Evaluating a Mechanistic Home Range Model for Elk (*Cervus elaphus*)

by

Dana Paige Seidel

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Abstract

Stable home ranges can emerge in a generic forager using a two-part memory system and rules derived from optimal foraging theory. My objective was to evaluate the underlying assumptions of this promising theoretical model using data from two populations of elk. Using a spatiotemporal scan statistic, I identified discrete foraging patches in GPS relocations of elk, thereby supporting the first assumption of the model that foraging occurs in discrete patches rather than diffusely across the landscape. Moreover, the model assumes that foraging patches have higher attractive value than other areas of the home range. During the 2012 growing season I identified patches based on GPS relocation data and sampled vegetation within each patch to estimate forage biomass. Points along elk paths not used for foraging were sampled identically for comparison. Using a matched-pairs conditional logistic regression on "patch" and "nonpatch" data points, I demonstrated foraging selection differences across herd, sex, and season and compared results to herd-scale resource selection functions for the area. Generally elk selected patches with higher biomass, cover, slope, and lower traffic on the nearest road; selection priorities that were mirrored at the larger scale. Exploring intra-home range movements in comparison to those predicted by the model, I used negative binomial regression to assess environmental characteristics that affect the frequency of returns, and thereby characterize the most successful patches. I found that elk return to known patches regularly over a season, on average after 15.4 (±5.4 SD) days. Patches in less-rugged terrain, farther from roads and with high productivity were returned to most often when controlling for the time each patch was known to each elk. My results demonstrate empirical support for the primary assumptions behind a mechanistic home range model and offer insight into the physiographic and anthropocentric features that define a successful foraging patch. These findings offer important insights that may be used to understand the movements, space use, and home range formation in free-ranging ungulates.

Preface

This thesis is an original work by Dana Paige Seidel. All data for this research project, of which this thesis is a part, were collected and animals captured according to guidelines approved by University of Alberta Animal Care and Use Committee (AUP#00000009). Chapters 2 and 3 have been formatted and submitted for publication in *Oikos* and *Movement Ecology* respectively prior to final submission of this thesis.

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Chapter 1

Modelling home range behaviour in the real world

Impetus

Territories and home ranges have been studied since the late 19th century but were not widely explored nor differentiated satisfactorily until the 1940s. In a seminal paper, W.H. Burt (1943) differentiated home ranges from territories and offered a definition of home range still cited widely today:

> "A home range is the area traversed in the normal activities of an individual including food-gathering, reproduction, and caring of young."

Although science now had a definition for this behaviour seen across a wide variety of species, we did not have an understanding of why or how this pattern of space use arose and our assessments of animals' ranges were limited by available data. In the mid to late 20th century, the understanding of animals space use was rapidly advanced by the use of VHF and GPS location systems. A plethora of GPS relocations for individuals allowed scientists to assess use, selection (Manly et al. 2002) and even behaviour (Fryxell et al. 2008) across larger areas with lower observation effort. Even with newly abundant data, the statistical methods developed for evaluating home ranges (e.g. minimum convex polygons, kernel density estimators) remained descriptive in nature, offering better and better estimates of the boundaries and nature of home ranges but no means of exploring how or why they develop or change.

These statistical methods are currently the most popular and accessible tools for the estimation and study of home ranges, however, the mechanistic models being explored today have significant advantages. A mechanistic model works by modeling the independent parts of a complex system and demonstrating how that system works via the coupling of those individual parts. In home range research, theoretical mechanistic models are essentially hypotheses of how the system works and test the biological mechanisms of home range development. Furthermore, because they are built on rules for movement, they have the potential to be predictive (Moorcroft and Lewis 2006, Mitchell and Powell 2008).

Mechanisms have been suggested for carnivores and central-place foragers but a gap in understanding how herbivores might develop their distinct home ranges remains (Moorcroft 1999, Moorcroft and Lewis 2006, Mitchell and Powell 2004). In response to this void, Van Moorter et al. (2009) proposed a mechanistic model using a two-part memory system and optimal foraging theory resulting in a stable home range for a generic forager. They hypothesize that animals forage optimally and return to successful patches allowing time for forage regrowth between visits. In so doing, their model is an extension of the original idea of the marginal-value theorem, whereby foragers should leave a patch when time to resource acquisition within a patch is greater than the time to find and acquire resources within a new patch (Charnov 1976). Van Moorter et al.'s (2009) model does not require an attractive center to the home range thereby allowing for more realistic foraging behaviour to define a stable home range for species that do not have a central place of attraction. Interestingly, emergence of stable home range based upon Van Moorter et al.'s (2009) model reflects more efficient resource use than simulated animals without a stable home range.

Although a promising new theory, like many mechanistic models, Van Moorter et al.'s (2009) has never been evaluated with empirical evidence. As such, the chief objective of my research was to evaluate the suitability of this home-range model for free ranging elk within the montane ecosystem of SW Alberta.

Study species

The elk (*Cervus elaphus*) is a wide-ranging, abundant, large-bodied ungulate distributed across much of North America. They are a charismatic species, economically valued for recreational hunting across their range. Ecologically, elk have a large impact on forage species distributions and abundance and can be an important prey species for wolves (*Canis lupus*) and other large carnivores (Beyer et al. 2007). Populations of elk can be nomadic, migratory, or resident (Hebblewhite et al. 2008); in our study area, elk are predominately migratory, staying faithful to the same winter and summer ranges annually. Because of their abundance, social, and ecological importance, elk have been studied widely, especially in regards to their foraging (Jiang and Hudson 1992, 1993) and habitat selection (e.g. Boyce et al. 2003). Furthermore, because of their similarities in behaviour to other North American deer, elk make an ideal study species for research of this kind. If Van Moorter et al.'s (2009) model were supported in elk, there are potential implications for understanding of home-range development in many deer species.

Chapter Objectives

In Chapter 2, I sought to examine four underlying assumptions to the Van Moorter et al. model. First, elk forage in discrete patches and not diffusely across the landscape. Second, patches selected for foraging have higher utility or value than other areas of the home range not used for foraging. Third, depletion and replenishment of biomass dictate departure from and attraction to patches. And finally, memory of patches produces the periodic return behaviour from which home ranges emerge.

In Chapter 3, I explore the intra-patch movements by elk within their home range as predicted by the Van Moorter et al. (2009) model. My objectives within this chapter were to assess whether elk make repeated returns to known foraging patches over the growing season and subsequently investigate what environmental covariates influence return likelihood and timing of returns over a season.

Chapter 2

Varied tastes: home range implications of foraging patch selection

Introduction

In recent years, accompanying the increase of GPS and satellite technology, abundant and accurate spatial data have enhanced the analysis of animal distributions and home range (Kie et al. 2010). Despite improved techniques and increased data availability, the processes for home range estimation remains mostly restricted to "probabilistic" or statistical approaches for home range description (Laver and Kelly 2008). The minimum convex polygon (MCP), the original estimator and still used widely today, is a conceptually simple method used to estimate a home range as a polygon containing some percentage of the individual's recorded locations (typically 95% or 100%). MCPs are not constrained to any statistical probability distribution of spatial use and thus are criticized for potentially including large areas unimportant to an individual's home range (Powell 2000). Reducing this error, utilization distributions are commonly estimated to assign a probability distribution to points on the landscape, predicting the probability that any point in space will be occupied by an individual at any given time (Powell 2000). The increased use of utilization distributions has encouraged inference as to why animals choose the home ranges they do, based upon correlations of the probabilities of use with landscape features (Kie et al. 2010).

Although MCPs and kernel estimation methods are widely used tools for the estimation of home ranges, these are descriptive, not predictive, methods for conceptualizing home-range behaviour. In contrast, mechanistic models for home range attempt to identify the biological mechanisms for stable home-range development; mechanisms that, despite the long tradition of home-range study, have yet to be identified (Börger et al. 2008, Van van Moorter et al. 2009). Range and distribution of animals is defined by more than just landscape structure because patterns of predators, conspecifics, and resource depletion also have the potential to influence where animals or groups of animals can be supported (Mitchell and Powell 2004, Haydon et al. 2008). Mechanistic models have the potential to use these influencing factors, e.g. resource distribution, conspecifics, predation, to forecast size and distribution patterns of home ranges through predictions about animal movement.

The first mechanistic models for territorial development were reliant on individuals' response to scent marking by conspecifics (Lewis and Murray 1993, Moorcroft et al. 1999, Moorcroft and Lewis 2006). These models informed movement of territorial animals but are insufficient for animals that do not predominately use a central den site or scent-marking behaviours to mark or defend their home range. As an alternative, Mitchell and Powell (2004) created mechanistic models for foraging carnivores, and validated them using radiotelemetry data on black bears (Ursus americanus). Their models proposed home-range mechanisms based on the distribution of resources across a landscape and the depression of resources, specifically driving two competing behaviours: area-minimization versus resource-maximization strategies. Additionally, both models incorporated an attractive center to the home range, e.g. a den site, which does not exist for many herbivores.

Extending the applicably of mechanistic models for foragers, Van Moorter et al. (2009) developed a theoretical home-range model for a generic forager, creating rules for movement based upon optimal foraging theory and memory parameters without requiring an attractive center. Van Moorter et al. (2009) propose that animals forage optimally and return to successful patches leaving time for patch renewal during a growing season. Based upon a biased correlated random walk, their model uses changing patch utility and value to direct animal movement across a simulated landscape. Interestingly, emergence of stable home range within their model reflects more efficient resource use than without a stable home range. Additionally, because this model is based not on the movements of animals (or the points in space that represent them) but upon the underlying rules for movement, it has the capability to predict an individual's spatial use, not only describe it (Moorcroft and Lewis 2006).

The model makes four assumptions: (1) foraging occurs in discrete patches not diffusely across the landscape, (2) these foraging patches have higher value than other areas of the home range, (3) short-term and long-term memory play a role in directing use and reuse of these patches producing movement patterns that (4) respond to depletion and replenishment dynamics of available biomass. To evaluate the efficacy of this model, support for these assumptions is needed from a free-ranging forager.

Although purely theoretical in its conception, this model offers a promising hypothesis for large-bodied ungulates, especially elk. During the growing season elk spend the majority of their time foraging (Owen-Smith et al. 2010), making a foraging-based model likely to be the most suitable to explain their ranging behaviour. Foraging studies have explored a diversity of factors important to fine-scale foraging decisions for elk, e.g., biomass, protein, and digestible energy (Wilmshurst and Fryxell 1995), which implies that elk are selecting particular patches of higher quality or "utility" as modeled by Van Moorter et al. (2009). Importantly, available biomass has been shown to influence ungulate movement both at localized and home-range scales. Comparing resident and migratory populations of elk in an evaluation of the Forage Maturation Hypothesis, Hebblewhite et al. (2008) found that migration indeed provided access to higher-quality forage than accessed by resident elk. At a finer scale, herbivorous ungulates, including elk, have been shown to execute prolonged movements across their home ranges and shift movement states from directed travel to highly tortuous foraging behaviour upon encountering high biomass areas (Johnson et al. 2002, Fryxell et al. 2008). Spatial familiarity and memory also have been shown to be important not just for home range but also for foraging: elk return to areas they "know" or have previously used, especially those most recently visited (Wolf et al. 2009). These movement patterns demonstrate unequal use of areas of the home range, and recollection of successful foraging patches which is a fundamental assumption in the Van Moorter et al. (2009) model.

To establish appropriateness of the Van Moorter et al. model for elk, it must be demonstrated that elk use discrete patches rather than forage diffusely across the landscape, and selected patches must be shown to have greater value than areas not used for foraging. We hypothesize that both these assumptions are valid representations of elk behaviour and seek to test them using a spatiotemporal clustering algorithm and matched-pairs regression on directly-sampled biomass and landscape data. Furthermore, Van Moorter et al.'s model suggests the influence of forager memory and sensitivity of foragers to patterns of depletion and replenishment, which has been demonstrated in recent studies on foraging behavior and movement of elk. Within Van Moorter et al.'s model, movement between patches is reliant on the dynamic utility of each patch as it is influenced by replenishment and depletion of available biomass. Van Moorter et al. acknowledge that utility may be influenced by more than available forage, recognizing the potential for external factors like predation risk, disturbance, or competition to contribute or detract from a patch's attractive value. We hypothesize that patch value will be influenced by more than available biomass, and our work seeks to identify environmental factors that affect the value of foraging patches for wild elk and subsequently quantify their influence on elk foraging selection within a home range.

Methods

Study Area

Our study area spans the montane region of SW Alberta with the Rocky Mountain divide as the western-most boundary and the US/Canada border as the most southern (see Ciuti et al. 2012 for greater detail). We focused on animals from two herds: Waterton (those from within the boundaries of Waterton Lakes National Park) and Livingstone (those ranging along the Livingstone Range, an eastern outer range of the Rocky Mountains). Waterton animals were concentrated in fescue grasslands of the park's northern hills and the aspen forests and wetlands surrounding the eastern edge of Lower Waterton Lake. West of the Livingstone Range, animals ranged in predominantly rugged, coniferous forests and cut blocks of the Forest Reserve (public land). East of the Livingstone Range the terrain is less rugged and dominated by private agricultural and range lands. Our animals ranged both east and west of the range. Table 2.1 details these differences in habitat and vehicular traffic across herds, and Figure 2.2A & B shows the spatial distribution of relocations and clusters.

Patch Identification

Using GPS radiotelemetry we followed 12 elk throughout the 2012 summer season to monitor their foraging and movements. Each elk was outfitted with Lotek 4400, Telonics, or Argos GPS radiocollars (each with a 2hr fix rate) during captures in January 2011, March 2011, and March 2012. Data from Lotek collars were collected weekly by remote downloads and ARGOS satellites; Telonics radiocollars allowed for monthly downloads. All captures and telemetry conformed to University of Alberta Animal Care protocol #AUP0000009.

To identify foraging patches, clusters of telemetry relocations were pulled from individual elk's GPS datasets weekly using a retrospective space–time permutation scan statistic and the program SaTScan®. Developed initially for identification of hotspots of infectious disease, Webb et al. (2008) adapted this method for use with GPS relocation data for identification of wolf (Canis lupus) kill sites. To reduce misidentification of patches used for resting or other activities than foraging, fixes between the peak hours of day and night (10:00-14:00 and 22:00-2:00) were trimmed from the datasets before clustering analyses took place. This leaves just relocations from crepuscular times of day, when elk are known to be most actively foraging (Owen-Smith et al. 2010). The scan statistic is defined by a moving cylindrical window with a base in geographic space and height defined by time. In this method, each relocation is considered to be the centre of a possible cluster in space (of varying radii) and using all possible time windows. This analysis uses a dynamic cylinder moving in space, rather than a simple moving window; tested clusters may be flat discs (wide space, short time) or tall poles (narrow space, long duration), and every size in between (Figure 2.3). For more information on this scan statistic and its adaptation for GPS data, see Webb et al. (2008).

