

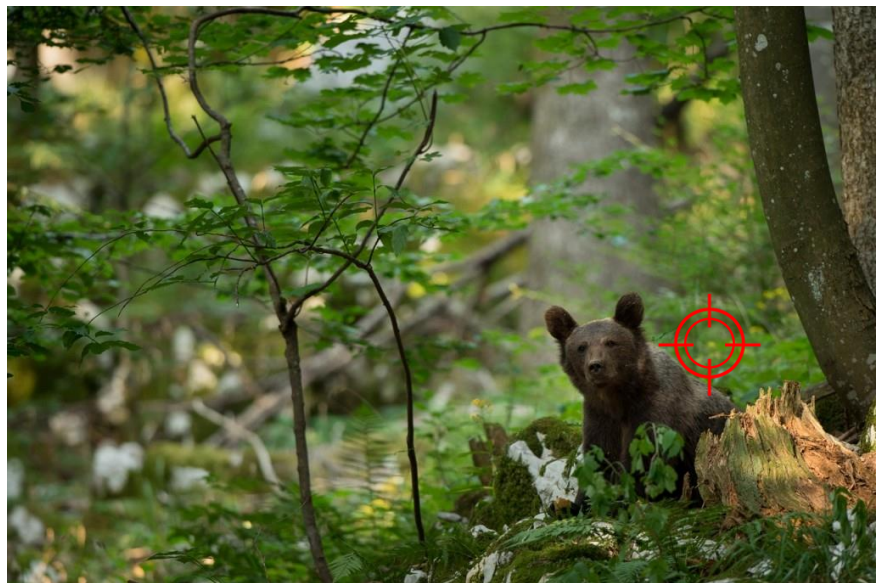
Laboratory of Geo-information Science and Remote Sensing

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Space-use strategies of brown bears (*Ursus arctos*) to avoid the human hunter

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Space-use strategies of brown bears (*Ursus arctos*) to avoid the human hunter

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ABSTRACT

Background: Tolerance for brown bears (*Ursus arctos*) in Sweden has had a long and complicated history, with ever-changing attitudes on human-bear coexistence in the last century. Currently, the population size is managed by establishing an annual quota for recreational hunters every year. The efficiency of hunters is impressive, and the quota is typically met within the first week of the hunting season. The hunt has a striking demographic impact, and the average lifespan of bears within the study site is now only five years. There are, however, several individuals (up to 22 years old) that appear to cope well with the hunting pressure, and have survived several successive hunting seasons. It remains unclear how these individuals adjust their behavioural strategies for avoiding being killed by hunters, what they are doing differently compared to individuals that are killed at younger age, and how that contributes to their survival. The bears in question are those occupying the wood-production forests of Dalarna and Gävleborg counties of central Sweden. Whether or not these bears display a habitat selection shift with the onset of the hunting season is established first. Following this, space-use between survivor and non-survivor bears is compared.

Methodology: To determine if a habitat shift occurs with the onset of the hunting season, resource selection functions were applied comparing used (recorded GPS) locations with available (randomly generated) locations. Models were created both at the population level (using a binomial GLMM with use vs. available as the response variable, and bear-year as a random effect) as well as for each individual bear-year (binomial GLMs with use vs. available as the response variable). The covariate “Hunt seasonality” is a binary variable, categorising locations by whether they were recorded before the hunting season began, or recorded during the hunting season. This variable was included as an interaction term for all landscape variables in the models, and sensitivity to this interaction term was evaluated by p-value of significance (chi-square test for GLMM, F-test for GLM). To then evaluate the magnitude of the habitat shift, parameter estimates for all landscape variables from individual bear-year models were entered into a principal component analysis. The distance between paired observations (before and after hunt began, for the same bear-year), were computed, and survivors were compared with non-survivors.

To analyse space-use amongst survivors and non-survivors, habitat use was estimated for each group using logistic regression with a binary response term of survivor (=0) and non-survivor (=1). Here, both hunt seasonality and bear-age were included as interaction terms.

Principal findings: Bears changed their resource selection in response to hunting (seasonality). This was evident for their habitat selection both at the population-level (e.g. “Habitat” variable, chi sq. test, p value < 0.01), and at the individual-level (e.g. 52% of individuals depicting shift in “Habitat” variable selection, and well over 5% of bear-years shifted selection for all other spatial features). The magnitude of this shift in behaviour did not differ significantly between survivors and non-survivors, and both groups appeared equally sensitive. In terms of habitat-use, when compared to non-survivors, survivors showed kept further away from most anthropogenic features such as minor roads and buildings, occupied locations with more rugged and elevated terrain, closer to major roads, and used habitats that offered more cover.

Conclusion: Most bears notice the onset of the hunting season and adjust behaviour accordingly. These adjustments have various degrees of success, and three distinct space-use strategies have been gleaned from successful survivors: 1) The use of impenetrable habitats; 2) The use of locations making bears less-detectable; and 3) Protection from the human-shield effect, by using areas close to major roads. Deeper exploration into the role that vegetation density and hunter distribution play is needed to further confirm the proposed strategies.

Keywords: brown bear, coexistence, collar data, GPS, habitat selection, hunting, positional information, Sweden, resource selection functions, *Ursus arctos*

LIST OF TABLES AND FIGURES

Table 3.1: Overview of all spatial variables processed for further statistical analysis	10
Table 3.2: Reclassification of SMD land-cover raster	11
Table 3.3: Description of habitat-use candidate models	18
Table 4.1: Significance of “hunt seasonality” interaction terms on the spatial variables	20
Table 4.2: Direction of the model coefficients as derived from the population-level RSF	21
Table 4.3: Overview of all principal components and their relative importance in describing overall variance	23
Table 4.4: Overview of all independent variables and their correlation with/‘loading’ on the principal components	24
Table 4.5: Results from the Welch two-sample t-test, measuring the distance in the PCA space between two paired observations. The observation pairs were grouped into “survivor” or “non-survivor”, and the mean difference size compared between these two groups	25
Table 4.6: Comparison of candidate models and their performance in AICc terms	26
Table A.1: $\Delta AICc$ values for the different anthropogenic density rasters	42
Table A.2: Comparing the two terrain roughness indices performance in AICc terms	43
Table A.3: Table with Variance Inflation Factors of final selection of variables	43
Table B.1: Parameter estimates of the spatial variables in the population-level model	44
Figure 3.1: Land cover over the study site and its location within the Scandinavian Peninsula	7
Figure 3.2: Pre-processing workflow and data preparation	12
Figure 3.3: Histogram of hunt “death-day” of all dead female collared bears	14
Figure 3.4: Visual overview of steps taken in the statistical analysis	15
Figure 3.5: Histogram showing the distribution of age of killed bears	18
Figure 4.1: Distribution of brown bear mortality sites between 2006 & 2016	19
Figure 4.2: Odds ratios of individual bear-years for the “midage forest” habitat type, distance to building, and elevation variables	22
Figure 4.3: PCA biplot, with observations colour-coded by survival-status that hunting season	24
Figure 4.4: Overview of habitat use model, with effects of all spatial variables depicted, unscaled	26
Figure 4.5: Effect of interaction term “Age” and “Hunt Seasonality” on response variable	27
Figure 4.6: Interaction effect of “age” on the anthropogenic and topographic variables	28
Figure 4.7: Interaction effect of “hunt” on the anthropogenic and topographic variables	28
Figure A.1: Correlation of all pairs of variables	43
Figure B.1: Effect plot for population-level model	45
Figure B.2: Odds-ratio plots of habitat types	46
Figure B.3: Odds-ratio plots of topographic and anthropogenic variables.	47
Figure B.4: Age distribution of all individual bear-years	48

Cover image by Slovenian Bears: Wildlife Photography Tours, 2015

LIST OF ABBREVIATIONS

AICc	Second order Akaike's Information Criterion
BB	Brownian Bridge
DEM	Digital Elevation Model
DOP	Dilution Of Precision
GIS	Geographic Information System
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
GPS	Global Position System
IT	Interaction Term
KDE	Kernel Density Estimation
km	kilometers
LiDAR	Light Detection And Ranging
LoCoH	Local Convex Hull
m	meters
MCP	Minimum Convex Polygon
PCA	Principal Component Analysis
SSF	Step Selection Function
Radar	Radio detection and ranging
RSF	Resource Selection Function
SBBRP	Scandinavian Brown Bear Research Project
SMD	Svenska Marktaggdata
TRI	Terrain Roughness Index
VIF	Variance Inflation Factor
WUR	Wageningen University & Research

TABLE OF CONTENTS

Abstract.....	v
List of Tables and Figures.....	vi
List of Abbreviations	vii
1. Introduction.....	1
1.1 Context.....	1
1.1.1 Human impacts on large predators.....	1
1.1.2 Effects of hunting on bears	2
1.2 Problem definition and study relevance.....	2
1.3 Research objective and questions	3
1.3.1 Objective	3
1.3.2 Research Questions.....	3
2. Concepts in habitat selection studies	5
2.1 Defining habitat selection and use	5
2.2 Understanding resources.....	5
2.3 Scales of habitat selection.....	5
2.4 Individual-level analyses.....	6
2.5 The extent of available resources & Home-range establishment	6
3. Methodology	7
3.1 Study site.....	7
3.2 Data Framework & Pre-processing.....	8
3.2.1 Bear Position Data	8
3.2.2 Spatial Data.....	8
3.2.3 Home-Range Estimation	11
3.2.4 Variable Selection.....	13
3.2.5 Selecting a study end-date.....	13
3.3 Distribution of mortality locations.....	14
3.4 Changes in habitat selection at the onset of the hunting season.....	16
3.4.1 Resource Selection Functions	16
3.4.2 Testing shift in behaviour with hunting onset.....	16
3.4.3 Degree of the shift – comparing survivors and non-survivors	17
3.5 Habitat-use differences between survivors and non-survivors	17
3.5.1 Modelling habitat-use	17

