

Understanding dispersal ecology of young male  
ungulates (*Cervus elaphus*) to design large scale  
wildlife corridors

Master Thesis

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## **Declaration**

This thesis was written in the department of biometry and environmental analysis, faculty of environment and natural resources at the University of Freiburg from May 2014 to November 2014 under supervision of Dr. Simone Ciuti.

I, Robin Benz, herewith declare that I have written this thesis on my own and that I have not used any other sources and materials than those indicated. I properly cited the materials I have relied upon. I have not submitted this document as a master thesis elsewhere.

Robin Benz  
Freiburg, November 2014

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## Abstract

Human modifications within natural habitats, such as linear clearings and roads, fragment the landscape into ever smaller habitat patches and reduce the permeability to wildlife movement. Habitat modifications have occurred exponentially over the last decades, with global biodiversity declining at the level of genes, species and ecosystems, while the majority of pressures showing increasing trends. Thus, conservation efforts focus on reservation and maintenance of wildlife corridors. In this study, I investigate the movement ecology of young male ungulates *Cervus elaphus* in order to design a large scale corridor matrix across the Northern Rocky Mountains. I used high-resolution satellite telemetry data of 54 young male individuals monitored from 2007 - 2011 to combine broad-scale habitat preference with fine-scale movement behavior. The majority of montane elk are migratory, meaning individuals move from wintering areas to summer ranges at higher elevations, with the exception of young males, which commonly disperse or make further exploratory movements. I used resource selection functions (RSFs) to identify best winter and summer hotspots selected by elk. For elk movement I separated long directional steps from short resting and foraging ones, and predicted fine-scale habitat selection using step selection functions (SSFs), while considering spatio-temporal differences in movement based on extrinsic factors, such as seasonality for spring and hunting in autumn. Elk showed marked habitat selection during both stationary and exploratory periods, and strong avoidance of roads, in particular high traffic highways. Based on SSF predictions, I build two cost friction surfaces for each season, where elk (i) moves on natural behavioral choice, and (ii) where elk is constrained by roads. Based on these, I mapped least cost corridors (LCCs) between winter and summer hotspots. Quantitative comparison of highway-corridor intersection lengths revealed significant effect of major highways on elk connectivity. This analytical tool can be used to define hotspots of elk connectivity along major roads, and can be easily applied to other large mammals and primarily aid conservation managers to make better informed management decisions based on animal movement behavior.

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# 1. Introduction

The decline of biodiversity during recent decades was merely explained by habitat loss and fragmentation, as well as degradation of habitat quality (Andren, 1994; Fahrig, 2003). Identifying regional conservation priorities at the level of genes, species and ecosystems has become targets to place different management strategies, including reservation (Butchart et al., 2010; Pressey & Logan, 1997). Recent analyses have shown that global biodiversity has continued to decline, while the majority of indicators of pressures show increasing trends (Butchart et al., 2010). Especially logging and the construction of roads are discontinuous due to land use suitability and accessibility to humans (Laurance et al., 2008). This leads to fragmentation of the landscape into a matrix of isolated habitat patches, surrounded by altered agricultural and forested landscape (Brühl et al., 2003; Hanski, 1998). This has a strong impact on the surrounding habitat configuration on a landscape level (Fahrig, 2003). Besides direct habitat loss, it also increases the number of patches, decreases patch size and increases isolation. Protected areas, as well as all other suitable habitats are increasingly isolated, as the surrounding is altered (Curran et al., 2004).

Previous research has shown that linear clearings, such as created by power lines, pipelines, railways and roads, have an intrinsic impact on the environment and ecosystems (Forman, 2003; Trombulak & Frissell, 2000). While some of them facilitate alien plant species invasions (Mortensen et al., 2009), they also negatively affect the demography of animal movement (Forman, 2003). Some species living in such a fragmented matrix are restricted in their movement and some even avoid crossing an anthropogenic impeded landscape, such as created by roads, to reach other habitat patches (Trombulak & Frissell, 2000; Laurance et al., 2008). Studies have shown that this is true for small, slow moving species, such as reptiles, small birds and arboreal mammal species (Laurance et al., 2009), but also for larger herbivores (Berger, 2004; Holdo et al., 2011; Sawyer et al., 2013; Van Oort et al., 2011). Seidler et al. (2014) demonstrated that major highways impede and even disrupt migratory ungulate movement.

The meta-population concept describes the dynamics of a population across such a fragmented landscape (Turner, 1996). Increased isolation can result in genetic drift, which is the loss of genetic diversity by chance within a subpopulation of a species (Hanski, 1998; Turner, 1996). One or just a few successful migrants per generation are needed to maintain genetic diversity (Slatkin, 1985). To allow demography and genetic exchange, individuals need the ability to disperse between subpopulations. Conservation efforts focus on identifying and maintaining wildlife corridors, as they facilitate the movement through such an anthropogenic modified landscape (Laurance et al., 2008). Poorly designed corridors on the other hand, may result in population sinks, waste financial resources or loss of stakeholder support (Killeen et al., 2014; Simberloff et al., 1992). Recent and most effective methods pursued were to model resistance surfaces using Geographic Information Systems (GIS) and radio-telemetry data to investigate least-cost-path (LCP) for best placement of corridors (Adriaensen et al., 2003; Rayfield et al., 2010).

Squires et al. (2013) combined broad scale residency with fine-scale movement behavior to depict linkages for Canada lynx (*Lynx canadensis*). In this study, I adapted this method to understand movement ecology of young male ungulate *Cervus elaphus* in the Northern Rocky mountains. Killeen et al. (2014) identified that it is almost exclusively the young males dispersing and undertaking exploratory movements, while females remain migratory or resident. As the target was to establish connectivity and maintain gene flow between subpopulations, females were not considered in this study. I identified landscape characteristics that influence male elk occupancy during summer and winter residency, as well as selection priorities during fast directional spring and autumn movements. This included the use of resource selection functions (RSF) to identify suitable habitat patches (Manly et al., 2002), and step selection functions (SSF) to calculate a cost friction surface (Fortin et al., 2005), to predict least cost corridors (LCC) between them (McRae & Kavanagh, 2011). I used this information to create a wildlife corridor matrix on a large scale following the recommendations by Sawyer et al. (2011). Lastly, I pointed out natural movement pathways lost to highways and highlight important corridor-highway intersections impeding the permeability for potential dispersers.

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## 2. Materials & methods

### 2.1 Study area

The study area covers a total of 46,000 km<sup>2</sup> and is mainly located in Southwestern Alberta (AB) Canada, but stretches into Southeastern British Columbia (BC) Canada and Northwestern Montana (MT) in the United States (Appendix: A.1). The main habitat type along the Rocky Mountains in this region consists of the transition zone of flat agricultural grassland in the East, to conifer and mixed hardwood and montane ecosystem in the West (Chetkiewicz & Boyce, 2009). The elevation range stretches from 900 meters in the East up to 3,400 meters in the montane area. There is considerable human activity in the study area, which is dominated by cattle ranching and crop farming in the lowlands of Alberta and forestry in the Rockies. The area has high recreational hunting activity from September to December (Ciuti et al., 2012b). Furthermore, the study area includes the Waterton National Park in Alberta and Glacier National Park in Montana. The wolf (*Canis lupus*), cougar (*Puma concolor*), and grizzly bear (*Ursus arctos*) are the main elk natural predators (*Cervus elaphus*) in the region (Muhly et al., 2011).

### 2.2 Elk capture and monitoring

In total, 182 elk were captured using helicopter net-gunning (animal care protocol no. 536-1003 AR University of Alberta), of which 62 were males. Capturing occurred during the month January through March, in each year from 2007 to 2011. For age determination, a vestibular canine was removed using dental lifters to assess age through cementum analysis (Matsons Laboratory, MT, USA). The age of females ranged between 1 to 19 years, while all males were ~1.5 years of age as net gunning allowed only capture for maximum one-point antlers. Individuals were fitted with a radio telemetry collar, programmed with a 2 hour relocation schedule. Data from male collars (Lotek ARGOS GPS Lotek Wireless Inc., Ontario, Canada) were received by email, while the data of females (Lotek GPS 4400 Lotek Wireless Inc., Ontario, Canada) were downloaded in the field. I

screened the data following the methods by Lewis et al. (2007) to remove location errors. I removed further outliers, such as locations prior capture and after collar loss or death, by hand after visual inspection in ArcGIS 10.1 (ESRI, 2012).

### 2.3 Digital data

Killeen et al. (2014) have shown recently that it is the males dominating dispersal almost exclusively, while most female individuals remain resident or migratory. Females were used to understand migratory timing and define seasons, while the males were target of this research. Of the 62 males captured, 54 individuals retained the collar or survived at least until September of each capture year from 2007 to 2011. From these individuals, a total of 225,800 GPS points were gathered for the analysis and referred as 'used' locations hereafter.

A number of environmental covariates are known to influence elk movement behavior in this region (Ciuti et al., 2012a). This included a combination of categorical land cover maps and continuous indices of terrain, vegetation and roads. I used these data layers as proxies of environmental variability (Table: 1).

**Table 1: Digital data layers.** Description of data layers and their characteristics used to quantify resource selection and movement behavior of montane elk.

Type	Name	Description	Resolution (m)
Terrain	DEM	Digital elevation model (m)	30
	ASPECT	Cosine transformed (North-South)	30
	SLOPE	% rise	30
	TRI	Topographic position index / ruggedness	30
Canopy cover	CC	% closure	30
Forage quality	NDVI.W	Average Jan. - March, 2007 - 2011	250
	NDVI.S	Average July - Aug., 2007 - 2011	250
Roads	DISTHWY	Distance to highways (m)	30
	DISTSMD	Distance to small & gravel roads (m)	30
MODIS land cover	CONIFER	Conifer forest (Categorical)	250
	DECIDUOUS	Deciduous forest (Cat.)	250
	MIXED	Mixed forest (Cat.)	250
	SHRUB	Shrub land (Cat.)	250
	GRASS	Grassland (Cat.)	250
	CROP	Cropland (Cat.)	250
	OTHER	Urban, water, ice (Cat.)	250

Predictors for terrain features included a digital elevation model (DEM), from which I derived aspect and slope. Furthermore, I calculated ruggedness according to Riley et al.

(1999), which describes the topographic elevation difference from one cell on a grid to its eight neighboring cells. I described land use characteristics using seven categorical land use types, split into seven binary layers for spatial application (MODIS, 2014). I used NDVI as a proxy for forage quality, which is a normalized difference vegetation index (NDVI) derived from 16 day MODIS satellite imagery. I averaged the NDVI values during the month where elk showed habitat residency across the years 2007 to 2011. Additionally, I created two road layers, containing the distance to double-lane highways and distance to smaller single-lane or gravel roads, referred to as gravel roads hereafter (Governments of AB & BC: National Topographic Database 1:50,000; U.S. Census Bureau Tiger/Line files, 2000). Ciuti et al. (2012b) have shown for that area that roads only influence elk movement behavior in close proximity. Therefore, I kept road distance layers constant 2 km distant to highways and 1 km distant to gravel roads, so that Step Selection Functions in remote areas are not forced to estimate road selection where it does not matter for the elk (Thurfjell et al., 2014). I focused on the use of broadly available data (resolution: 250 m) that are continuous across multi national borders of AB, BC and MT, in order to improve the applicability of this method as a tool for other regions on a large scale. I used fine scale environmental data when available for this large region (resolution: 30 m, Table: 1).