Prior to conducting the cluster analysis, three decision rules were set: the maximum diameter of the spatial window, the maximum duration of the temporal window, and permission for spatial overlap in resulting clusters. Using first passage time analysis to differentiate movement states from 2-hr fix data, Frair et al. (2005) observed elk step lengths when foraging were an average of 265.7m long. Given this average displacement and the logistic constraints of biomass sampling, we chose a diameter of 300m as an upper bound for cluster analysis. We used the software's default temporal window of 3 days because it did not significantly increase computational time and there was no biological reason to limit this window or the number of possible clusters tested. Finally, no geographic overlap was allowed between telemetry clusters in an individual analysis.

Unlike other clustering techniques, these decision rules do not directly define the number of points included or the size of the resulting cluster. Instead these maxima were imposed primarily to limit computational time and to ensure that clusters did not contain large unconnected areas. Due to the considerable energetic demands of large-bodied ungulates such as elk (Parker et al. 2009), we are confident that these clusters, representing a minimum of 4 hours in one location, identify sites where foraging took place. As such we considered the resulting clusters to be foraging patches. "NonPatches" were chosen from unclustered relocations of the elk during the same temporal window as the identified patch for that elk.

Field Sampling

Over 16 weeks from late May to early September 2012 (Victoria Day through Labour Day), patches and nonpatches of 13 elk from the Waterton (7, 3M, 4F) and Livingstone (6, 3M, 3F) herds were identified and sampled. Elevation, slope, aspect, species composition, and cover-type data were collected at the center of paired patches and nonpatches for 6 to 10 elk each week.

Biomass data were collected using a double-sampling technique (Coulloudon et al. 1999) for weeks 3 through week 16. Vegetation was sampled at 12 to 48 0.25-m2 quadrats along four transects at each site. The direction of the first transect was determined randomly and subsequent transects were lain 90, 180, and 270 degrees from the initial transect. Length of transect was determined by the radius of the patch identified by the cluster analysis. Patches with radii between 101m and 150m were sampled using 50m transects. Patches with radii between 51m and 100m were sampled using 25m transects. Patches with radii between 1m and 50m were sampled with 15m transects. Number of quadrats sampled along transects was determined by a heterogeneity assessment (Table 2.3).

Within each quadrat, we recorded species composition and estimated total aboveground biomass of forbs, graminoids, ferns, shrubs, and standing dead. Every 6th quadrat was clipped and vegetation types separated and weighed on site. A ratio estimator was then calculated for each vegetation type by dividing the measured wet weights by the field estimations for clipped quadrats. These ratios were then used to convert field estimates for all unclipped quadrats using the relationship between clipped wet weights and their field estimates. All final weight estimates for quadrats within a patch were used to calculate average above ground biomass for each patch and nonpatch. For transects dominated by shrubs, we used a line-intercept method to record percent cover of each shrub species on the line (Canfield 1941).

Covariates

Forage quality and availability have been shown to influence not only where elk range but also where they choose to forage (Langvatn and Hanley 1993, Hebblewhite et al. 2008). As such, the inclusion of forage biomass was crucial. Shrub percent cover (SPC) was calculated as an index for abundance in areas or on transects where shrubs dominated. For browsing animals, ranging predominately in shrub-dominated landscapes, SPC was considered another biomass predictor and possibly crucial for our foraging selection models – especially for Waterton males given their distribution in areas of high shrub density late in the season (Figure 2.2B, Table 2.2). Herbaceous biomass and shrub percent cover data were calculated from direct sampling at field sites using double sampling and line-intercept methods described above and informed the HerbBiom and SPC covariates respectively.

Although open areas are expected to provide the most high-quality forage, remaining close to or within cover is an important predator-avoidance strategy for ungulates (Altendorf et al. 2001). Foraging near or within cover may reduce the need for vigilance, especially in response to humans or roads (Altendorf et al. 2001, Frid and Dill 2002). Therefore forest cover was considered to be an important variable that could influence forage patch selection by elk and was included in the global model run for all model sets. The cover covariate, Forest, was estimated using a 2005 cover map created by the Foothills Model Forest Grizzly Bear Research Program (McDermid et al. 2009). This cover map is a composite of remotely sensed data on land cover and crown closure, as well as species composition, and agricultural and regeneration masks. Images for this cover map were collected at a 30m resolution by LandSat satellites. The cover map's 18 cover types were consolidated as either "forested" or "open." Forested cover type was made up of six types of vegetation (30% closure or greater): dense conifer, moderate conifer, open conifer, mixed forest, treed wetland, and broadleaf forest. Open cover type included herbaceous, shrub, regeneration, barren land, agriculture, snow/ice, water, and open wetland. To estimate the influence of cover on forage selection, the percentage of forested pixels within a patch was calculated in ArcMap 10.1.

Areas of higher slope highlight rugged terrain that is often a deterrent to elk that select areas that they can move through quickly, especially for foraging (Ciuti et al. 2012). As such it was hypothesized that increased slope might negatively influence forage-patch selection and thus slope was included in the global model set. Aspect has been shown to influence productivity, and thus forage quality, of a patch (e.g. southern slopes are more productive) and thus was considered a potentially important variable within the scope of our analysis. Slope and Aspect were calculated from a digital elevation model for the region. Covariate Aspect is the cosine of the aspect at the center point of the site for an assessment of northness.

Estimates for the distance to road and average summer daily traffic on the nearest road were obtained from the traffic model developed by Northrup et al. (2012) for the study area. We expect different magnitudes of response to roads and traffic across Waterton and Livingstone herds given the differences in traffic volume, habituation to humans, and hunting regulations across their ranges. Waterton animals are habituated to high traffic and tourism and face no hunting pressure within the boundary of the park. Rogala et al. (2011) demonstrated in Banff National Park (380 km north of Waterton Lakes, with even higher levels of tourism), that areas adjacent to trails and roads with low levels of human activity are concurrently used by elk in the area. Conversely, in populations facing hunting pressure roads and high traffic have been shown to reduce use of areas adjacent to roads (Rowland et al. 2000). East of the Livingstone Range, animals encounter many small roads with low traffic and are hunted by private land owners and any hunter to whom the landowner has granted access, generally on foot. West of the Livingstone range is public land and animals face far more hunting pressure off the main forestry road. Previous research has shown that human disturbance may incite vigilance, reduce foraging efficiency and time spent foraging (Frid and Dill 2002, Ciuti et al. 2012). As such, both Traffic and DistRd were included in the global model.

Model Analysis

To evaluate the assumption that patches have higher quality than non-patches, a matched-pairs conditional logistic regression was done in Program R using the clogit function. The paired regression allowed us to compare habitat differences between patches and nonpatches stratifying across each animal and each week, thus reducing the confounding effect that time and animal might have on the overall patterns of forage selection (Breslow and Day 1980). The analysis is analogous to a paired t-test: the values for all habitat variables at each “control” (nonpatch) are subtracted from those at each “case” (patch), and standard logistic regression procedures fit a response vector excluding an intercept term (Compton et al. 2002). The coefficients are interpreted as odds ratios adjusted for the effects of stratification variables (in this case individual elk and sampling week): thus the n-unit increase of explanatory variable, β, results in an $e^{\beta n}$ increase in the odds ratio of foraging occurring at a site (Breslow and Day 1980, Compton et al. 2002). As explanatory variables in this paired logistic regression represent the difference between paired patch and non-patch locations, these models should be interpreted in terms relative differences rather than absolute differences in values of habitat variables (Compton et al. 2002).

To avoid collinearity, pairs of covariates were compared and for those with a correlation coefficient greater than 0.6 the covariate producing the lower Akaike's Information Criterion, AIC, was included in the global model run, and the other was dropped from analysis. Covariates were standardized before analysis for ease of interpretation.

To investigate the differences in patch selection across herd, sex, and season, paired conditional logistic regression models were estimated across the global dataset and 6 subsets using data from both herds, both sexes, and within the female subset, two times of year, calving and later summer. Comparison of females during the first 7 weeks of the season (late May through June) versus the last 9 weeks (July through early September) was considered to be an assessment of the effect of calving season on foraging patch selection. To demonstrate the driving factors behind elk forage selection across herd, sex, and season, regressions were estimated across each of the 7 sets, using an identical global model. Nested models were compared to identify the driving components of each subset and the most parsimonious models, i.e., with the lowest AIC, were reported. Models within 2 AIC units of the top model were model averaged.

To compare patch selection results to selection assessed at the home range scale, a resource selection function (Manly et al. 2002) was estimated using remotely sensed correlates to the covariates included in the patch model analysis: NDVI, DistRd, Ruggedness, and Canopy Cover. Used as a corollary to the herbaceous biomass parameter sampled for the patch model, peak NDVI, or the Normative Difference Vegetation Index, was used as a metric of relative forage productivity across the area. This value was calculated from MODIS satellite imagery from July 2012, the peak image of productivity in this study area (Seidel and Boyce 2014b). DistRd was calculated from the global road model as a metric of human disturbance on the range (Northrup et al. 2012). Ruggedness, calculated from a digital elevation model for the region, is highly correlated with the slope parameter included in patch models to estimate the influence of terrain on habitat selection. Canopy Cover, a corollary for the Cover covariate used in the patch model, was calculated from a 2005 map created by the Foothills Research Institute (McDermid et al. 2009). The map includes data on land cover and crown closure, as well as species composition, and agricultural and regeneration masks at a 30m resolution using LandSat technology. Daytime code was included in the analysis to account for autocorrelation of GPS relocations and to account for individual variation. ElkID was included as a random effect. This RSF model was estimated using relocation data from animals within the Livingstone and Waterton herds during June through August of 2007-2012. Data from 8 individuals in the Waterton herd and 12 animals across the Livingstone Range were included in the RSF analysis. These data include but are not limited to the data used for identification of patches and non-patches in the previous analysis. For animals within a single herd, availability was considered constant and available points pulled randomly from within a 95% kernel representation of herd ranges calculated using the kernel density tool in ArcGIS with a search radius of 5 km. To compare selection estimated using the RSF with the estimates of patch selection, we used the cor.test function in R.

Finally, to visualize the distribution of foraging patches within individual home ranges, adaptive kernels were estimated using all summer telemetry relocations (i.e. those collected June-August 2012) from the 12 elk sampled for this study. Using the kde function in the Geospatial Modelling Environment (GME) software and least-squares cross validation bandwidth estimation, kernel density estimation was used to demonstrate range-use patterns and a home-range estimate for each individual animal (Worton 1989). The season's patches (as identified by SatScan) were overlain on these home range estimates to illustrate the distribution of foraging patches throughout the home range and how they contribute to the underlying UD structure (Figure 2.5).

Results

Field Sampling and Ratio Estimation

In total, vegetation was sampled at 209 sites over 16 weeks; forage biomass data were collected at 178 sites. Field collection was done at an average of 6.5 site pairs per week. Of the pairs sampled for biomass, 58 and 31 site pairs were visited by cow and bull elk respectively. Waterton males consistently ranged in areas easily accessed for downloads and therefore were sampled more frequently than other groups. Consequently, of the 31 site pairs sampled for bull elk, only 29% were within the Livingston Range. Sampling of sites visited by cows was more even between the two groups with 55% of female cluster pairs sampled in the Livingstone range; 45% in Waterton.

Regression Analyses

Seven variables were included in the global model: HerbBiom, SPC, Forest, Slope, Aspect, Traffic, and DistRd. Across all best model sets HerbBiom and Forest were the most frequently included covariates after AIC model selection (Table 2.4). HerbBiom was included in the top models for 5 of 7 model sets; in all cases we observed that elk foraged more in patches with greater herbaceous biomass than the nonpatch sites. Forest was included in 6 of the top models but its impact differed between sexes: patches selected for foraging by cows had more forest cover than their nonpatches but bull elk selected patches in more open cover types than their nonpatches. Road parameters were included in top models for all but the Calving model set. Vehicular traffic reduced foraging likelihood in 4 top models, and DistRd was included in 5 top patch models indicating reduced likelihood of patch occurrence with increased proximity to roads except in the Livingstone model.

From analysis of the entire data set, three models were reported with AICs within two units of the top model and their coefficients were model-averaged. Analysis of Waterton sites resulted in three top models, and two top models resulted from analysis of Livingstone patches. Four models within two AIC units of the top model resulted from analysis of cow data, and two from the bull subset. From the within-season subsets, three top models were reported from the summer subset and two models from calving data. Top models within each data subset were model-averaged. Top models for each data subset are reported in Table 2.4. See Table 2.5 for model-averaged coefficients.

Model-averaged coefficients for the top models across the entire dataset suggest that elk select patches in areas with low traffic, high forest cover, steeper slopes, and high herbaceous biomass. Coefficients indicating an effect of shrub percent cover and distance from roads also were estimated but large standard errors reduced our confidence in their importance (Table 2.5). The coefficient with the largest magnitude was Traffic, however, the standard error was also highest (0.88) relative to its coefficient estimate (-1.05) lessening confidence in the estimate and effect. HerbBiom and Forest had the most robust coefficients when standard error was considered and thus likely have the greatest effect on patch selection.

Patch selection across Livingstone animals was best characterized by high levels of herbaceous biomass and steeper slopes. Notably, the averaged Livingstone model reported a negative coefficient estimate for the DistRd parameter nearly 14 times greater than the next largest estimate across all average models, indicating that Livingstone animals increased patch selection nearer to roads. Standard error on the estimate was also large, thus the negative effect is likely small or inestimable from our data. The odds ratio of the herbaceous biomass parameter was larger in the Livingstone model than the global model, anticipating a 97% increase in odds of patch selection across a standard deviation increase in herbaceous biomass, but reported higher standard error. In Waterton, patches were defined primarily by increased forest cover and increased distance from roads. A negative traffic and a positive shrub percent cover coefficient were included in the final averaged model for Waterton patch selection.