4. Results.....	19
4.1 Distribution of mortality locations.....	19
4.2 Data preparation and variable selection.....	20
4.3 Changes in habitat selection with hunting onset.....	20
4.3.1 Testing shift in behaviour with hunting onset.....	20
4.3.2 Degree of shift with hunting onset: Comparing survivors and non-survivors	23
4.4 Habitat-use differences between survivors and non-survivors	25
5. Discussion & Recommendations	29
5.1 Design limitations	31
5.2 Recommendations.....	32
6. Conclusion	34
Acknowledgements.....	35
References.....	36
Appendix A: Variable selection – Supplementary Information.....	42
Appendix B: Habitat selection shift with seasonality – Supplementary Information	44

1. INTRODUCTION

1.1 Context

With rising human populations and increased habitat fragmentation, anthropogenic pressures on wildlife continue to grow (Woodroffe 2000; Tilman et al. 2001; Treves & Karanth 2003; Athreya et al. 2014). Large predators are particularly vulnerable to these pressures because of their large spatial requirements, forcing them to move through mixed-use and suboptimal landscapes dominated by humans as protected areas shrink (Purvis et al. 2000; Cardillo et al. 2005; Balme et al. 2010; Estes et al. 2011). The frequency of human-predator interaction is on the rise in many parts of the world, and human-caused mortality (referred to as anthropogenic mortality hereafter) is currently the greatest threat to apex predators (Woodroffe & Ginsberg 1998; Woodroffe 2000; Castley et al. 2002; Schwartz et al. 2006; Loveridge et al. 2007; Darimont et al. 2015).

Humans have lower tolerance for predators compared to other taxonomic groups, regardless of how much damage the predators cause (Kansky et al. 2014). This low tolerance is in part what drives the intentional killing of large predators. Anthropogenic mortality can be broadly categorized as legal hunting, management removals, traffic accidents, and poaching (Bischof et al. 2009; Nowak & Mysłajek 2016; Kuijper et al. 2016). The impact each category has on predators varies with its context. In Scandinavia, the brown bear (*Ursus arctos*) faced immense hunting pressure and approached near-extinction in the 1800s due to conflict with humans (i.e. depredation of domestic livestock) and generous bounties set by the government (Swenson et al. 1995). Efforts were made to recover the dying population – Sweden eliminated the bounties in 1893 and introduced more protective policy (Swenson et al. 1995). There has been substantial recovery of the population since the 1970s, with a consistently positive trend in population size and growth rate until 2008 (3298 bears estimated), after which the population started to decrease at a rate of 3.2% per annum in accordance with new management targets (Kindberg & Swenson 2014; Steyaert et al. 2016; Swenson et al. 2017).

The success of these management efforts demonstrates how prevailing attitudes and tolerance of large predators is a great determinant of their survival success. However, the stagnation in population growth after 2008 is primarily due to the high hunting pressure in the area. Legal harvesting continues to be the greatest mortality risk to brown bears, with at least 73% of all anthropogenic mortality attributed to hunting (Bischof et al. 2008, 2018; Steyaert et al. 2016; Swenson et al. 2017).

1.1.1 Human impacts on large predators

In order to reduce risk of anthropogenic mortality, large predators display a spatio-temporal partitioning of activity so as to avoid humans as much as possible (Oriol-Cotterill et al. 2015). Such adaptations can have varied impacts on apex predators at different biological organisational levels, i.e. at the individual, population and ecosystem level. At the individual level, black bears (*Ursus americanus*) for example, shift their activity towards crepuscular and nocturnal periods to avoid humans, which are mostly active during the day (Beckmann & Berger 2003). At the population level, apex predators can show a reduction of population numbers, altered distributions and sex ratios (Noyes et al. 1996; Hertel et al. 2016; Leclerc et al. 2017), and indirectly, a reduction in genetic integrity due to habitat fragments acting as barriers to wildlife and creating subdivisions in the population (Jaeger et al. 2011). Finally, at the ecosystem level, the role of apex predators in generating top-down trophic cascades can be compromised in landscapes of

coexistence, because human-induced fear in top predators can further alter the landscape of fear of prey species which may use anthropogenic features as refuges (Hebblewhite et al. 2005; Berger 2007; Muhly et al. 2011), or because of a direct reduction of apex predator numbers due to persecution and/or hunting (Ordiz et al. 2011).

1.1.2 Effects of hunting on bears

Brown bears are the study animal of this thesis, and previous research has garnered much insight into various aspects of their behaviour. Brown bears are omnivorous animals with high energy requirements and spend much of their time foraging and resting (Moe et al. 2007). A great driver of habitat selection is therefore the food resources a habitat has to offer. A mixture of forested and open forests are thought to be favoured because of higher food availability (Herrero 1972; Nielsen et al. 2004b). They also show a seasonal selection of clearcut forest areas during mid-summer, when herbaceous greenness and ant foraging is at its highest, and show a greater selection for forested areas during late-summer periods where fruit foraging is at its peak (Nielsen et al. 2004b; Hertel et al. 2016). Temporal aspects are also important, as brown bears are most active during nocturnal and crepuscular hours, and select habitats differently when foraging than when resting (Moe et al. 2007).

There has been some research into the impacts of hunting on bear behaviour. Hertel et al. (2016) showed that bears undergo a foraging trade-off, where they forage less during peak hunting risk periods once the hunting season has begun. Frank et al. (2018) showed that when a bear is hunted, other bears in the population undergo a spatial reorganisation following the removal of that individual. The vacated home-range is mostly taken over by individuals of the same sex who are the least related to the hunted bear (Frank et al. 2018). The combination of this spatial reorganisation and that an unfamiliar bear occupies the vacated home-range also impacts the social behaviour: Work by Gosselin et al. (2017) showed that during the mating season, sexually-selected infanticide increases when a male bear is killed during the hunting season. This is because of “increased male turnover” i.e. males moving into the home-range of the deceased bear, and coming into contact with unfamiliar females and their cubs. Those females whose home-ranges neighboured that of the deceased male will suffer increased cub loss because of this increased male turnover (Leclerc et al. 2017). The spatial reorganisation caused by hunting is also an important consideration when formulating management goals aimed at reducing human-bear conflict (Frank et al. 2018). Finally, recent research is also shedding insight into how high hunting pressure has driven slow life histories in bears, where females provide longer maternal care to offspring to safeguard offspring and themselves against hunting risk (Van de Walle et al. 2018)

1.2 Problem definition and study relevance

The hunting season in Sweden begins on the 21st of August and last until the 15th October, or until the hunting quota is met. Bear hunting requires no specific license, and there is no limit on the number of bears an individual hunter may kill during a hunting season (Bischof et al. 2008). Bears are mainly hunted with baying dogs, where up to three dogs track down a bear and keep it in place until the hunter arrives and shoots it (Bischof et al. 2008). As the bear population recovered and showed a steady growth, the hunting quota too was increased, and has doubled between 2006 and 2014 to 120 individuals per year, for the counties Dalarna and Gävleborg of central Sweden (Hertel et al. 2016). This quota is typically reached within the first week of the hunting season, and the efficiency of hunters has resulted in a shift of the Swedish bear demography such that the average life-span of an individual bear is only about five years,

whereas females can reach up to 32 years old and die from natural senescence when there is no anthropogenic mortality pressure (Schwartz et al. 2003).

In the study area of this research, there are individuals who have consistently survived the hunting seasons and are over fifteen years of age (well over the average). What factors are influencing the survival of these individuals is therefore of interest. There has not yet been an assessment of brown-bear survival, as influenced by their space-use “strategies”. As most bears killed do not reach reproductive-age, the health of the population can be jeopardized (i.e. in terms of genetic integrity). Because of this, an understanding of successful behaviours and strategies is relevant in order to assess how adaptable this population is to adversity. A greater focus on older individuals can also inform management practice. Identifying and understanding which space-use “strategies” surviving bears may depict, and whether or not they can be linked to bear longevity will be the focus of this research.

1.3 Research objective and questions

1.3.1 Objective

To determine if and how space-use patterns facilitate the survival success and longevity of individual bears in south-central Sweden across consecutive hunting seasons.

1.3.2 Research Questions

In order to achieve the research objective, two research questions have been formulated:

Research Question 1. Do bears show a habitat selection shift once the hunting season has commenced?

If so, is there a difference in the degree of shift between survivors and non-survivors?

Research Question 2. What habitat use patterns can be observed in survivor bears that are different to their non-survivor counterparts?

The first research question will be answered by studying bear habitat *selection*, whilst the second research question will be answered by studying bear habitat *use*. How this is conducted will be detailed in the consecutive chapters.

Based on previous research on bears and other species impacted by hunting, the following hypotheses have been formulated (numbered by the research question they target):

Hypothesis 1

Bears do show a shift in habitat selection behaviours once the hunting season has begun.
Survivors show a greater shift than non-survivors.

This hypothesis is based on work done by Ordiz et al. (2012), who showed that when the hunting season began, bears responded with a change in movement patterns. It is therefore possible that this change in movement patterns would influence a change in habitat selection. Presuming that bears who are survivors are more adaptable and sensitive to hunting onset than bears who do not survive, it is therefore also hypothesized that survivors will show a greater shift in habitat selection than non-survivors.