### 2.4 Defining elk movement and residency periods

I defined the movement and resident periods of elk according to female elk migration in conjunction with net displacement (ND) of males (Bunnefeld et al., 2011; Ciuti et al., 2012a). The plotted straight line distance of each data point to the starting location indicates animal movement or residency period, as well as exploratory movements. I recorded dispersal and exploratory moves only in the first year of elk tracking, when males show exploratory and dispersal movements which match with my goal to understand connectivity in the region. Therefore, I restricted the data to the first year (146,233 GPS points), as I considered young male elk as inexperienced in moving through and exploring new territories after leaving the herd (Killeen et al., 2014).

In accordance with previous studies describing the elk migratory behavior in this area (Ciuti et al., 2012a; Paton, 2012), male elk did not show variation in ND during the months from January to March. Locations during this time period have been considered as winter residency. Using the same rationale, I considered the time July/August as summer residency period (Appendix: A.2 - A.5). During the summer residency, only minimal

movements occurred except short lasting exploratory movements. I considered the period from early April to late August as spring/summer movements, referred to as spring movements hereafter. Elk movements in autumn, back towards a winter habitat, started earliest from September and lasted to November. NDs were calculated and plotted in R (R Core Team et al., 2014) and concur with the migration period of females in the same study area (Ciuti et al., 2012a; Killeen et al., 2014).

## 2.5 Winter and summer habitat selection prediction using RSF

I followed the methods introduced by Squires et al. (2013), which I adapted by taking into account of elk ecology. Resident habitat ranges were quantified by relating the environmental characteristics to those available across the study area (Squires et al., 2013). I modeled population-level resource selection by elk using Resource Selection Functions (RSFs) following Manly et al. (2002)s design II. With this design, individual animals are identified (individually relocated) and the use of resources is measured for each, but availability is measured at the population level (Manly et al., 2002). As a representative for available habitat, I scattered sample locations randomly across the study area, weighed 10:1 to each individual elks' 'used' locations. Prior to build my habitat model, I screened the environmental parameters for collinearity using Pearson correlation coefficients ( $r < 0.7$ ) and used a variance inflation factor of higher than 3 to drop multi-collinear variables (Zuur et al., 2009). The model coefficients were estimated using general linear mixed models (GLMM) with binomial distribution of errors, with individual elk as a random intercept (Bolker et al., 2009). I started with a full model, and variables that did not contribute towards the model based on Wald statistics ( $p < 0.05$ ) were not included. Actually, all starting variables were retained with the exception of aspect, confirming habitat selection patterns documented for elk in this region (Ciuti et al., 2012a; Killeen et al., 2014). For statistical modeling I used the R package lme4 (Bates et al., 2014). Using the coefficients estimated by the GLMM, I built a RSF of winter and summer according to Manly et al. (2002), which takes the exponential form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i), \quad (1)$$

where  $\beta_i$  is the coefficient of each predictor variable ( $i$ ),  $x_i$  is the associated environmental value in the vector, and  $w(x)$  is the predicted value relative to the probability of selecting this resource unit (Boyce et al., 2002). The predictions of the RSFs' were used to identify

winter and summer hotspots in the GIS environment (ESRI, 2012).

The models performance were tested with area-adjusted frequency of binned cross-validated 'used' locations (5-fold cross-validation), according to Boyce et al. (2002). I randomly divided the 'used' locations in five subsets and then, I withheld one subset from model prediction, while using the remaining four as model training data. This procedure was repeated for each of the subsets. The RSF scores gathered from each of the training datasets were placed into 10 bins. Subsequently, I assessed each withheld subset against the predictions by the training model and compared them to each other using spearman-rank correlation (Boyce et al., 2002).

### 2.6 Elk movement prediction using SSF

The straight line distance (step length) between two subsequent locations was calculated using GME and R (Beyer, 2012; R Core Team et al., 2014). I used a broken stick model in R with the package *segmented* to distinguish between long distance dispersal and exploratory movements from those associated to foraging and resting. (Johnson et al., 2002; Muggeo, 2012). The same amount of locations were selected per animal and included in the broken stick model to have equal weight for each animal and avoid biased estimates. For spring movements, this included all 54 animals with 800 randomly drawn steps. Due to the shorter movement time period in autumn, as well as many elk were shot early in the hunting season, only 33 elk contributed equally with 600 steps to the broken stick model. All locations of spring and autumn movements that had a greater movement speed than the investigated breaking points were used for large scale movement predictions and are referred to as active movement hereafter. The turning angles between the previous and subsequent locations were used as a proxy for directionality. To ascertain true step length, movement speed and turning angles, I only considered locations that were recorded within 10 minutes of the typical two hour interval as true movement steps. Steps recorded between much shorter or longer time intervals were removed from the dataset.

In order to incorporate the active movement behavior into small scale habitat selection, each observed active step was matched with five random steps that were expected to be available at each location (Thurfjell et al., 2014). I reclassified the step lengths and turning angles of the long directional steps into bins of 50 m and  $10^\circ$  respectively, to create probability distributions. Subsequently, five random steps were drawn from these probability

distributions, that were created from observed steps. Prior to build my fine scale habitat model, I screened the environmental parameters for collinearity using Pearson correlation coefficients ( $|r| > 0.7$ ) and used a variance inflation factor of higher than 3 to drop multicollinear variables (Zuur et al., 2009). Model coefficients were estimated using a mixed conditional logistic regression model (Fortin et al., 2005, 2009), where individual steps with their five associated random steps were treated independently as strata and individual elk set as a random intercept. Elk movements were modeled with the R package *mclogit* (Elff, 2013). The Step Selection Function (SSF) provides a fine scale comparison of elk movement on a single step level using observed and random steps (Fortin et al., 2005) and uses like the RSF, the same exponential form as in Equation 1. I built two SSF models in spring: one model did not include distance to the closest road as a predictor, while the second one did. We repeated the same procedure for the autumn SSFs. Hereafter, these models are simply referred to as SSFs with or without roads. Model robustness was evaluated using  $k$ -fold cross-validation for case-control design according to Fortin et al. (2009). SSFs were built using 80% of randomly selected strata. This SSF was then used to predict the SSF scores for the remaining 20% of strata. The observed location of each stratum was ranked against its associated random locations and tallied. The bins' ranking and associated frequency was carried out with spearman-rank correlations ( $\bar{r}_s$ ). This procedure was repeated 100 times and the mean and 95 % CI of  $\bar{r}_s$  are presented for each model. The mean ( $\bar{r}_s$ ) and 95 % CI were also presented under assumption of complete random patterns of habitat selection by following the same steps except that random steps were ranked against withheld random steps.

Lastly, I applied the SSF spatially in ArcGIS and scaled it from 0 to 1 by dividing each cell by the maximum predicted value to give a probability surface. In order to use the SSF map as a source of cost friction, I inverted the map by subtracting the probability surface from one. In a cost friction map, each cell reflects a value of energetic cost, difficulty or mortality risk of moving across that cell (McRae & Kavanagh, 2011). In this study, the cell reflects habitat selection preference of young male elk of moving through the yet unknown environment.

### 2.7 Elk connectivity

In order to connect seasonal preference elk habitat, I connected true winter source locations with potential summer and further winter locations. Firstly, using the isopleth tool in GME (Beyer, 2012), I created 6 winter source core polygons from 50% volume

of male locations during winter, grouped by herd. Secondly, I depicted 11 winter and 15 summer core areas across the study area, depending on high RSF scores gathered from winter and summer RSF. I did not consider adjacent core areas, as they are assumed to be intra-connected. I used the Linkage Mapper tool kit (McRae & Kavanagh, 2011) to identify least-cost-corridors (LCCs) between core area pairs. I examined 200 core area pairs that have a maximum Euclidean corridor distance of 80 km, as I expected long corridors to move through other core areas. Linkage Mapper sums the cost-weighted distance (CWD) rasters from each core area pair, and normalizes least-cost-corridors (NLCCs) by subtracting the least-cost path distance (LCD) from the raw corridor (Equation: 2; McRae & Kavanagh (2011)).

$$NLCC_{AB} = CWD_A + CWD_B - LCD_{AB} \quad (2)$$

Finally, Linkage Mapper combines all NLCCs' into one corridor map, using the mosaic function of ArcGIS (ESRI, 2012). The final corridor layer contains in each cell the minimum value of all NLCCs', which I cropped at a maximum CWD of 200,000.

### 2.8 Effect of roads on elk movements

I attached the CWD values of the corridor matrix to the highway layer at a 50 m interval using ArcGIS and split into 20 highway segments (ESRI, 2012). Proportions of corridors lost to highways were investigated by comparing intersections under (i) exclusion and (ii) inclusion of roads for spring and autumn movement predictions using a paired t-test.

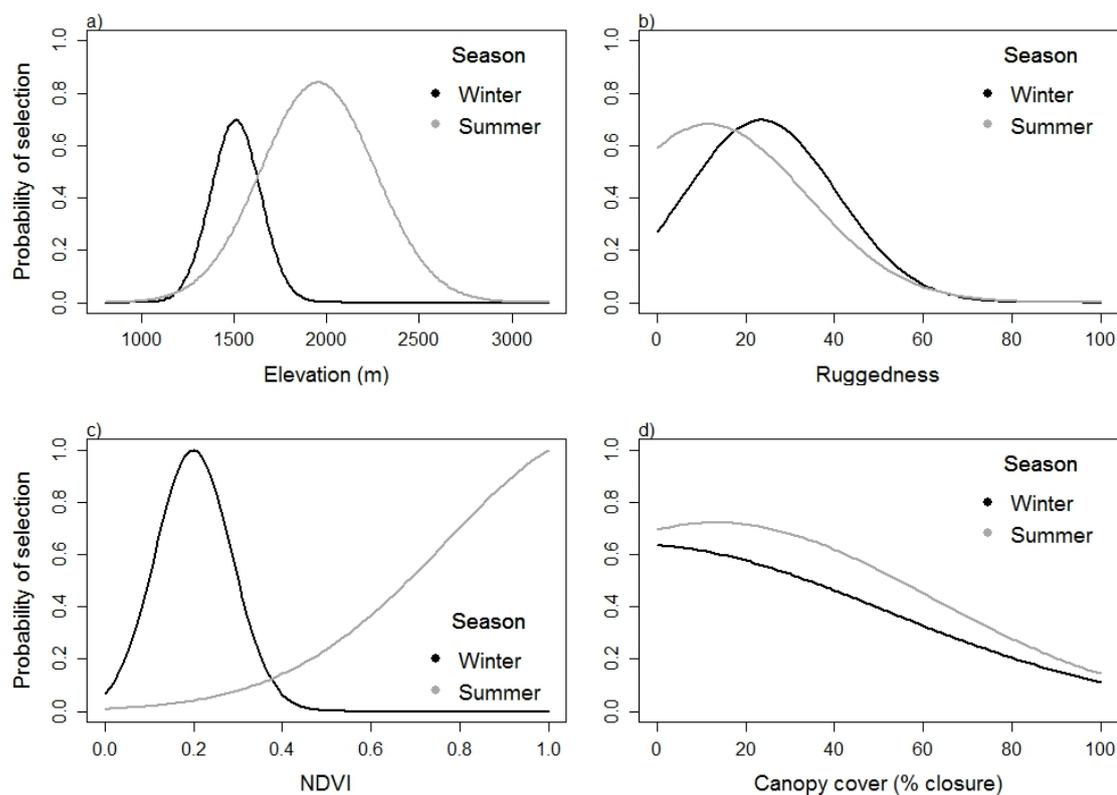
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## 3. Results