The model-averaged coefficients for bull elk indicated that decreased cover, steeper slopes, higher levels of shrub presence and greater distance from roads increased patch likelihood. This was also the only top model set that included Aspect but the standard error was greater than the estimate itself. The cover coefficient in the top model for bull elk, $\beta = -1.23$, indicates that the patches in which bulls foraged had lower cover than the nonpatches that they passed through. Coefficients for slope and shrub percent cover were the most robust estimates in the top model for bull elk. Patch selection by cow elk was best supported by a model including increased cover and greater biomass, echoed again in the top models for calving and summer seasons for cow elk. The model-averaged model for cow elk patch selection also included increased slope, increased proximity to roads, and reduced traffic. During calving, the model-averaged coefficients included only selection for herbaceous biomass. Later in summer, cow elk selected for cover, herbaceous biomass, and reduced traffic.

With the RSF for Waterton animals, the most important predictor was Ruggedness, seconded by CanopyCover, DistRd and lastly NDVI (Table 2.6). Animals within the Waterton herd were attracted to cover and areas further from roads, but avoid rugged terrain and areas with high NDVI values, an index for productivity. Across Livingstone, model results suggest animals select strongly for areas with higher levels of productivity. In fact, NDVI, was the model most important predictor as ranked by z-score. Livingstone animals tended to select for productive sites further from roads, and avoid dense canopy cover and rugged terrain.

Calculating the correlation between the relative probability of selection at a patch given by an RSF and the relative probability of being selected as a patch given our conditional patch models is a means to test agreement in predicted value of pixels between two differently scaled analyses. Using the model-average coefficients from entire patch dataset (the "pooled" model, Table 2.5), we calculated the predicted value of each patch location. Predicted selection values for each patch were also calculated using model-averaged coefficients from each herd subset. Using the coefficients from the RSF outputs for respective herds, we calculated the predicted selection value at each patch location. As opposed to the data used within the patch models that were already collected at a scale to characterize the value of an entire patch, at the herd scale, selection values within the extent of each patch had to be averaged to assign a selection value. Adapting the minimum cell size of its inputs, the habitat selection layers created from our RSFs had a resolution of 30m2 .To characterize selection value of a patch from these layers an average of all pixel values within each patch was calculated. Correlation between predicted site values from the "pooled" patch model and the Waterton RSF model was 0.306 (n=46, P =0.034). When the predicted selection was calculated using coefficients from the patch model assessed from solely Waterton animals, the correlation with predicted RSF value increased to 0.715 (n=46, P <0.001). Correlation between predicted site values from the "pooled" patch model and the Livingstone RSF model was 0.178 (n=39, P = 0.267). Using the Livingstone patch model, the correlation with predicted RSF value was -0.553 (n=39, P < 0.001). This result was highly sensitive to the inflated DistRd coefficient within the Livingstone model (Table 2.5); without it, correlation between the models was 0.266 (n=39, P = 0.093).

Kernel density estimates (kde) of home range for 12 elk are presented in Figure 2.5. Tested against alternative bandwidth estimators in the GME software, the least-squares cross validation bandwidth estimator provided the most biologically relevant representation of our data and was used to estimate an optimized bandwidth in each kde. Darkness represents high density of use and 95% isopleths are presented to demonstrate a general boundary to each home range. In 7 out of 12 home ranges, multimodal use pattern is evident with multiple dark patches appearing within the extent of non-circular home range boundary. Utilization distributions (UDs) created for bull elk E178, E175, & E179, display more centralized activity which may be a result of their smaller ranges and concentration in available forested habitat (Table 2.1 and Table 2.2). Relative to habitats that Waterton bulls frequented for the majority of the summer, habitats used by Waterton cows and Livingstone animals were apparently more heterogeneous. E176, a cow elk, appears to have centralized use and a unimodal home range however no data for this animal nor E178 were collected for the latter half of the season due to data download issues. The spatial distribution of foraging patches overlain on the individual UD's appears visually to be well correlated with the density of use as indicated by increasing darkness in the figures. Identified foraging patches occur throughout the UDs, dispersed even where the smoothing depicts a unimodal home range. Varied patch use is occurring amongst this fine scale patch structure, even when lost to the smoothing inherent in UDs.

Discussion

Van Moorter et al.'s (2009) model offers promise for explaining home range formation. Evaluation of assumptions put forth here is a crucial step towards validation of a model that may have profound impacts on how we understand the movement strategies and space use of the world's large-bodied ungulates. Using field sampling and a matched-pairs design to compare used patches and unused areas of the home range, we evaluated foraging-patch selection and underlying assumptions of a theoretical home-range model. Our statistical results demonstrate clearly that forage availability alone does not define the value of a foraging patch for elk. Generally, our analyses demonstrated that elk select foraging patches with higher forage biomass, greater forest cover, and lower traffic on nearby roads. Presumably these characteristics offer protection from predators and human disturbance, and may allow for reduced vigilance and more efficient foraging (Altendorf et al. 2001, Frid and Dill 2002). Sex, habitat availability, and time of year also influenced selection criteria, illuminating the complexity of foraging decisions within the home range.

Patch Quality

Van Moorter et al.'s (2009) model for home range assumes that foraging patches have higher value than other areas of the animal's home range, but Van Moorter et al. do not offer details on what biological and environmental covariates might define this value. Van Moorter et al. imply that available forage alone drives utility of a patch. Explored by our study, we found the predicted pattern to be true, i.e., available forage is a driving factor in foraging-patch selection by elk, especially in the Livingstone and cow datasets. Herbaceous biomass and shrub percent cover, both directly measuring forage biomass, appeared in all top models. In all cases, coefficients were positive indicating that increased biomass increased the likelihood of patch selection. Notably, our top model for the calving period was predominately driven by attraction to herbaceous biomass supporting current theory that higher biological demands of this time can change the selective behaviours of mothers, resulting in selection for highly nutritious and digestible forage (Gedir and Hudson 2000).

Our results show that biomass is not the only driver of forage selection and subsequent patch value. Slope, Forest, and Traffic also were included in the top model for all data points. Attraction to areas of steep slope was supported in 5 out of 7 model sets and might be ascribed to predator avoidance behaviours (as in Frair et al. 2005) or, in the presence of cattle in Livingstone, necessary habitat segregation to locate available forage not consumed by cattle that predominately range in lower elevation and less-rugged terrain (Muhly et al. 2010). In the top model for all data point and the top models for Waterton, cow, and summer subsets, elk demonstrated selection for increased forest cover at foraging sites. Absent the threat of predation, habitat selection in deer is driven largely by forage abundance (Massé and Côté 2009), and leads to selection of open areas where herbaceous forage is often the most productive and abundant. For prey in the presence of predators, however, open areas also might be burdened by risk, resulting in a common trade-off between access to quality forage and risk of predation (Verdolin 2006). Forest cover offers reduced visibility from predators and could allow ungulates to reduce their vigilance (Altendorf et al. 2001). Our metric for forest cover, % patch within forest, might be confounded by the existence and use of edges by elk, which offer a balance between security of cover and the productivity of open habitat attractive to many ungulates (Tufto et al. 1996). In future work, more specific metrics indicating visibility or distance to open/forest edge could help tease apart the attraction to cover for foraging.

Opposed to the selection for increased forest cover seen in the cow data, greater openness was found to define the difference between patches and nonpatches for bulls. Clutton-Brock's work anticipated forage differences between sexes of red deer but predicts quite the opposite result: red deer stags were found to forage in lower-quality habitat than hinds.   His, now disproven, theory supported indirect “scramble” competition between sexes pressuring the stags into lower-quality habitat (Clutton-Brock and Guinness 1982, Conradt et al. 1999). Females tend to forage more selectively than males; indeed, across species with significant (>20%) size dimorphism, the Jarmin-Bell theory suggests that males can support diets of higher fiber and may thus be more adaptable to lower-quality diets (duToit 2005). The higher energetic needs of bulls may incentivize browsing in areas where forage is more available but lower quality – like the dense stands of Amelanchier, Symphoricarpos, and Populus shrubs that Waterton males used late in the study period. On the home-range scale, there might be support for these dynamics in our study because Waterton bulls increasingly selected forest cover over the season while cows maintained larger more-diverse home ranges (Table 2.2). At the fine scale, the apparent contrast in patch selection between bulls and cows is likely a reflection of difference in habitat availability rather than a genuine difference in selection. Selecting for more-open foraging sites within a dense forest likely reflects a selection for areas containing higher-quality, more-productive forage, a behaviour we would expect (Rumble and Gamo 2011).

Beyond variables influencing foraging patches, human disturbance can influence fine-scale foraging decisions and, in cases of high disturbance, may overwhelm the importance of site-specific vegetation characteristics. Roads and associated traffic represent a disturbance pervasive over much of elk habitat. In Waterton Lakes National Park, where traffic was highest, HerbBiom was not included in the top model. Instead patch selection by the Waterton herd was driven predominately by attraction to cover and areas further from roads. Based on predictions of a traffic model for our study area (Northrup 2012), the main road entering Waterton Lakes National Park experiences 27 times the number of cars per hour during a summer day than the North Burmis Road bisecting a majority of the elk activity east of the Livingstone Range. In context of Rogala et al.’s (2011) work demonstrating elk use of areas adjacent to human activity within a national park, 54 cars per hour is significantly past their identified threshold of two people per hour reported to deter elk use of areas surrounding trails. Additional research has shown that elk may avoid roads due to increased risk of mortality caused by vehicles or hunters (Cole et al. 1997, McCorquodale et al. 2003),but the effect of roads is often muddled by attraction to the increased biomass, openness, and edge environment associated with roads. These conflicting risks and values of roads may reflect why related parameters in our analyses were supported in only some top models. Ciuti et al. (2012) showed that high levels of traffic provoke vigilance behaviour in elk and disrupt active foraging. Our results demonstrate that traffic and road disturbance also can affect animal decisions about where to forage, at least in populations with the highest disturbance levels. What may seem to be an outlier, the DistRd coefficient for Livingstone models likely demonstrates a landscape saturated with mostly small low-use roads. Additionally, in the western range, terrain along the Forestry Trunk Road north of Coleman, Alberta restricts available foraging areas to those in close proximity to roads. These factors may do more to influence a large negative coefficient for DistRd than does a genuine attraction to human disturbance in the form of roads. Similar to the sex differences in Cover, these results depict the importance of availability in understanding selection especially of an environmental covariate with conflicting risks and rewards for foragers.

Comparison of scale

When interpreting the results of a resource selection function, availability is a central consideration. This is also true within our analysis. Assessing availability at different scales, Boyce et al. (2003) used multiple RSFs to demonstrate sensitivity of habitat selection metrics to scale and remind us of the dynamic nature of selection in space and time. Creating an "available" set from animal relocations not within foraging patches, therefore used but not for foraging, we have produced a highly restricted RSF asking what elk are selecting while foraging rather than where or what are elk selecting overall. An unrestricted RSF using all relocations from an animal does not differentiate between two used areas, even when used in different ways. What is more, when using all relocations within a herds range as we did, an RSF reflects the probability of selecting a resource unit given the use patterns and habitat availability across the extent of that range. At a much finer scale, our patch model reflects habitat contrast between two used sites, individual patch and nonpatch pairs (i.e., comparisons of a maximum area of 141,300 m^2, given patches with a 300m diameter). Correlation between the predicted selection values of patches calculated using both scale analyses was positive ($r = 0.178$, $n=39$, $P = 0.267$, and $r = 0.306$, $n=46$, $P = 0.034$) and improved when estimated between Waterton specific patch and RSF models (0.715, $n=46$, $P < .001$, Table 2.6; Figure 2.4). Notably the correlations were significant only when patch likelihood values were calculated using coefficients from the top model from each herd subset, not the top model coefficients from analysis of all patches, which seems reasonable given that the distribution of availables was quite different between the two areas (see Table 2.1 & Figure 2.2). Even with low correlation, estimated coefficients demonstrated similar direction and relative strength across both analyses with the exception of the DistRd covariate across Livingstone models. For instance, at the herd-scale Waterton animals select denser canopy cover and Livingstone animals seek less canopy cover, similar to top models reported by our analysis. Within the RSF, Livingstone animals are only nominally influenced by distance to road but Waterton animals are sensitive to a much higher degree. Productivity of biomass, as measured by peak NDVI, was a positive selective coefficient in Livingstone whereas in Waterton, higher levels of productivity seemed to marginally detract from selection reflecting the inclusion and exclusion of HerbBiom in respective top herd models.

Central differences between temporal and spatial scales of the analysis explain the reduced correlation between model predictions. Availability within the large-scale RSF models was assumed to remain constant across all animals within a herd and across all 5 years of relocations. Patch/nonpatch models were interpreted at the scale of a single growing season and result from a series of within week comparisons, restricting the temporal variability and noise drastically. Furthermore, available points are limited to the movement path of the animal within a week rather than the entire spatial area of a seasonal home range as in the RSF model. These restrictions were useful for clarifying fine-scale foraging decisions but for prediction or extrapolation, our herd-scale models are more powerful inherently because these incorporate sites of greater contrast (used and available versus the comparison of two differently used sites), more animals, and a larger spatial extent. Additionally, at the larger scale there is greater variance over which the RSF is calculated (Boyce et al. 2003). These scale differences and the alternative natures of these analyses change interpretation of the models as well. Our RSFs assess relative probabilities of selection across the extent of each herd on a 5-year interval whereas the conditional approach is intended to highlight habitat contrasts between foraging patches and otherwise used areas within a single growing season. The patch-scale analysis indeed only identifies the selection of patches by individuals whereas the herd-level RSF model yields selection of the landscape being used as well as the patch within that landscape.

Figure 2.5 is a visual representation of the season's identified patches within individual home ranges. Displaying our identified foraging patches across adaptive kernels that represent the seasonal home range and smoothed use patterns of individual elk is a strong visualization of Van Moorter et al.'s model in action. Across the majority of animals, separate use areas or hot spots are evident, with the density of identified patches strongly correlated with intensity of use over the season exactly as conceptualized by Van Moorter et al. This correlation between densities of patches and densities of use suggest visually that the locations of successful foraging patches may be important factors determining size and shape of home ranges, echoing the central hypothesis of Van Moorter et al.'s model. For those animals where the home range appears to show a single central place, instead of the multiple loci pattern (e.g. E176, E175, E178, E179), the home range may be too homogenous or confined an area to see the underlying patterns of patch use. For the Waterton males, E175 and E179, this concentration of use is the result of underlying habitat availability and their more limited home range size (as shown in Table 2.1 & Table 2.2). These animals are still moving between different patches and areas of the home range, just within a smaller area over the summer season. In other words, varied patch use is occurring within this area, but is visually lost due to the sheer density of points within the constrained area, and the smoothing inherent to the kernel analysis. The patterns displayed by E176 and E178 are limited by data: no relocations were downloaded after June 2012 and full use within their summer range could not be captured within this shortened period. Despite individual variation, this visualization of patches across existing home ranges is an important presentation of support for the use patterns and movements predicted by Van Moorter et al.'s theory.

