Individual Heterogeneity

Out-of-sample model evaluation, based on 10 repetitions of 4-fold block cross-validation displayed positive rank correlations ($\bar{\rho} = 0.92$; $SE = 0.03$) between observed and expected counts in the 8 area-adjusted NSR bins. However, out-of-sample rank correlations for the dynamic model were highly variable among rolling windows (Appendix A, Figure A.5.A). This was likely due to constraining the temporal domain of presence locations to a 10-day period, but maintaining the annual level of availability (i.e., where the animal could have been present). This can result in relatively isolated regions of relatively high NSR values, and large areas of negative selection, or avoidance, with relatively low NSR values (e.g., Appendix A, Figure A.5; mean day = 35.5). This inverse relationship between NSR values and geographic area can result in similar area-adjusted NSR bin midpoints (i.e., U_i ; Johnson et al. 2006, page 352). When this occurs, small differences between expected and observed bin counts can result in poor alignment of bin rankings in the Spearman rank correlation. To overcome this we conducted an alternative post-hoc goodness-of-fit using the root-mean-square-deviations of NSR bins:

$$(RMSD = \sqrt{\frac{\sum_{t=1}^8 (x_{observed,t} - x_{expected,t})^2}{n}})$$

For each 10-day rolling window we created 1000 random permutations of the observed bin counts and calculated the probability of obtaining an equal or smaller value than the observed RMSD for each 10-day rolling window (Appendix A, Figure A.5.B). As expected, when use was proportional to availability (mean near days 5.5 and 35.5) the probabilities of obtaining a smaller RMSD than the observed level RMSD were relatively high. Probabilities were also relatively high for time periods when selection showed a bivariate response, possibly suggesting the day-based fold allocations to the different regions of positive selection were highly variable.

The static NSR estimate from the pooled 50-day period showed a moderately complex pattern of nonlinear selection for elevation: slight to moderate negative selection at lower elevations, moderate positive selection at mid elevations, and decelerating positive selection at higher elevations transitioning to negative selection and leveling off at approximately one-half the expected intensity of use (Figure 4.A).

The smoothed NSR surface of the 41 stage-1 models illustrated the temporal dynamics of selection for elevation and captured the fundamental patterns defined by the dynamic simulation scenario (Figure 4.B, see Appendix A, Figure A.2 for graphical schematic of selection dynamics). The range of the dynamic NSR surface (0.13–3.18) was approximately 3 times larger than the range of the static NSR curve (0.46–1.48), and more closely matched the simulated intensity levels (*e. g.*, $\overline{day}_{15.5} = 2x$; $\overline{day}_{25.5} = 3x$; $\overline{day}_{45.5} = 2x$), demonstrating the attenuating bias of pooling data and ignoring temporal dynamics.

Application: Inter-Individual Grizzly Bear Habitat Selection

External 4-fold, cross-validation of Stage-1 models ($n = 31$) displayed high Spearman rank correlations among expected and observed counts in area-adjusted NSR bins ($\bar{\rho}_{bear-year} = 0.84$; $SE_{bear-year} = 0.07$), suggesting little evidence of poor model performance across individuals bears. One individual, grizzly bear 610 in 2009, had low out-of-sample performance ($\bar{\rho} < 0.70$) and was censored from the stage-2 analysis. Estimated degrees of freedom of stage-1 models ranged from 1.0 to 12.7 ($\bar{x}_{edf} = 4.94$; $sd_{edf} = 2.49$) suggesting that most individuals had moderately complex responses to whitebark pine density.

Stage-2 population-level inferences based on the mean of stage-1 NSR responses, $\overline{NSR}_{pop}$, indicated areas without whitebark ($WBP_{500m} = 0$) were used approximately 10% less ($\overline{NSR}_{pop} = 0.91$) compared to the baseline of use proportional to availability ($NSR = 1$). An increasing trend in selection was observed up to densities around 0.75, where the strength of selection was approximately 2.35 times greater than baseline selection ($\overline{NSR}_{pop} = 2.35$). At densities above 0.75, the strength of selection remained relatively constant at about twice the baseline ($\overline{NSR}_{pop} = 1.96$; Figure 5. A).

The hierarchical clustering of DTW-transformed stage-1 NSR curves suggested multiple levels of plausible structure in habitat selection within the population. Using a “cut” value of DTW distance = 45, we classified 90% of individuals into 4 groups, leaving 10% of individuals ($n = 3$) as non-classified outliers (Figure 5.B). Mean cluster-level NSR curves, $\overline{NSR}_{group}$, provided graphical descriptions of the unique group-level

selection strategies for the density of whitebark pine habitat (Figure 5.C; see Appendix A, Figure A.6 for individual curves). Kruskal-Wallis tests failed to detect differences among groups (1-4) for relative whitebark pine availability (area of whitebark pine/area of home range) [$H = 3.28, d.f. = 3, p = 0.35$], absolute area of whitebark pine [$H = 7.04, d.f. = 3, p = 0.07$], area-weighted mean Landscape Assessment System [LAS] score [$H = 0.70, d.f. = 3, p = 0.87$], and total area [$H = 2.15, d.f. = 3, p = 0.54$] (all measured at home range-level; see Appendix C.1-C.6 for boxplots of group level distributions). Similarly, we found no differences among groups relative to the non-spatial attributes age [$H = 1.11, d.f. = 3, p = 0.77$], year [$H = 2.29, d.f. = 3, p = 0.51$], sex [$LRT, \chi^2_{3,23} = 0.85, p = 0.84$], or mast production [$LRT, \chi^2_{3,23} = 2.49, p = 0.47$].

Using the 4-group clustering solution, 23% of the population (group 3; $n = 7$) showed positive selection ($\overline{NSR}_{group-3} = 1.38; sd = 0.27$) for non-whitebark pine habitats ($WBP_{500m} = 0$) and avoidance of all whitebark habitat ($WBP_{500m} > 0$; Figure 5. C, group 3). The hierarchical clustering dendrogram showed little support for subgroup structure within group 3 without cutting the tree below a DTW distance below 20. The proportion of whitebark pine in group 3 availability domains ranged from 2% to 33% ($\bar{x} = 21\%; sd = 12\%$) and absolute areas ranged from 6.1km^2 to 73.9km^2 ($\bar{x} = 43.6\text{km}^2; sd = 20.8$). Although the lowest relative availability (2%; bear-year 492–2008) seems small, the associated absolute availability (6.1 km^2) was suitable for strong positive selection ($NSR \approx 6.0$) by this individual during the subsequent year (group 2, bear-year 492–2009). Whitebark pine mortality level in group 3, as indexed by the LAS score (Macfarlane et al. 2013), ranged from moderate to severe and was heavily skewed

by individual 645 (years 2010 and 2011), who resided in a region of post-outbreak conditions with virtually complete overstory mortality ($\bar{x}_{645} = 5.5$). Whitebark pine stands in home ranges of remaining bears in group 3 indicated moderate to severe mortality levels ($range = 2.15 - 3.27$; $\bar{x} = 2.97$; $sd = 0.47$).

The remaining 77% of the population showed positive selection for varying densities of whitebark pine and general avoidance of non-whitebark habitats ($WBP_{500m} = 0$). As a cohort that selects for whitebark pine, home ranges varied from moderate to severe whitebark pine mortality (LAS score; $range = 2.15 - 3.27$; $\bar{x} = 3.31$; $sd = 0.67$). We failed to detect any differences in relative availability of whitebark pine, whitebark pines mortality based on the LAS score, home-range size, year, age, sex, or seed production among groups 1, 2, and 4. However Kruskal-Wallis test suggested a possible difference in absolute availability of whitebark pine [$H=4.75$, $d.f.= 2$, $p=0.09$], and boxplots indicated group 1 had, on average, less area of whitebark pine in home ranges (Appendix C, Figure C.5).

Group 1 ($n = 8$) displayed positive selection for a broad range of mid-level densities of whitebark pine but an overall declining strength of selection for densities above 0.6 (Figure 5.C). There was moderate support for sub-clustering into two equal-sized groups (Figure 5.B) and the location of NSR peaks relative to density suggest a subgroup with NSR peaks in low-to-mid densities (<0.5) and a group with NSR peak at densities >0.5 . As indicated in the dendrogram tree, grizzly bear 752 in 2013 was the most dissimilar individual of group 1 with a narrow peak of strong selection at mid-level densities but closely following the sub-group trends in other regions of the covariate

space. We failed to detect any differences in relative and absolute availability of whitebark pine, whitebark pine mortality based on the LAS score, home-range size, year, age, or sex between subgroups of group 1.

Group 2 ($n = 9$) demonstrated moderate avoidance of low-density whitebark pine habitats, use proportional to availability at mid-densities, and an approximately linear trend at higher densities (>0.5). The highest $\overline{NSR}_{group\ 2}$ values occurred at the maximum whitebark pine density of 1.0, about 2.65 times that of baseline selection (Figure 5.C). Hierarchical clustering indicated a plausible substructure of 2 groups of equal size. Kruskal-Wallis tests showed significant differences between these subgroups relative to proportional ($(\bar{x}, (sd)_{sub1} = 0.17(0.08); \bar{x}, (sd)_{sub2} = 0.30(0.04)$, [$H = 6.00, d.f. = 1, p = 0.01$]) and absolute ($(\bar{x}, (sd)_{sub1} = 49km^2(19); \bar{x}, (sd)_{sub2} = 126km^2(54)$, [$H = 3.84 d.f. = 1, p = 0.05$]) availabilities of whitebark pine. The subgroup with smaller whitebark pine availability measures (relative and absolute) was associated with positive selection (i.e., $NSR > 1$) at lower densities, whereas the subgroup with higher availability metrics showed negative selection in this region. However, both subgroups showed strong selection for whitebark pine at high densities. We failed to detect any subgroup difference among whitebark pine mortality, home-range size, year, age, or sex for group 2.

Group 4 ($n = 3$) exhibited the strongest group-level positive selection ($NSR \approx 4$), which was relatively stable and occurred at whitebark pine densities greater than 0.65 (Figure 5.C). Selection for density of whitebark pine declined with density, although bear 557 in 2007 showed strong selection for low density whitebark pine, suggesting

dissimilarity from the other group members at low densities. The small samples sizes prevented statistical analyses of subgroups but graphical examination of home range-level characteristics showed no obvious patterns (Appendix A.5).

Outliers ($O_1 = 551-2007$; $O_2 = 758-2013$; $O_3 = 584-2009$) selected against areas without whitebark pine and selected strongly ($NSR > 7$) for whitebark pine, but at different densities, ranges, and regions (Appendix X.X). Outliers O_2 and O_3 displayed strong selection ($NSR \approx 6$ and 10) for higher density whitebark pine ($0.7-0.8$), and most closely resembled group 4, as indicated in the dendrogram. However, the higher magnitude of selection, rapid declines in selection at high densities (>0.8), and multimodality caused earlier branching from the group-4 cluster. Outlier O_1 selected strongly ($NSR \approx 10$) for a narrow region of mid-density whitebark pine and displayed strong avoidance of densities >0.5 . The early branching from all other individuals in the dendrogram suggests a fundamentally different response from other groups or outliers.

Although the temporal window of selection (August-September) represented the majority and peak season of whitebark use, the possibility of variation in the timing of whitebark use among individuals, or years, could not be ruled out. Thus, if selection for whitebark pine occurred, but only during the late season (i.e., October), then classification into group 3 would represent a type-II error. Coincidentally, all individuals in group 3 had October data to assess (post-hoc) the presence of type-II errors in group 3 from late season whitebark pine use. For all individuals in group 3, we repeated the original NSR analysis but included active-only used locations, excluding those associated with denning behavior, during the month of October. The NSR curves and hierarchical

clustering of the late-season analysis provided strong support for the original classification and absence of type-II errors, except for grizzly bear 584 in 2008 (Appendix A, Figure A.7). The post-hoc NSR (August 1-October 31) for this individual showed strong selection for higher densities of whitebark pine most similar to group 2 and avoidance of non-whitebark areas ($(WBP_{500m} = 0)$), confirming the classification into group 3 was a type-II error caused by late-season use of whitebark pine. Given the post-hoc nature of this result and the inability to include late-season use for all individuals in the analysis, we chose to not reclassify and re-run the original hierarchical clustering of individuals, but instead address the implications of this type-II error in the discussion section.