Hypothesis 2

- A. Survivors use locations where hunters have difficulty accessing or targeting them
- B. Survivors use locations offering greater cover to them (might not be that significant for such a large animal)

Hypothesis 2 is supported by studies on different ungulates and their response to hunting pressures, where survival was directly measured. Hypothesis 2A was formulated based on research done by Thurfjell et al. (2017), where elk (*Cervus elaphus*) showed differential use of rugged terrain depending on whether it was during the rifle-hunting season or the bow-hunting season. Steeper terrain was favoured during the bow-hunt, as it made the elk more difficult to target, but relatively flatter terrain was favoured during the rifle-hunt, which the researchers believed may be because of reduced detection (Thurfjell et al. 2017). Here it is expected that survivor bears may be using locations that hunters find difficult to access.

Hypothesis 2B is based on research done by Jacques et al. (2010), where pronghorn (*Antilocapra americana*) neonate survival from hunters was linked to microhabitat features such as understory density in both horizontal and vertical structure. These features offered the pronghorn neonates cover from hunters and reduced visibility and in turn vulnerability to them. Based on this principle, it is hypothesized that survivor bears may use habitats offering more cover and thicker vegetation than open areas such as clearcuts, which is influencing their survival.

Finally, other aspects that have been shown to be important in survival studies are age, season, and personality. Age and learning have been central to the survival of white-tailed deer (*Odocoileus virginianus*) and elk (Delgiudice et al. 2002; Ciuti et al. 2012; Thurfjell et al. 2017). Though space-use is the focus of this study and underlying temporal aspects are beyond the scope here, the temporal elements will be incorporated to some degree when answering the second research question, as is detailed in Chapter 3.

2. CONCEPTS IN HABITAT SELECTION STUDIES

As a great proportion of this study is based on habitat-selection and habitat-use analyses, this chapter is devoted to describing their concepts and providing a brief overview on different design choices. More attention is put on the choices relevant to the research objective of this study.

2.1 Defining habitat selection and use

A habitat can be thought of as the sum of all the resources available to the animal (Johnson 1980). All animals must fulfil basic requirements of food, cover, and water, not only for survival but also to ensure reproductive success (Johnson 1980). A single habitat typically does not fulfil all these needs, which is why an animal makes trade-offs between habitats and the resources available within them. *Habitat use* is the way in which an animal uses a particular habitat (be it for foraging, denning, or cover from predators), whereas *habitat selection* is the disproportionate use of a particular habitat compared to its relative availability (Manly et al. 2002).

2.2 Understanding resources

In habitat selection terms, “resources” are considered to be the different attributes that contextualise a location. These attributes can be characterised in various ways, but for bear-ecology, the following categories are the most relevant: topographic information, landscape and vegetation attributes, and attributes that quantify anthropogenic disturbance (particularly when studying human-wildlife interaction). Topographic attributes may act as an indicator of food accessibility/hunting success for the animal of interest, and also as markers of accessibility of a location to humans. This category is often characterised by features such as elevation, slope, terrain ruggedness and variability of a location (Johnson et al. 2000; Nielsen et al. 2004a; Martin et al. 2010). The avoidance or selection for certain topographic attributes can vary greatly even with closely related species (Johnson et al. 2000). The vegetation metrics give detailed information on behavioural choices regarding food and shelter at the individual or population level (depending on the chosen scale). These are typically characterised by using attributes such as vegetation density, proportional canopy cover/openness, and land cover type. For example, habitat type can act as an indicator of food availability (Davidson et al. 2012), shelter selection (Elfström et al. 2008), or vulnerability to anthropogenic mortality (Nielsen et al. 2004a). Vegetation density and thickness are also good indicators for resource availability and shelter opportunity (Johnson et al. 2000; Kittle et al. 2014). Attributes of anthropogenic disturbance are often incorporated by creating continuous variables such as distance-to- or density-of- anthropogenic features, such as road or building features (Martin et al. 2010; Roever et al. 2010; Sánchez et al. 2013; Morrison et al. 2014). Anthropogenic features such as these are associated with increased mortality risk (Loveridge et al. 2017), but also can offer increased resources such as increased food availability (Roever et al. 2008). This is why often the individual has to make a trade-off between risk associated with the location and resources it has to offer (Stillfried et al. 2015).

2.3 Scales of habitat selection

Habitat selection can be considered at different spatial and temporal scales – a hierarchical ordering of which was first presented by Johnson (1980). At the broadest spatial scale, habitat selection considers the entire physical/geographical range of a species i.e. “first-order selection”. When looking at a smaller group such as social groups or individuals within the species, home-range is the next scale and is termed

“second-order selection”. “Third-order selection” determines the usage of habitat components within the defined home-range of an individual/social group. Finally, “fourth-order selection” looks at a yet finer scale, where a defined use site within the home-range is then further analysed for differences in use within the site – for example, preferential feeding within a defined feeding site of an individual (Johnson 1980).

2.4 Individual-level analyses

Individuals of a species can show variation in behaviours amongst one another. Research by Leclerc et al. (2016) showed that there are repeatable patterns of individual variation in habitat selection behaviours that cannot be observed at the population level, and also that selection observed at the population level does not necessarily translate to selection at the individual level. This was a reflection the trade-offs an individual makes regarding resource use (Johnson 1980; Leclerc et al. 2016). Studies on other animal species have shown that variation in habitat selection amongst individuals can affect their fitness. As this thesis is concerned with variation in space-use behaviours and the influence it has on the survival success of the individual, habitat selection at the third-order is the most relevant scale. Coarser scales would instead reflect the intra-specific competition over resources within a population and not the differences in individual choices (Leclerc et al. 2016).

2.5 The extent of available resources & Home-range establishment

The home-range of an individual establishes the spatial extent within which resource availability is defined. The concept of a home-range, as first introduced by (Burt 1943), refers to the area utilised by an individual for all their basic activities such as for foraging, shelter, mating, and rearing young. The home-range area utilised is not constant over the lifetime of an individual, and can vary with season. Other factors such as age and sex and the presence of young can influence the size of the individual’s home-range (Burt 1943). Advancements in radio-telemetry and animal tracking methods make it possible to collect positional information of an individual at increasingly high frequencies, remotely. This positional information can be employed to determine an individual’s home-range. There are various methods that can be used, each accompanied with its advantages and disadvantages. They can be broadly categorised into point-based calculations and trajectory-based calculations of home-range (Steiniger & Hunter 2013; Kooij 2015). Common point-based calculations include “Minimum Convex Polygon” (MCP) (by far the most commonly employed method) and the “Kernel Density Estimation” (KDE) (Gula & Theuerkauf 2013). Common trajectory-based calculations of home range include the “Brownian Bridge” (BB) method and the “Local Convex Hull” (LoCoH) method. Each of these methods can show disparity with one another, and Gula and Theuerkauf (2013) state that this demonstrates a need for standardisation in the field of home-range estimation.

3. METHODOLOGY

3.1 Study site

The study site is between longitudes 60° 23'N – 62° 39'N, and latitudes 12° 25'E – 16° 39'E. It is approximately 25800 km² in size, and falls between the counties Dalarna and Gävleborg of central Sweden. Elevations range from 175m to 725m above sea level (Martin et al. 2010). Most of the area (80%) is dominated by intensely managed boreal forest for wood production and is at various stages of growth (Moe et al. 2007). The dominant tree species are Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), lodgepole pine (*Pinus contorta*), and birch (*Betula* spp.), with heather (*Calluna vulgaris*) and berry shrubs (e.g. *Vaccinium* spp.) present in the understory (Lodberg-Holm 2015; Leclerc et al. 2017).