### 3.1 Winter and summer habitat selection prediction using RSF

Montane elk selected for rugged open terrain at elevations around 1,500 m in winter and flatter terrain with more cover at higher elevations (~2,000 m) in summer (Figure: 1). NDVI was the main driver for selection in winter and in summer, followed by elevation, ruggedness and canopy cover (Figure: 1). In summer however, selection was stronger driven by elevation and canopy cover than in winter. In winter, elk favored open areas, such as grasslands, croplands, and deciduous forests, while the land cover OTHER was avoided (Table: 2). Strongest selection in summer was for deciduous forests and mixed forest, as cover is high. Open habitat, such as shrub- and grass land, as well as crop fields, were less selected. Least selection in summer was for conifer forest and land cover type OTHER. All MODIS land cover types are in relation to the reference category conifer forest (CONIFER).

The Spearman rank 5-fold cross-validation suggests a very good predictive fit for each fold of the data, with  $\rho = 1$  for each fold of summer, and  $\rho = 0.997, 1, 0.997, 0.997$  and  $0.997$  for winter.



**Figure 1: Selection probability during winter and summer residency as depicted by RSFs.** Relative probability of selection in winter and summer for a) elevation, b) ruggedness, c) NDVI and d) canopy cover.

**Table 2: Resource selection function (RSF) for winter and summer.** General linear mixed model RSF coefficients ( $\beta$ ), standard errors (SE), Wald statistics (Z) and probability values (P) comparing used with available locations across the study area from 2007 to 2011.

Variable	Winter				Summer			
	$\beta$	SE	z	p	$\beta$	SE	z	p
DEM	8.37e-02	9.20e-04	91.23	<0.001	2.06e-02	3.17e-04	64.89	<0.001
DEM <sup>2</sup>	-2.78e-05	3.12e-07	-89.01	<0.001	-5.26e-06	9.15e-08	-57.51	<0.001
TRI	8.13e-02	2.81e-03	28.94	<0.001	2.43e-02	2.11e-03	11.51	<0.001
TRI <sup>2</sup>	-1.73e-03	5.67e-05	-30.59	<0.001	-1.04e-03	3.71e-05	-28.12	<0.001
CC	-1.69e-03	1.00e-03	-1.68	0.092	5.74e-03	8.01e-04	7.17	<0.001
CC <sup>2</sup>	-1.57e-04	1.43e-05	-10.94	<0.001	-2.15e-04	1.05e-05	-20.53	<0.001
NDVI	2.71e-03	4.57e-05	59.32	<0.001	8.42e-04	6.83e-05	12.33	<0.001
NDVI <sup>2</sup>	-6.80e-07	1.17e-08	-58.20	<0.001	-3.70e-08	5.09e-09	-7.27	<0.001
DECIDUOUS*	1.46e+00	3.21e-02	45.38	<0.001	1.00e+00	2.63e-02	28.17	<0.001
MIXED	1.68e-02	4.53e-02	0.37	0.710	6.86e-01	3.23e-02	21.25	<0.001
SHRUB*	5.70e-01	2.87e-02	19.86	<0.001	3.62e-01	1.90e-02	19.02	<0.001
GRASS*	1.47e+00	3.30e-02	44.62	<0.001	1.57e-01	2.84e-02	5.52	<0.001
CROP*	1.56e+00	3.66e-02	42.48	<0.001	-4.35e-01	4.95e-02	-8.80	<0.001
OTHER*	2.40e-02	2.25e-01	0.11	0.915	-2.54e-03	7.49e-02	-0.34	0.735

\* CONIFER, reference category

### 3.2 Elk movement prediction using SSF

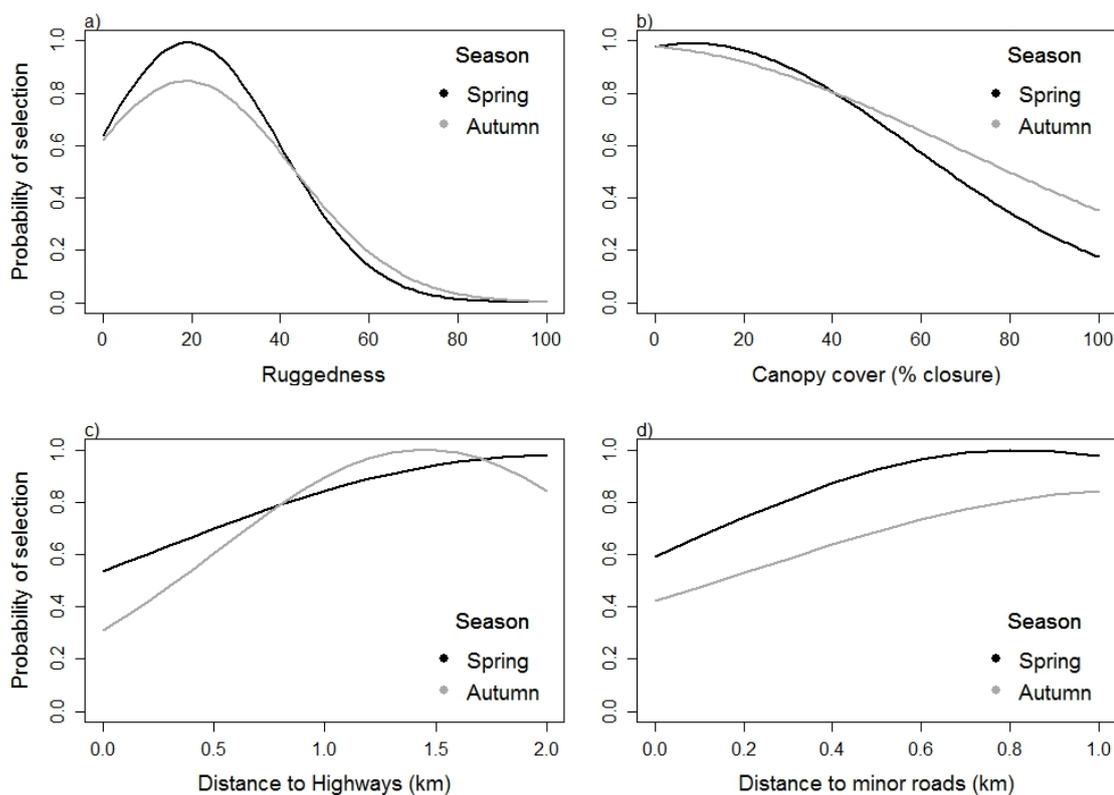
The broken stick model identified active movement speeds during spring slightly faster with  $6.97 \text{ m min}^{-1}$  than in autumn with  $5.87 \text{ m min}^{-1}$  (Appendix: A.6). Movement steps faster than the identified thresholds showed a forward directional tendency (Appendix: A.7).

According to SSF predictions, elk favored deciduous forests, grass- and crop lands, in slight rugged terrain and little canopy cover ( $\sim 20\%$  closure) in spring (Table: 4, Figure: 2). In autumn, elk favored mixed-, deciduous- and conifer forest, as well as grass land (Table: 4). However, high canopy cover was avoided (Figure: 2). The land cover type 'OTHER', as well as close proximity to roads was strongly avoided in both seasons. Friction maps were shown in Figure 3c and 4c.

The  $k$ -fold cross-validation suggests a very good predictive fit of my SSF models (Table: 3).

**Table 3:  $k$ -fold cross-validation of SSFs**, showing model robustness based on observed  $\bar{r}_s$  and  $\bar{r}_s$  expected under random patterns, as well as the 95 % CI for each model. Excellent predictive fits are achieved when of 95 % CI of observed and randoms do not overlap.

Model	Observed		Randoms	
	$\bar{r}_s$	95 % CI	$\bar{r}_s$	95 % CI
Spring no roads	0.989	0.985 – 0.994	-0.181	-0.270 – -0.091
Autumn no roads	0.989	0.984 – 0.993	-0.189	-0.280 – -0.098
Spring including roads	0.982	0.987 – 0.976	-0.181	-0.268 – -0.094
Autumn including roads	0.857	0.830 – 0.884	-0.050	-0.159 – 0.058



**Figure 2: Selection probability during spring and autumn movements as depicted by SSFs.** Relative probability of selection in spring and autumn movements for a) ruggedness, b) canopy closure, c) distance to highways and d) canopy cover.