The late-season type-II error based on grizzly bear 584 in 2008 discovered in the post-hoc analysis, in combination with the opportunity to illustrate a dynamic application using empirical data, prompted us to include an additional supplementary post-hoc analysis: intra-individual annual variation in habitat selection for whitebark pine. Grizzly bear 584 locational data from 2008 and 2009 met analysis criteria from August 1 to October 31, providing an opportunity to compare ecological inferences between static and temporally dynamic habitat selection models. Using a 20-day rolling window and the methods described in the *Intra-individual heterogeneity* section, we examined the dynamic selection process for the density of whitebark pine. For comparison, we re-computed the static models extending the upper limit of the temporal range from Sept 30 to October 31, following the previously outlined methods.

Both the static and dynamic analyses indicate different NSR responses between years, with stronger selection during 2009 for all but the lowest densities of whitebark pine (Figure 6). The difference in magnitudes between the two selection strategies was a function of more time spent (i.e., number of relative locations) in non-whitebark pine habitats during 2008, and is indicated in both the static and dynamic plots. However, unlike the static analysis, temporal dynamics demonstrate that selection for whitebark pine occurs primarily during late season in both years, but at fundamentally different densities and intensities. More than 97.8% of the inter-point distances between GPS locations in October 2008 and 2009 were >500m apart ($\bar{x} = 3606$; $sd = 2620$; Appendix A, Figure A.8), supporting the use of different areas of whitebark pine (i.e., stands) in successive years. As with the dynamic simulation analysis, short periods of intense use produced much higher NSR indices that are attenuated under the static analyses.

4. DISCUSSION

Simulations

Our study findings demonstrate the utility of the adaptive penalized regression splines and the Poisson point model (PPM) framework for capturing complex nonlinear relationships between intensity of use and habitat availability. The flexibility of the adaptive smoothing functions allowed us to extend the concept of individual variation in habitat selection models from simple variation in strength and direction (e.g., random slopes in mixed-effects exponential HSFs) to unlimited and unspecified variation in the functional form of responses among individuals. This is particularly useful given the exploratory stage of most GPS-based habitat studies, where scientific knowledge is typically insufficient to specify a priori mechanistic models (Aarts et al. 2013).

Our development of the NSR index solved several issues related to interpreting intensity of use (λ) in habitat selection models. First, the reference intensity (λ_{Ref}) accounts for differences in sample size and area of the availability domain (i.e., home-range size), allowing direct comparison across different models. Second, it provides an intuitive and useful user interface to habitat selection modeling by conveying relationships as a response curve. Thus, ecological interpretations explicitly make use of effect sizes and precision of estimates (i.e., confidence intervals) and avoid the potential of misinterpretation and misuse of null hypothesis significance testing and p -values (Nakagawa and Cuthill, 2007), especially as applied to HSFs (Boyce et al. 2002). Furthermore, as a ratio, the NSR directly expresses the effect size in terms of the defining characteristic of habitat selection: the disproportionality between use and availability

(i.e., $NSR \neq 1$). Finally, unlike inter-class correlation coefficients (ICC) and standard deviations of random effects in mixed-effect models, the NSR response curve is easily interpreted and does not require advanced statistical knowledge.

As with other spline regression techniques, a danger exists of overfitting our models. We implemented multiple overfitting protection measures including the use of adaptive splines, optimizing the smoothing penalty basis (m), and increasing the penalty per degree of freedom (γ) from 1.0 to 1.4. Out-of-sample validation of the static simulation and empirical models provided strong support that these measures performed well and prevented overly complex response curves. Importantly, these are adaptive strategies that can be adjusted based on external cross-validated performance. For example, an iterative process of increasing γ (penalty per degrees of freedom) and re-testing out-of-sample performance could further improve overfitting protection by allowing the penalty to vary among individuals. Such measures are primarily a concern of computation time, although in certain contexts an issue of multiple-testing may exist as optimization routines (for m or γ) represent a form of model selection.

Although overfitting is a concern, the principal challenge of our approach, or any two-stage nonlinear analysis, is how to scale up stage-1 models for population-level inference (i.e., stage-2 analysis). If functional relationships (Mysterud and Ims, 1998) exist between stage-2 covariates and individual stage-1 functional forms, then a functional response surface provides a straightforward solution for population-level inference. However, if functional responses are not detected among the set of measured covariates, then alternate metrics for population-level inference must be used. Our

simulations demonstrate that the most frequently used methods, measures of central tendency of stage-1 models (e.g., Nielsen et al. 2002; Osko et al. 2004), may not translate well to a population of diverse nonlinear response curves. This may be particularly true for populations of “generalist” species, in which the wide diversity of resource use is actually a heterogeneous collection of specialized strategies (Bolnick, 2007).

Our approach of classifying the stage-1 NSR curves into similar groups via hierarchical clustering provides a powerful alternative to global measures of central tendency for population inference. Without the use of a priori information, our stage-2 analysis accurately described the unique simulated processes and their relative contribution to the population. Group-level means provided intuitive descriptions of how selection patterns vary among groups and the hierarchical nature of the clustering allowed for inferences at multiple levels of increasing similarity in habitat selection. The ability to identify the subpopulation structure is particularly important to better inform management because our results suggest that managing for the “average” resource response may have unintended consequences to particular groups of individuals (Bolnick, 2003).

Finally, the dynamic application of the NSR shows strong potential to address the need to incorporate ecological dynamics in HSFs (e.g., Mcloughlin et al. 2010). The rolling window approach is a conceptually simple means of dissecting habitat selection over time. Our dynamic simulations demonstrate the ability to detect patterns of selection that can be attenuated, and even masked, when pooling locations over time. This is particularly important for research trying to identify the underlying mechanisms of

habitat selection based on temporally, or seasonally, pooled data. Furthermore, the ability to detect, strong, but ephemeral, responses to habitat selection is important because it may provide managers information on when protection of habitat can be most effective (e.g., closures of calving areas for ungulates). Although this approach holds potential, our findings indicate the current recommended methods for out-of-sample cross validation for HSFs (Boyce et al. 2002; Johnson et al. 2006) may be problematic in the nonlinear dynamic setting. The restricted range of the temporal moving window can isolate narrow regions of covariate space of selection, and animals can indeed be using resource proportional to availability during short periods of time. Such scenarios are problematic for bin counting and rank correlations currently used to evaluate HSFs. Although our use of randomization tests of RMSDs showed improvement over the rank correlation approach based on simulations, further development of cross-validation techniques are needed to fully leverage the potential of the dynamic models.

Application: Inter-Individual Grizzly Bear Habitat Selection

We found support for heterogeneity in the functional forms of habitat selection across individuals, although we were unable to detect associations with home-range or individual-level covariates to explain this variation. With traditional two-stage approaches, failure to detect such functional relationships would lead to inferences based on the average response of all individuals. For our study population, this would have resulted in the conclusion that grizzly bears used whitebark pine more than expected and avoided areas without whitebark pine during August and September. However, using the hierarchical clustering of response curves, we were able to detect intra-population

structure, providing evidence of 4 distinct selection patterns in the sample population. Differences among those groups selecting for whitebark pine (groups 1, 2, and 4), was explained by the density of whitebark pine used and the magnitude of selection. For example, group 1 selected for intermediate densities whitebark pine, whereas group 2 avoided low densities and showed increasing selection for densities >0.5 (Figure 5). Group 4 showed the strongest response which occurred at whitebark pine densities greater than 0.65. Such group-level differences support the idea that habitat selection at the population-level may be better described by the collective patterns of individuals rather than a single measure of their central tendency (Nielsen et al. 2002; Osko et al. 2004). Importantly, we were able to identify a cohort of the population (group 3; 23% of the study population) that selected strongly for non-whitebark habitats and avoided whitebark pine. Failure to detect this response would have resulted in a type II error in population-level inference.

Our results provide several ecological insights into grizzly bear selection of whitebark pine habitat. Within the cohort of the population that avoided whitebark habitat (group 3) one individual's home range (bear 645 in 2010 and 2011) had extreme whitebark pine mortality levels, $>99\%$ overstory mortality (i.e., LAS score > 5). Interestingly, fidelity to its home range persisted, despite whitebark pine making up approximately 30% of the home range. Numerous mammalian studies demonstrate increased home-range size in response to insufficient resources (Linders et al. 2004; Wauters et al. 2005; Chaverri and Kunz 2011), including several ursids (Garshelis et al. 1981, Moyer et al. 2007; Brodeur et al. 2008; Koike et al. 2012). Thus, the lack of home-

range abandonment or expansion by bear 645 (a 14- and 15-year-old female) suggests sufficient resources were available to meet nutritional requirements. A second individual in group 3, grizzly bear 492, had a low relative availability of whitebark pine in its home range (6 km^2 ; 2%) and did not use whitebark pine during the poor mast year of 2008 but showed positive selection in 2009, the year of highest cone production during the study. Although these cases represent a small sample, both findings support previous research (Interagency Grizzly Bear Study Team 2013; Costello et al. 2014) suggesting that selection of whitebark pine, when available, can be strong but that there is no clear dependency between grizzly bear occupancy on the landscape and whitebark pine at the individual level.

The remainder of the individuals in group 3 ($n = 4$; 14% of sampled individuals) did not fundamentally differ in terms of sample year, whitebark pine availability, or whitebark pine mortality level from bears that selected for whitebark pine (see Appendix C). This may simply reflect spatial variation in whitebark pine cone production not captured by monitoring transects coinciding with sampling years for this subset of bears (i.e., nondemonic intrusion; Hurlbert 1984). Other resources may also influence selection for whitebark pine. For example, a post-hoc examination of GPS data from group 3 showed bears 600 and 721 in 2012, a year of good whitebark pine seed production (Haroldson 2015), occupied agricultural fields in an area where wild caraway (*Carum carvi*), an invasive plant species, are consumed by numerous grizzly bears during late summer through fall (IGBST, unpublished data). Although data are insufficient to test the hypothesis of preference for caraway over whitebark pine, the high density of bears

congregating to feed in these areas supports the notion of a valuable food resource and diverse diet among individual grizzly bears in the GYE. Such diversity is further supported by several other members of group 3 that selected for non-whitebark habitats. For example, bear 584 in 2008 and 622 in 2010 had >80% of its August and September locations at elevations above 3,200m, consistent with feeding on dense aggregations of army cutworm moths (*Euxoa auxiliaris*; French et al. 1994; D. Bjornlie, Wyoming Game and Fish Department, personal communication). The years 2008 and 2010 had poor whitebark pine seed production throughout the ecosystem and therefore, similar to the caraway example, we are unable to determine if this represents preferential selection or simply use of an alternative resource during years of poor whitebark pine seed production. However, bear 584 showed strong selection for whitebark pine during 2008 and 2009 (group 3), but this selection occurred late in the season and subsequent to use of army cutworm moth sites. Although we did not have sufficient data for bear 622 during 2009 to be included in the analysis, a post-hoc examination showed 95% of locations during September and October were in areas with whitebark pine densities >0. One possible explanation for these patterns is that whitebark pine seeds cached by squirrels for overwinter use can be acquired later in the season than other more phenologically-sensitive bear foods, such as army cutworm moths. If this is the case, bears may forage on alternate food when they are at peak availability and delay use of whitebark pine until later in the fall when other resources become scarce. Although such hypotheses need further testing, it suggests the need to carefully consider foraging flexibility when evaluating habitat selection of grizzly bears.

Among the 3 groups and outlier individuals that selected for areas with non-zero whitebark pine densities, our results contribute to our collective understanding of grizzly bear habitat selection. First, despite the substantially diminished state of whitebark pine in the GYE during our study period (2007-2014), the majority (>80%) of the study population used whitebark pine more than expected and areas without whitebark pine less than expected during August and September. Second, 38% of the individuals selecting for whitebark pine (groups 1, 2, 4, and outliers) did so even during years of poor whitebark pine seed production. As stated previously, the observed selection for whitebark pine during years of poor seed production may reflect spatio-temporal variation in mast production not captured by the ecosystem-level measure of cone production. If this were the case, home ranges with larger areas of whitebark pine habitat may be more likely to have stands with active squirrel middens in any given year. However, we cannot rule out that selection for whitebark pine in years of poor seed production may be due to grizzly bears acquiring alternative resources in mapped whitebark pine habitat, such as ungulate carcasses and false truffles (*Rhizopogon* spp.; Fortin 2013).

The diversity in habitat selection responses among individual grizzly bears highlights the difficulty of addressing research questions that are conditional on observing specific behaviors (e.g., avoiding whitebark pine). Although GPS telemetry provides the fine-scale data that allowed us to observe important patterns in habitat selection, its use comes at the cost of smaller sample sizes (i.e., animals instrumented) compared with VHF-based telemetry and may affect population-level inference (Cagnacci et al. 2010). For example, larger sample sizes may result in a more continuous

gradient or additional groupings of habitat selection responses. Although our sample size was relatively large compared with many bear studies, long-term research efforts can overcome sample size challenges. As datasets grow over time, results from this study can be re-evaluated and additional research hypotheses can be tested.