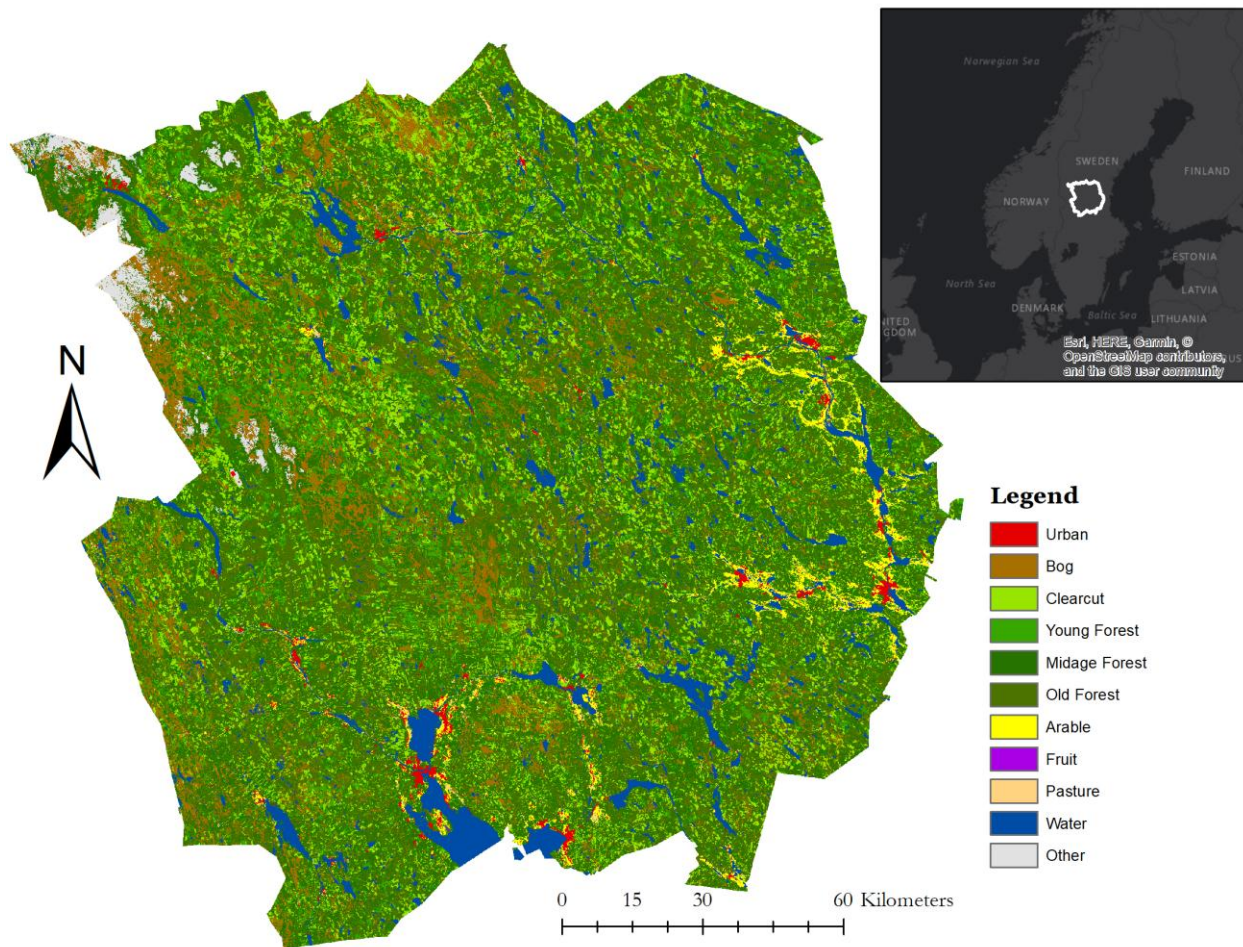


Figure 3.1: Land cover over the study site (as of 2000), and its location within the Scandinavian Peninsula

The clear-cutting of entire forest stands is common, with a rotation age typically lasting between 80-120 years. Less than 60% of the forest is older than 35 years (Swenson et al. 1999; Moe et al. 2007). There is also a significant proportion of bogs and lakes throughout the area, as well as a dense network of gravel roads that make the study site very accessible for humans for a host of recreational activities (Elfström et

al. 2008; Lodberg-Holm 2015). There are also several small urban areas, farms and pastures in the study site, with a human density of ~5-7 inhabitants/km² in 2011 (Ordiz et al. 2014).

3.2 Data Framework & Pre-processing

See Figure 3.2 for an overview of the entire pre-processing scheme.

3.2.1 Bear Position Data

The Scandinavian Brown Bear Research Project (SBBRP) has been studying brown bear ecology since 1984, but individual bears have been equipped with Vectronic GPS-Plus collars since 2003 to track movement (VECTRONIC Aerospace GmbH, Berlin, Germany). The bears within the study area have been followed consistently for several years. This project, however, included data only from the years 2006 to 2017. Information regarding the sex, reproductive status, and age of each collared bear is monitored following standardized protocols, and positional information is collected at least every hour. At each location, whether it was a 2D or 3D fix was known and the dilution of precision (DOP) was recorded. 2D fixes rely on a minimum of three satellites to record positional information, i.e. the latitude and longitude. 3D fixes need a minimum of four satellites and record altitude in addition to positional information. To remove erroneous locations and reduce uncertainty of measurement accuracy, only 3D positions with DOP<10 and 2D positions with DOP<5 were deemed reliable and selected for this study (Bjørneraas et al. 2010).

As the survival of female bears is vital for population growth, and because there is great variation in the home-range size of the individual between the sexes, only females will be considered in this analysis (Martin et al. 2010). Females accompanied by their cubs receive protected status during that hunting season. Therefore, I excluded all females accompanied by cubs (recorded in a July cub count) from all analyses, and only data of lone females between July and August were used.

3.2.2 Spatial Data

The bear location data were linked to topographic, vegetation, and anthropogenic attributes on the landscape, i.e., information that has been shown to be relevant when studying bear ecology (Martin et al. 2010; Ordiz et al. 2011; Steyaert et al. 2016).

Topographic variables

All topographical variables were generated from a digital elevation model of the area of 50×50m pixel size (GSD-Höjddata, grid 50+, from Lantmäteriet 2016). From this DEM, four variables were extracted. First, elevation was extracted at each location. Next, slope was calculated from the DEM using the slope tool from the “Spatial Analyst” toolbox in ArcGIS 10.4. Finally, the DEM was also used for calculating two terrain roughness variables. The first (called “ruggedness” was calculated following Ascione et al. (2008), Dorresteijn et al. (2014) and Steyaert et al. (2011). Here, ruggedness was calculated using a focal approach, where the mean elevation and range in elevation of the 8 neighbouring cells to the central pixel was used, using the “Focal Statistics” tool of the Spatial Analyst toolbox (Steyaert et al. 2016). Accordingly, these three raster layers (DEM, mean DEM, and range DEM) were used as inputs to calculate ruggedness as done in the following equation:

$$Ruggedness = \frac{(mean\ DEM - DEM)}{range\ DEM}$$

This equation gives scaled values ranging from -1 to 1, where negative values indicate peaks and areas of higher elevation compared to the surroundings, and positive values indicate dips and areas of lower elevation compared to the neighbouring cells. Values close to 0 suggest low roughness.

Roughness was also calculated using the terrain roughness index (TRI) developed by Riley et al. (1999). This was also done with a focal approach, where a raster of the maximum altitude and minimum altitude at a 3 by 3 cells processing window was created (again, using the “Focal Statistics” tool of the Spatial Analyst toolbox), and were incorporated using the following equation:

$$TRI = \sqrt{|maxDEM^2 - minDEM^2|}$$

Here, the values range from 0 to 4367m, with higher values indicating more roughness. Riley et al. (1999) further groups the values into the seven following classes: Level (0 – 80m), Nearly-Level (81 – 116m), Slightly Rugged (117 – 161m), Intermediately Rugged (162 – 239m), Moderately Rugged (240 – 497m), Highly Rugged (498 – 958m), and Extremely Rugged (959 – 4367m).

Anthropogenic variables

Road and building shapefiles (line and point respectively) were provided by the SBBRP. Accordingly, distance and density variables were calculated for each. For the distance variables, a simple Euclidean distance metric was chosen, with kilometres as the output unit, creating a raster with each pixel denoting distance to the nearest feature (be it building, major road or minor road). The “Euclidean Distance” tool from the “Spatial Analyst” toolbox in ArcGIS v 10.4 was used for this purpose. For the building density, the “Point Density” tool was used (as it was a point shapefile being processed), and for the major and minor road densities, the “Line Density” tool was applied instead (for polyline features). For each of the three shapefiles, 13 processing windows were used to create 13 rasters for each variable. The processing window sizes used were 50m, 100m, 150m, 200m, 300m, 400m, 500m, 1000m, 1500m, 2000m, 3000m, 4000m and 5000m. Creating such a large set of density variables was done in order to choose the most optimal spatial scale to answer the research questions.

Land use variable

The land cover raster used in this study was provided by Svenska Marktäckedata (SMD and is at a 25m x 25m resolution. It consists of over 80 classes, but for the purposes of this research these were reclassified into the 11 classes described in Table 3.2. The reference year is 2000 (Statistics Sweden 2000). Land cover was not static as much of the area is wood production forest. Clearcuts that occurred after the year 2000 were used to update the land cover data. A polygon shapefile of clearcut patches and the date on which the clearcut event occurred was available at the Swedish National Forest Service, and was used for updating the SMD land cover raster. Following a clearcut event, the existing land cover type (as established by SMD) was changed into a “clearcut” land use type, and remained a clearcut for 8 years following the clearcut event date (Steyaert et al. in prep). After this, the forest regrowth time is incorporated by changing clearcut events that were over 8 years ago into a “young forest” land use type. The transition from young to mid-age forest was not considered here, as the greatest time difference between the reference year and the earliest clearcut event (16 years) is still considered “young” in terms of forest ecology.

Table 3.1: Overview of all spatial variables processed for further statistical analysis. For the density variables, the ‘XXXX’ in the shorthand notation/label refers to the optimal search radius (in meters) that was selected. See section 3.2.4 for more details on this selection.

	Variable	Description and units	Cell size	Label
Topographic	Elevation	Digital elevation data (in m)	50x50m	Elevation
	Slope	Slope (in °), derived from the DEM. Ranges from 0° to 90°	50x50m	Slope
	Terrain Roughness	Calculated as the standard deviation of altitude (derived from the DEM). Scaled, with values ranging from -1 to 1	50x50m	Ruggedness
		Calculated using Riley’s Terrain Roughness Index (Riley et al. 1999). Units in meters.	50x50m	TRI
Anthropogenic	Distance to Settlement	Euclidean distance to the nearest settlement, measured in km	25x25m	BuildDist
	Distance to major road	Euclidean distance to the nearest major (high traffic) road, measured in km	25x25m	MajDist
	Distance to minor road	Euclidean distance to the nearest minor (low traffic) road, measured in km	25x25m	MinDist
	Density of settlements	Density of point features (buildings) in number of points/km ²	25x25m	BDXXXX
	Density of major roads	Density of line features (major roads) in road-length/km ²	25x25m	RDMajXXXX
	Density of minor roads	Density of line features (minor roads) in road-length/km ²	25x25m	RDMinXXXX
Land Use	Habitat type	Classified into 11 classes: urban, bog, clearcut, young forest, midage forest, old forest, fruit farming, pasture lands, arable lands, and other.	25x25m	Habitat

Locations with land-use classes that were used extremely infrequently (>0.5% of all use-locations) were removed, due to their small sample size relative to the overall sample. These could include classes such as water bodies, and classes that make up a very small proportion of the overall study area (such as fruit farms and pasture lands).