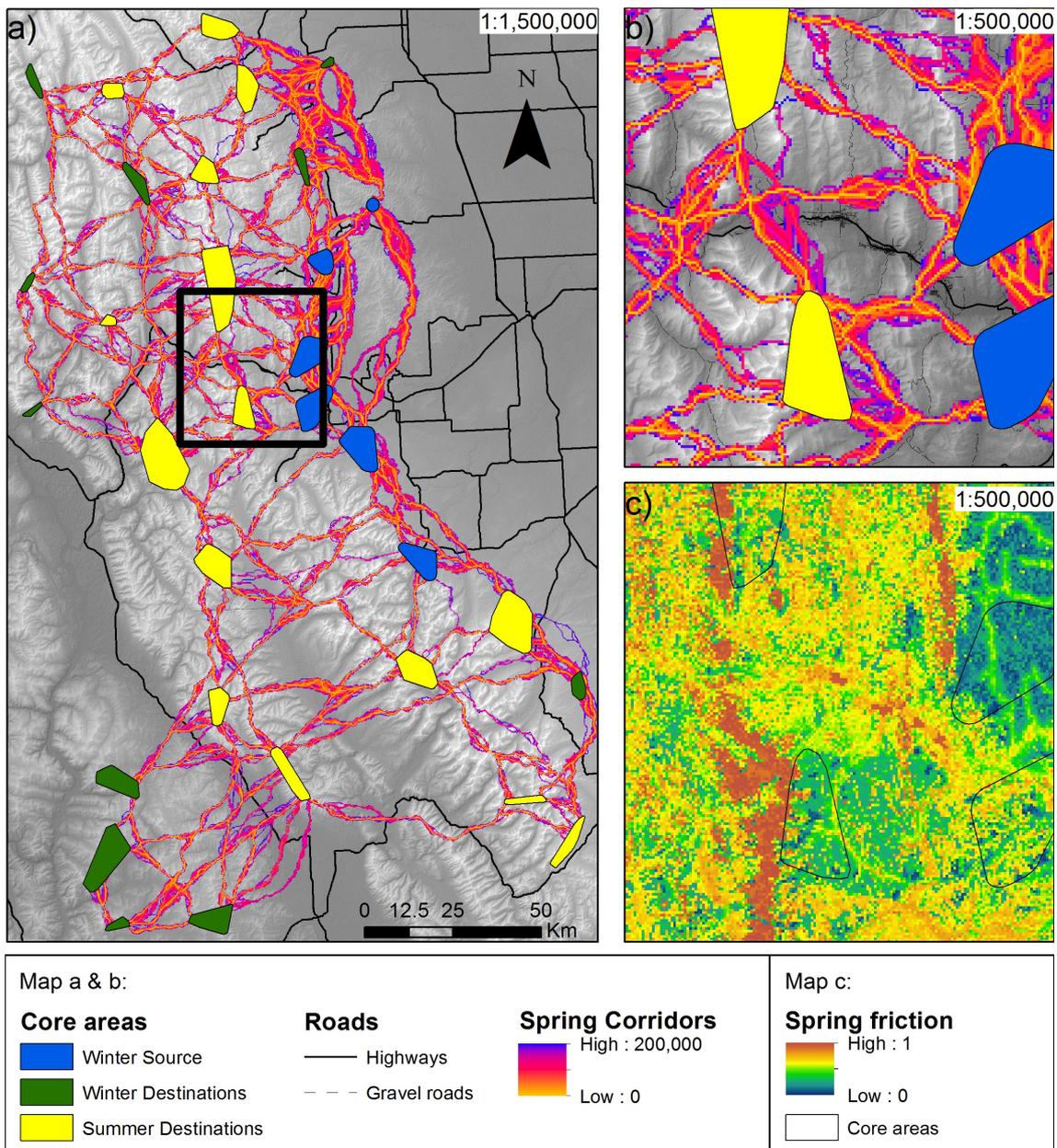
**Table 4: Step selection function (SSF) for spring and autumn movements.** Mixed conditional logit models SSF coefficients ( $\beta$ ), standard errors (SE), Wald statistics (Z) and probability values (P) comparing true steps with available locations at step level from 2007 to 2011.

Variable	Spring				Autumn			
	$\beta$	SE	z	p	$\beta$	SE	z	p
TRI	4.56e-02	4.90e-03	9.30	<0.001	3.29e-02	7.09e-03	4.64	<0.001
TRI <sup>2</sup>	-1.18e-03	9.72e-05	-12.13	<0.001	-8.72e-04	1.33e-04	-6.56	<0.001
CC	3.53e-03	2.19e-03	1.61	0.107	-1.30e-03	3.18e-03	-0.41	0.681
CC <sup>2</sup>	-2.07e-04	3.22e-05	-6.45	<0.001	-8.91e-05	4.45e-05	-2.01	0.045
DISTHWY	6.02e-04	2.12e-04	2.84	0.005	1.63e-03	3.91e-04	4.16	<0.001
DISTHWY <sup>2</sup>	-1.51e-07	8.59e-08	-1.76	0.078	-5.61e-07	1.58e-07	-3.55	<0.001
DISTSMD	1.28e-03	2.81e-04	4.54	<0.001	1.26e-03	4.83e-04	2.61	0.009
DISTSMD <sup>2</sup>	-7.77e-07	2.32e-07	-3.35	<0.001	-5.67e-07	3.95e-07	-1.43	0.152
DECIDUOUS*	2.13e-01	6.06e-02	3.52	<0.001	5.96e-03	9.56e-02	0.06	0.950
MIXED*	5.32e-02	9.12e-02	0.58	0.559	4.47e-02	1.39e-01	0.32	0.748
SHRUB*	-3.57e-02	5.85e-02	-0.61	0.550	-9.71e-02	8.53e-02	-1.14	0.255
GRASS*	1.71e-01	6.32e-02	2.71	0.007	1.55e-03	1.04e-01	0.02	0.988
CROP*	1.35e-01	7.74e-02	1.75	0.081	-1.75e-01	1.46e-01	-1.20	0.232
OTHER*	-1.82e+00	2.66e-01	-6.83	<0.001	-1.97e+00	4.67e-01	-4.22	<0.001

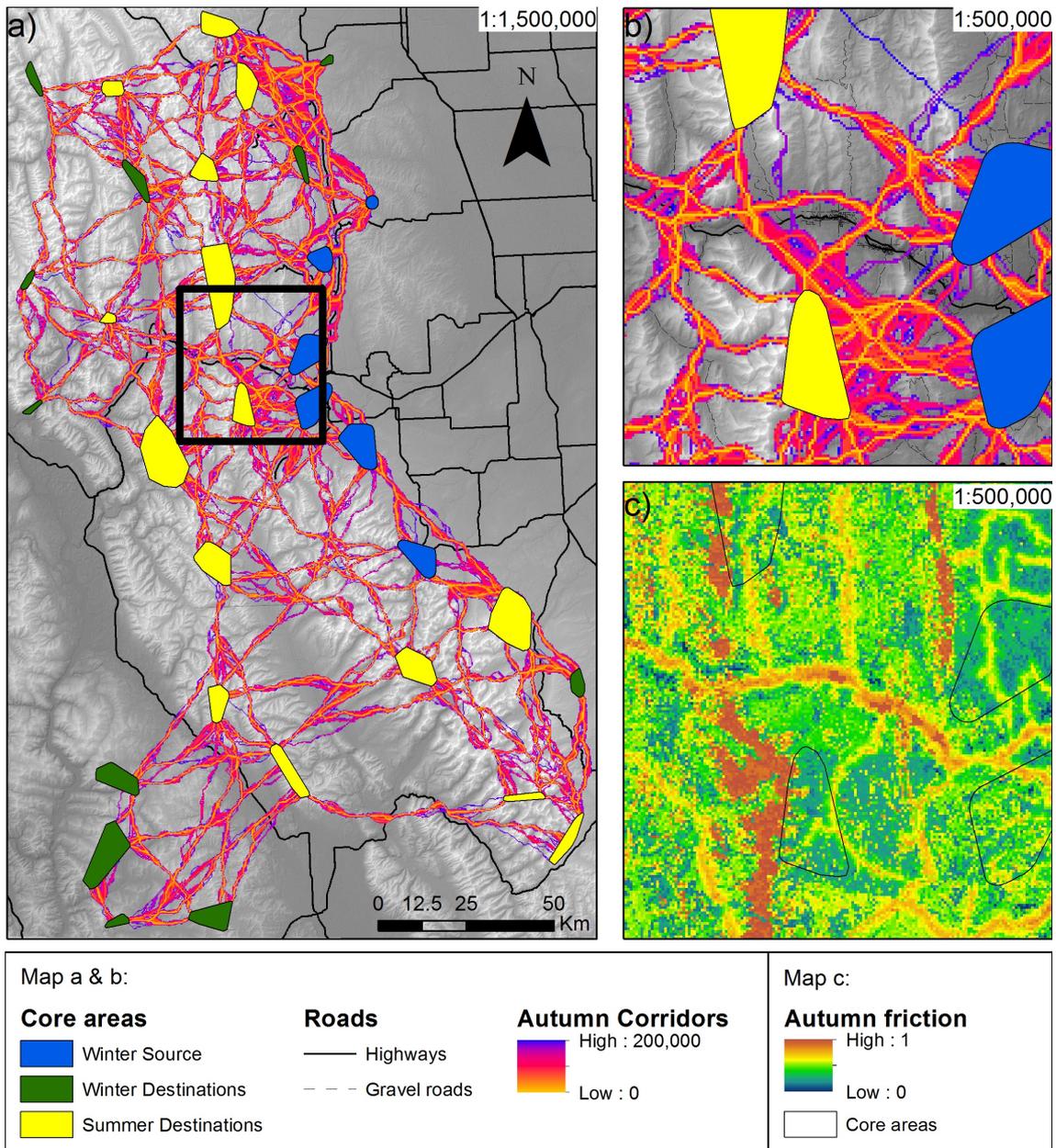
\* CONIFER, reference category

### 3.3 Elk connectivity

Linkage Mapper produces a continuous raster with cost distance values reflecting how costly it is to move between core areas. The values range from zero, where least-cost-path are optimal, upwards, reflecting higher cost for movement. For final corridor maps of spring and autumn movements, a cutoff value for CWD of 200,000 was used (Figure: 3 and 4).



**Figure 3: Corridor map of spring movements.** a) Normalized least-cost-corridors, with low values as optimal, connecting winter with summer core areas, b) close up section along highway 3, c) close up friction map produced from spring movements.