5. CONCLUSIONS

We presented a new analytical tool based on a Normalized Selection Ratio, or NSR, to add to the extensive collection of technique available for habitat selection modeling. There are 3 main advantages to our approach. (1) The use of NSR allows individuals to vary in their functional forms of habitat selection without imposing rigid assumptions about what those should be. (2) the NSR is an intuitive and easily interpreted habitat selection metric that does not require advanced statistical knowledge for interpretation. Furthermore, the basis for inference of NSR is effect size, rather than statistical significance testing accompanied by p -values. Thus, the NSR presents an easily interpreted graphical view of biologically important (i.e., effect size) information from habitat selection estimates. (3) Our technique allows identification of a hierarchy of habitat selection patterns by grouping individuals that respond similarly within the population. This hierarchy effectively enhances ecological interpretation when scaling up from individual models (stage 1) to population-level inference (stage 2).

We demonstrated application of our approach within a dynamic framework using both simulated and empirical data. Although validation techniques proved to be problematic, the dynamic analyses highlighted several important issues related to habitat selection. First, seasonal dynamics in HSFs are well documented and a general strategy is to develop separate models for different times of year (Nielsen et al. 2002; McLoughlin et al. 2009). However, correctly identifying the appropriate break-points of different seasons can be difficult when applied at the population level. This is especially true when individuals or cohorts can exhibit dietary specialization (e.g., grizzly bears; Edwards et

al. 2011), whereby selection for different habitat types can translate into different temporal dynamics in habitat selection among individuals (Turney and Roberts 2004). As illustrated by our dynamic analysis of grizzly bear data, the presence of alternative resources (e.g., moth feeding sites) can have profound impacts on the timing of selection for other resources. Regardless of the cross-validation issue, preliminary analyses using dynamic rolling window models can be used to evaluate the assignment of temporal domains (e.g., seasonal breaks) at the individual level which may improve ecological inference.

More generally, we demonstrated that accounting for individual heterogeneity in habitat selection can enhanced ecological interpretation at the population level. However, the degree to which this affects population-level inferences is likely species- and context-specific. We believe our approach will particularly benefit habitat studies involving species that (1) experience high temporal variation (e.g., seasonal, inter-annual) in the distribution of resource availability such as opportunistic omnivores (Leclerc et al. 2016), (2) express contrasting life-histories (e.g., migratory vs. non-migratory [Cagnacci et al. 2011] or niche separation among sympatric species [Nichols and Racey 2006]), and (3) cover large ecosystem-level scales where spatial heterogeneity in habitat among individuals may be large (e.g., Gustine et al. 2006; Gillaird et al. 2010). In such scenarios, the NSR approach facilitates interpretation because individual differences in habitat selection can be quantified and organized, an important ecological challenge with direct management and conservation consequences (Fortin et al. 2008).

Simulation scenario	Functional form	Selection interval	Strength of selection	<i>P</i> (selection interval)	
				Availability domain = 5-km radius	Availability domain = 10-km radius
1	Univariate (200m)	2900-3100m	2x	0.18	0.19
2	Univariate (200m)	3100-3300m	2x	0.21	0.12
3	Bivariate (200m x 2)	2500-2700m; 3100-3300m	2x; 2x	0.14; 0.21	0.20; 0.12
4	Univariate (400m)	2900-3300m	2x	0.39	0.31
5	Univariate (200m)	2900-3100m	3x	0.18	0.19

Table 1. Scenario definitions used to simulate “use” locations for single-stage simulation models of habitat selection. Parentheses in the functional form field indicate the width of the selection zone. The strength field indicates the simulated magnitude relative to a reference level of 1, where use is proportional to availability. *P*(selection interval) indicates the relative probability distribution value for the selection interval demonstrating which simulation scenario have similar availabilities (1,5) and those that have different availabilities (2,3,4).

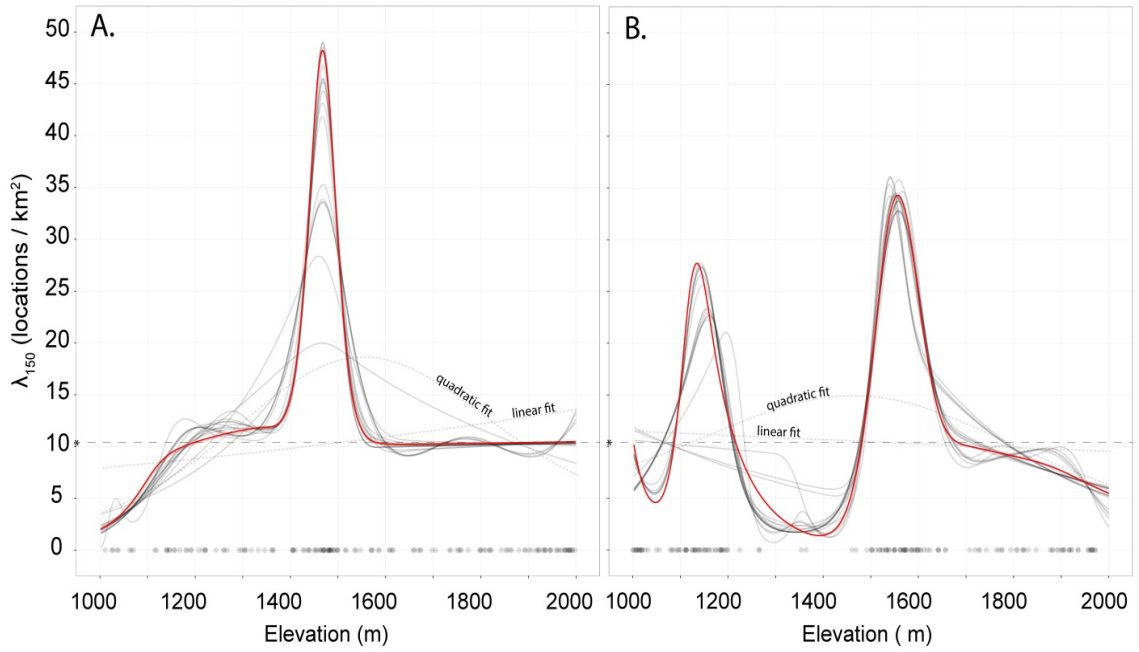


Figure 1. Examples of nonlinear smooths and optimal smoothing penalties (m) for elevation ($elev_{100}$) based on the IPP model:

$$\lambda(u) = \exp(B_0 + f(elev_{100m}))$$

Grey lines represent individual models of different smoothing penalty ($m = 1, 2, \dots, 17$). The red lines show the “best-fit” penalty based on the minimum UBRE score. The horizontal dashed line and corresponding “*” on the y-axis shows the intensity of use proportional to availability. Points on horizontal line at $y = 0$ represent the distribution of simulated locations as a function of $elev_{100}$. Dotted lines show smooths with effective degrees of freedom of 1 and 2 and are approximately equivalent to linear and quadratic fits.

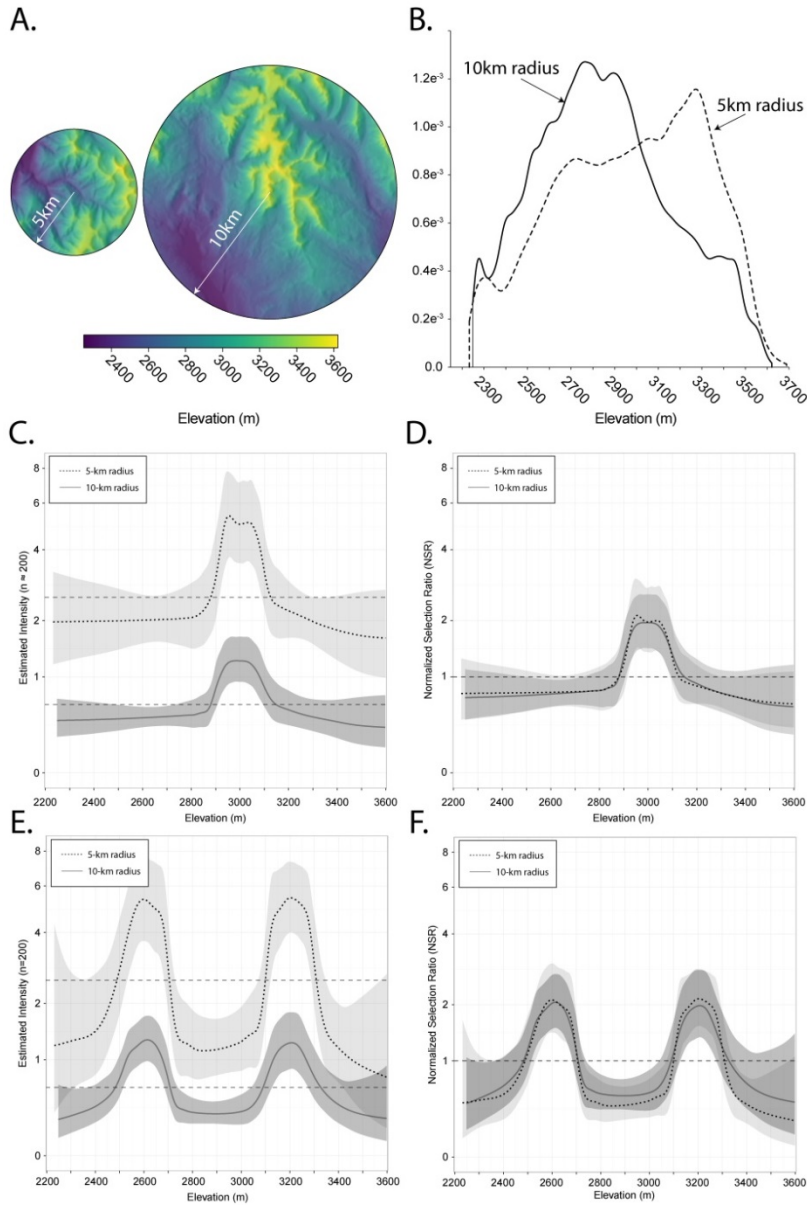


Figure 2. Mean ($n = 10$) simulation results for single-stage models of habitat selection. A) Spatial distribution of elevation between the 5- and 10-km availability domains. B) Probability density functions for elevation in each availability domain (area under each curve = 1). C) Raw estimated intensities for 5- and 10-km availabilities for scenario 1. D) NSRs associated with panel C for scenario 1. E) Raw estimated intensities for 5- and 10-km availabilities for scenario 3. F) NSRs associated with panel E for scenario 3. To aid in visualization the scaling of the y-axis is log transformed (i.e., $\log(\text{NSR} + 1)$), but values at the tick marks are the untransformed NSR scale. The dashed line at 1.0 represents use proportional to availability. See Appendix A, Fig. A.3 for similar figures for scenarios 2, 4, and 5.

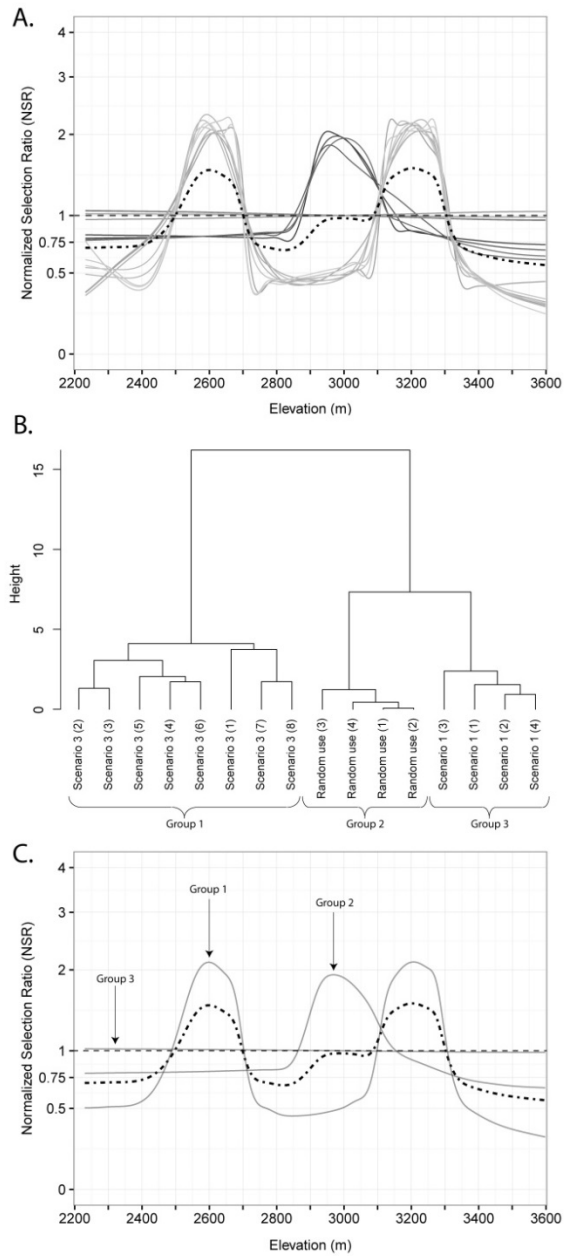


Figure 3. Two-stage (i.e., population-level) simulation results of habitat selection. A) NSR stage-1 results for a simulated population ($n = 16$). To aid in visualization the scaling of the y-axis is log transformed (i.e., $\log(\text{NSR} + 1)$) but values at the tick marks are the untransformed NSR scale. The dashed line at 1.0 represents use proportional to availability. The dark dashed line represents the global mean of all individuals. B) Hierarchical clustering dendrogram of the DTW transformed NSR curves in A. C) Group-level mean curves defining the selection response for each hierarchical clustering group (see Table 1 for scenario definitions). The dark dashed line represents the global mean.