Table 3.2: Reclassification of SMD land-cover raster (reference year 2000)

Class	Description	Composition (%) in study site
Mid-age Forest	Forests above 15m in height	32.36
Old Forest	Old growth boreal and conifer forests	24.22
Clearcut	Freshly-felled forest for wood production. Class remained clearcut for the next 8 years after the date of cut	11.95
Swamp	Wetlands of different types: bogs, swamps, peatlands, and other wetlands	11.47
Young Forest	Forests (both conifer and boreal) between 8 and 15m in height	10.02
Water	All natural water bodies present in the area, including lakes and streams	6.14
Arable land	Land not yet utilised for crops but tilled or deemed suitable for agriculture	1.52
Other	All other small land cover classes that did not fit in the above categories, included small natural grasslands, rock or sandy areas	1.10
Urban	Areas utilised by humans. This included buildings, villages and larger residential areas, urban green spaces (golf courses and urban parks), construction sites and airports.	0.79
Pasture	Lands set aside for livestock to graze	0.45
Fruit farming	Fruit and berry farm lands	0.001

3.2.3 Home-Range Estimation

The annual home-range of a bear was determined by constructing a minimum convex polygon (MCP) around GPS locations recorded by that individual throughout the year and across the multiple years it was recorded.

Each MCP was used to randomly create ('null') points representing what was available in a given bear's annual home range. These points were used to extract landscape attributes (e.g. elevation; Figure 3.2) or inherit that of used ('true') positions (e.g. bear sex) to which they are compared (see RSFs in 3.4.1).

MCP was the method selected because of its rapid calculation time, and the relatively strong results it produces when estimating home-range as compared to other methods (Kooij 2015). Though a kernel density estimation method may have produced a more realistic home-range shape, for this study's purposes the MCP was deemed sufficient to determine habitat availability for individual bears.

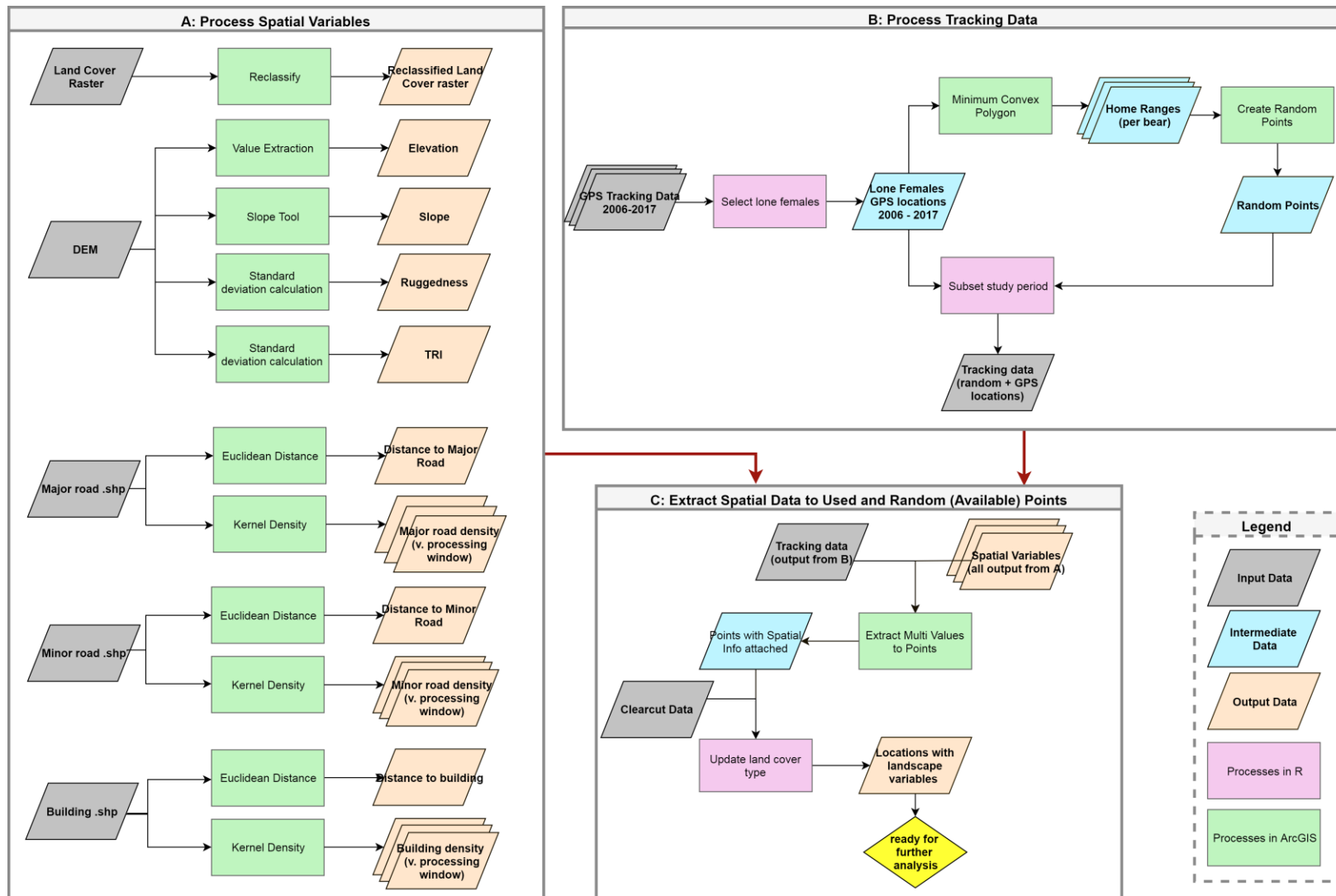


Figure 3.2: Pre-processing workflow and data preparation. Box A = processing spatial data; Box B = processing bear position data; Box C = integrating spatial variables (Box A output) to the positional data (Box B output).

3.2.4 Variable Selection

There were three anthropogenic features considered in this study: major roads, minor roads, and buildings. For each feature, 13 density rasters were constructed with varied search-radii. In order to select the most optimal density raster for each feature, regression models were constructed (density variable = explanatory variable, predicting GPS vs. null locations), and performance compared with the second order Akaike's Information Criterion (AICc) (Boyce et al. 2002). AICc has no meaning in absolute terms but is useful when comparing models. Lower AICc values are indicative of better model fit as balanced out by the number of parameters incorporated in the model, so as to avoid over-fitting (Boyce et al. 2002; Burnham & Anderson 2002). For this, I used the package "AICcmodavg" in R (Mazerolle 2017). Accordingly, the best fitting search-radius for each feature was determined, and that density raster that was used for further analysis.

As two terrain roughness variables were created, including both in further analyses is excessive. Because of this, AICc was employed again to choose which of the two roughness metrics performed better in predicting the response variable (GPS vs. null locations).

Finally, once the density and roughness variables were selected, correlation between all variables was evaluated. Any strongly-correlated variables were then removed, and multicollinearity was evaluated by means of variance inflation factors (VIF). VIF values above 10 suggest high collinearity, and any variables with high VIF values were removed (Salmerón et al. 2018).

3.2.5 Selecting a study end-date

For bears that did not survive the hunting season in a particular year, the end-date of their study was the day on which they are shot by the hunter during the hunting season. For survivor bears on the other hand, data were often available throughout the whole hunting season. Deciding where to cut off the analysis of these survivors is therefore an important decision in order to effectively compare the two groups. For this, the distribution of kill dates by hunter of non-survivors was derived, and "end-dates" were randomly drawn from this distribution and assigned to survivor bear years (red dashed line in Figure 3.3). The bears' space-use was then studied up until this end-date. This avoids over-representing survivor bears in the hunting season, as the data on non-survivors in the hunting season is limited. The distribution of the hunt day on which bears died is presented in Figure 3.3 (of lone females only). Many of the deaths occurred in the first few days of the hunting season – the strong peak on Day 0 marks the first day of the hunting season.

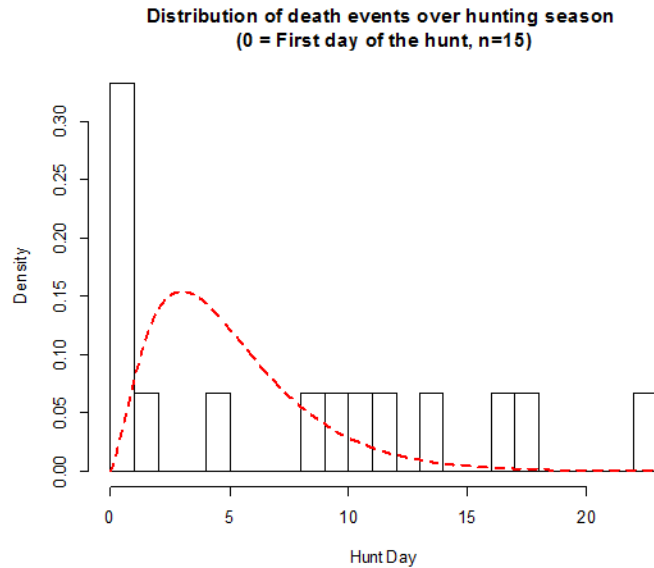


Figure 3.3: Histogram of hunt "death-day", of all dead female collared bears (n=15) who were shot in the hunting seasons of 2006 – 2016. The red dashed line shows the distribution curve of death events, and it was from under this curve that end-dates were sampled and assigned to survivor bear-years.