Conclusions

In evaluation of the first assumption we have clearly demonstrated that elk forage in discrete patches and we have offered a novel method for identifying discrete patches in grazers. Furthermore we established that patches are selected for their higher value as compared to nearby use areas. This value is indeed dynamically defined by external environmental factors including human disturbance, and can be influenced by sex, habitat availability, and season. Our work supports Van Moorter et al.'s (2009) second assumption that patches have higher utility than the surrounding matrix while also demonstrating greater complexity of variables defining the value of foraging patches for elk.

The third assumption of the Van Moorter et al. (2009) model is that foragers remember successful patches. Van Moorter et al.'s model includes both long-term and short-term memory, over a time scale of a growing season. Long-term memory includes recollection of successful patches across the home range. Van Moorter et al.'s short-term memory keeps animals from backtracking over patches recently depleted. Across numerous ungulate species, site fidelity and philopatric behaviours have been demonstrated repeatedly. Across years, migratory elk return to same natal or established seasonal ranges using the same migratory routes (Boyce 1991), which demonstrates the potential for long-term recollection in space. These multiyear return migrations exhibit the same processes that presumably are used to remember successful patches at a shorter time scale. Recent work has even shown reuse and recursive behaviour in large ungulates across shorter time scales such as season (Conradt et al. 2001, Bar-David et al. 2009, Wolf et al. 2009). Seidel and Boyce (2014b) demonstrate returns to patches identified in the study area occur an average of 9 to 23 days apart, dependent on individual variability. These results suggest that animals are not immediately backtracking on nor interminably camped at patches, and thus the existence of some mechanism delaying reuse of patches. Well-designed experiments are needed to establish the existence of short-term memory as Van Moorter et al. suggest, however, the philopatric life history patterns well established in ungulates, makes the existence of complex cognitive processes such as short term memory more than plausible.

Finally, although we demonstrated that biomass was central to patch value, due to the scale of our analysis, we did not examine the replenishment and depletion dynamics that are central to Van Moorter et al.'s fourth central assumption. Optimal foraging theory which underlies this assumption has been evaluated in ungulates repeatedly and at smaller scales, previous foraging literature already provides rigorous examples of the Marginal Value Theorem (MVT) driving patch use. For example, Jiang and Hudson (Jiang and Hudson 1993) confirmed predictions of the MVT in penned elk, observing that elk gave up a foraging patch when the cropping rate dropped below the seasonal expectation, staying longer when growing conditions were less favourable. Although replenishment rates were not evaluated in the study, Seidel and Boyce (2014b) demonstrate additional support for replenishment/depletion mechanism. Individual elk returned to known foraging patches after an average of 1-3 weeks (a reasonable time to allow regrowth, Jiang and Hudson 1993) and return more frequently to those patches with higher relative productivity. Results demonstrating that increased biomass and productivity positively affect selection and movement in grazing species (Bergman et al. 2001, Hebblewhite et al. 2008) and offer further support that these processes play an important role in elk foraging selection and ultimately home range development.

Mechanistic models can help us understand why and predict where home ranges might develop in novel or changing environments based on the available landscape. Our results demonstrate strong initial support for the Van Moorter et al. (2009) model in two populations of elk, a large bodied ungulate. Further validation of this model for elk and similar ungulates could have broad implications for the management of these species in a rapidly changing environment. Ungulates are widespread, economically valuable species with enormous impact on the distribution of forage; anticipation of their response to land-use change, changing climates, and natural or human disturbance may be integral to anticipating local and distributional range shifts in the short and long term.

Chapter 2 Tables and Figures

		Use (% of relocations)	**Availability (% of cells)**				
	n	**Open***	**Forest**	**Open**	**Forest**	**total cells**	**Cars/hr**
Waterton	**6**	21.5	78.5	32.0	68.0	75202	.06-54.85 (μ= 14.22)
Bull	3	9.9	90.1				
Cow	3	24.8	75.2				
Livingstone	**7**	65.5	34.6	45.8	54.2	602113	.07-260** (μ=4.46)
Bull	2	68.1	31.9				
Cow	5	65.1	34.9				
East Livingstone	4	69.9	30.1	75.6	24.4	275138	.07-260**
West Livingstone	3	51.5	48.5	20.7	79.3	326975	.08-10.79

* Open is defined as <15% canopy cover

**Hwy 3 is a semi-impermeable boundary at the southern end of the range with a rate of weekday traffic at 260 cars per hour

Table 2.1. Availability and use of forest cover & traffic across herds, sex, and range for May 17, 2012 – September 3, 2012. Availability represents the percentage of cells within each summer home range extent (as calculated from MCPs) and use is calculated from values at elk relocations. This table demonstrates the variation in availability across herds and the selection differences across sexes, habitats and herds. Waterton animals have less strictly open habitat than Livingstone animals and it is used far less, particularly by bull elk. The differences in habitat on either side of the Livingstone Range are very apparent: availability figures for open and forested habitat are nearly inverses of each other on either side. On the much more forested west side, the selection for open habitat seems to be even more pronounced. Notably a very conservative 15% canopy cover has been chosen for the differentiation of open versus forested cells, but this pattern is consistent using a wide margin of thresholds. The range and mean of traffic values, number of cars per hours on a weekday day, were provided for each herd to demonstrate differences in traffic levels affecting elk in different locations across the study area.

	May	June	July	August
% MCP with ≥15% canopy cover				
Bulls	71.0	91.0	95.7	95.9
Cows	56.7	56.9	56.7	61.0
Area MCP (Bull) (km^2)	56.61	28.98	15.30	11.40
Area MCP (Cow) (km^2)	46.36	46.98	46.35	39.71

Table 2.2. Temporal changes in Waterton home range sizes and available canopy coverage. Minimum Convex Polygons (MCPs) are considered a general metric for size of a home range. Above, percentages of open area within Waterton elk home ranges are reported. In cow elk, use of cover and size of home range remains consistent over the summer months while bull elk transition into nearly complete use of covered areas and especially restricted home ranges.

Patch Radius		**Homogeneity (1 most homogenous, 3 most heterogeneous)**		
	Transect Length	**1**	**2**	**3**
101-150 m	50m	24 plots	32 plots	40 plots
51-100 m	25m	16 plots	24 plots	32 plots
0-50 m	15m	12 plots	16 plots	24 plots

Table 2.3. Sampling Protocol. When approaching a novel patch or nonpatch for sampling, homogeneity of the patch species composition was assessed as a means of streamlining the time-intensive sampling process. Number of quadrats sampled at a site was determined by relative heterogeneity on a 1-3 scale and quadrats were laid, evenly spaced, along 4 transects whose length was determined by the radius of site. Heterogeneity of the patch was determined visually to be between 1, mostly homogeneous (fewer than 5 species in a sample quadrat), and 3, highly heterogeneous (greater than 10 species in a sample quadrat). This rudimentary scale was intended to maximize sampling efficiency by adjusting the number of quadrats sampled based on heterogeneity of the plot: those patches with greater diversity required more quadrats sampled than extremely homogenous patches.

Model Sets (n pairs)	Top Models	AIC	w_i
Pooled (89)	~ **HerbBiom** + **Forest** + Traffic + **Slope**	117.545	0.424
	~ **HerbBiom** + **Forest** + Traffic + **Slope** + **DistRd**	118.178	0.309
	~ **HerbBiom** + **Forest** + Traffic + **Slope** + **DistRd** + **SPC**	119.100	0.195
Waterton (48)	~ **Forest** + **DistRd**	60.714	0.302
	~ **Forest** + Traffic + **DistRd**	60.889	0.277
	~ **Forest** + Traffic + **DistRd** + **SPC**	61.268	0.229
Livingstone (41)	~ **HerbBiom** + **Slope**	53.216	0.456
	~ **HerbBiom** + **Traffic** + **Slope**	54.016	0.306
Bull (31)	~ Forest + **Slope** + **DistRd** + **SPC**	41.096	0.501
	~ Forest + **Slope** + **DistRd** + **SPC** + **Aspect**	42.043	0.312
Cow (58)	~ **HerbBiom** + **Forest**	74.213	0.310
	~ **HerbBiom** + **Forest** + Traffic	74.620	0.253
	~ **HerbBiom** + **Forest** + Traffic + **Slope**	74.858	0.225
	~ **HerbBiom** + **Forest** + Traffic + **Slope** + **DistRd**	75.672	0.142
Summer (42)	~ **Forest**	54.144	0.359
	~ **Forest** + **HerbBiom**	55.115	0.221
	~ **Forest** + **HerbBiom** + Traffic	55.584	0.175
Calving (16)	~ **HerbBiom**	20.501	0.529
	~ **HerbBiom** + **Slope**	21.850	0.270

Table 2.4. Top reported models across all data subsets ranked by Akaike Information Criterion (AIC). For the pooled dataset and each of the 6 subsets, top models are reported. Models within 2 ΔAIC units of the best model were considered non-differentiable and reported along with AICs and Akaike weights (w_i). Positive coefficients are reported in bold.

	Pooled	**Livingstone**	**Waterton**	**Bulls**	**Cows**	**Calving**	**Summer**
Covariate							
Forest	0.367		0.999	-1.227	0.531		0.617
	(0.208)		(0.509)	(0.905)	(0.228)		(0.272)
HerbBiom	0.695	0.969			0.807	1.172	0.560
	(0.342)	(0.554)			(0.463)	(0.869)	(0.545)
Slope	0.582	0.697		1.667	0.534	0.507	
	(0.327)	(0.383)		(0.784)	(0.409)	(0.643)	
DistRd	0.383	- 16.736	0.693	1.215	0.489		
	(0.333)	(15.720)	(0.446)	(0.835)	(0.476)		
Traffic	-1.046		-1.042		-1.075		-0.991
	(0.878)		(0.990)		(0.928)		(0.925)
SPC	0.195		0.301	0.839			
	(0.189)		(0.242)	(0.478)			
Aspect				.500			
				(.501)			

Table 2.5. Model-averaged coefficients and standard errors for all data subsets. Presented above are the model-averaged coefficients for all data subsets. Standard errors are presented in parentheses below the average coefficient estimates for each included covariate.

Resource Selection Model (RSF)	**Waterton**		**Livingstone**	
	Coefficient	z value	Coefficient	z value
NDVI	-2.56E-05	-1.59	6.22E-04	41.56
Ruggedness	-1.00E-01	-32.36	-8.09E-03	-8.32
Distance to Road	3.26E-04	14.31	1.70E-04	10.51
Canopy Cover	9.17E-03	16.86	-9.40E-03	-24.3
Correlation between RSF and Pooled Model	0.306	n= 46, P= 0.034	0.178	n=39, P=0.267
Correlation between RSF and Herd Model	0.715	n=46, P<0.001	-0.553*	n=39, P<0.001

*When *DistRd* not included, correlation between Livingston RSF value and Livingstone Patch Model is 0.266 (n=39, P=0.093)

Table 2.6. Patch Model and Resource Selection Function Correlation. A RSF model was calculated using remotely sensed correlates to top model covariates included in the patch model analysis for the pooled dataset. Availability within the RSF was assumed to be the same for animals within a single herd but was calculated separately for Livingstone and Waterton animals. Directions of coefficients were the same in both RSF and Patch model outputs across herds, excluding the *DistRd* coefficient in the patch model for Livingstone animals. Correlation between selection value at patches as assessed by the RSF model and the top pooled and herd models are reported.

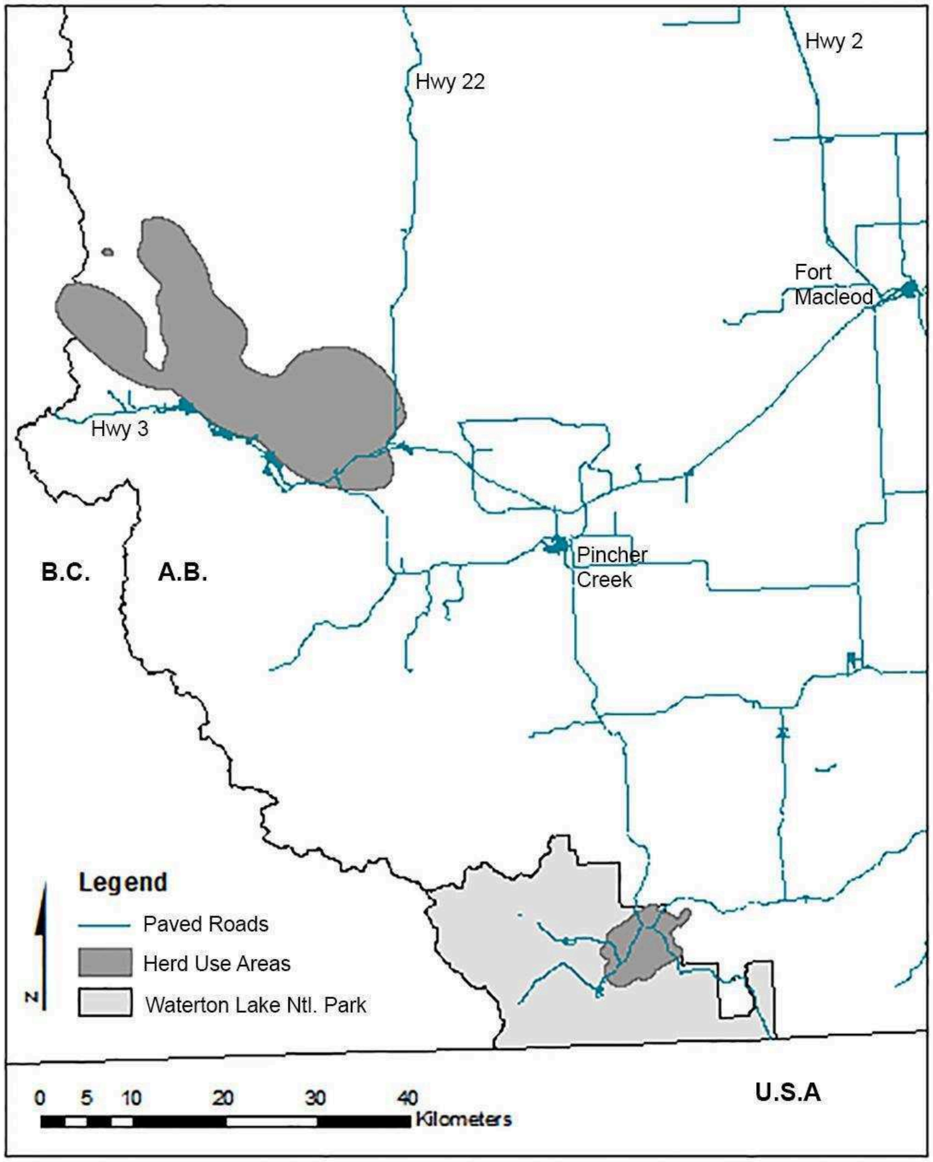

Figure 2.1. Study Area. Animals were sampled from two herds in southwestern Alberta: the Livingstone herd to the north and the Waterton herd to the south. Waterton animals were sampled within the park boundary marked on the map and typical elk use over the summer season is depicted by dark gray polygons. Notice that Livingstone animals cover a substantially larger area than the concentrated use seen in Waterton.