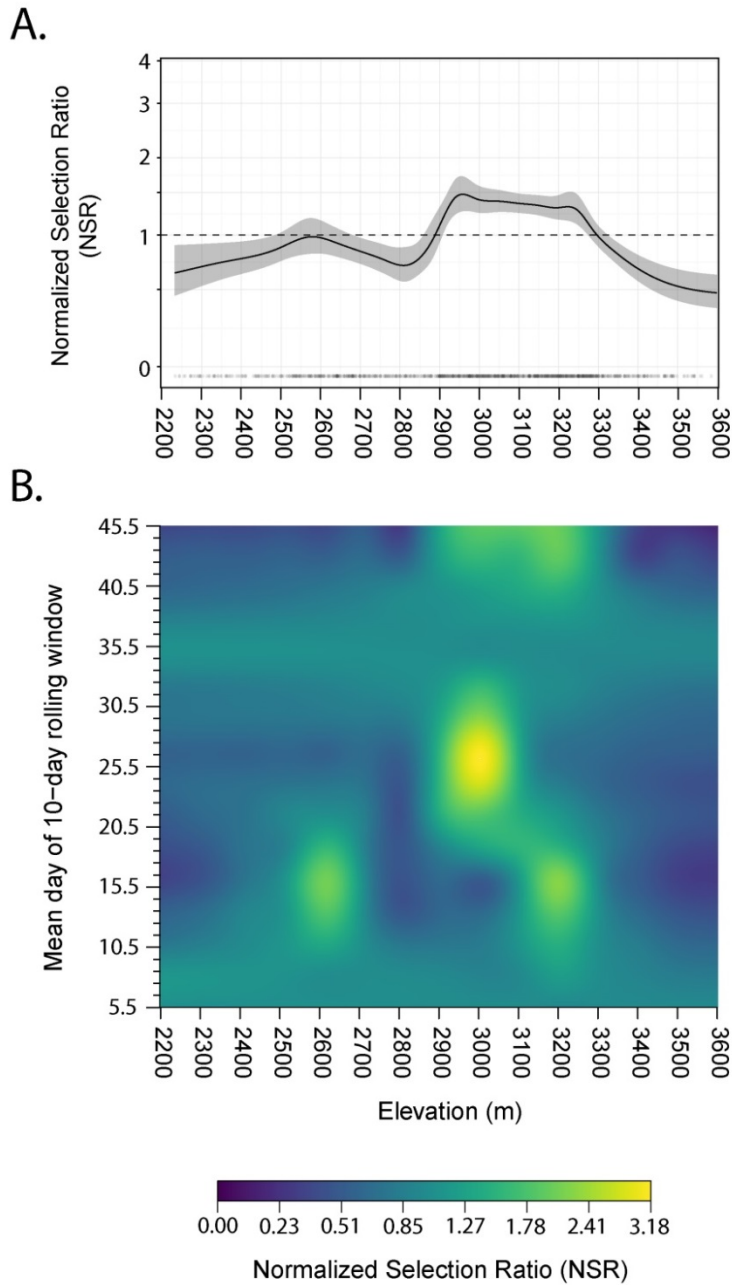


Figure 4. Dynamic simulation results. A) Static NSR curve using the “pooled” dynamic simulated-use data. The dashed line at 1.0 represents use proportional to availability. B) NSR surface for the dynamic simulation model based on a 10-day rolling window of the dynamic simulated use data. To aid in visualization the scaling of the y-axis (A) and color scheme (B) is on the log scale (i.e., $\log(\text{NSR} + 1)$) but the y-axis and legend values are on the original NSR scale.

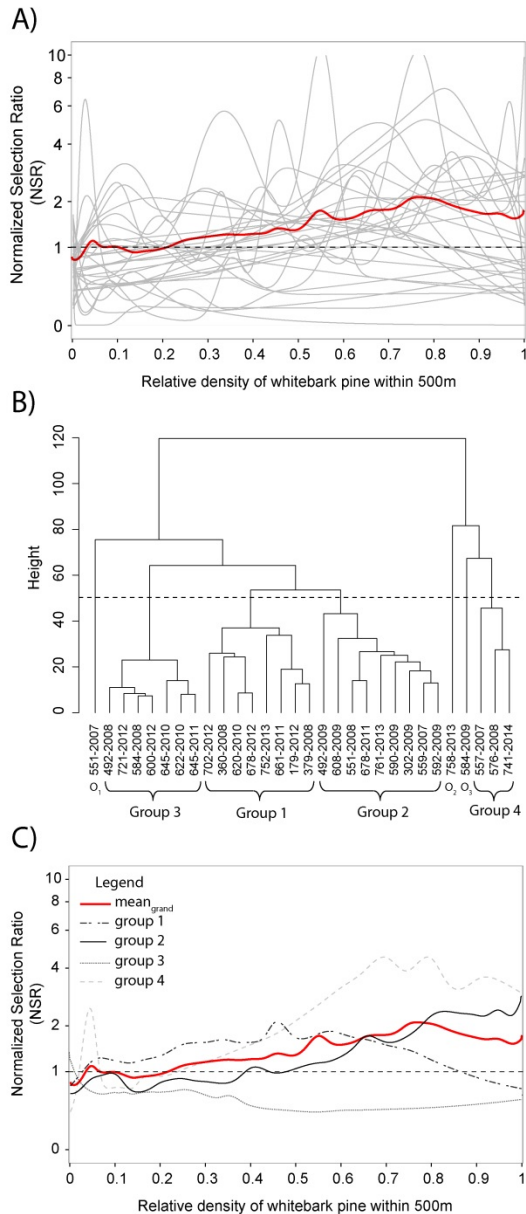


Figure 5. NSR curves, hierarchical clustering, and group-level responses for 27 grizzly bears in the Greater Yellowstone Ecosystem 2007-2014. A) NSR response curves for 27 grizzly bears. The red line represents the global mean from averaging all 27 curves, weighted by their standard errors (not shown for visual clarity). To aid in visualization the scaling of the y-axis is log transformed (i.e., $\log(\text{NSR} + 1)$) but values at the tick marks are the untransformed NSR scale. The dashed line at 1.0 represents use proportional to availability. B) Hierarchical clustering dendrogram of the DTW-transformed NSR curves in A. C) Group-level mean curves defining the selection response for each hierarchical clustering group (see Appendix A, Figure A.6 to see individual curves relative the group level means).

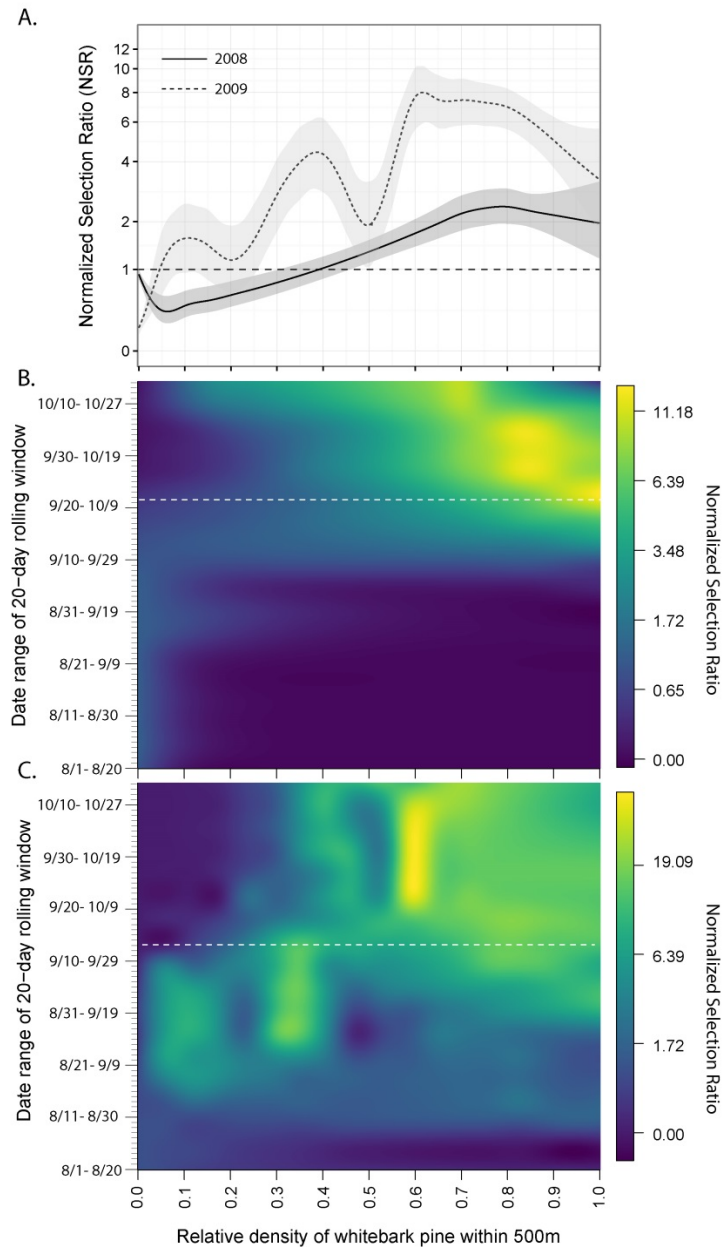


Figure 6. Dynamic NSR results (post-hoc) for grizzly bear 584 from Aug 1 to Oct 31 in 2008 and 2009 in the Greater Yellowstone Ecosystem based on a 20-day rolling window. A) Static pooled results. The black dashed line at 1.0 represents use proportional to availability. B) NSR surface for 2008. C) NSR surfaces for 2009. The dashed white line in B) and C) indicates the temporal limit of the original static analysis for whitebark pine density (i.e., from Aug 1 to Sep 30). To aid in visualization the scaling of the color scheme is log transformed (i.e., $\log(\text{NSR}+1)$), but values in the legends are on the untransformed NSR scale. Note the difference in scaling between 2008 and 2009, showing the stronger selection for late-season whitebark pine use in 2009.