3.3 Distribution of mortality locations

Before directly answering the two primary research questions, the distribution of mortality locations will be presented, in order to quickly identify areas of higher mortality concentrations within the study site, as well as make a quick assessment on differences between the sexes. All mortality events that occurred during the hunting season were collated for both male and female bears. The point location at which the bear was killed was determined, and then spatial densities were estimated at three scales. Median home-ranges as determined by Dahle & Swenson (2003) for bears of this area were used to inform kernel window size for each of the three scales, as males and females have widely different home-range sizes. They reported separate home-range sizes for the north and south of the study site, but for this thesis an intermediate of those two medians was used for each sex. The scales used were thus as follows:

1. Male bear home-range: 944km^2 (kernel window radius = 17.33 km)
2. Female bear home-range: 249km^2 (kernel window radius = 8.90 km)
3. Intermediate home-range size: 597km^2 (kernel window radius = 13.79 km)

When estimating spatial density of male mortality locations, the male bear home-range estimate was used, and similarly for female mortalities, the female bear home-range was applied. When collating both male and female mortalities and estimating total spatial density, the intermediary home-range estimate was applied. All spatial density estimations were conducted in ArcGIS 10.4 using the "Spatial Analyst" toolbox. A total of 68 collared bear mortalities (due to hunting) fell within the study site between the years 2006 – 2016, of which 32 were female and 36 were male.

The research questions were answered by employing a mixture of study periods and statistical analysis techniques. An overview of all these and which research questions they tackle is presented in the workflow of Figure 3.4. Each step of the workflow has been detailed in the sections mentioned within the figure. The remainder of this chapter describes these analyses.

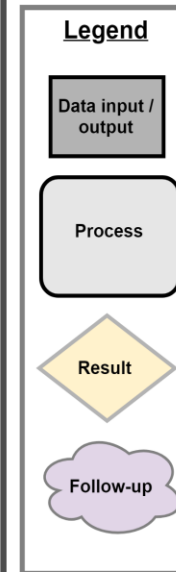
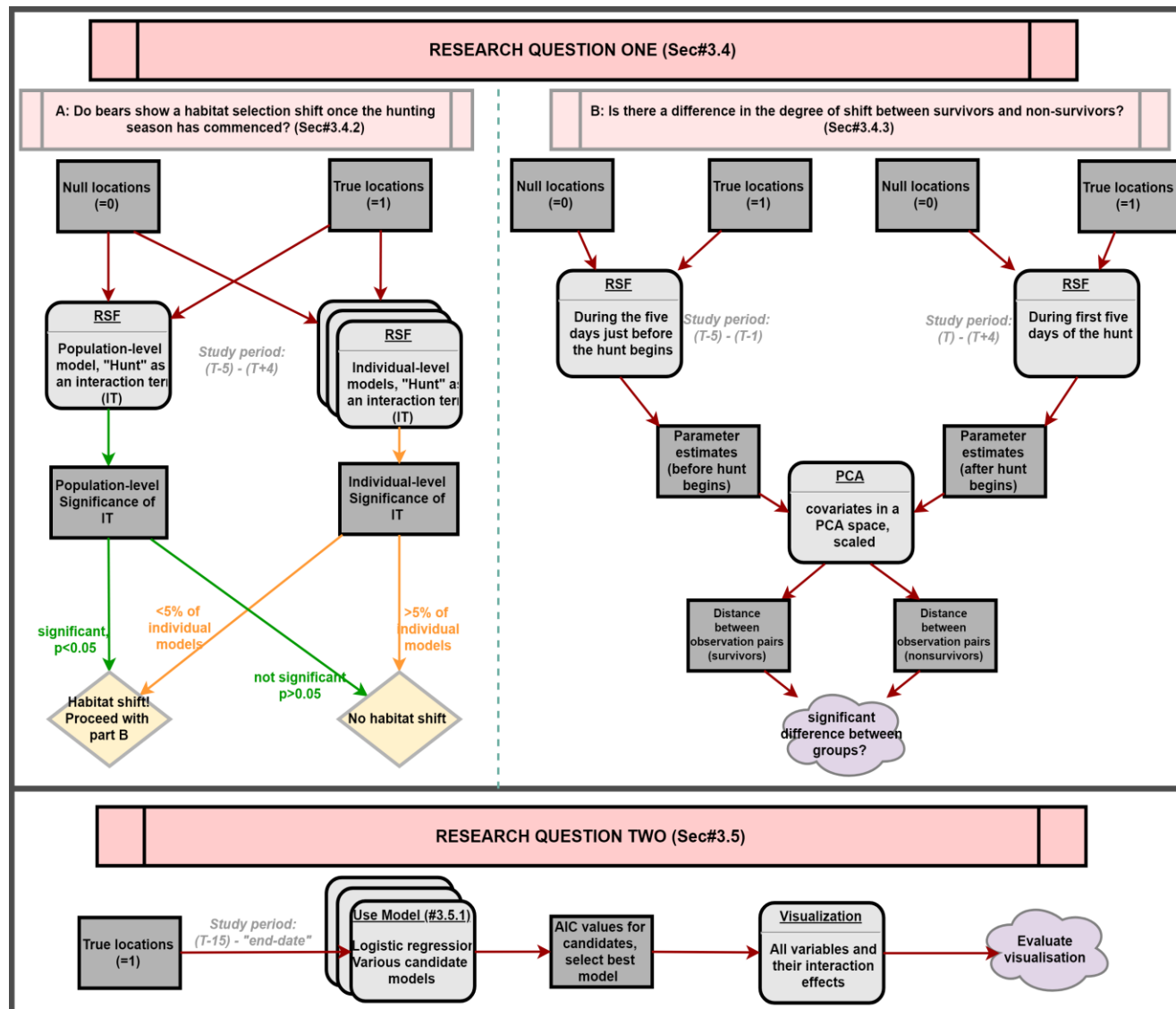


Figure 3.4: Visual overview of steps taken in the statistical analysis to answer the study research questions. The study period for each model and RSF is detailed next to its process box in blue. "T" is referred to as the first day of the hunting season, and the numbers following refer to the temporal distance from T (in days). Sec# refers to where in the text (section number) that part of the workflow is described.

3.4 Changes in habitat selection at the onset of the hunting season

The first research question assesses whether or not individual bears show a shift in habitat selection behaviours once the hunting season begins. To quantify selection, resource selection functions (RSFs) were applied.

3.4.1 Resource Selection Functions

RSFs discern the disproportional use of resources relative to what is available. For these functions, all the output spatial variables (see Figure 3.2) were input as independent variables in logistic regression models, with the outcome “null” (=0) or “true” (=1) location as the binary dependent variable. Logistic regression models are suitable for estimating RSFs. RSFs were constructed in R using the package “lme4” (Manly et al. 2002; Bates et al. 2015). These models use an exponential function to relate probability of an event (in this case, a true bear location) to the explanatory variables (in this case, the measured spatial variables). A presence/available design was chosen, as the null locations measured are not direct absences but pseudo-absences. It had the following log-linear form:

$$W(x) = \exp(b_1x_1 + b_2x_2 + \dots + b_kx_k)$$

Where $W(x)$ represents the probability of a location being characterised by true bear presence, b_k represents the coefficient as estimated from logistic regression, and x_k represents the environmental predictor variable (Manly et al. 2002; Nielsen et al. 2004a; Johnson et al. 2006).

3.4.2 Testing shift in behaviour with hunting onset

To assess whether a change in resource selection by bears occurred at the onset of the hunting period, I designated two seasons: 5 days prior to the onset of the hunting season (16th – 20th August), and 5 days after the hunt began (21st – 26th August). Resource selection functions (RSFs) were created with this “seasonality” as an interaction effect for all independent variables within the functions. “Hunt seasonality” was thus an additional categorical variable, with pre- and post-hunt commencement as the two categories considered.

The influence of the “Hunt seasonality variable was studied at two levels, with two types of RSFs:

- *Population level*: A general RSF was created (generalised linear mixed model, i.e. GLMM pooled across all bear-years), with bear ID and year included as random effects, and with hunt as an interaction term to each spatial variable
- *Individual level*: RSFs (generalised linear models, i.e. GLMs) were created for each individual bear-year, with hunt as an interaction term to each spatial variable

The significance of the interaction term “Hunt Seasonality” was measured in all RSFs. For the general RSF, this tested by a chi-square test of the interaction term (as is appropriate for mixed-effect-models) and evaluating the p-value. For the individual bear-year RSFs, this was done by calculating the F-test p-value significance of the interaction term (appropriate for logistic regressions), and then calculating the proportion of individual bear-year RSFs that showed the interaction term to be significant ($p < 0.05$) for each spatial variable in the model.

Next, trends shown by the individual bear-year models between the two hunt “seasons” was evaluated per variable and compared to the trend shown by the population-level RSF. For this, parameter estimates for

each bear-year model before and after the hunt began were plotted, with each bear-year pair connected visually (with a trend line). The bear-years were then visually evaluated, and compared to the median bear-year and population-level estimates.

3.4.3 Degree of the shift – comparing survivors and non-survivors

Presuming there is a change in behaviour, this section is concerned with quantifying the difference in this shift between survivor and non-survivor bear-years. In order to do this, two RSFs were created per bear-year: one before the hunting season began (from 6th- 20th August), and one after the hunting season has begun (21st August – end-date assigned to that bear-year, see section 3.4.2). The parameter estimates from each RSF were extracted, and the variation across individual bear-year models was evaluated by employing multivariate analysis techniques. Techniques such as principal component analyses (PCA) and other ordination techniques are useful in exploring variation in the dataset by rearranging distances between values such that the overall variation is reduced as much as possible. Original spatial variables that correlate strongly with the corresponding principal components exploring the highest variation in the dataset can be thought of as being particularly important in exploring trends in the dataset. Only continuous variables can be incorporated in PCA, therefore explanatory variables such as survival status and seasonality cannot be integrated. Bear-years with no-data values cannot be processed by PCA, therefore such bear-years were removed. In order to minimize the number of no-data values, habitat classes that are greatly under-represented were removed. The PCA space was first visualised, and any extreme outliers were also removed in order to best represent variation in the entire dataset without having a strong skew by these anomalies. Correlation of explanatory variables with PCA axes were also evaluated – values above 0.4 were considered moderately correlated with the axis.