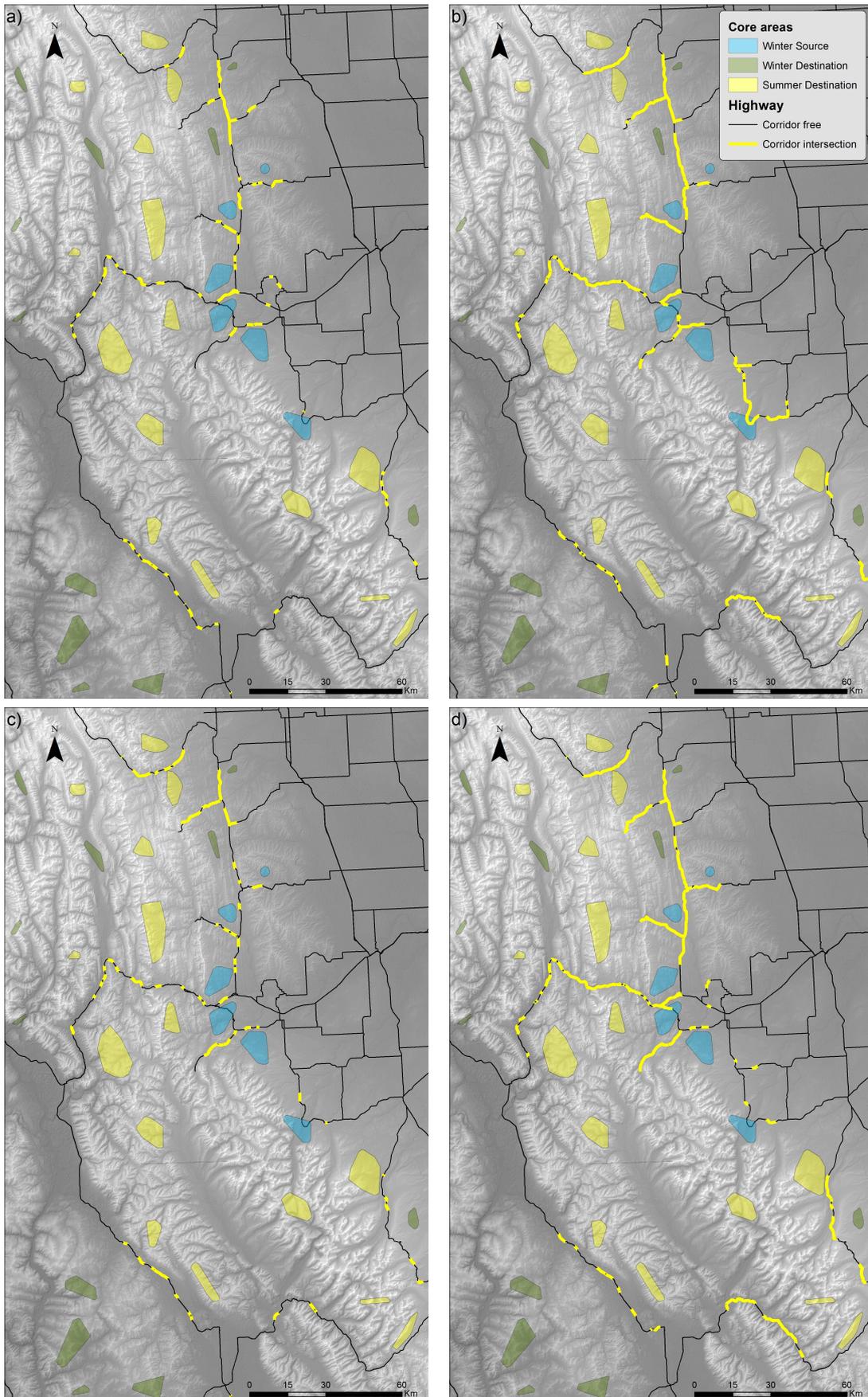
**Figure 4: Corridor map of autumn movements.** a) Normalized least-cost-corridors, with low values as optimal, connecting summer with winter core areas, b) close up section along highway 3, c) close up friction map produced from spring movements.

### 3.4 Effect of roads on elk movements

Total corridor intersection lengths were 358.6 km and 382.2 km for spring and autumn, respectively, under natural movement conditions when (i) roads were excluded (Figure: 5b, 5d). After inclusion of distance to roads as predictors in habitat models (ii), total measured corridor highway intersection lengths were reduced to 172.9 km for spring movements, and 171.7 km for autumn respectively (Figure: 5a, 5c). I found a significant loss of corridor-highway permeability in both seasons (in spring, paired t-test,  $t=-2.452$ ,  $df=19$ ,  $p=0.024$ , in autumn, paired t-test,  $t=-4.979$ ,  $df=19$ ,  $p<0.0001$ , Table: 5), after taking into account of the effect of roads on connectivity.

**Table 5: Road crossings.** Paired sampled t-test of mean ( $\bar{x}$ ) CWD values of 20 road segments between corridor road crossings under inclusion and exclusion of roads as predictors in models of spring and autumn movements.

Season	Roads		No roads		N	t	p
	$\bar{x}$	SE	$\bar{x}$	SE			
Spring	0.366	0.061	0.518	0.067	20	-2.452	0.024
Autumn	0.347	0.063	0.593	0.068	20	-4.979	<0.0001



**Figure 5: Corridor-road intersections** of a) 172.9 km in spring considering roads, b) 358.6 km in spring under exclusion of roads, c) 171.7 km in autumn considering roads, and d) 382.2 km in autumn under exclusion of roads, where movement is impeded by highways.

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## 4. Discussion

### 4.1 Ecology of young male elk

First key improvement to previous work by Squires et al. (2013) is that I adapted to the seasonal habitat preference of elk by targeting the connection of suitable winter with summer habitat using differing spatio-temporal movement behavior. Most elk herds in this area are migratory, which means they move to higher elevation to gain access to better quality food or escape predators (Bischof et al., 2012). This means the habitats for summer and winter differ considerably. Varying seasonal environmental conditions, such as bare deciduous forests in spring or leaf fall as well as hunting pressure in autumn alter movement behavior of elk depending on time of the year (Ciuti et al., 2012b; Bischof et al., 2012; Frair et al., 2005). I built SSFs taking into considerations these key periods of elk ecology. Spring friction maps were built to understand the effort required by elk to move from winter ranges (capture sites) to summer ones, while autumn friction maps were deployed to depict the corridors from summer hotspots to new winter areas potentially targeted by dispersers. The novel approach I introduced here strongly takes into account of elk ecology, because elk move through the landscape and disperse to novel areas through a sequence of steps that are synchronized with spring and fall migration periods (Killeen et al., 2014).

Second key improvement, which is novel about this study, was that I particularly focused on the large scale movement ecology of young male elk (*Cervus elaphus*). Wildlife corridors for any large mammal can be designed for different purposes, depending on specific movement types, such as foraging, searching, migration and dispersal (Chetkiewicz et al., 2006). Depicting large scale wildlife corridors in order to improve gene-flow across a landscape has to be focused on facilitating the movement of individuals potentially dispersing. Studies however, have been limited due to difficulty of maintaining an adequate sample size of identified true dispersers, especially in hunted populations (Petersburg et al., 2000). Killeen et al. (2014) pointed out, that dispersal is inextricably dominated by males, as young males leave their mother group during their second year spring migra-

tion, after snow has melted, exploring new and unknown landscapes (Killeen et al., 2014). Focusing on large scale movement behavior of all young males, best reflects dispersal behavior in regards to gene-flow (Broquet & Petit, 2009).

## 4.2 Dispersal corridor matrix

The wildlife corridor matrix provided in this study differs to most other output of LCP analysis (Cushman et al., 2009; Squires et al., 2013). In other studies, source and destination locations are often placed in regular intervals or along a border rather than inside high suitable residency areas across the landscape. Especially over large distances, these LCP run into the drawback that they run together into a single main corridor as seen in Cushman et al. (2009) and Squires et al. (2013). A young and unexperienced male elk does not follow a single and most suitable route during dispersal. There are other extrinsic factors, such as competition, high population density or the encounter of a predator, which is not accounted for here, that potentially influence the movement or force a change of direction (Fortin et al., 2005). Therefore, it is important to map multiple potential habitat patches across the landscape, that act as nodes, to create a matrix of corridors between them. Furthermore, the common 'Cost distance' and 'Cost path' tools of ArcGis provide a corridor output of one grid cell width, which is not biologically meaningful (ESRI, 2012; Sawyer et al., 2011). Linkage Mapper on the other hand, allows to produce a continuous output with CWD from the optimal LCP between core area pairs. This output is ecologically much more meaningful, compared than buffered single line corridors (McRae & Kavanagh, 2011).

Roads strongly impact the biological diversity and integrity of wildlife communities (Trombulak & Frissell, 2000). Whittington et al. (2005) highlighted with the example of the wolf (*Canis lupus*) that high road density seems to have a strong impact on animal movement, especially in mountain valleys. Ciuti et al. (2012b) found that ungulates are negatively affected by roads (e.g. increased vigilance, decreased foraging) with increasing human activity (high vehicle traffic combined with recreational and hunting activities). Seidler et al. (2014) also identified that major highways induce increased stopover in movement or provide complete barriers in migration patterns of pronghorn (*Antilocapra americana*). Therefore, I modeled two scenarios with roads as part of the friction across the landscape that reflect movement behavior for each spring and autumn. The first model, where roads are absent, shows natural movement of elk lost to the current road network, and the second model highlights highway sections that are of primary con-

servation concern, regarding dispersal ecology of young male elk moving between core areas.

### 4.3 Application and future directions

I depicted summer and winter hotspots based on high RSF scores and connected them using the Linkage Mapper tool, following the rules of friction maps depicted by SSFs. I showed how elk would naturally move in absence of roads (i), and then imposed the restriction of roads (ii). Subsequently, I quantified the loss of connectivity across the study area due to major highways.

Primarily, this information can be used to make better informed conservation management decisions, and in particular to improve gene-flow of elk populations across the landscape in the northern Rocky Mountains. Focus should be on facilitating movement, as well as identifying areas, where it is impeded (McRae et al., 2012). However, the corridor map provided is not a single end stage result. The friction maps can be used to investigate the connectivity and loss to roads by linking any areas of interest, such as protected areas, within the study area. Furthermore, this information can be used in road development. Before placement of new roads, the influence of these on current movement corridors can be investigated by integrating them into the road model prior construction. A next step in this study could be to use this spatio-temporal movement behavior model of elk dispersal and compare it with the genetic differentiation of elk across the landscape. In this way it is possible to understand the actual effect of road barriers on the genetic diversity and population structure in the study area (Storfer et al., 2006).

Better understanding the dispersal ecology of any species is essential to adapt landscape resistance values, in order to design functional wildlife corridors for dispersers. Focusing on the young male individuals to improve gene-flow, as it is them among many cervid species, is applicable to many other ungulate species (Long et al., 2008; Petersburg et al., 2000). Lastly, this method aids conservation managers as a tool to make better informed management decisions, not only for migratory ungulates, also for any other geographically restricted populations in other regions such as Africa or Asia (Bolger et al., 2008; Sodhi et al., 2010)