APPENDICES

APPENDIX A

SUPPLEMENTAL FIGURES

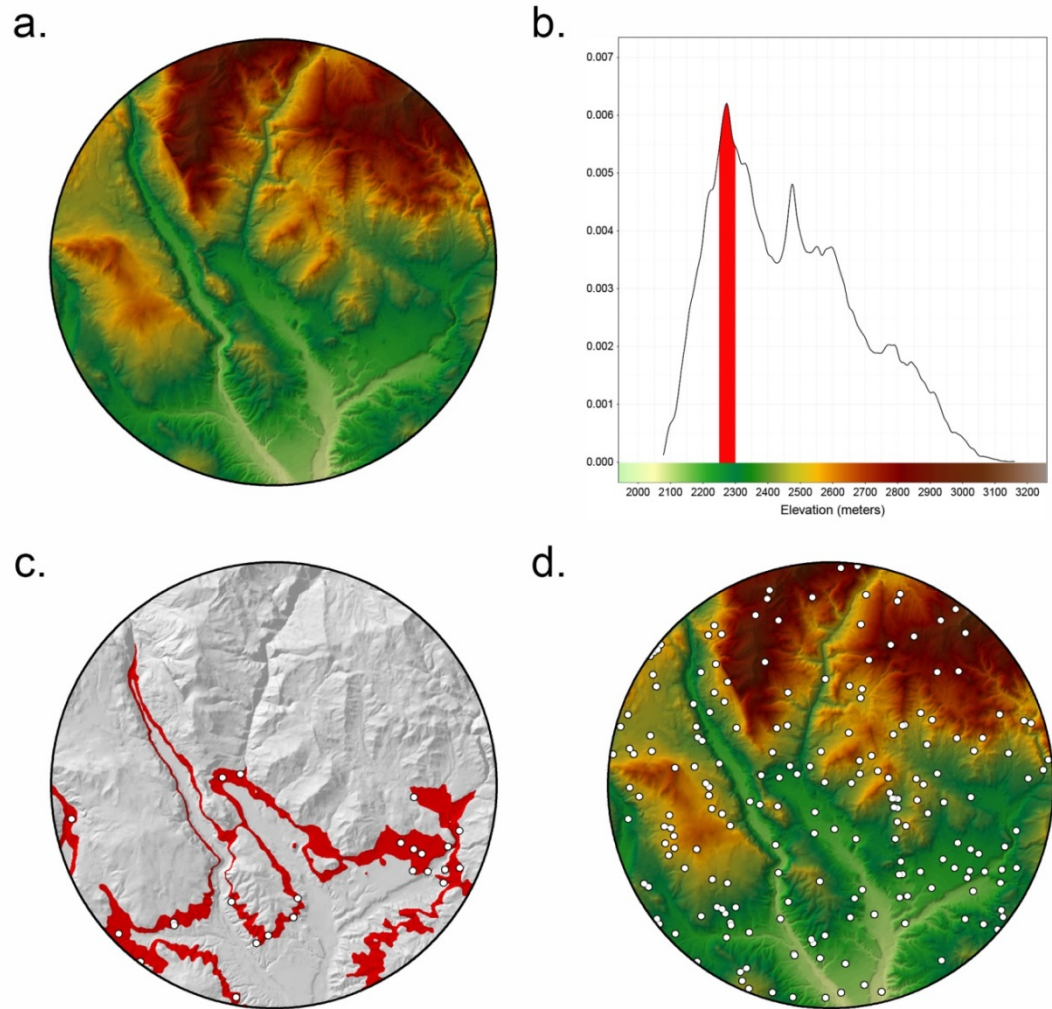


Figure A.1. Schematic of the simulation point generating process based on the spatial trend covariate elevation ($elev_{100m}$). a) Simulated circular home-range showing spatial distribution of elevation. b) Kernel density estimate showing distribution of elevation (area under the curve sums to 1). The red vertical band shows the sub-region 2250-2300m depicted spatially in c, approximately 12% of the home range area. c) Red region shows the spatial window defined by the 2250-2300m sub-region. White points show the random locations for the proportional allocation (12% of total locations) constrained to be inside the sub-region. d) Merging all 50m sub-regions together creates a simulated dataset ($n=200$) where use of elevation is approximately proportional to availability.

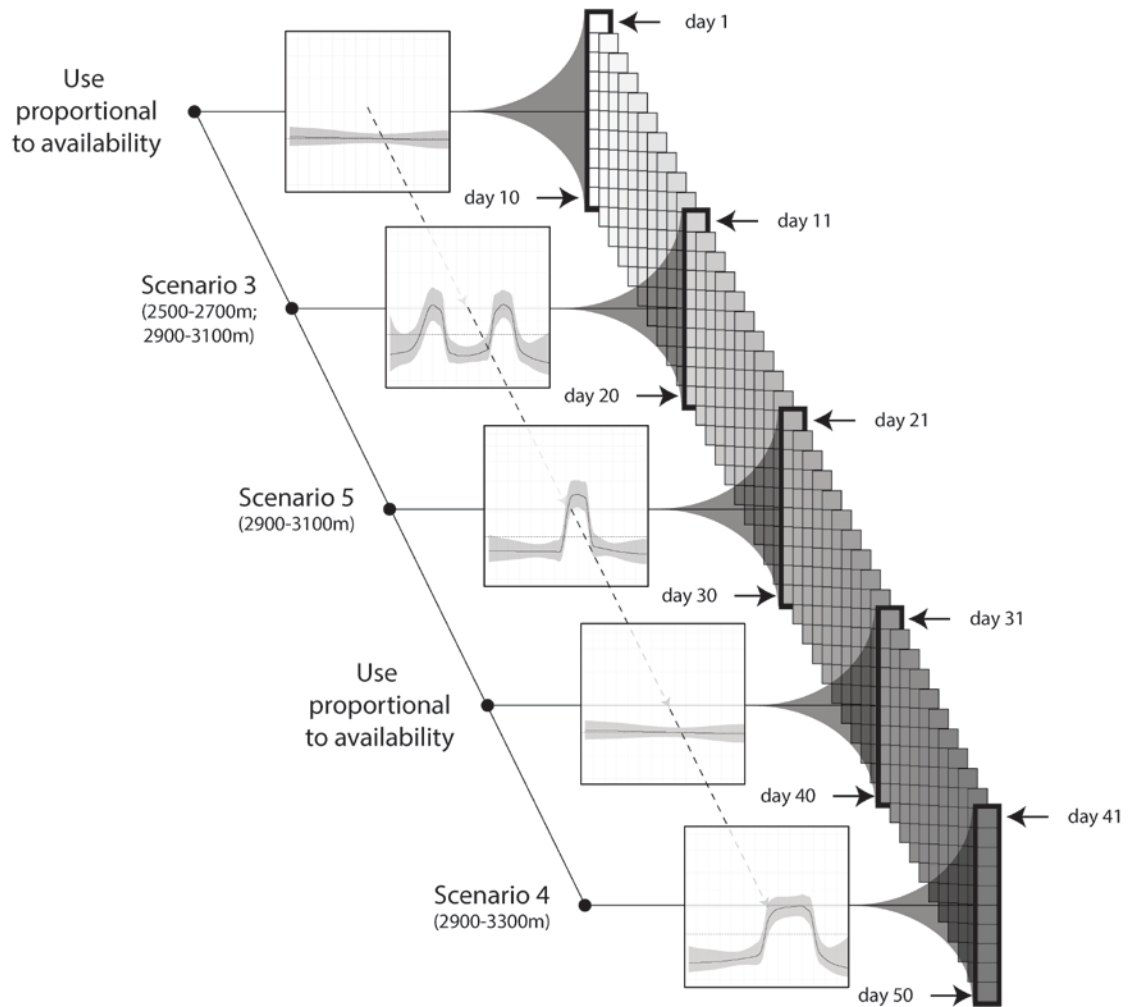


Figure A.2. Conceptual diagram of the temporally dynamic “known-use” simulation process. Each square represents a day and vertical blocks of squares illustrate 10-day rolling windows ($n=41$). Each unique day can be represented up to 10 times (only once per moving window and at different vertical positions). The relative position can be followed horizontally through the stack of columns. Columns with bolded outlines represent the rolling windows for the 5 predetermined scenarios, where used locations ($n \approx 200$) within the 10-day rolling window were simulated according to the scenario type. Simulated locations for rolling windows between scenarios were defined by linearly interpolating (between scenarios) the expected use in each 50-meter elevation bin (see *Habitat covariate, availability, and simulated use* section in main text for details on simulating “known use”).

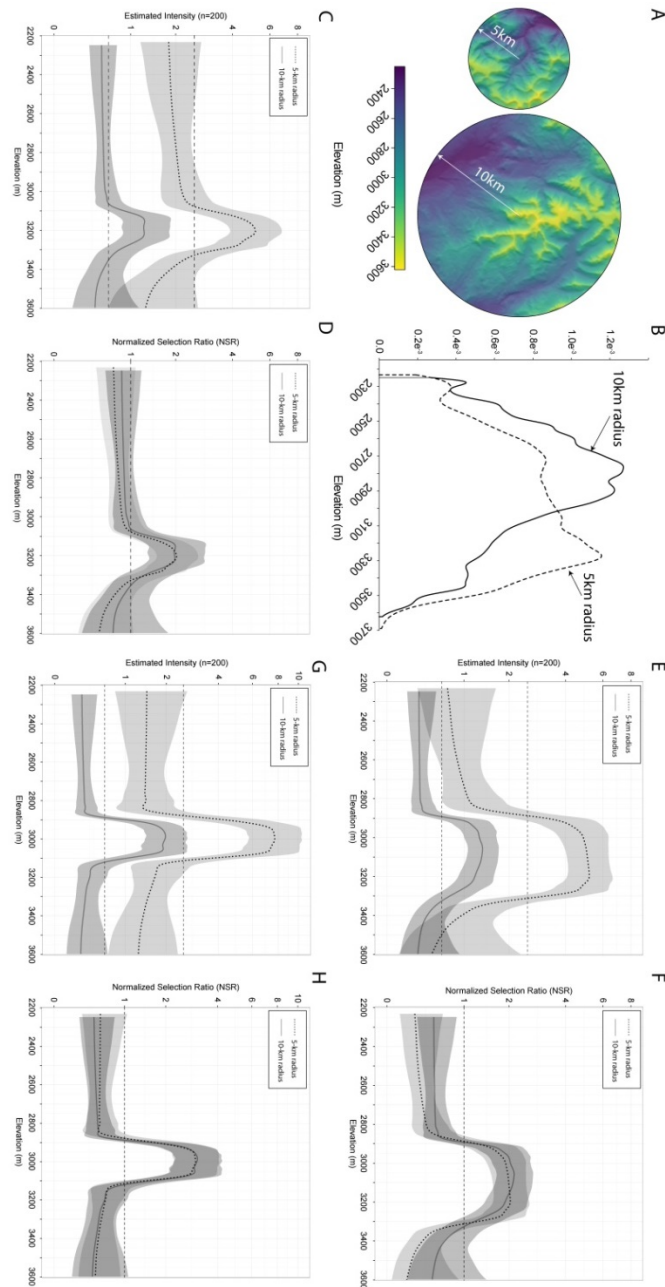


Figure A.3. Mean ($n=10$) simulation results for single-stage models. A) Spatial distribution of elevation between the 5- and 10km availability domains. B) Probability density functions for elevation in each availability domain. C) Raw estimated intensities for 5- and 10km availabilities. D) NSRs associated with panel C for scenario 2. E & F) Raw estimates and NSR curves for scenario 4. G & H) Raw estimates and NSR curves for scenario 4. To aid in visualization the scaling of the y-axis is log transformed (i.e., $\log(\text{NSR}+1)$), but values at the tick marks are the untransformed NSR scale. The dashed line at 1.0 represents use proportional to availability.

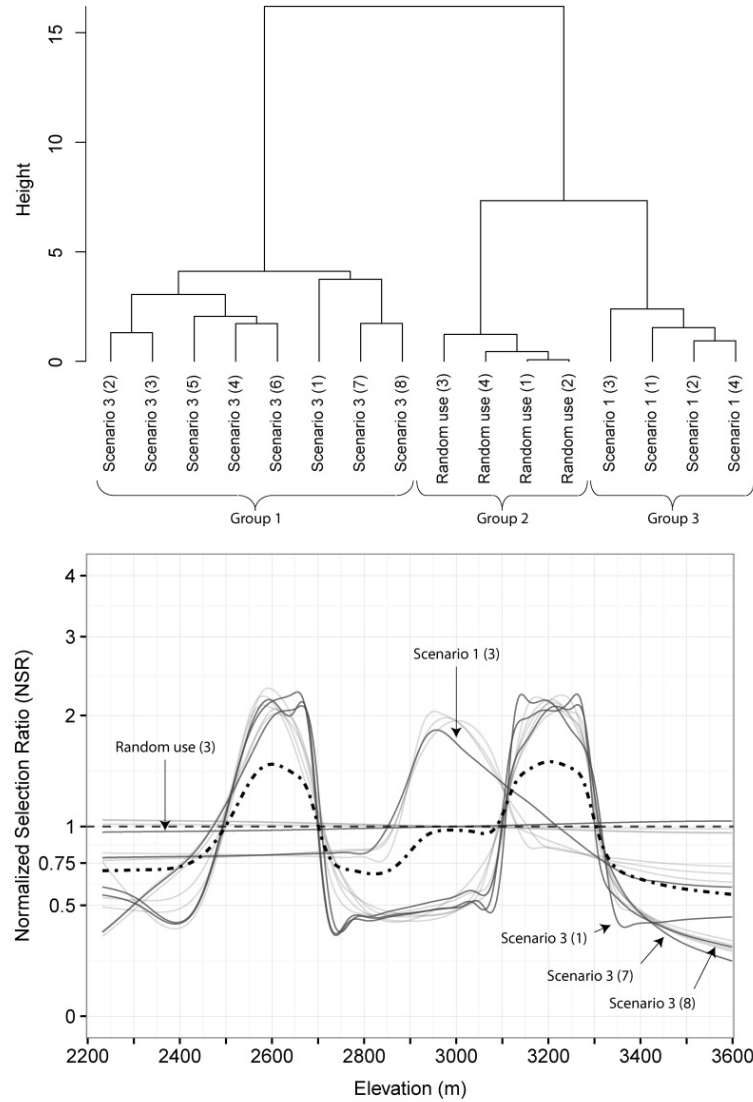


Figure A.4. Top) Hierarchical clustering of the DTW transformed NSR curves. Bottom) NSR stage-1 results for simulated population ($n=16$). Arrows and identifiers indicate subgroup structure identified in the top panel. To aid in visualization the scaling of the y-axis is log transformed (i.e., $\log(\text{NSR}+1)$), but values at the tick marks are the untransformed NSR scale. The dashed line at 1.0 represents use proportional to availability. The dark dashed line represents the global mean of all individuals.