Each bear-year had a pair of values in the PCA space (one before the hunting season began, and one after). The distance between the pairs can be calculated, and the magnitude of these distances can be compared between survivor and non-survivor bear-years. This gives an indication as to whether one group (survivors or non-survivors) show a greater shift in habitat-selection once the hunting season begins (i.e. greater distance in the PCA space), or whether there is no difference between the groups. . The absolute difference in the principal component scores was calculated, to illustrate the *magnitude* of the shift in habitat selection between two observations. A Welch’s two-sample t-test was employed to compare the difference in the mean difference between the two groups. This test is appropriate because the two groups were of unequal sample sizes and variances.

3.5 Habitat-use differences between survivors and non-survivors

3.5.1 Modelling habitat-use

This section aims to answer the second research question, and decipher patterns amongst bears that may contribute to their survival. Logistic regression was used to identify patterns in habitat use in relation to survival status, with “Survived” (=0) and “Dead” (=1) as the two outcomes, depending on whether the bear was killed that year by a hunter or not. Here, two weeks before the hunting onset was considered the start date and the bear-year was modelled until that individual’s death date (if the bear was killed) or the randomly-assigned end date of those bears that survived that hunting season (see section 3.2.5).

Modelling habitat-use in this way provides a good overview on the influence that spatial predictors have on the response variable. However, temporal elements have already been demonstrated as important in habitat selection analyses. To add more depth to the habitat use analysis here, two additional variables were also added: hunt-seasonality (temporal) and age of the bear (demographic) – see Figure 3.5. I set up candidate models where in some instances these two variables were added as extra independent variables, and in other instances they were incorporated as interaction terms. The candidate models (listed in Table 3.3) were cross-compared using AICc values (Burnham & Anderson 2002).

Table 3.3: Description of habitat-use candidate models. The “+” indicates that the extra variables were added simply as additional independent variables in the regression. The “ \times ” indicates that the variable succeeding this symbol was incorporated as an interaction term, and acted on all independent variables in the model. The base-model (M1) was a simple linear combination of all spatial variables discussed, excluding the density to major roads and buildings

Model	Attributes
1	M1: Independent spatial variables only
2	M1 + age
3	M1+ season
4	M1 + age + season
5	M1 \times age
6	M1 \times season
7	M1 \times age \times season
8	(M1 + age) \times season
9	(M1 + season) \times age

I then used the “Effects” package in R to visualise the results (Fox et al. 2018).



Figure 3.5: Histogram showing the distribution of age of lone female bears that were killed during the hunting season. Age is plotted against the density, and a smoothed density curve is plotted in blue. The red vertical line denotes the mean age here (4.4667 years)

4. RESULTS

4.1 Distribution of mortality locations

Spatial densities were calculated at the female, male, and intermediate home-range scale for the study area. The distribution of these mortalities is depicted in Figure 4.1. The central and western parts of the study site appear to have a higher density of hunt-mortalities, common to both male and female casualties.

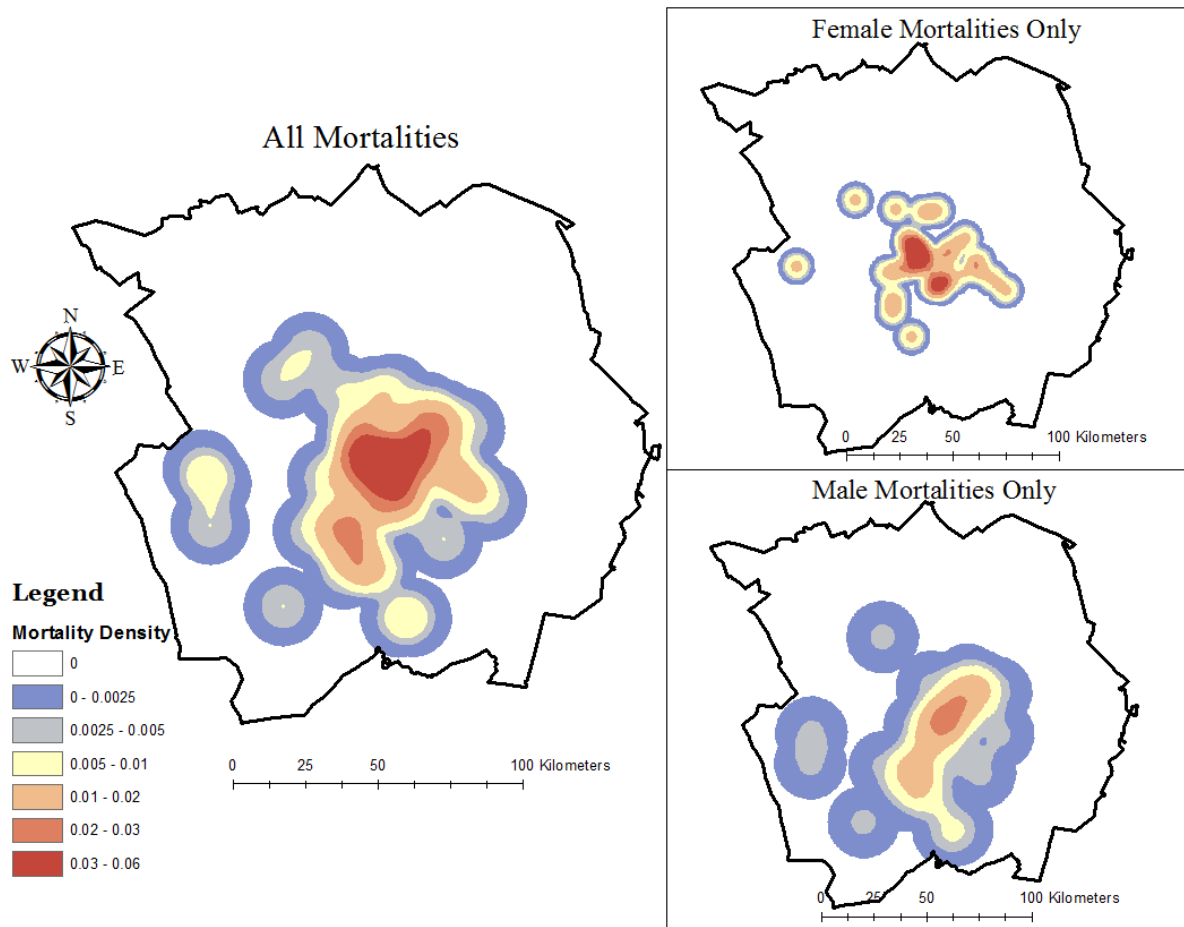


Figure 4.1: Distribution of brown bear mortality sites between 2006 & 2016. Only collared brown bears have been included. The mortality density unit is the number of bears killed per square kilometre. Males and females show considerably different home-range sizes, which is why different processing windows were applied for the two sexes when visualising the mortality densities. The size of the processing window used was the median home-range size of that sex. Accordingly, the female mortality density (top right, $n=32$) was calculated using a home-range estimate of 249km^2 , while the male mortality density (bottom right, $n=36$) was calculated using a home-range estimate of 944km^2 . The density with both male and female mortalities combined ($n=68$) is displayed on the left using an intermediary home-range estimate of 597km^2 . The cell size of these rasters was $100\times 100\text{m}$.

Keep in mind these are mortalities of collared bears only, a small proportion of all bears killed in the area.

4.2 Data preparation and variable selection

After applying the bear selection criteria, 167 bear-years were available for analysis. Bear-years with too few data points (<100 locations) either before or after the hunt began were removed as well.

From the set of density variables, the most optimal spatial scale for building density was 300m, and 500m and 200m were the most optimal scales for major and minor road densities, respectively. See Table A.1 for an overview of model selection results.

Habitat variables that were rarely used (<0.5% of all use-locations) were removed. After removals, the remaining classes were “bog”, “clearcut”, “young forest”, “midage forest” and “old forest”. These were incorporated as dummy variables in the regression models, with “midage forest” as the reference category as it was the most prevalent habitat type here. “TRI” performed better than “Ruggedness” (see Table A.2), and as it was excessive to have two roughness indices included in this study, “Ruggedness” was excluded from further analyses. When examining correlation between all variable pairs, “Slope” and “TRI” were strongly correlated, and “TRI” and “Elevation” were moderately correlated. Because of this very high correlation with “Slope”, “Slope” was excluded as well from further analyses. See Figure A.1 for an overview of all correlation pairs.

There was no multicollinearity observed with the final set of variables (see Table A.3). However, when creating habitat selection models for individual bear-years, many bears only had 0’s in the dataset for the major road density and building density variables. This is because the home-range of these individuals was outside of the small search-radius for these features, giving many pixels a value of 0. For this reason, the density variables “Major Road Density 0500m” and “Building Density 0300m” were also removed. The distance-to- variables were relied on instead to represent these anthropogenic features.

4.3 Changes in habitat selection with hunting onset

4.3.1 Testing shift in behaviour with hunting onset

The sensitivity of each variable to the interaction term “hunt seasonality” i.e. before/after hunting onset was determined by an F-test for the individual-level models, and a chi-square test for the population-level model. A chi-square test was chosen because it a generalised mixed effects model was applied, with random effects included. The results of this significance test are presented in Table 4.1.