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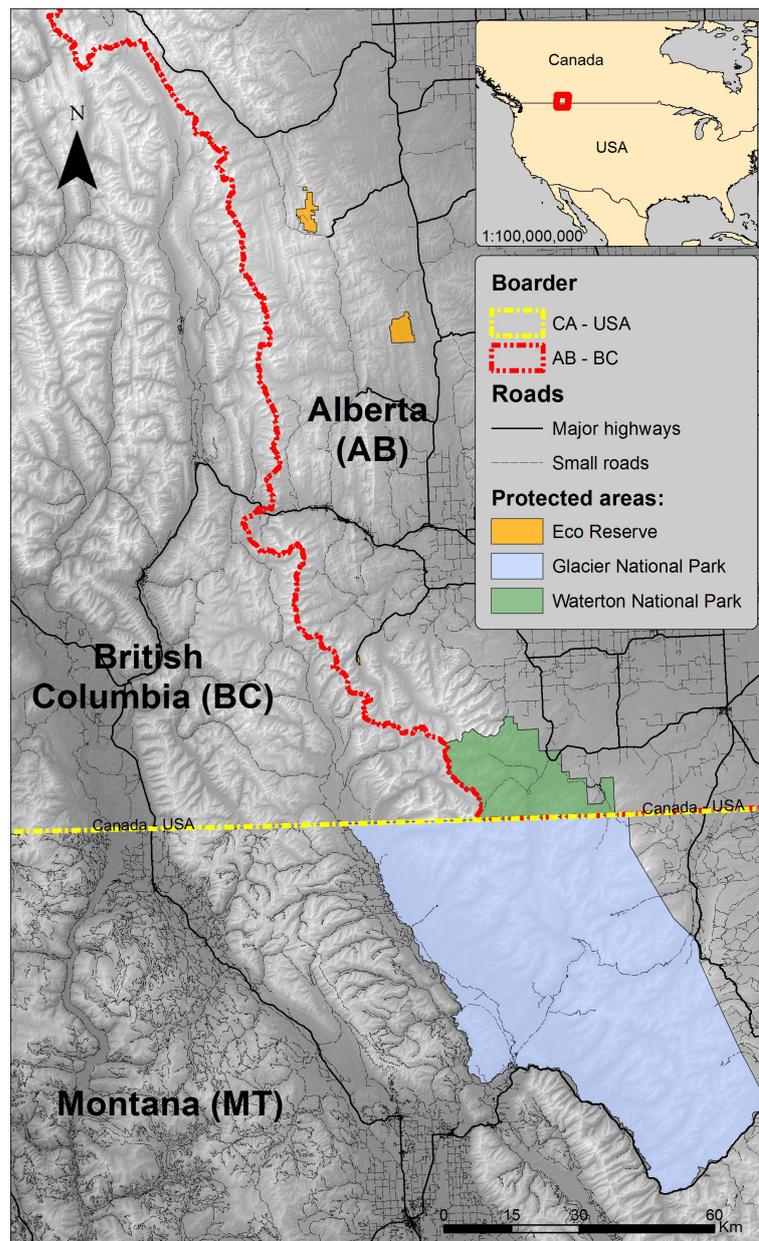
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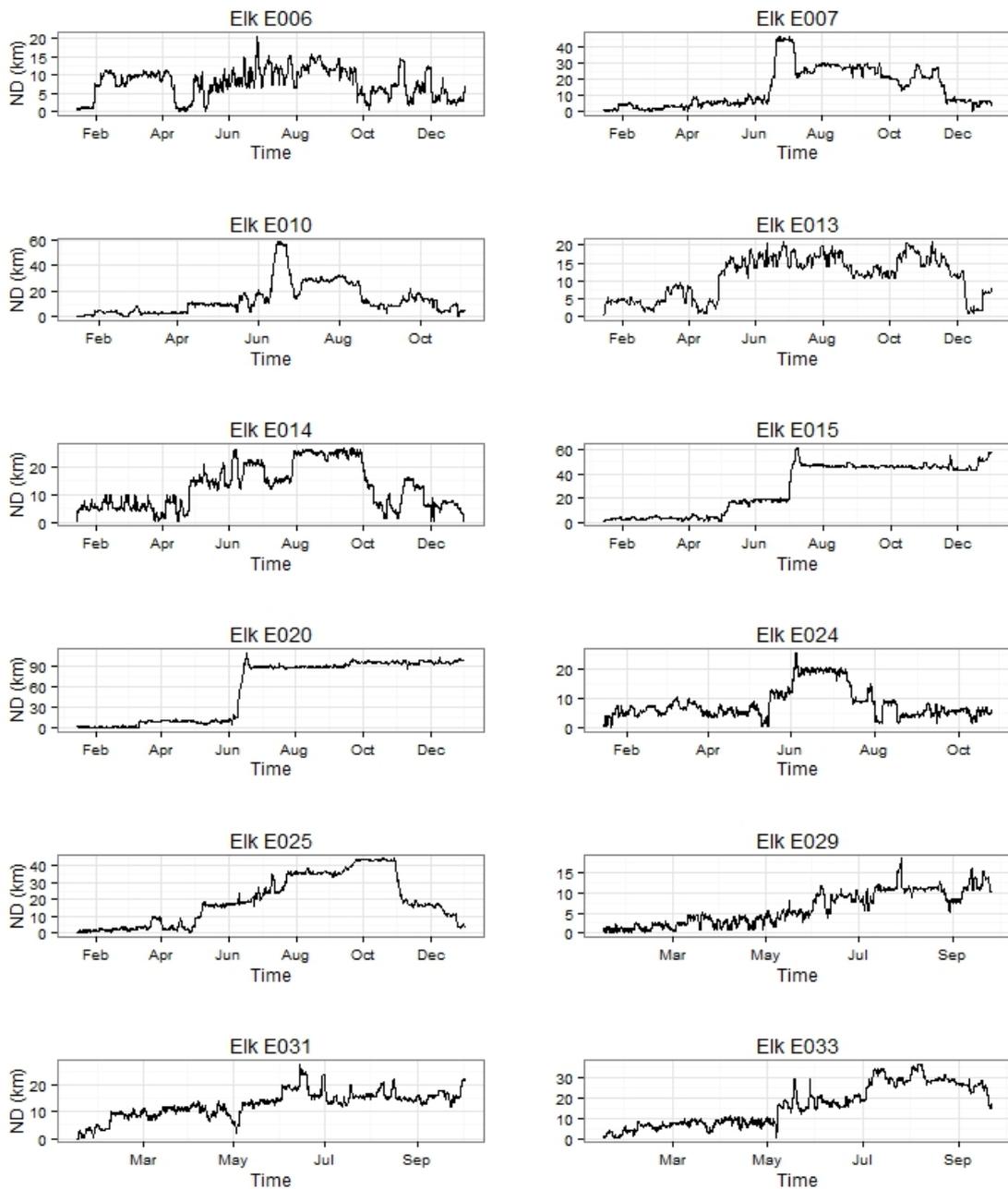
# Appendices

# Study Area

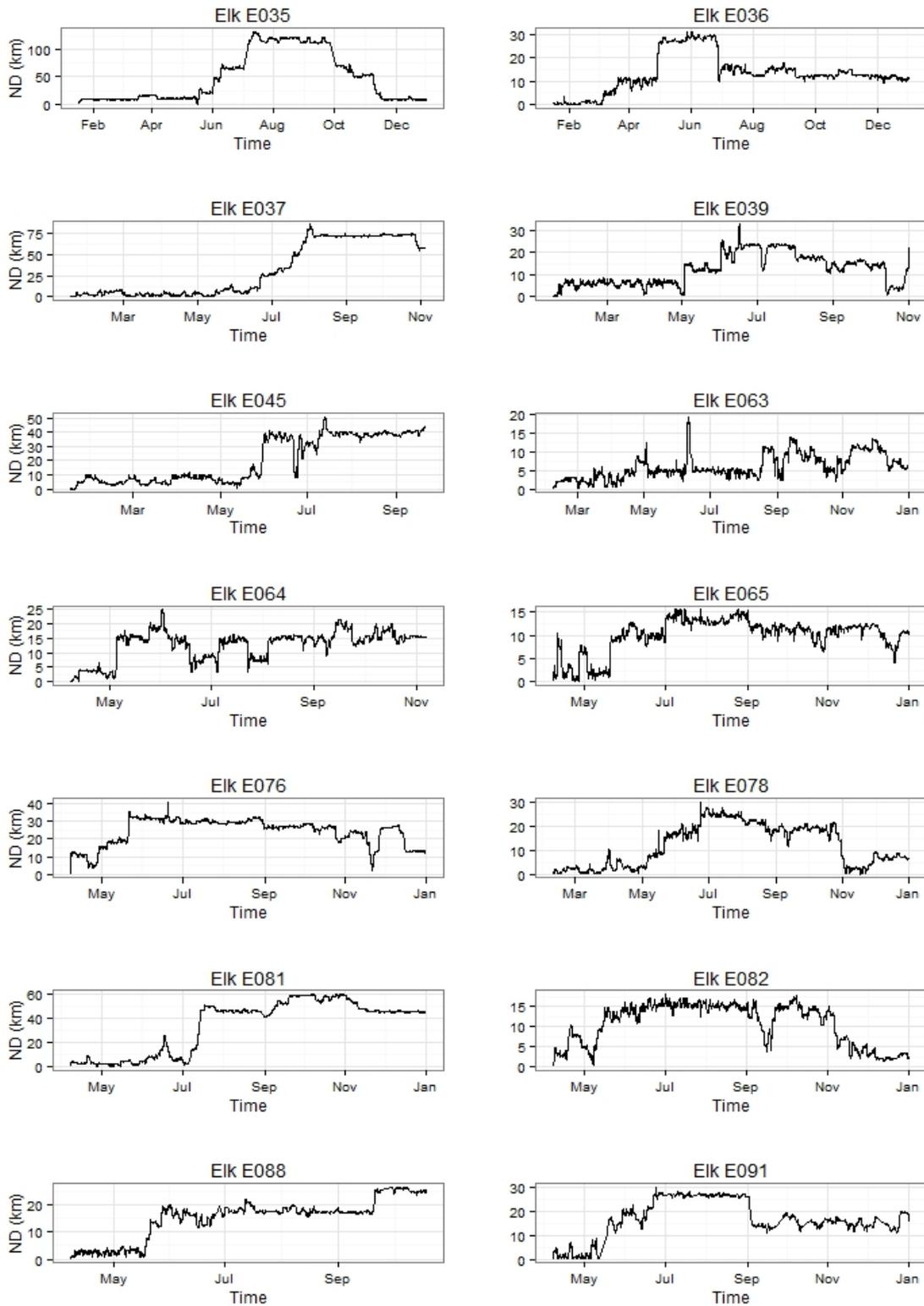


**Figure A.1:** Study area at the multi-border of Montana, Alberta and British Columbia, with protected areas and road network.