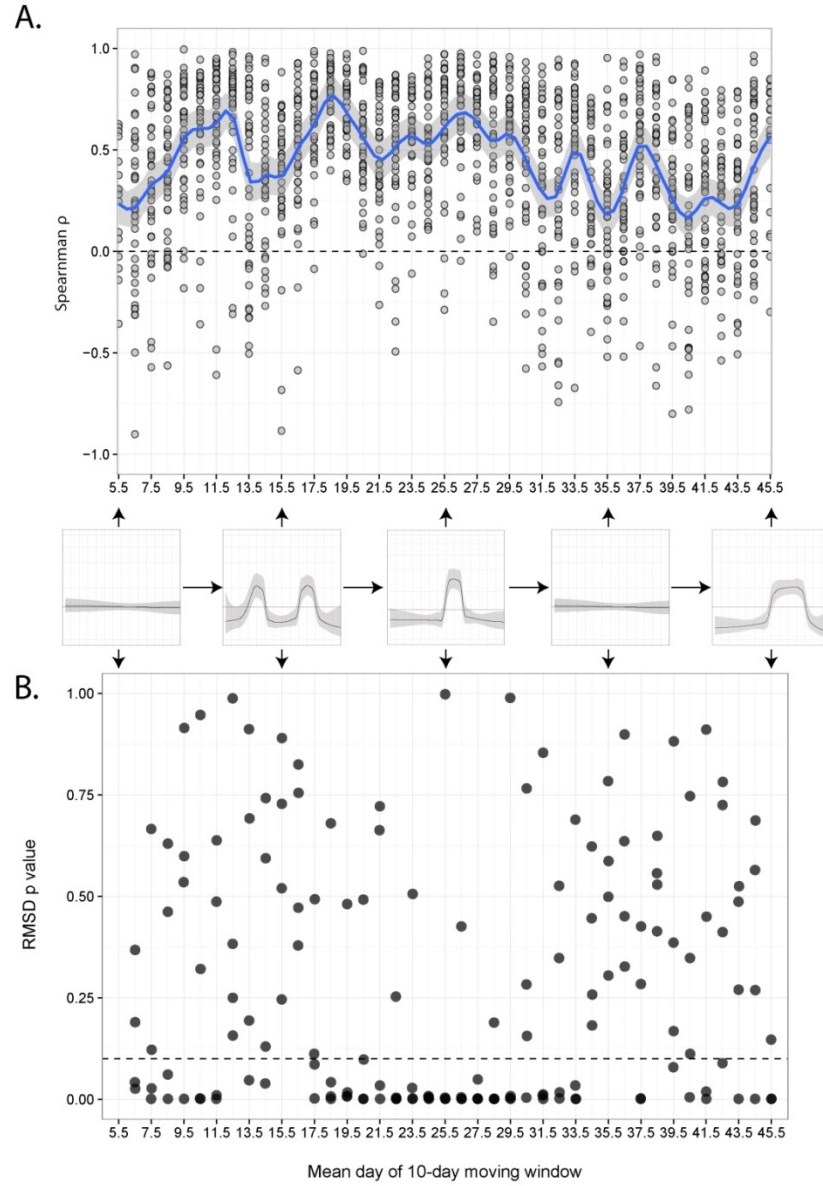


Figure A.5 A) Spearman's ρ (10-replications) for the 4-fold cross-validation for the dynamic simulation model using 8 area-adjusted NSR bins. B) Root-mean-square-deviations p-values (4-replications) for 8 area-adjusted NSR bins. Dashed line represents $\alpha=0.01$.

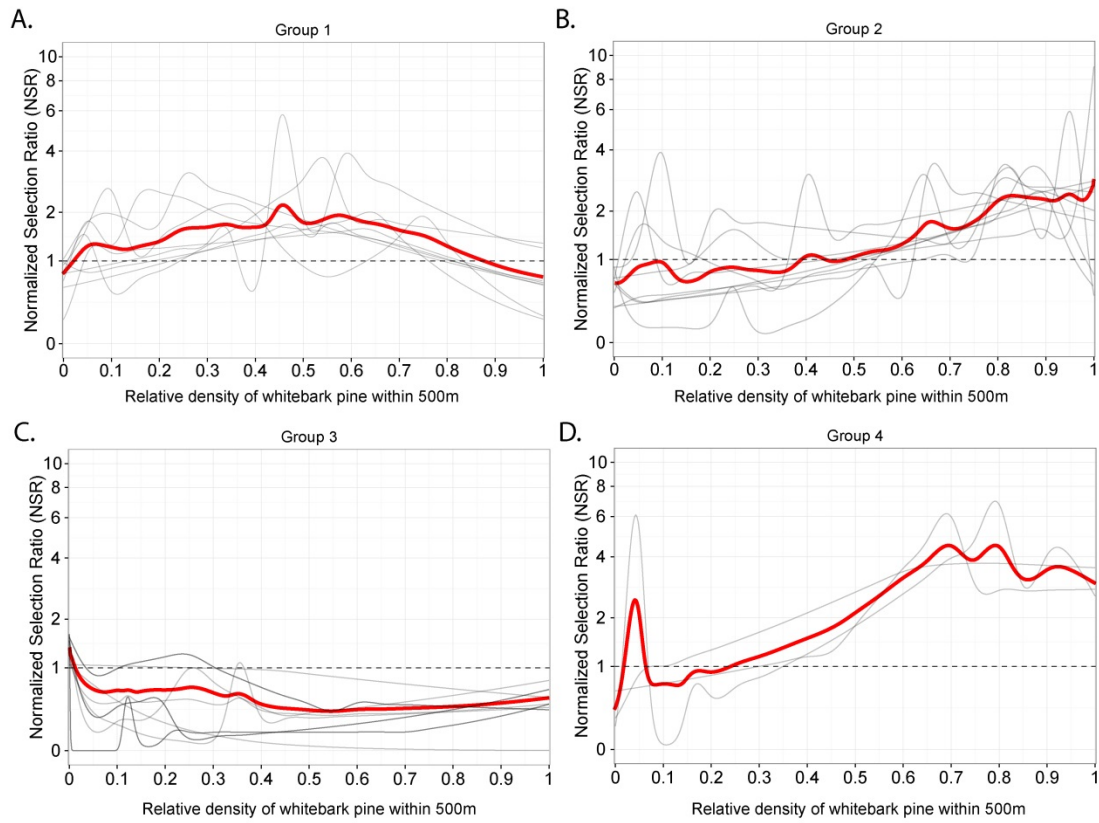


Figure A.6. Group-level means (red) and individual bear NSR curves for relative whitebark pine density in 27 grizzly bears in the Greater Yellow Ecosystem from 2007-2014. Means are weighted by inverse of the stage-1 level NSR standard errors.

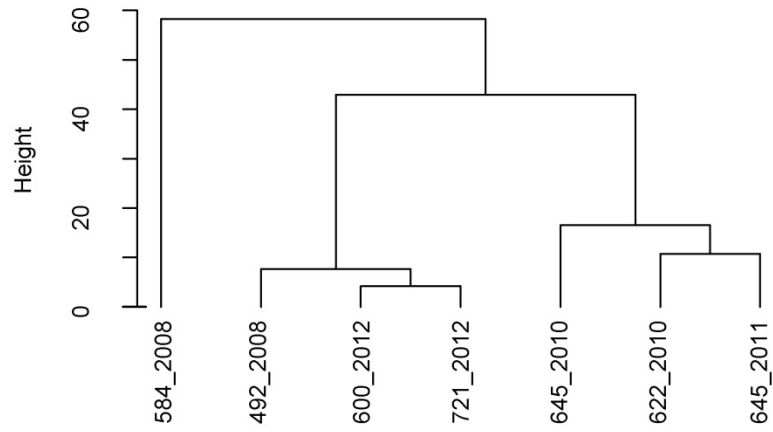


Figure A.7. The hierarchical clustering dendrogram of stage-1 NSR locations from the post-hoc late-season type II error checking analysis for group-3.

APPENDIX B

DICHOTOMIZING GPS DATA INTO ACTIVE
AND NON-ACTIVE LOCATIONS

We used a two-stage process for dichotomizing GPS data into active or inactive behavioral states. Our objective was to partition pooled behavioral data into two general categories that would differentiate between active behavior (e.g., movement and foraging) and sustained periods of inactivity associated with bedding, or resting, behavior. Resting bouts for grizzly bears vary seasonally and across populations as a function of food sources (McLellan and McLellan, 2015), but resting bouts of 3 – 10 hours are common in the GYE (IGBST unpublished data) and facilitate detection using the acquisition intervals that occurred during our study.

GPS collar data was separated into individual bear-years beginning with den emergence or capture and ending with den entrance or casting of the GPS collar. For each bear-year we first applied the Density-Based Spatial Clustering Application with Noise (DBScan) to assign cluster membership to all successfully acquired GPS locations. This algorithm does not require a priori specification of the number of clusters, excels at finding clusters of non-uniform shape, and allows locations to belong to a non-cluster class (Ester, 1996). We selected a parameter set for the DBScan algorithm which would identify short and long term clusters (minimum cluster size = 2 locations), yet be spatially sensitive to the high spatial accuracy of GPS locations (search radius = 20m). Individual cluster identification numbers were generated and appended to the GPS time-series (Figure B.1 *Cluster ID* column).

For each bear-year we combined cluster identification numbers with GPS collar activity sensor data as the input data for a serial time-series analysis (Díez-Noguera, 2013). Failed GPS fix attempts in grizzly bear telemetry data most often caused by behavioral influences of bedding, when bear body position may result in the GPS antenna having a poor view of the satellites (Figure B.2; Moe et al. 2007, Schwartz et al. 2009). GPS activity sensors record data regardless of acquisition success, which allowed us to assign activity state (active/non-active) for missed locations by incorporating information from adjacent success fix locations in the time series. For example, a missed fix with a low activity value buffered by successful fixes that are members of the same non-active cluster indicate a high probability of no movement and an overall sustained period of inactivity including the failed GPS fix attempts. Assigning an activity state to missed fixes is important for our analysis as it allows assessment of the potential for habitat influenced bias from missed fixes (Frair et al. 2004) for active-only locations. Given the propensity for missed locations in grizzly bears GPS fixes to be a function of resting behavior, subsetting the data to only active locations may improve the fix success rate over that of the pooled data and prevent the need to account for habitat bias in parameter estimates (e.g., fix success $\geq 90\%$; Frair et al. 2004, Frir et al. 2010). Therefore, we included the entire GPS data stream (successful and failed fixes) in the serial time-series analysis (Figure B.1. *GPS fix success* column).

Each serial analysis on an individual bear-year time-series began by assigning each record an activity state (non-active = 0, active = 1) based on the Schwartz et al. (2009) grizzly bear specific activity threshold value of 210 (Schwartz et al. 2009; Figure B.1, *Activity value* column). The short window of time (10-15 minutes) that activity data is recorded relative to GPS interval (range 105-120 minutes) may result in low activity values for some behaviors, or simply indicate a brief period of inactivity nested within a

longer period of active movement or foraging. Accordingly, non-active classification based exclusively on activity data may result in elevated Type I (false positive) error rates. Integrating spatial information with activity data can greatly reduce the type I error rates for resting behaviors. For example, consecutive locations with low activity values that are members of the same spatial cluster indicate a sustained lack of spatial displacement and bodily movement, the hallmark signs of resting behavior. Therefore, we updated activity states by incorporating cluster membership information: locations assigned to the non-active state that were not members of spatial clusters were switched to active status (Figure B.1, locations 2 and 9). Although switching non-clustered low activity locations to the active state may increase Type II (false negative) errors, we believe our approach is conservative in the context of resource selection of active locations. Furthermore, it avoids the nonsensical situation of non-active locations “migrating” across the landscapes.