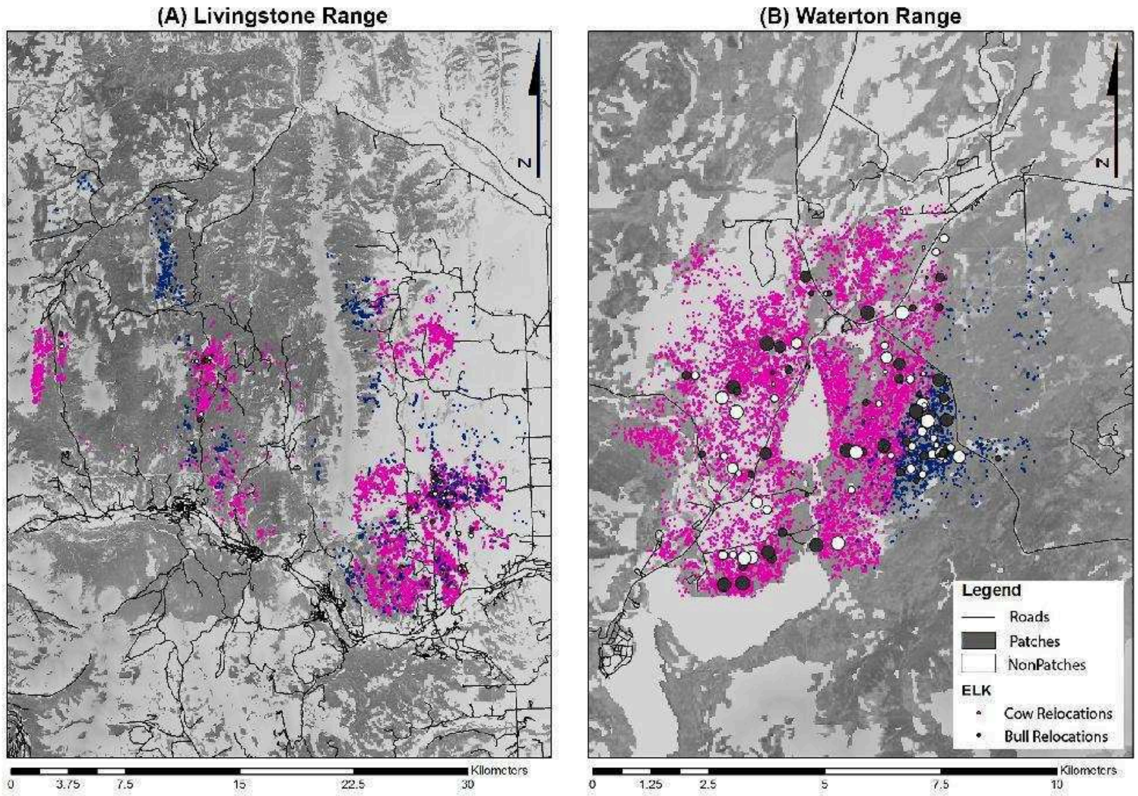

Figure 2.2. Distribution of patches, nonpatches, and GPS relocations displayed against Canopy Closure in the Livingston (A) and Waterton (B) ranges.

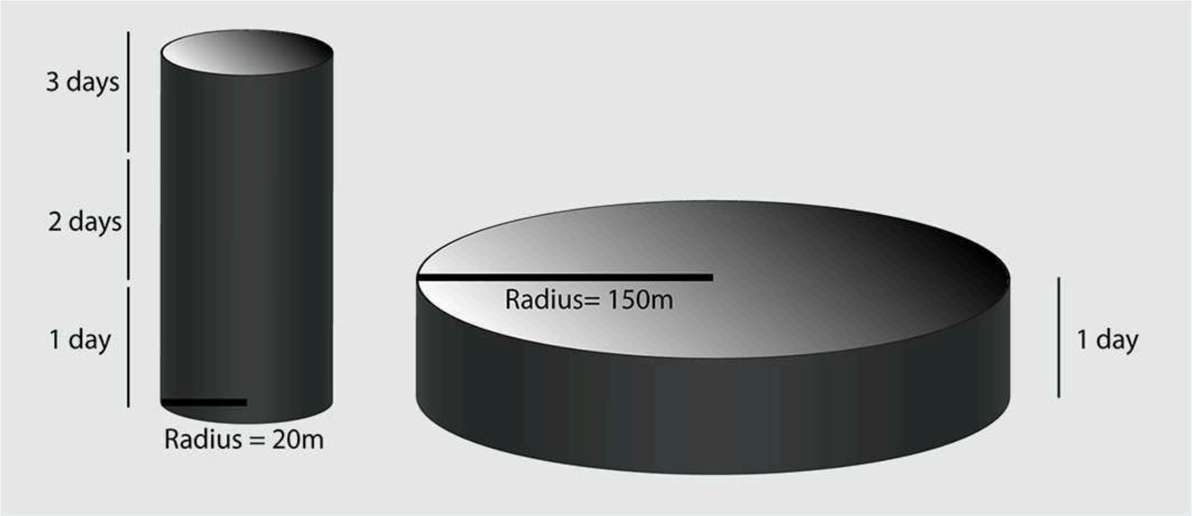

Figure 2.3. Visualization of the cylindrical clustering window. The space-time permutation scan statistic (STPSS) procedure uses a cylindrical moving window to screen for clusters within GPS relocations. The cylindrical windows can range in size both spatially and temporally: being wide and flat (over a large area but only a single day in time) or narrow and tall (a cluster over a small area but across many days) and everything in between. Here we provide a visualization of two potential cylindrical windows.

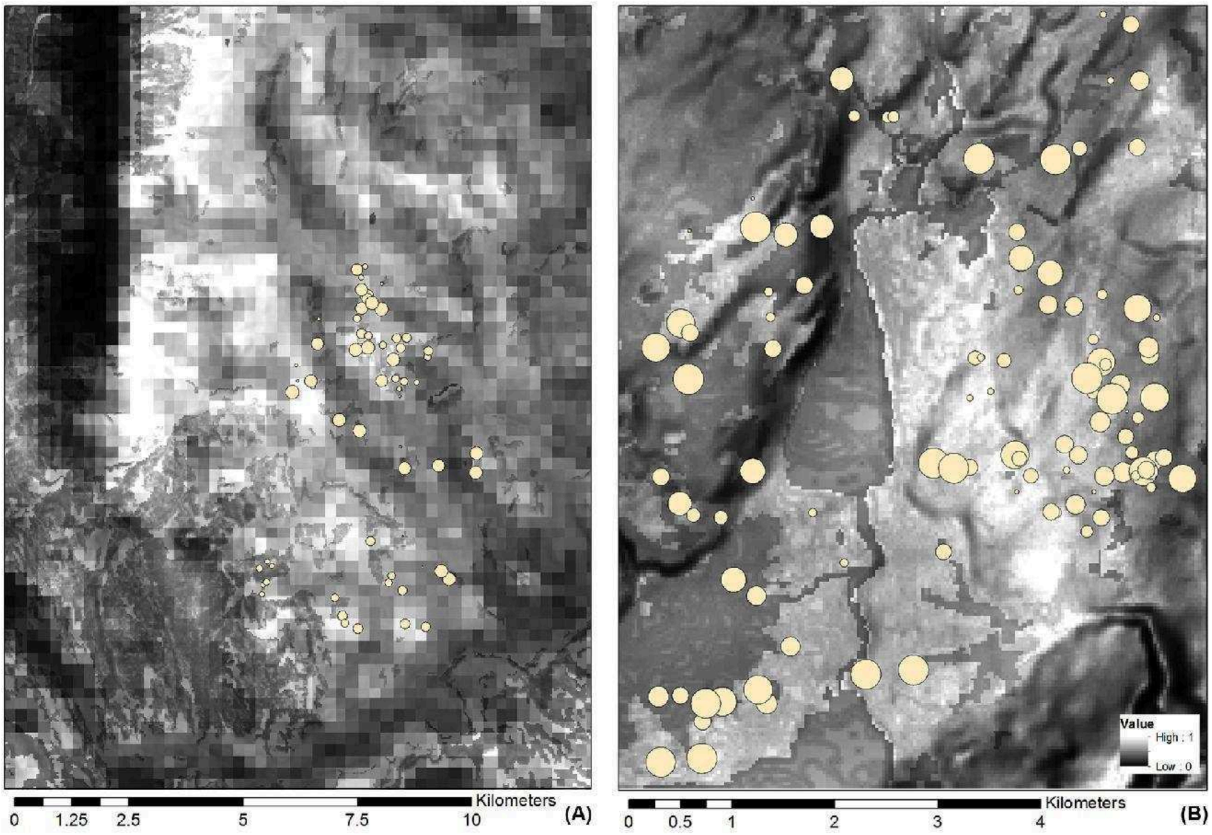

Figure 2.4. Patch distribution on RSF surfaces for Livingstone (A) and Waterton (B) herds. A resource selection surface was constructed using elk relocations from summers 2007- 2012, assuming identical availability within herds, and considering *Peak Productivity (NDVI)*, *Canopy Closure, Distance to Roads,* and *Ruggedness*. Patches identified by the STPSS procedure and sampled over the 2012 season are overlain on the RSF surface to offer a visual comparison of the two methods (clips from both ranges are presented).

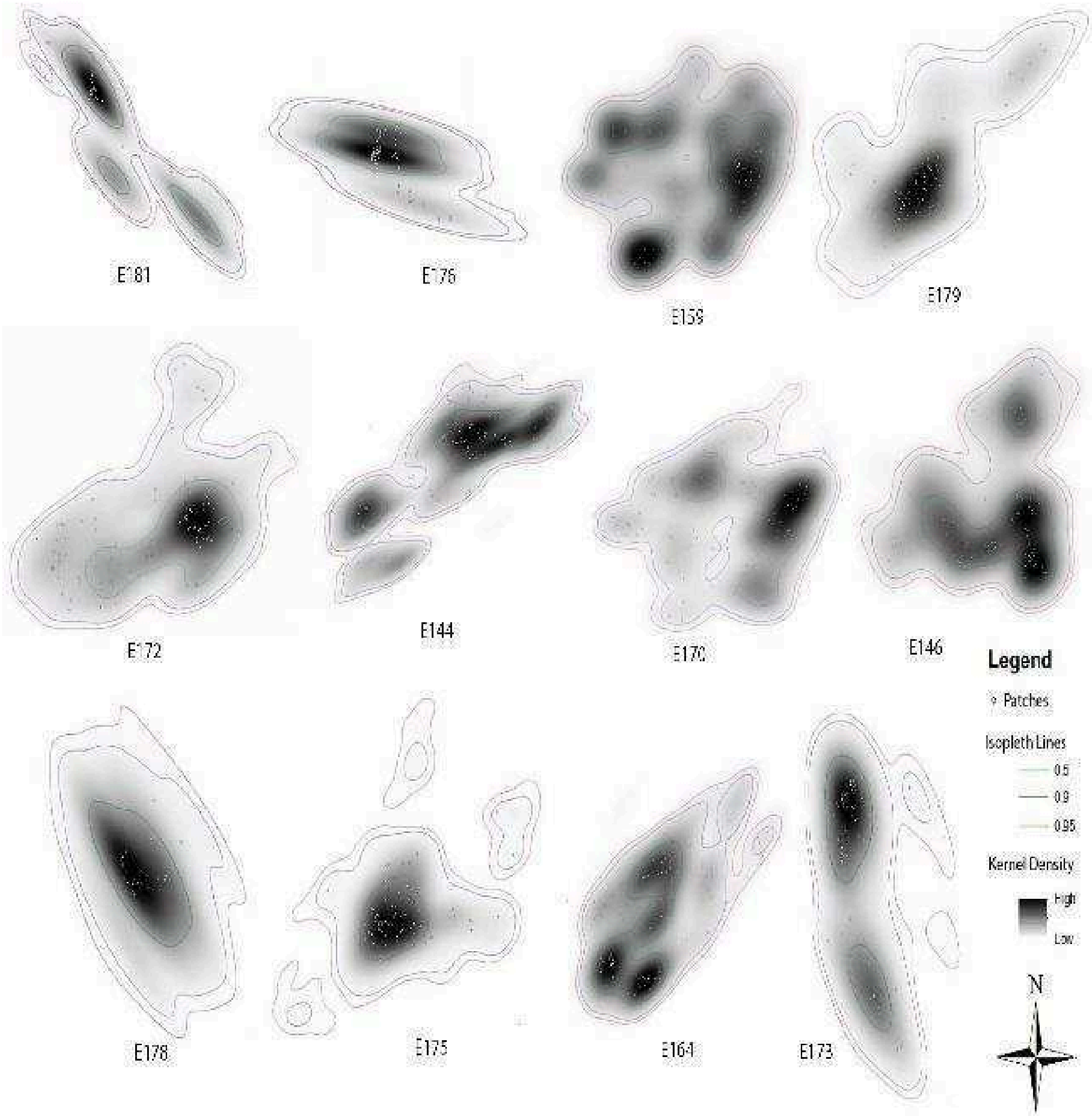

Figure 2.5: Patches distributed across kernel density estimations (KDEs) for individuals. KDEs were calculated for all 12 individuals tracked over the summer using all 2-hr relocations during the study period. Smoothing parameters were estimated using optimized bandwidths calculated using a least-squares cross validation algorithm in the Geospatial Modelling Environment. Darker tone indicates high density of relocations, or "use". Each animal's patches, calculated using SatScan across all 16 weeks of the study period, were overlaid on the home range

estimates for that individual. Patches overlap extensively with areas of high use supporting the idea that foraging patches may influence the organization of stable home ranges in elk. Importantly this also demonstrated that varied patch use and fine scale foraging structure exist even where UDs suggest unimodal or centralized use of the landscape.