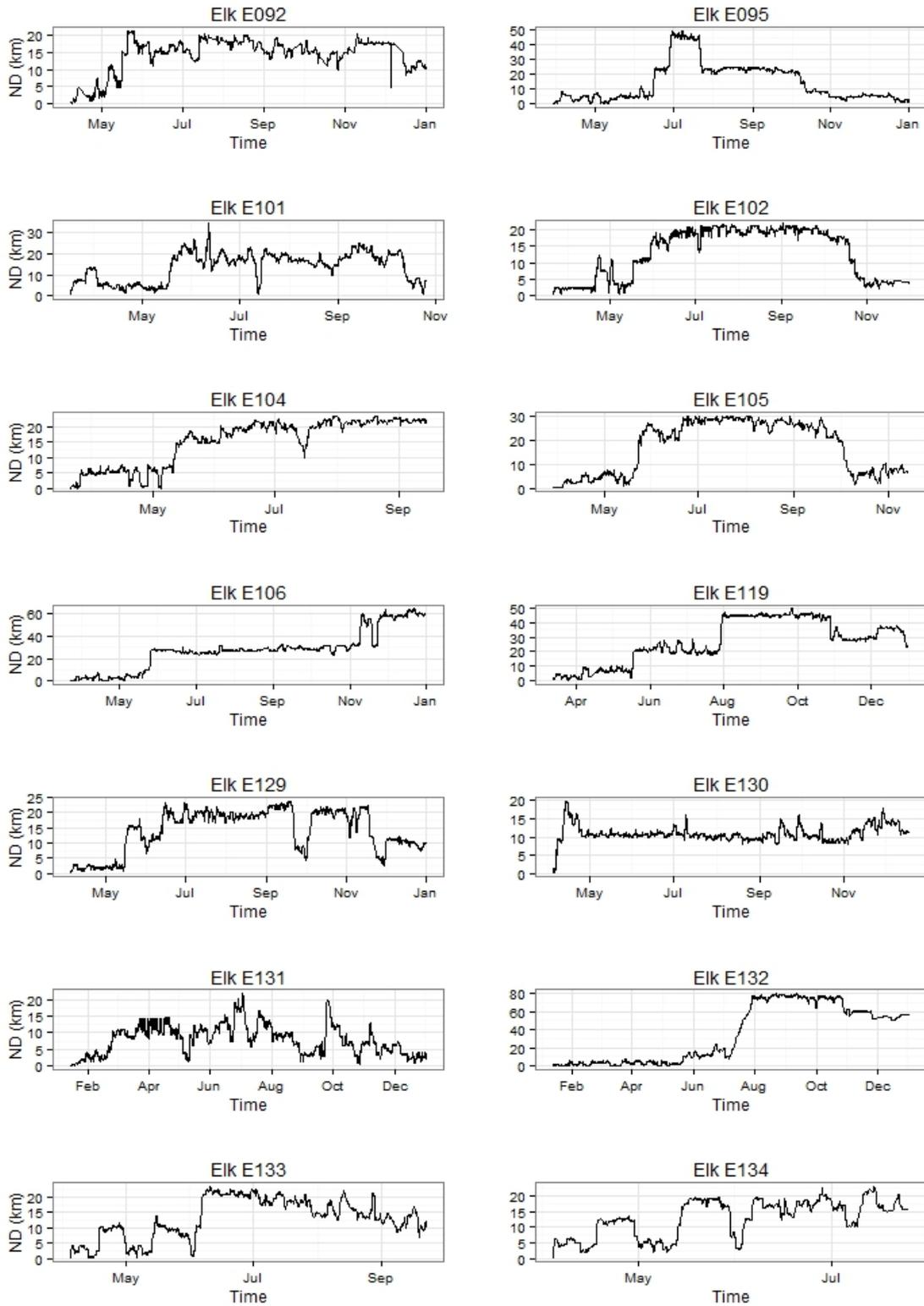
# Elk movement



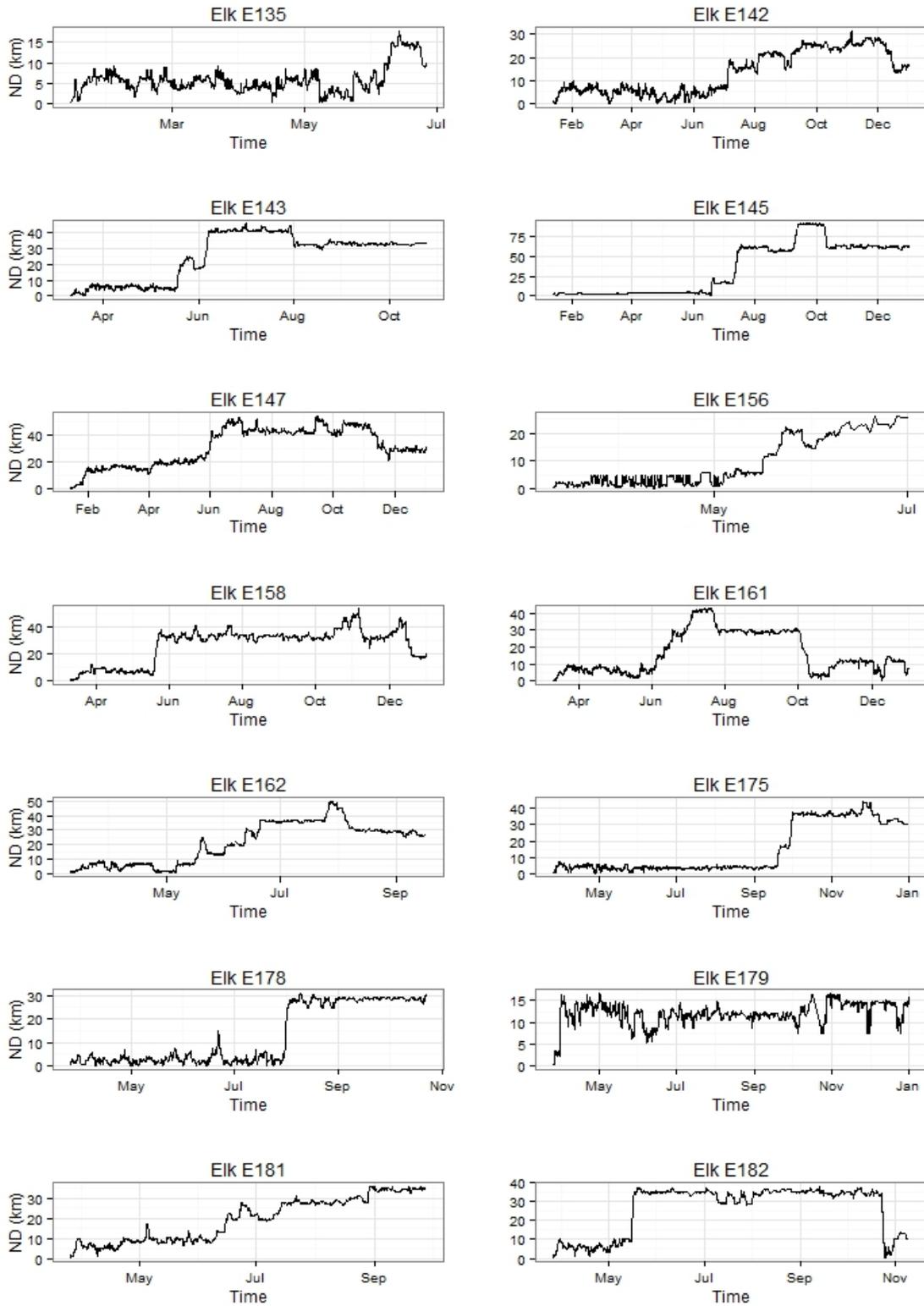
**Figure A.2: Net displacement.** First year net displacement (ND, in km) of all young male elk.



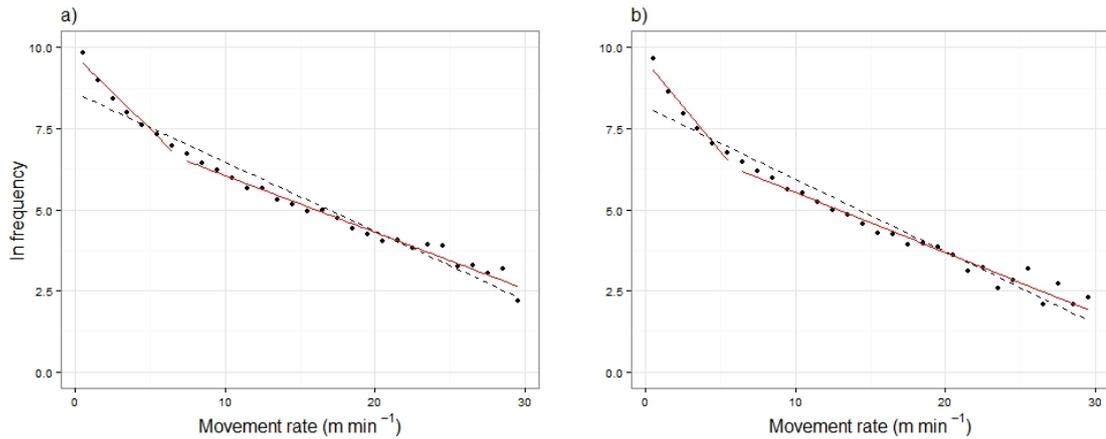
**Figure A.3: Net displacement (continued).** First year net displacement (ND, in km) in km of all young male elk.



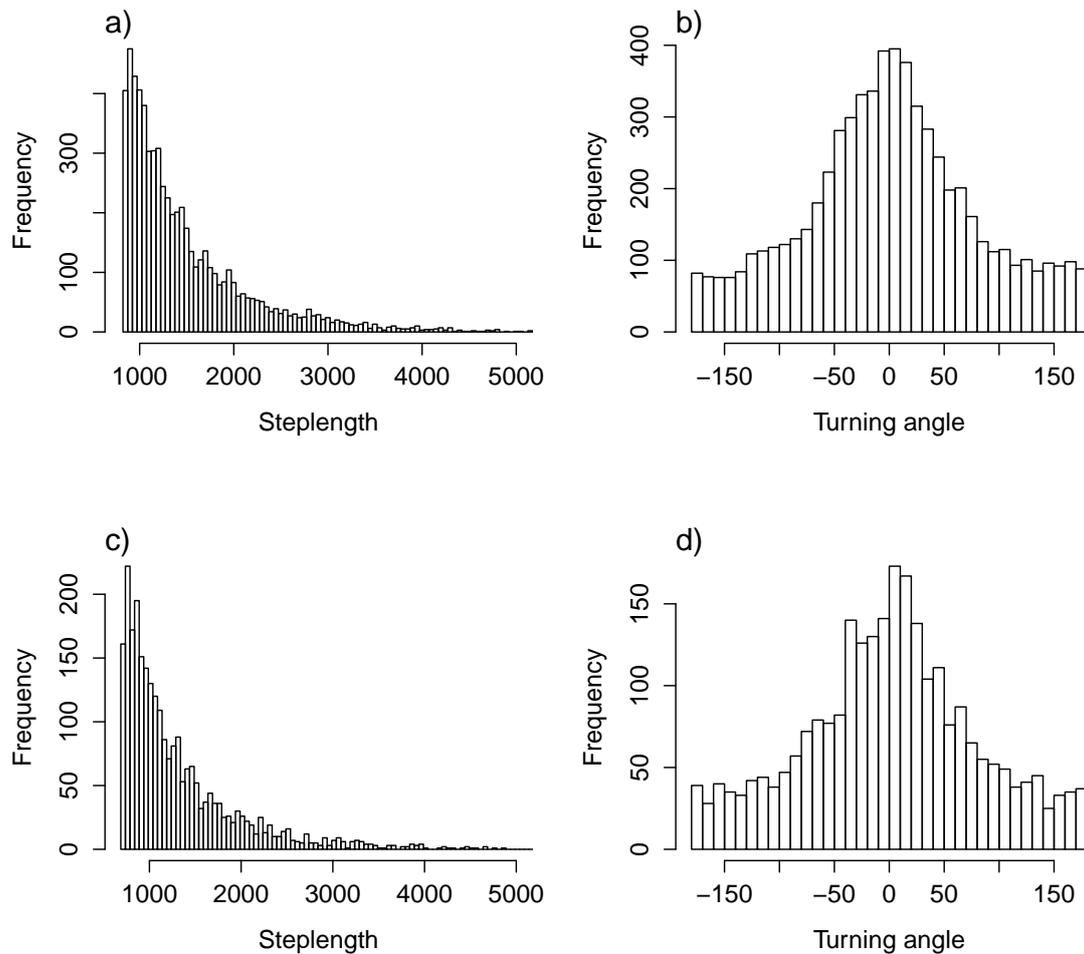
**Figure A.4: Net displacement (continued).** First year net displacement (ND, in km) in km of all young male elk.