Next we assessed missing GPS fixes which lack the required spatial information for clustering procedures. We used the previous and subsequent successful locations surrounding missed fixes to adjust the initial activity state determined by the Schwartz et al. (2009) threshold. Missing locations, or consecutive blocks of missing locations, with non-active status that were adjacent to non-active clustered locations were left in the non-active state (Figure B.1, locations 5, 6, 19, 20). However, in order not to artificially inflate GPS fix success for active locations we assigned all missing locations that were not adjacent to non-active clusters to the active state regardless of their activity values (Figure B.1, location 22). We consider the allocation of these non-clustered missing locations to the active class as conservative because they only influence the analysis by reducing the active-only location fix success rate.

GPS positional error occasionally caused single low-activity locations to be outside a group of non-active clustered locations. As previously described, these single (i.e., non-clustered) low activity locations were set to an active state. However, unlike single low activity locations adjacent to active values in the time series, or those incorporating movement across the landscape (Figure B.3., location 7), these cluster outliers represent a brief movement away from a non-active cluster, followed by non-active locations at the same spatial cluster (Figure B.3, location 4). In such cases, the continuous stream of low activity data, combined with small displacement distances suggests GPS locational error slightly exceeded the cluster search radius, causing exclusion from the cluster. Therefore, we adjusted the activity state of these locations back to the original non-active state as if they were members of the non-active cluster (Figure B.3, locations 2-7).

The results of the dichotomizing procedure improved fix success when assessing active only locations for individual grizzly bear bi-weeks periods. Using the Friar et al. (2004) cutoff of 90% acquisition success, we were able to substantially increase the available sample size for our analysis (Figure B.4).

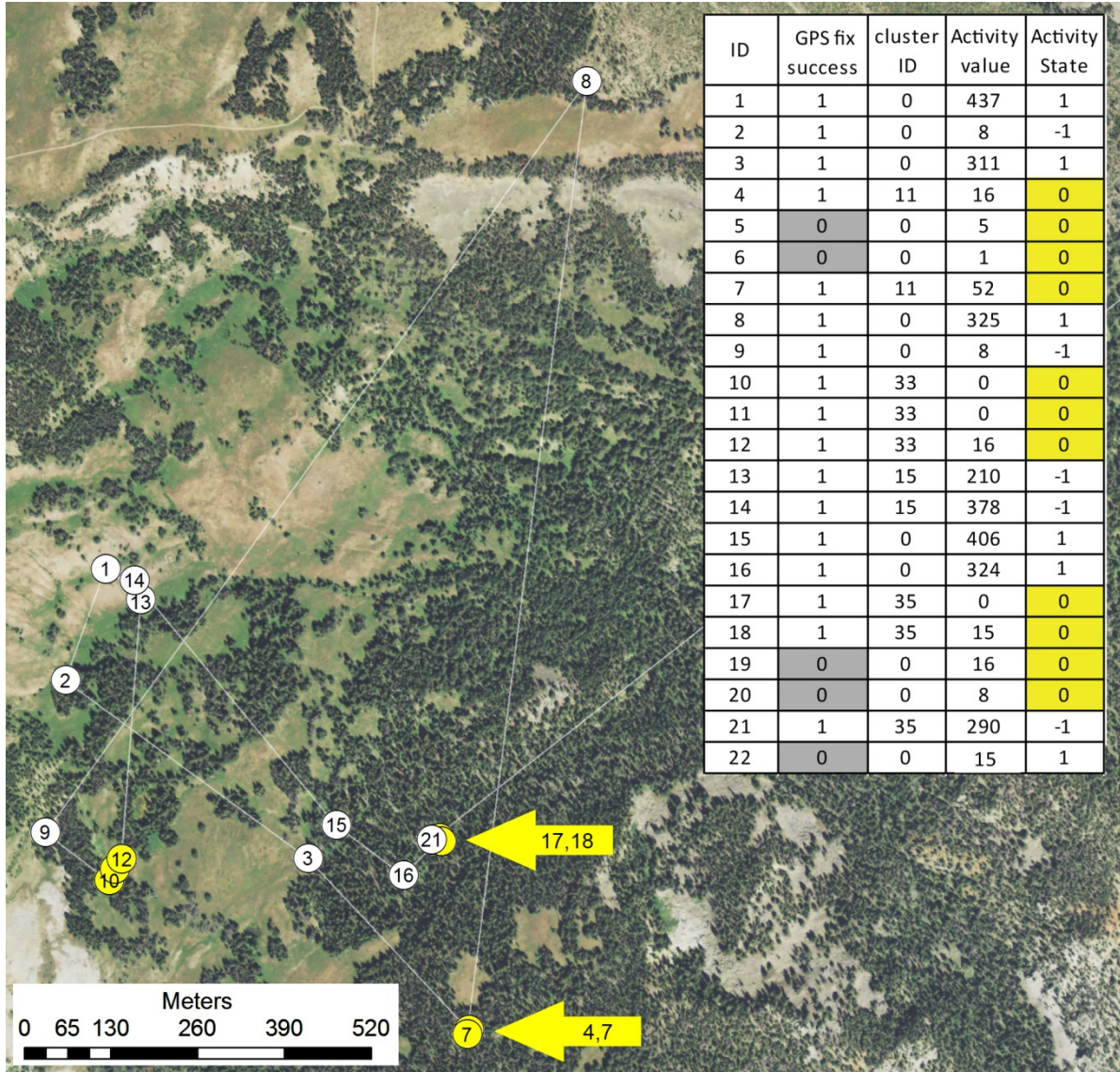


Figure B.1. Spatial data and associated attribute data (inset table) for 21 consecutive GPS locations from a 5 year-old male grizzly bear during August, 2013 in the GYE. Sequential numbers (ID) indicate the temporal sequence of 105 minute GPS location fixes. Failed GPS fixes (GPS fix success = 0) are shaded grey in the table. Clustered locations (results of the DBScan algorithm) are shown in yellow and cluster membership (Cluster ID) are provided in the data table inset. Activity value represents the GPS stored activity sensor data associated with each location. Activity State (0 = non-active; 1=active) is output behavioral state for each location. Yellow arrows indicate ID number of locations obscured by overlapping points.



Figure B.2. An example of a bedded collared grizzly bear in Pelican Valley, Yellowstone National Park taken during a routine VHF telemetry monitoring flight in 2007. Note that the body position of the bear on its side places the antenna close to the ground and toward two trees. This would greatly reduce the visible sky for satellite communication. Photo courtesy of Steve Ard.

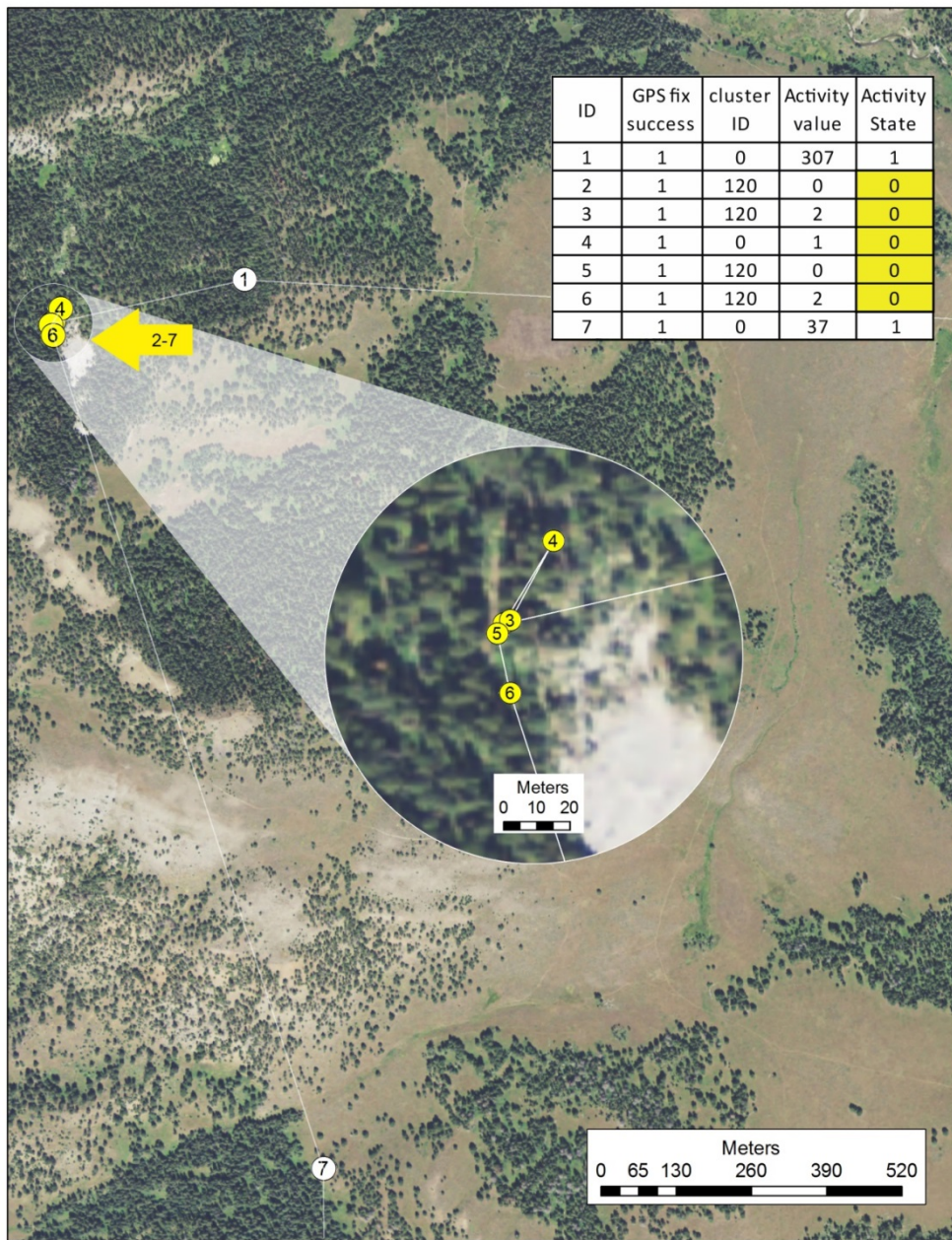


Figure B.3. Spatial data and associated attribute data (inset table) for 7 consecutive GPS locations from a 5 year-old male grizzly bear during October, 2013 in the GYE. Sequential numbers (ID) indicate the temporal sequence of 105 minute GPS location fixes. Failed GPS fixes (GPS fix success = 0) are shaded grey in the table. Clustered locations (results of the DBScan algorithm) are shown in yellow and cluster membership (Cluster ID) are provided in the data table inset. Activity value represents the GPS stored activity sensor data associated with each location. Activity State (0 = non-active; 1=active) is output behavioral state for each location. Yellow arrows indicate ID number of locations obscured by overlapping points.

APPENDIX C

GROUP-LEVEL BOXPLOTS

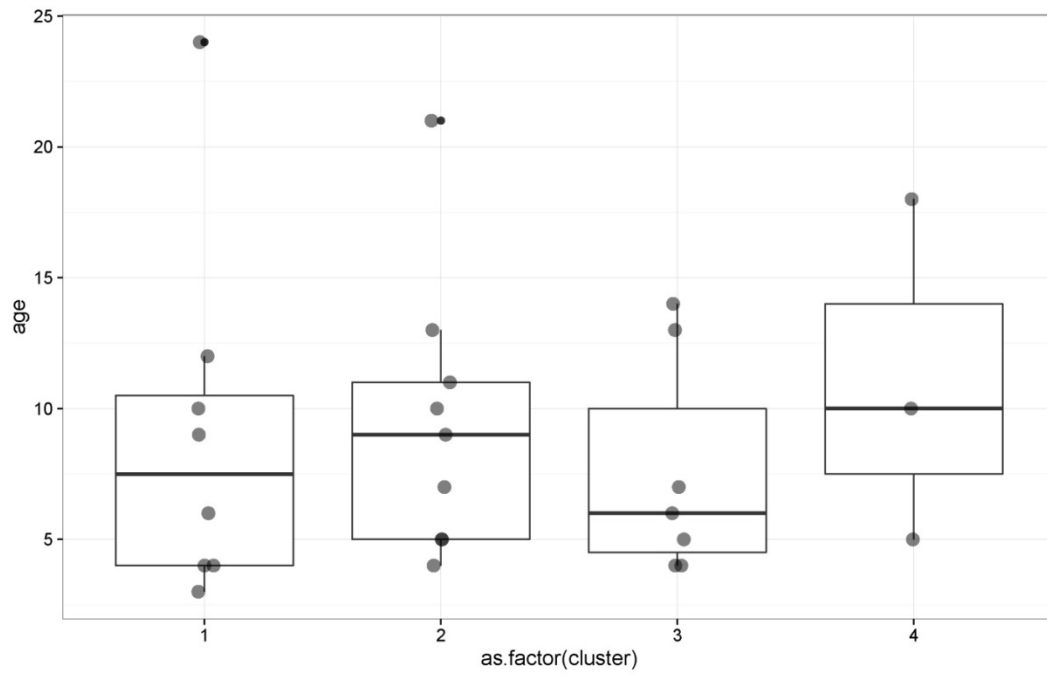


Figure C.1. Boxplot of age by stage-1 hierarchical clustering group.