Chapter 3

Patch-use dynamics by a large herbivore

Introduction

Home-range development and range-use dynamics are key components of foraging behaviour with implications for animal movement, habitat selection, and fitness (Powell 2000, Börger et al. 2006). The home range often is defined to be the area known by the animal and remembered or maintained because of its value, presumably in resources required by the animal for survival and reproduction (Powell 2000, Börger et al. 2008, Gautestad 2011). However, simulations of memory processes alone have failed to yield stable home ranges (Van Moorter et al. 2009, Gautestad and Mysterud 2010) and the biological mechanisms underlying the development and maintenance of home ranges are still missing. In response to this void, there is a growing body of literature on mechanistic home range models hypothesizing the underlying rules for movement or landscape structure that might define or result in the development of stable home ranges (see Mitchell and Powell 2004, Moorcroft and Lewis 2006, Mitchell and Powell 2007, Van Moorter et al. 2009, Nabe-Nielson et al. 2013).

Compared to traditional techniques that describe home ranges, mechanistic models are more comprehensive attempts to unveil the processes that result in home-range behaviour. Because these models are based not only on the movements of animals but upon the underlying rules for movement, they have the ability to predict an individual's spatial use, not only describe it (Moorcroft and Lewis 2006, Mitchell and Powell 2008). As such these models, when validated, are especially powerful tools for predicting responses to changes in habitat (Moorcroft and Lewis 2006, Vanderwel et al. 2012) either by human land-use change, or natural perturbations to the environment.

A model by Van Moorter et al. (2009) simulates home-range development combining the rules of optimal foraging theory and a two-part memory system. Foragers move between dynamically valued patches distributed across the landscape, removing food from a patch until depletion stimulates departure according to the marginal value theorem (Charnov 1976). Their movement is biased by the utility of surrounding patches and both short-term memory and long-term memory that prevents backtracking over depleted patches while maintaining knowledge of successful patches and allowing time for forage regrowth prior to return.

Seidel and Boyce (2014a) evaluated four formative assumptions of Van Moorter et al.'s model in two populations of elk in SW Alberta. Their work formed the first empirical support for this model but they did not investigate the predicted movement patterns or returns to foraging sites. Although directed movements between areas of resource abundance where animals linger to forage have been demonstrated (Johnson et al. 2002, Fryxell et al. 2008, Owen-Smith et al. 2010), very few studies have shown returns or recursive movement patterns in ungulate populations and none exhibit returns directly to identified foraging patches (Bar-David et al. 2009, Wolf et al. 2009). As such, our objective was to evaluate movement within home ranges according to predictions of a proposed mechanistic home range model for foragers.

We used a flexible space-time permutation scan statistic to identify and approximate the scale of discrete elk foraging patches in space and time. We first sought to establish whether and how frequently elk return to these patches. Secondly, our goal was to identify the characteristics of a patch that increased the likelihood of reuse. Connecting patch-return likelihood to attributes of these patches and surrounding landscape lays the groundwork for understanding why and how animals use various areas within their home range and allows us to evaluate the expectation that those patches that are revisited should be of higher quality than other available patches.

Methods

Study Area & Animals

Elk in this study ranged freely within the montane ecosystem of SW Alberta. The study area is characterized by steep mountainous terrain to the west, abruptly transitioning in the east to rolling grasslands and agricultural land. Seven cow elk from two herds (Waterton and Livingston) were included in these analyses. The three Waterton animals ranged within the boundaries of Waterton Lakes National Park, and were predominately associated with the Park's northwestern hills and the aspen forests and wetlands southeast of Lower Waterton Lake. Tourism to the national park during summer is a unique disturbance for animals in this herd. The four radiocollared Livingstone animals ranged on both sides of the Livingstone Range, an eastern ridge of the Rocky Mountains where they encountered timber cut blocks of varying age and dense forests of lodgepole pine (*Pinus contorta*) to the west, and rolling agricultural and range lands to the east.

Clustering

To identify patches used for foraging, a retrospective space–time permutation scan statistic (STPSS) was used to identify clusters in the relocation data for each individual elk using SaTScan® (Kulldorff et al. 2005). The scan statistic is defined by a moving cylindrical window with a base in geographic space and height defined by time. Using this method, each relocation was considered to be the centre of a possible cluster across multiple spatial windows and at each available time window (i.e., over 1 day, 2 days, or 3 days). The analysis considers all relocations within a wide range of cylinders when evaluating for clusters: considering everything from relocations within tall poles, i.e. small spatial windows but across many days, to those that might be described to occur within wide flat discs, i.e. large spatial windows during a single day (Webb et al 2008). For detailed information on the probability function underlying this clustering method, see Kulldorff et al. (2005).

Following adaptations explained by Webb et al. (2008) to use this method with GPS relocation data, we let c_{zd} = number of locations at geographic coordinate z during day d, and defined C, the total number of observed GPS elk locations, as

$$C = \sum_{z}\sum_{d} c_{zd}$$

On day d at location z the expected number of GPS locations (U) is

$$U_{zd} = \frac{1}{C}\left(\sum_{z} c_{zd}\right)\left(\sum_{d} c_{zd}\right)$$

Because each relocation point in a GPS dataset is unique, the number of GPS locations at a location z across all days sums to one and, subsequently, U_{zd} =1. Expected number of locations U_A in a cylinder A is the summation of these expectations within that cylinder:

$$U_A = \sum_{(z,d)\in A} U_{zd}$$

When there is no space–time interaction, c_A, the observed number of locations within the cylinder, is distributed according to a hypergeometric distribution with mean U_A and probability function:

$$P(c_A) = \frac{\left(\frac{\sum_{z \in A} c_{zd}}{xA}\right)\left(N - \frac{\sum_{z \in A} c_{zd}}{\sum_{d \in A} c_{zd} - c_A}\right)}{\left(\frac{c}{\sum_{d \in A} c_{zd}}\right)}$$

When both the number of geographic locations and the number of days within cylinder are small compared to C, c_A is expected to be approximately Poisson distributed with mean and variance U_A. As such, the evidence that a given cylinder contains a cluster can be measured by a Poisson Generalized Likelihood Ratio.

Elk most actively forage during crepuscular periods (Green and Bear 1990, Ager et al. 2003, Ensing et al. *in press*) thus, to help ensure that clustering could identify patches primarily used for foraging and not some other activity, e.g., grooming or bedding, data from peak hours of day and night were removed (10:00-14:00 and 22:00-2:00 hr) prior to clustering. In addition, all resulting clusters with a radius ≤ 15m were removed because these likely represent GPS error on resting or bedded animals (Frair et al. 2005). Three decision rules had to be made prior to running the scan statistic: the maximum spatial window, the maximum temporal window, and permission for geographic overlap of clusters.

Frair et al. (2005) used a first-passage time analysis, assessing how long an animal spends in an area of a given size, to identify the scales at which three separate movement processes occurred: resting, foraging, and travelling from 2-hr fix data. When foraging, female elk travelled an average of 265.7m (42.5m SD) between fixes; accounting for this previous work and given the logistical constraints of our field sampling, a maximum diameter of 300m was chosen as an upper spatial bound for analysis. The maximum number of sequential days evaluated for clusters of points, i.e., the maximum temporal window, was left broad: including up to 3 days of points. Finally, within an individual scan (over the data of one elk for a single week), no geographic overlap was allowed between reported clusters; this is a constraint imposed to ensure that we captured unique patches in space.

Counting Returns

After identifying the boundaries of foraging patches, we recorded all revisits by an elk to its known patches during the summer season. Patches were identified weekly for each animal and were aggregated from June-August 2012 for return analyses. Returns to each patch were calculated for the entire duration of the summer season. Sampling began the first week of June to reduce the likelihood of including patches encountered on spring migration to the summer range as these patches are unlikely to be used again within the season.

For purposes of our analysis, a return was defined to be a series of 2 or more sequential fixes within 300m of the cluster point separated by more than 3 days (i.e., 36 fixes) from the previous visit. This mirrored the spatial rule used for defining clusters by the STPSS (maximum 300m diameter) and required a temporal window that would help to ensure that animals left the general area and subsequently returned in a separate event. Elk often spend several days encamped in one area and then relocate to another distant area of their home range (Fryxell et al. 2008); we expected these rapid relocation events to occur within our 3-day buffer and to separate one series of cluster visits from another. Single fix events within the appropriate spatial and temporal definition were denoted as “singles” but were not assumed to represent a foraging event. Biologically, we hypothesize these single fix events could represent exploratory returns to assess biomass regeneration in the presence of competing herbivores (e.g., cattle) but given their duration were not considered to be a foraging return for this analysis.

To count returns to each patch, we first imposed the spatial boundary of the patch and then tallied return events. Distances between sequential relocations for an animal and each cluster for that animal over the study period were calculated using Geospatial Modelling Environment (GME) (Beyer 2012). In Program R (R Core Team 2014), we identified the subset of fixes within 300m of a cluster point. This subset contained all returns to the 300m buffer including the foraging event originally clustered, but at this point they are undifferentiated events (See Figure 3.1). To accurately count the number of returns to a site, we used the sequential fix numbers (adjusted for missing fixes) included in the subset table to isolate clusters in time. Using the diff function in GME the table was read separating events of sequential fixes. In this way, nonsequential points outside the 3 day buffer represented start points of events that were isolated and tallied, separating single-fix events from multi-fix events, or returns. Based on this method, the number of returns to an area equals the (number of events in the area) – 1, accounting for the originally clustered foraging event. A correction to the returns count was needed in instances when the final record was a single-fix return: in this case, returns equal (number of events in the area) – 2, accounting for both the last single event and the original cluster point.

Return Analysis

Using the counts of returns to a patch as our response variable, we sought to understand how environmental covariates might influence an elk's decision to return to patches later in the season.

Ungulates move to maximize forage intake. They seek out areas of intermediate biomass that optimize quality and quantity available (Hebblewhite et al. 2008) and respond to physiogeographic features that impact where forage is most available (e.g. ruggedness, slope, elevation, aspect). Differences in elevation, slope, and aspect can create microclimates that affect localized productivity and available forage (Frair et al. 2005) and subsequently may affect elk movement (Fortin et al. 2005b). Higher productivity is expected to shorten regrowth times and provide more available biomass over the season, potentially increasing the number of returns occurring over the time window by decreasing the number of days between returns. As such, aspect was hypothesized to influence the frequency of returns and northness, or cos(Aspect), was included in the global mode. Additionally, movement by elk is restricted by rugged terrain and we hypothesize that the returns would be more frequent at less-rugged patches because they likely require less energy for travel to and within (Mao et al. 2005, Northrup et al. 2012, Ciuti et al. 2012). Terrain ruggedness, Ruggedness, was calculated from a digital elevation model for the area and included in the model to reflect this predicted influence on movement.

In addition to seeking out forage, research has shown that elk movement may be driven by predator avoidance (Fortin et al. 2005a, Frair et al. 2005). Remaining close to or within cover is an important predator avoidance strategy for elk (Ciuti et al. 2012). To evaluate the influence of cover on return frequency, CanopyClosure was extracted from a 2005 map created by the Foothills Research Institute (McDermid et al. 2009). This cover map is a composite of remotely sensed LandSat data with 30-m resolution on land cover and crown closure, as well as species composition, and agricultural and regeneration masks. The global traffic model developed by Northrup et al. (2012) was used to obtain estimates for the distance to road, DistRd, and average summer daily traffic on nearest road, Traffic. Traffic varies widely across the two herds. In Waterton, high levels of tourist traffic push through the park's few roads daily. In Livingstone, the landscape is dominated by small, seldom-travelled roads. Due to the wide variation in road density and traffic between the two herds, a binary and categorical covariate of Herd was included in models and allowed to interact with Traffic and DistRd parameters. This parameter specifies whether a patch occurs within the boundaries of the Livingstone or Waterton herd and was included to account for differences in the impact of roads and traffic on return likelihood to patches across the two herds.

Data for dynamic environmental covariates were available at all points in time when returns occurred. As such, because visits that comprise the dependent variable of "RETURNS" occurred through time, only covariates that remain static through time were included. In spite of this limitation, we hypothesized vegetation productivity would have a large influence on the frequency of returns to a patch. The normalized difference vegetation index, NDVI, an index of above-ground primary productivity, was compiled from images collected by MODIS remote sensing satellites in May through September 2012 at a 250m resolution every 16 days. The mean NDVI value of all clusters in each reporting period demonstrates the typical parabolic trend in productivity values over the summer (see Figure 3.2). Extracting the NDVI value at each cluster during the peak productivity period of the summer (early July), in combination with a parameter acknowledging the average and variance of NDVI values within each cluster over the summer, allowed us to include peak NDVI as a covariate indicating the relative productivity of each patch during the summer season.

The TmKnown covariate was included in the global model to account for our right-censored sampling period. TmKnown equals the number of days elapsed between the first ever visit to the patch and the end of the time period and can account for the increased likelihood that some patches have over others in the dataset just based on when they were first encountered in the season and the length of our sampling period. Accounting for even this most simplistic temporal dynamic was crucial to the accuracy of our model. The longer a patch is known to an animal, and the longer we monitored returns to it, the more returns that patch was likely to accrue.

The final environmental covariates added to the global model included DistRd, Traffic, CanopyCover, peak NDVI, cos(ASPECT), Ruggedness, TmKnown , DistRd:Herd, Traffic:Herd. All included covariates were hypothesized to affect movement of elk within their home range: attracting elk to areas where forage potential is maximized and threat is minimized. Individual variation in return patterns was substantial (See Figure 3.3A) and ElkID was included as a random effect to account for this variation and address issues of pseudoreplication in the sample. Although differences in terrain ruggedness were visually identifiable across herds, an interaction between ruggedness and herd was not expected to influence return frequency. That is to say, the return behaviour of Livingstone animals was not influenced differently by ruggedness than was the behaviour of Waterton animals, despite the greater overall ruggedness of Livingstone terrain. Although unconventional, Herd was not forced to be included in all models where an interaction between Herd and a road parameter was included. All of the expected difference between herds was attributable to the difference in tourism levels between areas and other individual variation accounted for by the random effect.

All covariates were standardized to mean = 0 and SD = 1, and using mixed negative binomial regression through the glmmadmb package in Program R, we investigated which environmental covariates influenced the incidence of return count data at 768 clusters. Using the MuMIn pkg and dredge function in Program R, all nested covariate combinations of the global model were tested and ranked according to the AICc. Models within 2 AIC units of the best model were considered indistinguishable and their coefficients model-averaged.