**Figure A.5: Net displacement (continued).** First year net displacement (ND, in km) in km of all young male elk.



**Figure A.6: Broken stick model** for a) spring movements showing the breaking point at  $6.97 \text{ m min}^{-1}$  and b) autumn movements with the breaking point at  $5.87 \text{ m min}^{-1}$



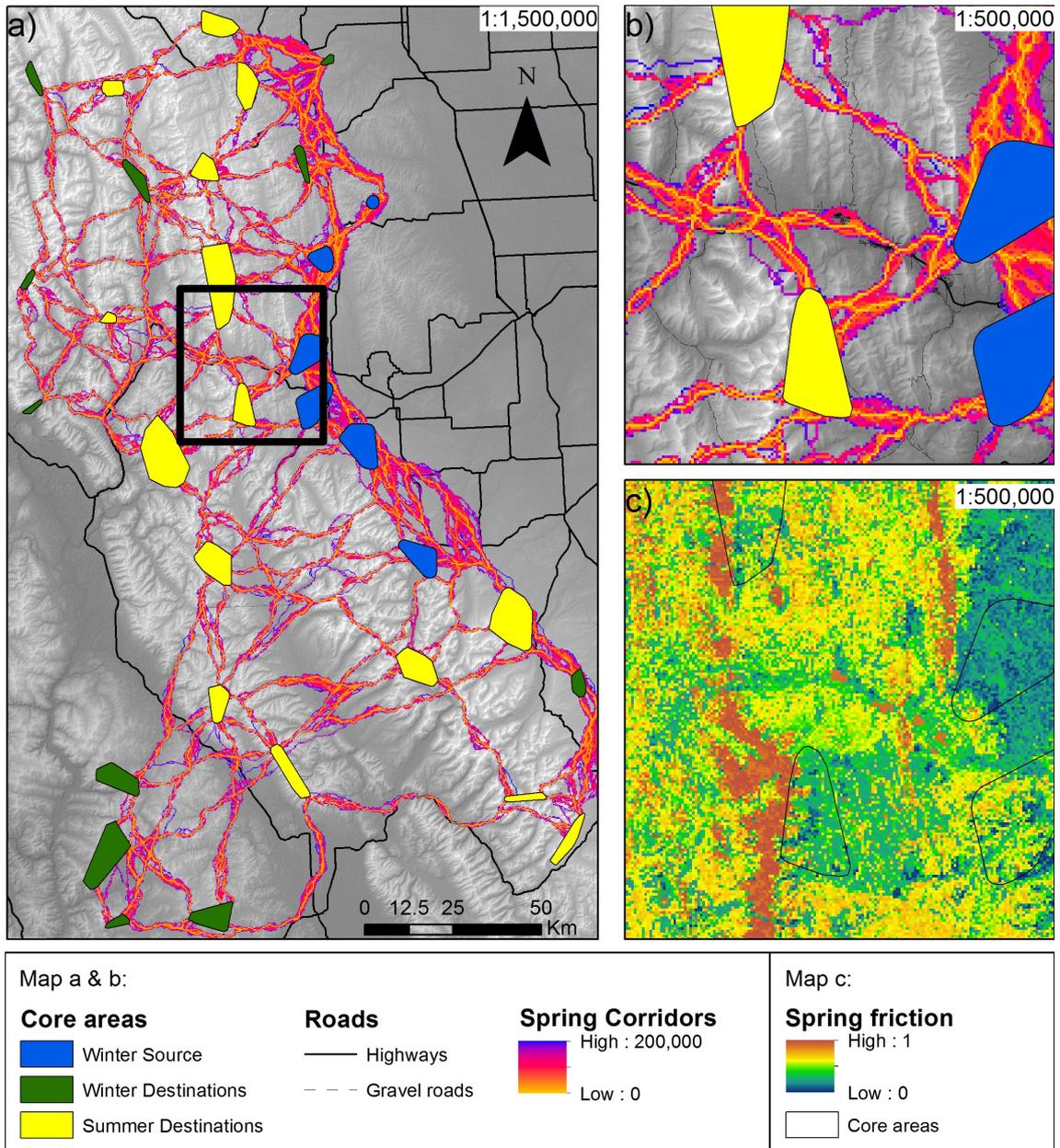
**Figure A.7: Movements** of steps larger then the indicated breaking point in figure A.6, showing a) steplength and b) turning angles for spring, and c) steplength and d) turning angles for autumn movements.

## SSF without roads

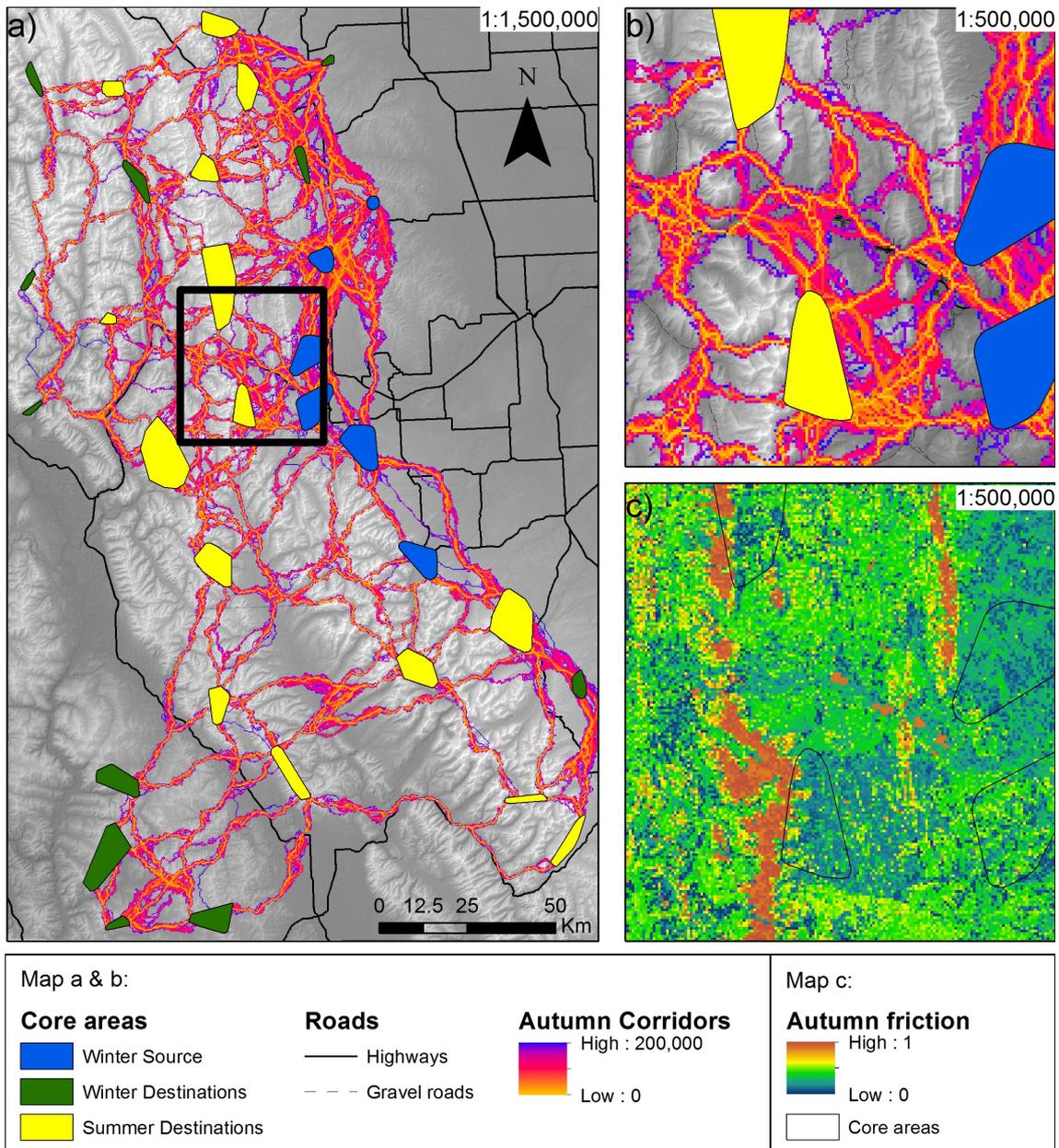
**Table A.1: Step selection function (SSF) for spring and autumn movements excluding roads.** Mixed conditional logit models SSF coefficients ( $\beta$ ), standard errors (SE), Wald statistics (Z) and probability values (P) comparing true steps with available locations at step level for from 2007 2011.

Variable	Spring				Autumn			
	$\beta$	SE	Z	P	$\beta$	SE	Z	P
TRI	4.86e-02	4.89e-03	9.95	<0.001	3.64e-02	7.07e-03	5.15	<0.001
TRI <sup>2</sup>	-1.22e-03	9.72e-05	-12.5	<0.001	-9.01e-04	1.33e-04	-6.83	<0.001
CC	3.59e-03	2.19e-03	1.64	<0.001	-1.23e-03	3.17e-03	-0.39	0.697
CC <sup>2</sup>	-2.05e-04	3.21e-05	-6.39	0.101	-8.58e-05	4.43e-05	-1.94	0.053
DECIDUOUS*	2.01e-01	6.05e-02	3.32	<0.001	-3.73e-02	9.50e-02	-0.39	0.695
MIXED*	4.33e-02	9.11e-02	0.48	<0.001	1.88e-02	1.38e-01	0.14	0.892
SHRUB*	-5.48e-02	5.82e-02	-0.94	0.349	-1.16e-01	8.48e-02	-1.36	0.173
GRASS*	1.25e-01	6.28e-02	1.99	0.047	-6.27e-02	1.03e-01	-0.61	0.542
CROP*	8.41e-02	7.69e-02	1.09	0.275	-9.70e-02	1.46e-01	-1.70	0.089
OTHER*	-1.82e-00	2.66e-01	-6.83	<0.001	-1.96e-00	4.66e-01	-4.21	<0.001

\* CONIFER, reference category



**Figure A.8: Corridor map of natural spring movements under exclusion of roads.** a) Normalized least-cost-corridors, with low values as optimal, connecting winter with summer core areas, b) close up section along highway 3, c) close up friction map produced from spring movements.



**Figure A.9: Corridor map of natural autumn movements under exclusion of roads.** a) Normalized least-cost-corridors, with low values as optimal, connecting summer with winter core areas, b) close up section along highway 3, c) close up friction map produced from spring movements.