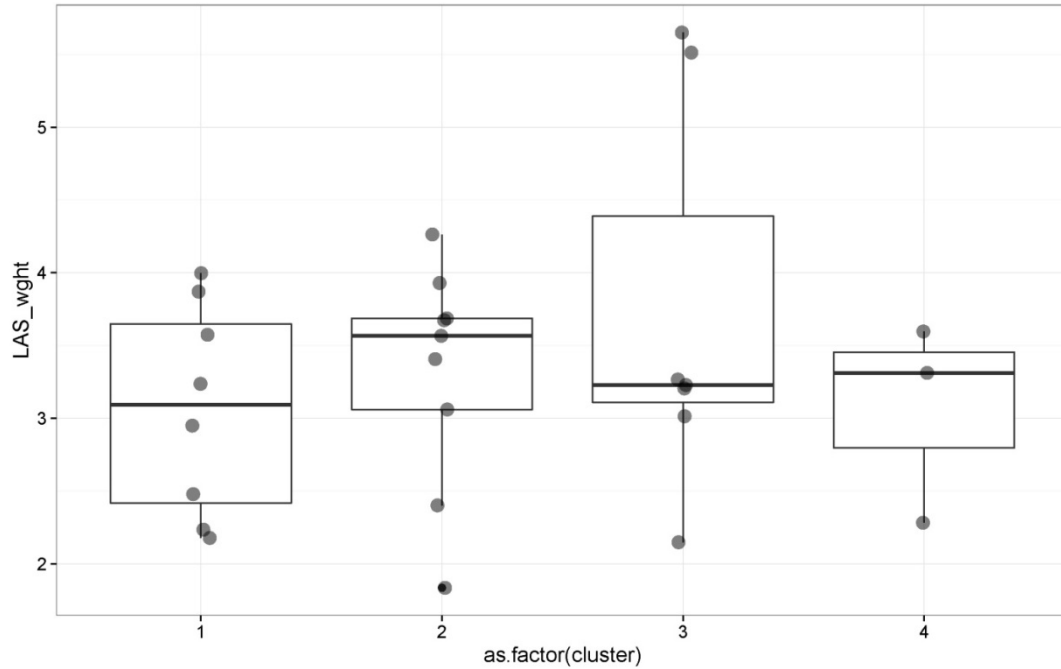


Figure C.2 Boxplot of whitebark pine mortality level (LAS score; Macfarlane et al. 2013) by stage-1 hierarchical clustering.

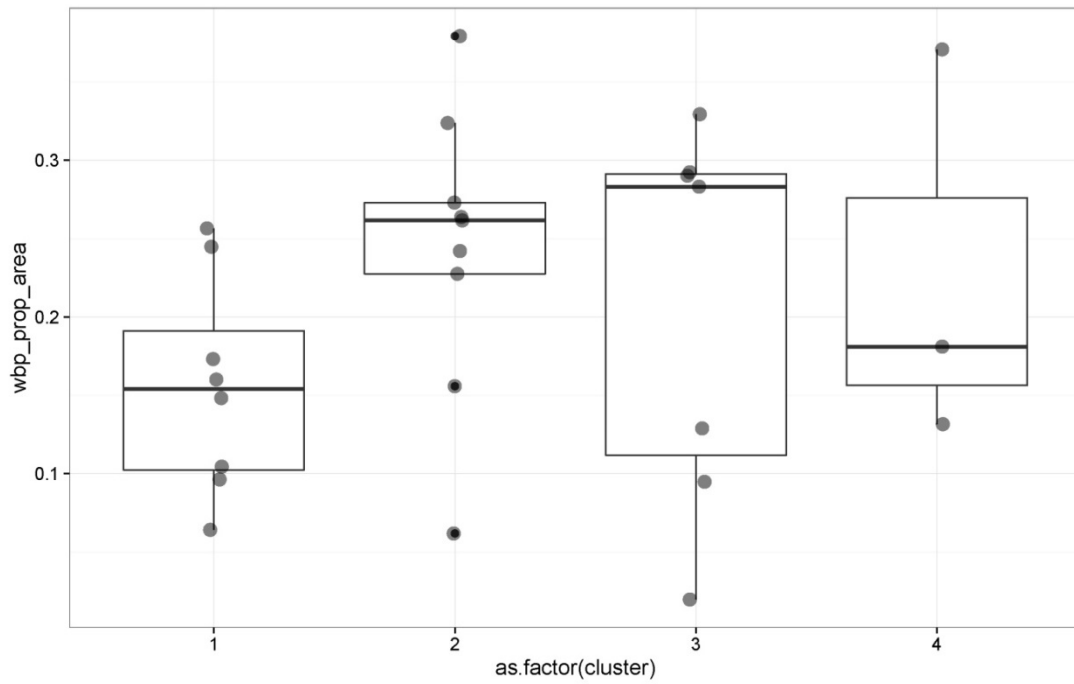


Figure C.3 Boxplot of proportion of home range composed of whitebark pine habitat by stage-1 hierarchical clustering group.

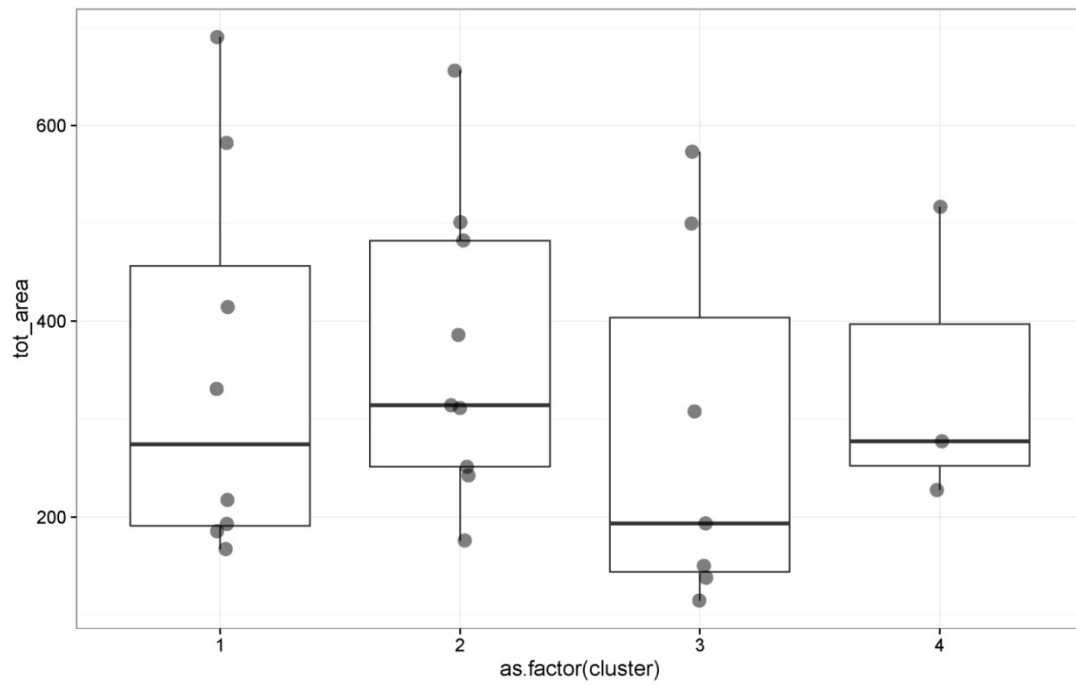


Figure C.4 Boxplot of total home range area by stage-1 hierarchical clustering group.

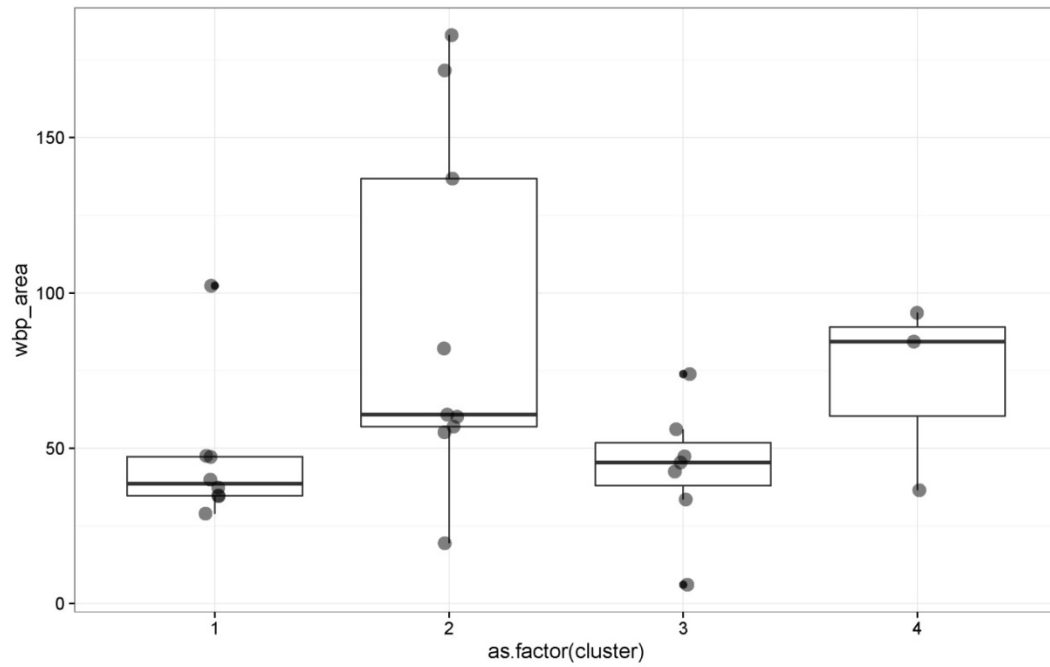


Figure C.5 Boxplot of absolute whitebark pine area by stage-1 hierarchical clustering group.

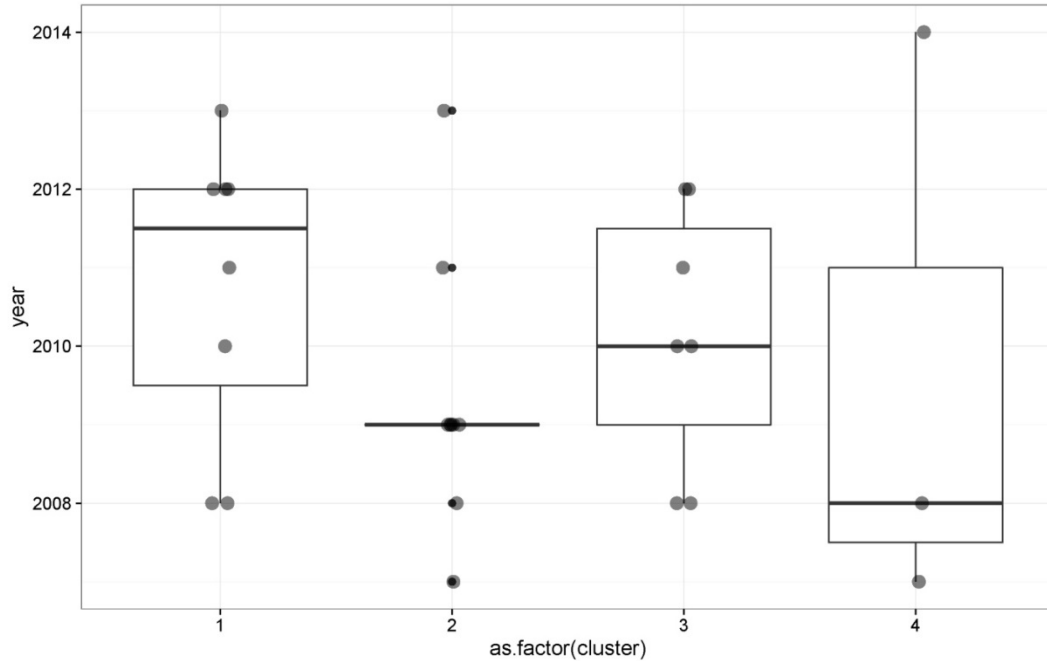


Figure C.6 Boxplot of year by stage-1 hierarchical clustering group.

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