Results

SatScan Clustering

Using the STPSS procedure, 815 clusters were identified over the summer season. Clusters with radii less than 15m in length were removed, 47 (5.8%) qualifying clusters, leaving 768 clusters for analysis. The average number of clusters identified in total each week was 54.86 (±8.24 SD) clusters (minimum: 42, maximum: 63).

An average of 109.7(±8.36 SD) clusters per individual was identified over the 3 month season. The average radius of analysed clusters was 92.4m (±39.1 SD) and included an average of 2.63 (±1.21 SD) fixes in each cluster. SatScan output also provides number of observed fixes within the cluster. This value is often larger (but never smaller) than the number of fixes included in the cluster and represents the total number of fixes within the spatial boundaries of the cluster over the entire analysed temporal period, i.e.7 days. The average number of observed fixes in each cluster was 2.77(±1.47 SD) indicating that animals frequently revisited the cluster within the same week but not within the chosen temporal window.

Investigating Returns

Our calculations suggested that across all animals, clusters were returned to an average of 2.75 (± 2.37 SD) times over the 3 month season (including single fix returns). Animals returned to each cluster after an average of 15.38 days (±5.39 SD) and the average rate of return (#returns/timeknown) was .034 (±.027 SD) returns per day (or 3.34 returns per patch over the study period). Some clusters (17.1%) were not revisited in a foraging event. See Table 3.1 for additional summary statistics on returns.

A high frequency of zeroes is often best explained by length of time known – especially evident in Livingstone animals (Figure 3.4). For example, because E144 moved to a new area of her home range just 3 weeks before the end of the sampling period, her late season clusters had a much shorter period of time for revisitation and account for 69.6% of her non-returned patches over only 21% of the study period.

Returns were overdispersed (mean = 2.75, variance = 5.63) and a negative binomial distribution examined for better fit. As expected, a fixed negative binomial outperformed a fixed Poisson model by 23 AIC (Akaike Information Criterion) units and reduced the Pearson $\chi 2$ dispersion coefficient from 1.39 to 1.10. When mixed-effects models were estimated with Poisson and negative binomial families, fit was improved compared to fixed models. Unexpectedly, the mixed-effects models differed only by 0.8 AIC units (mixed Poisson 2866.36, NB 2865.56) but again the Pearson $\chi 2$ coefficient indicated less over dispersion with the negative binomial (1.20 to 1.11 respectively).

We fitted 288 nested variations of the global model, and 7 were observed to be within 2 AIC units of each other. We calculated relative variable importance over the entire nested model set and determined that *Distrd, herd:distrd, TMKnown, Ruggedness,* and peak *NDVI*, to be the most important explanatory variables for the pattern of returns and included in all 7 models (see Table 3.2). Of the variables included in the global model, only *herd:traffic* was not included as an explanatory variable in these top models.

The best fit model by AIC indicates that time known, ruggedness, distance to road and productivity at the site most significantly influenced the likelihood of return across all patches. The dispersion parameter for the top reported model was 30.166 (19.58 SE). The width of this standard error and the magnitude of the corrective parameter were large but the parameter estimates were stable across mixed Poisson and Negative Binomial approaches and the Pearson $\chi 2$ dispersion parameter, 1.11, indicates that the remaining 11% overcorrelation is within suitable bounds for use of the negative binomial distribution (Hilbe 2011).

For interpretation of effect sizes for estimated parameters, model averaging was done over all 7 nested models within 2 AIC units of the top model (See Table 3.2). Relative productivity of a patch increased likelihood of return in all reported top models. Elk preferred to return to patches farther from roads; the interaction parameter between herd and distance to road was included in all top models indicating the road effect on returns was magnified in the Waterton herd. The censorship parameter, *TmKnown*, proved to have the largest effect size, positively impacting return likelihood almost 3 times more than any other variable. The longer that a patch is known by, i.e. available to, an animal the more likely it will receive a return visit.

Differences between herds were included in 45% of the top 7 models and indicated that Waterton animals return less often than Livingston animals overall. Denser canopy cover increased likelihood of returns in 25 % of the top models, with a slightly positive coefficient and a small effect size. Standard error swamped both traffic and aspect parameters when included. Traffic on nearest road was the only parameter with an unstable coefficient estimate, but in all cases standard error on the estimate overlapped with zero and the effect was thus considered negligible.

Discussion

Our results confirm that individual elk make repeated foraging visits to patches within a growing season. Furthermore, we demonstrate that distance from roads, as well as landscape ruggedness, and productivity contribute to increased returns at foraging patches indicating that patch value influences the likelihood of return to a patch, just as proposed by Van Moorter et al.'s (2009) home-range model.

To our knowledge, this is the first empirical demonstration of recursive movements specifically to identified foraging sites. Return behaviours have been shown before in wild ungulates. Wolf et al. (2009) and Bar-David et al. (2009) both identified recursion events to previously used or "known" locations related to resources, or foraging behaviours, though neither estimated returns directly to identified foraging areas. By analysing return patterns to a specific location and use, we uniquely explored how foraging selection might drive movement patterns.

Differences across return distributions of individuals and across herds were noted (Figure 3.3A&B), with Waterton animals returning less often overall. These distributions are likely influenced by subtle range shifts over the season and by individual movement behaviours. Van Moorter et al. (*in prep*) demonstrate that larger home ranges lead to fewer returns and longer time between returns at individual patches. This is a logical result because when there is more space to cover and more patches to visit, the time between returns will be longer leading to fewer returns over a single season. We observed that the Waterton cows expanded their home ranges over the course of the season, but maintained returns to the entire area, even as it expanded late in the summer down into the aspen forests and wetlands of the east shore of lower Waterton lakes where bull elk typically spent their summers. Maintenance of larger home ranges may explain a portion of the reduced return likelihood of Waterton patches.

Our top models demonstrate that at the population level, productivity, time known**,** distance to road and an interaction between distance to road and herd were the most influential environmental covariates determining return counts at patches across the season. These four parameters had the highest relative importance and were included in all models within 2 AIC units of the top.

The importance of productivity, calculated by peak *NDVI*, in return models supports the underlying thesis of Van Moorter et al.'s (2009) model which values patches based on replenishment of resources. As expected our results demonstrate that productive patches are returned to more often than less productive patches. An attraction to productive forage is consistent with previous work demonstrating that elk migration often follows the start of spring photosynthetic activity, or greenup; as new growth extends into higher elevations over summer so do elk (Boyce 1991). Forage research on elk also shows attraction to intermediate levels of biomass, often more digestible and productive than tall late-season stands, and forage abundance has been shown to encourage site fidelity in nonmigratory elk populations on short time intervals, supporting our results that productivity may strongly influence returns (Wilmshurst et al. 1995, Frair et al. 2005, van Beest et al. 2013).

Distance to nearest road and its interaction with the Herd variable appeared repeatedly in the top model set, with Waterton animals being more sensitive to road proximity. Animals in national parks often seem undisturbed by roads, habituated to traffic and people, and attracted by the roadside vegetation and protection from predators that roads and human settlements offer (Rogala et al. 2011), but in other populations, especially in those facing hunting pressure, roads and high traffic have been shown to alter movement near roads (Rowland et al. 2000, Frair et al. 2008). From the perspective of foraging, human disturbance has been shown to increase vigilance, reducing time spent foraging, foraging efficiency, and intake (Frid and Dill 2002, Fortin et al. 2004, Ciuti et al. 2012) and, recently, to deter foraging patch selection in elk (Seidel 2014a). Our analysis demonstrates that disturbance may also affect whether or not that animal returns to patches over time.

Inclusion of the TmKnown variable markedly improved the fit of our model to the data and emphasizes the temporal dynamics at play driving returns. TmKnown was the strongest indicator of return likelihood, with an effect size three times that of any other predictor; this is a logical and likely trivial result. Patches visited earlier in the season have a longer period of time during which they can be returned to. Return behaviour overall however indicates that animals are not avoiding previous locations and that previous use may increase subsequent use, just as demonstrated by Wolf et al. (2009). If this coefficient had been diminished or even negative, we would expect that animals were likely moving into novel environments, not cycling back over the season either due to range drift or possibly resource depletion or predator avoidance.

Traditionally, simple random-walk or diffusion models were used widely to model animal movement and, dependent on the time scale in question, can provide a realistic approximation of movement for many species (Smouse et al. 2010). Diffusion alone however does not result in emergent home range behaviour: using a diffusion approach, eventually the paths of an animal will expand to fill any available extent. Diffusion models with an attraction vector to a central place (e.g. a den, a nest) can result in a circular, unimodal, home ranges but empirical observation shows that animals' real home ranges generally exhibit multimodal use with non-circular edges (Smouse et al. 2010). Mechanistic home-range models have evolved in an attempt to identify and model the movement processes that can simulate emergent multimodal utilization distributions and realistic home-range boundaries (Please see Börger et al. 2008 and

Smouse et al. 2010 for further review of recent movement and home-range modelling). The Van Moorter et al. (2009) model, based on foraging and memory, provides a promising model for the intra-home-range movement in wild ungulates, without requiring presupposition of home range centers or a single attractive nuclei. Although not a direct validation of the movements prescribed by the model, our work demonstrated repeated movement behaviour between multiple nodes of attraction, indicative of memory processes, and negates simple diffusion or central place models for ungulate home range development.

We have demonstrated that elk will return to foraging patches repeatedly over the season. Return behaviour should be driven in part by patch value, and indeed, we show that productivity, terrain ruggedness, and proximity to road all influenced the likelihood that elk would return to foraging patches. These results demonstrate that the Van Moorter et al. (2009) model for home-range development appropriately characterizes key aspects of elk foraging and movement behaviour and furthers understanding of within home range movement of free ranging elk. Increased research into the mechanisms driving space use and empirical evaluation of theoretical home range models will improve our understanding of the dynamic nature of animal space use and movements, especially in response to human land use change.

Chapter 3 Table and Figures

ELKID	**N**	**% not returned**	**#UnRet (SingleRet)**	**Avg Returns**	**MAX Returns**	**Avg # Singles**	**Avg Return Rate**
E144	111	20.72	23 (4)	5.22	11.00	1.10	11.96
E146	118	24.58	29 (6)	2.06	5.00	0.29	12.66
E159	117	6.84	8 (3)	3.14	7.00	0.80	20.24
E164	117	11.97	14 (7)	3.29	7.00	1.20	24.82
E170	96	15.63	15 (8)	3.21	9.00	0.83	15.54
E172	105	8.57	9 (4)	3.67	10.00	0.90	13.17
E173	104	31.73	33 (9)	2.49	7.00	0.65	9.24
AVG	**110**	**17.15**		**3.30**		**0.82**	**15.38**
SD	**8.4**	**9.03**		**1.00**		**0.30**	**5.39**

Table 3.1. Summary statistics on returns for cow elk, Summer 2012. Across 7 cow elk, an average of 109.7 clusters per animal was detected in GPS relocations from summer 2012. An average of 17% of these clusters, presumed foraging patches, were unreturned to, however the percentage of patches unreturned to drops 2.6-8.7% when including single fix returns over the season which were not immediately considered foraging returns. The average number of returns per cluster, as well as maximum number of returns recorded, are presented for each animal and then averaged for the population. The “average return rate” is the average number of days between return events, not including singles and not accounting for differences in time known to the individual

	AIC_c	**Δ AIC**	**w_i**	**Intercept**	**ASP_C_s**	**Canopy_s**	**DistRd**	**HERD**	**NDVI_s**	**RUGGs**	**TMKnwn_s**	**Traffic**	**DistRd:HERD**
M1	2860.750	0.000	0.238	0.830			0.044		0.052	-0.148	0.521		0.118
M2	2860.917	0.168	0.218	0.937			0.045	-0.250	0.052	-0.155	0.521		0.117
M3	2861.911	1.161	0.133	0.949		0.032	0.044	-0.279	0.045	-0.159	0.526		0.116
M4	2862.097	1.348	0.121	0.829		0.026	0.042		0.046	-0.151	0.525		0.118
M5	2862.377	1.628	0.105	0.830	0.015		0.043		0.052	-0.149	0.521		0.117
M6	2862.551	1.801	0.097	0.937	0.015		0.045	-0.250	0.052	-0.156	0.521		0.116
M7	2862.737	1.988	0.088	0.830			0.044		0.051	-0.148	0.521	0.007	0.118

Model Averaged Coefficients	**Estimate**	**Standard Error**	**Adjusted SE**	**zvalue**	**Relative Variable Importance**
(Intercept)	0.88	0.12	0.12	7.50	--
DistRd	0.04	0.04	0.04	1.24	1.00
NDVI_s	0.05	0.03	0.03	1.98	1.00
RUGGs	-0.15	0.04	0.04	3.86	1.00
TMKnwn_s	0.52	0.03	0.03	15.02	1.00
DistRd:HERDWATERTON	0.12	0.05	0.05	2.28	1.00
HERDWATERTON	-0.26	0.17	0.17	1.51	0.45
Canopy_s	0.03	0.03	0.03	0.93	0.25
ASP_C_s	0.02	0.02	0.02	0.64	0.20
Traffic	0.01	0.03	0.03	0.23	0.09

Relative variable importance over entire model set

DistRd	**NDVI_s**	**RUGGs**	**TMKnwn_s**	**DistRd: HERDWATERTON**	**HERDWATERTON**	**Canopy_s**	**ASP_C_s**	**Traffic**	**HERD:traffic**
1	0.71	1	1	0.83	0.51	0.4	0.31	0.36	0.1

Table 3.2. Top Models and Model Averaged Coefficients. The top 7 models are reported, displaying coefficient estimates and Akaike weights. All are within 2 AIC units of each other. All models were model averaged, and new averaged coefficients estimated, with relative variable importance values reported below. *TmKnown*, *Ruggedness*, and *DistRd* were the covariates included in all top models and were the covariates contributing the greatest effect on the return frequency. Aspect, canopy cover, and traffic parameters were included in a minority of the top reported models, and thus the averaged model, but the standard errors associated with these coefficients resulted in their effects being indistinguishable from zero.

RECNO	DISTANCE
5094	165.7443
5095	168.6976
5096	169.9055
5097	169.3984
5144	261.1286
5145	206.4126
5154	219.7317
5155	218.1231
5156	257.1246
5157	261.0635
5158	0
5159	17.96821
5160	38.69315
5161	105.8742
6213	212.8553
6270	209.9958
6276	54.09491
6277	97.4556

Figure 3.1. Example subset table for differentiating return events

This example patch has received 2 returns and 1 single fix event over the season. Note that a return can occur prior to the event clustered by the space-time permutation scan statistic.

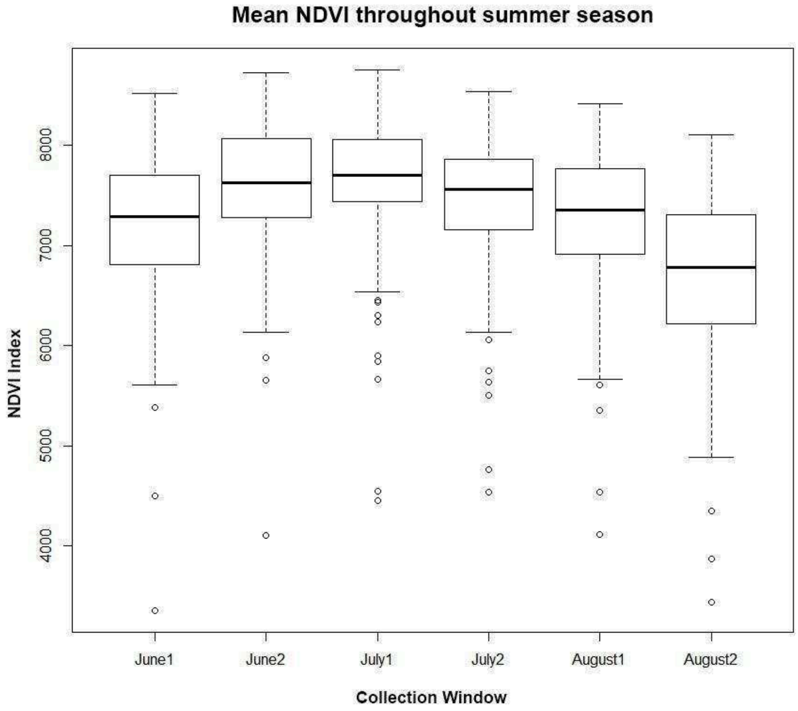

Figure 3.2. Boxplot demonstrating mean NDVI and its variance throughout summer

MODIS satellites retrieve imagery from the study site every 16 days, twice each month. The 6 boxplots present the average and variance of Normalized Difference Vegetation Index (NDVI) values for each photoperiod. These averages and variances are calculated from NDVI values reported at all clusters identified. The first reporting period of July (July1) has the highest mean and the lowest variance making it the best choice for a parameter demonstrating relative productivity of each cluster. The higher variance early and late in the season is likely due to timing variation of snow melt, growth, and die-off along elevation and cover gradients all of which influence NDVI values.

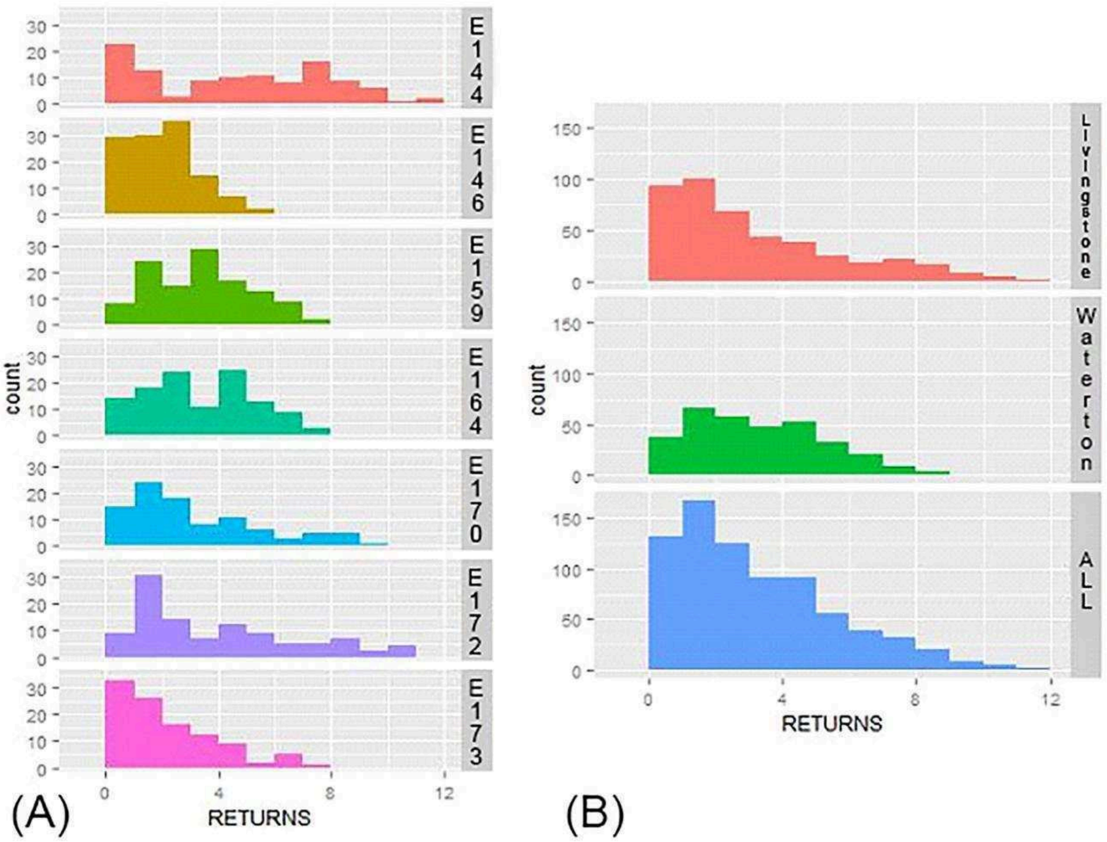

Figure 3.3 . Distribution of return frequency to clusters by (A) Individual and (B) Herd across the summer season.

Histograms depicting frequency of returns to identified foraging patches are presented for each individual cow and each herd cumulatively. These histograms demonstrate the wide variation present across individual and herd return frequencies, potentially influenced both by differences in habitat and behaviour across the season.

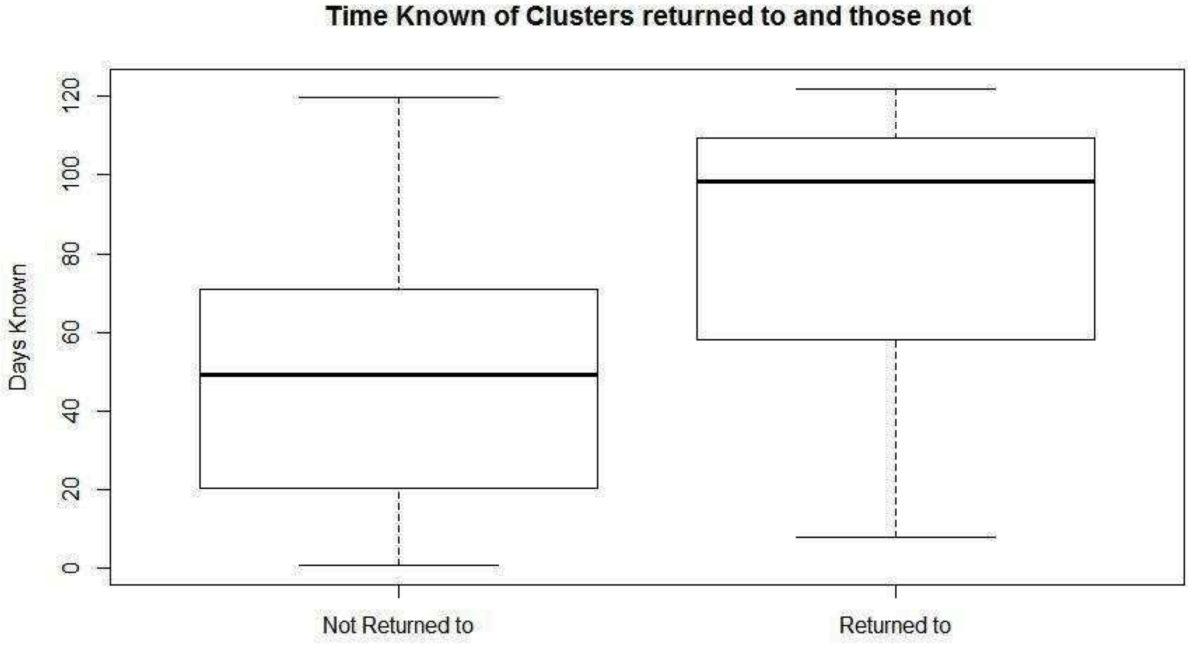

Figure 3.4 . Examining the influence of *TMKnown* on clusters not revisited. *TmKnown*, or the number of days between an individual's first visit to a patch and the end of the study period, has a noteworthy effect on the likelihood an identified patch will be revisited. Revisited patches have, on average, been known for at least 100 days, suggesting that many clusters not returned to were potentially not known long enough to be returned to within the sampled season.

Chapter 4

Concluding Thoughts

Chapter Review

The central chapters of this thesis have explored underlying assumptions to a mechanistic home-range model designed for a generic forager. In the first known empirical evaluation of this model, my work has used Van Moorter et al.'s (2009) initial theory as a framework for further exploration of foraging, movement, and home-range patterns in an ungulate species.

In chapter 2, I tackled an evaluation of the four fundamental assumptions to Van Moorter et al.'s (2009) theory. First I identified foraging patches using a unique numerical method that clearly indicates foraging patches within home ranges. My data analysis approached the central question of heterogeneity across a home range. I then asked if foraging patches are different, specifically of higher forage quality, than areas of the home range used outside of foraging. Van Moorter et al.'s model suggests that attraction to foraging patches is determined by a dynamic utility or value, with the dynamics predominately driven by depletion and replenishment of available forage. Using matched-pairs regression, my analysis and results demonstrate that available biomass is indeed one of the most important influences to a patches' quality reflected by selection, but patch likelihood also is simultaneously affected by site conditions like proximity to and level of traffic at nearest road, slope of site, and available forest cover. In an additional layer of analysis, top models reported from subsets of the directly sampled sites indicate that patch selection preferences can differ across sex, season, and herd. This variability is likely influenced by the different metabolic requirements across sex and season, and differing habitat availability across distant ranging herds.

Overlain on utilization distributions created for all animals in the area, patches imitated the use patterns visualized by the kernel density estimation calculated for individuals' relocations. The multimodal distribution of patches across the home range not only reflects nearly full coverage of the utilization distribution but also a use pattern similar to that expected by Van Moorter et al.'s patch-based model. The scale of my patch-selection analysis is considerably restricted to focus narrowly on what it is about the patch that attracts a cluster of use points by the animals. To compare this narrow patch-selection scale with selection on a broader scale I also calculated a habitat-selection model where I contrasted used resource units with those associated with random landscape locations within the home range. Waterton animals selected strongly for canopy cover and less rugged terrain distant from roads. Livingston animals selected strongly for productive areas and avoided canopy cover, rugged terrain and roads. These results mirrored the direction and importance of comparative coefficients in the patch scale models.

In Chapter 3 I explored within-home-range movements among patches in comparison to the expectations of Van Moorter et al.'s model. I established that elk return to distinct foraging patches over the summer with an average of 15 days between revisits. Using mixed negative binomial regression, I showed that productivity, distance to road, and terrain ruggedness were the most influential environmental covariates affecting number of foraging returns to a patch. Returns frequency was positively associated with distance to road and productivity but negatively associated with terrain ruggedness, suggesting returns were made most frequently to patches that were easy to get to, highly productive, and further from roads. Across herds, return rates and sensitivity to roads varied. Beyond environmental covariates, *TmKnown,* or the number of days since the elk first encountered the patch, was the most influential predictor overall. Intuitively, the longer a patch was available to or "known" by an elk, the more returns it accrued. The importance of this parameter establishes that elk are not avoiding previously used areas or known patches and along with regular returns, suggests the potential for long-term recollection of patches within a season.

Implications of the research

In separate reviews on animal movement and home-range models, Smouse et al. (2010) and Börger et al. (2008) reiterated the need for validation of theoretical models with data. These models can strengthen our understanding of the underlying cause for home-range development beyond what decades of descriptive statistical methods have taught us, but only when theories are validated with ecological data and the predictive strength of the model assessed. In my chapters I demonstrate that elk exhibit the patterns of habitat selection and movement exactly as projected by the Van Moorter et al. theory and I further demonstrate empirical support for the mechanisms proposed. The Van Moorter et al. model promises to offer important insights into home range formation behaviours of ungulates and my work has offered the first step towards its validation.

Ultimately, knowledge of underlying home-range mechanisms can aid managers in anticipating change in animal space use in response to land-use change or disturbances including those caused by changing climate and patch composition.

Future Work

Van Moorter et al.'s model simulates movement during the growing season but it remains unknown how this model might function for the emergence of winter home ranges when replenishment is not at play. Feeding behaviours in the winter consist mostly of digging in search of buried biomass, switching to browse species, or using winter hay where available (Fortin et al. 2005b). None of these sources replenish as expected by the patches simulated in the Van Moorter et al. (2009) model. Despite this difference, work by Fortin et al. (2005b) suggest that elk may use many of the same movement and patch dynamics during winter forage as expected in summer. Their work reports elk making directed movements between foraging areas where they linger and dig for food. These dynamics suggest that the patch structure and movements expected by the Van Moorter et al. model may still be present in the winter season, but the research simply has not been done to assess winter home range behaviours in this way.

Although there is developing evidence for memory and cognition in animals such as elk, and little doubt that it affects animal movement substantially (Smouse et al. 2010), there is much left to be understood about memory in animals. In terms of further evaluation of Van Moorter et al.'s (2009) model, spatial and temporal extent of memory within wide-ranging animals must be explored and ideally experimentation should be used to elucidate the functioning of "short-term" memory and learning in foragers. Data from animals in novel environments, either relocated or dispersing, is often not as readily available as data from mature or resident animals, but observation in novel environments should be increasingly undertaken to provide further understanding about how animals learn in their environment and how home ranges develop (Frair et al. 2007).

Ultimately, Van Moorter et al.'s (2009) model is individual based and does not explore the influence of intra- and inter-specific competition for resources. This leaves a gap to be filled in understanding how competition and/or social behaviour might affect ranging in social foragers like elk. Furthermore, I would be interested to understand how competition for resources could influence the periodic patch foraging described by this model specifically because of pressures on the underlying replenishment/depletion cycle as a population reaches or exceeds carrying capacity.

Conclusions

In an era of scientific research that incentivizes the novel and exciting, too often the drudgery and repetition that is required to evaluate promising theories is not undertaken. Offering a bridge between a theoretical model and applied research, my work provides the first evaluation of a theoretical home-range model for an herbivore and ultimately enhances our understanding of the foraging selection and movement patterns underlying home-range development in elk.

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