Table 4.1: Significance of “hunt seasonality” interaction terms on the spatial variables. The population-level tests model sensitivity to the interaction term (IT) by evaluating the p-value of a chi-sq test. The individual level tests the *proportion* of bear-year models (n=168) where spatial variables were sensitive to the IT (F-test, $p < 0.05$).

Variable	Individual Level	Population Level
Habitat	52%	0.0015 **
Minor Road Density (200m)	25%	0.9654
Distance to Minor Road	34%	0.1893
Distance to Major Road	52%	0.3193
Distance to Building	49%	0.0005 ***
Elevation	46%	0.0004 ***
TRI	30%	0.7557

The effect of the interaction term “hunt-seasonality” is assumed to be minimal if fewer than 5% of individual bear-year models showed the interaction term to be significant. For all included spatial variables, well over 5% of bear-year models showed seasonality to be a significant interaction term. Only the variables “Habitat”, “Distance to building” and “Elevation” appeared to be significantly influenced by hunt seasonality at the population level (see Figure 4.1).

Table 4.2: Direction of the model coefficients as derived from the population-level RSF. Non-significant variables are indicated with a ‘0’, while significant variables are indicated with a ‘+’ or ‘-’ depending on the direction of the coefficient, i.e. whether they were selected-for- or averted-from-. This is a summary of the population-level model: standard errors, parameter estimates, p-values of the model are detailed in Table B.1.

Variable		Pre-hunt	During hunt
Habitat	Bog	+	-
	Clearcut	0	+
	Young forest	-	+
	Midage forest	-	+
	Old forest	-	+
Elevation		-	-
TRI		0	+
Distance to Major Road		0	+
Distance to Minor Road		0	+
Distance to Building		+	+
Minor Road Density (200m)		0	-

In the five days prior to the hunt, bears select bogs, whilst avoiding all forested habitats (Table 4.2). They preferred areas of lower altitude and further away from buildings. However in the first five days of the hunt, many selection behaviours switched. Bears showed a selection for all forest ages and clearcuts, but avoided bogs. There was still a selection for areas of low altitude; however they also show preference for more rugged terrain. Additionally, they avoided areas close to major and minor roads, as well as buildings. There was also a selection for areas of low densities of minor roads.

What is most striking here is the significant shift in behaviour of selected habitat types once the hunt began, with mostly opposite selection shown. Only the habitat types, “Distance to Building” and “Elevation” showed significant selection both before and after the hunt began – perhaps unsurprising as they were shown to be sensitive to hunt seasonality at the population-level as well (see Table 4.1).

The population-level trends generalise bear habitat selection behaviours. They do not however capture the full degree of individual variation in behaviour and how that relates to survival. Plots such as the one in Figure 4.2 help make these comparisons. Here, the figure shows the variety in selection for midage forest, distance to building, and elevation parameter estimates, all of which were sensitive at the population level (Table 4.2). For all other variables, see Figure B.2 and Figure B.3.

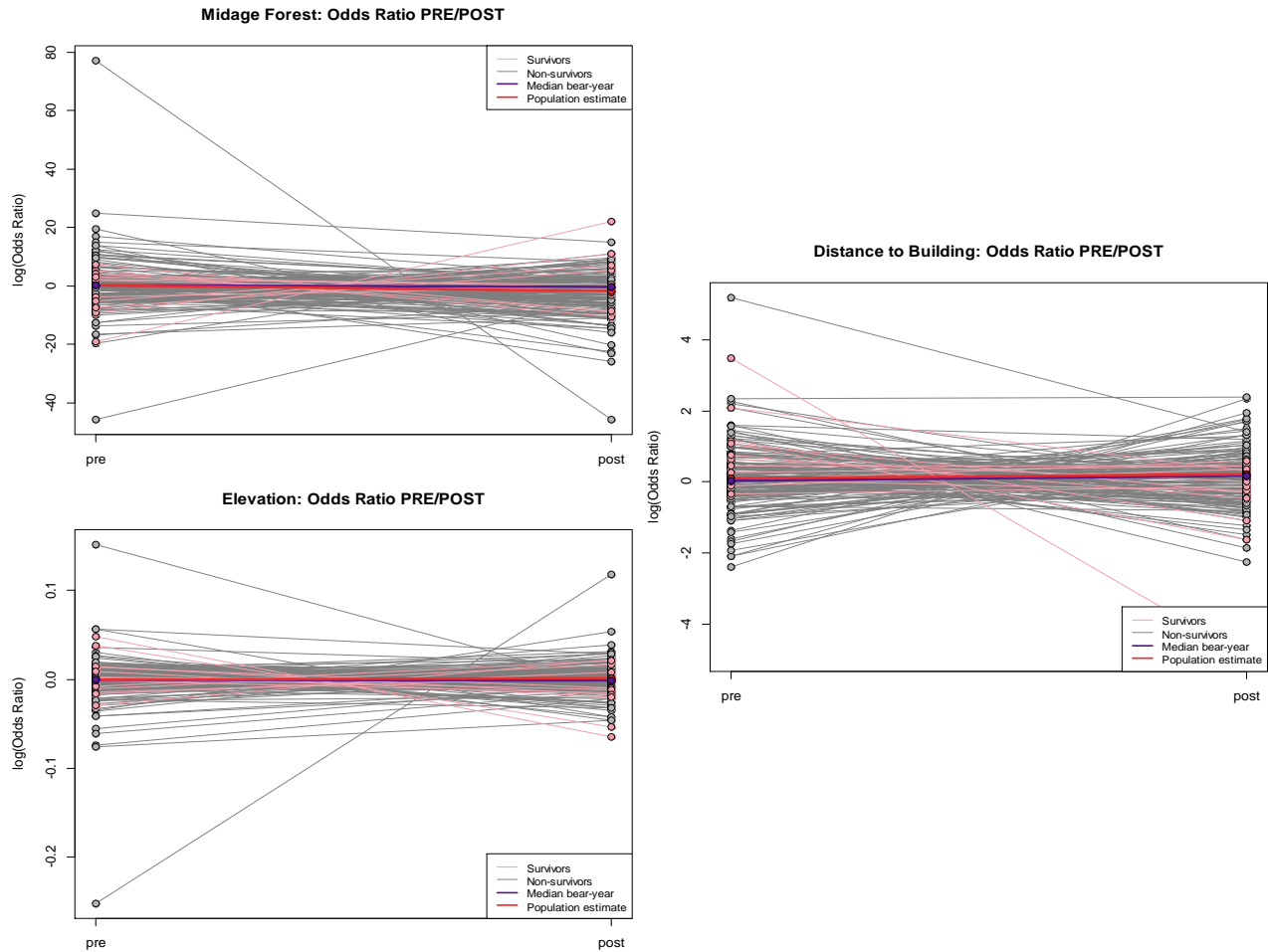


Figure 4.2: Odds ratios of individual bear-years for the “midage forest” habitat type (top left), distance to building (right), and elevation (bottom left). The log-values of the odds-ratios have been plotted here as the range in values was extremely large. The thick purple line shows the odds ratio shown by the population-level model, while the thick red line shows the median bear-year model values. “Pre” and “Post” denote the odds-ratio values of this variable before and after the hunt began. It must be noted that because the log-odds-ratio values are plotted, small differences observed in the plots are more dramatic than they appear.

Midage forest goes from being avoided in the pre-hunt period, to being selected-for once the hunt begins (Table 4.2). The slight incline of the red trend-line in Figure 4.2 (top left) mirrors this. However, what is most striking for these three plots as well as for all other variables is that there is a great variety in trends across bear-years. Some bear-years show an opposite trend to that shown by the population-level model, others show a much more extreme shift, in the same direction as the population model. There is no clear grouping of survivors and non-survivors (color-coded in grey and pink in the plots of Figure 4.2). The variety amongst bear-years emphasizes that strategies and habitat selection can vary greatly amongst individuals. Though the population-level model does make an attempt to generalise this, with such variety it does not appear that useful.

In summary, bears do indeed show a habitat selection shift once the hunting season commences. Though the most sensitive variables at the population-level are “Habitat”, “Distance to Building” and “Elevation”, the wide variety these variables show at the individual-level make population-inferences difficult.

4.3.2 Degree of shift with hunting onset: Comparing survivors and non-survivors

The first four principal components were deemed the most relevant by the Kaiser criterion, as they all had an eigenvalue above 1 (Kaiser 1960). Together they explained over 75% of the total variation in the dataset (see Table 4.3).

Table 4.3: Overview of all principal components and their relative importance in describing overall variance

#	Eigenvalue	Proportion Explained	Cumulative Proportion
PC1	3.813	0.347	0.347
PC2	1.840	0.167	0.514
PC3	1.479	0.134	0.648
PC4	1.202	0.109	0.758
PC5	0.907	0.082	0.840
PC6	0.807	0.073	0.913
PC7	0.495	0.045	0.958
PC8	0.301	0.027	0.987
PC9	0.098	0.009	0.995
PC10	0.042	0.004	0.998
PC11	0.017	0.002	1.000

Selection for most of habitat types is moderately correlated with the first principal component, whereas the selection for the variables “Minor Road Distance”, “Elevation” and “bog” were more strongly correlated with the second principal component (Table 4.4 and biplot of Figure 4.3). This suggests that these variables are more relevant in portraying the overall variance in bear habitat selection behaviour of this area.

The other anthropogenic variables and “TRI” were more strongly correlated with the lower principal components (Table 4.4).

Table 4.4: Overview of all independent variables and their correlation with/‘loading’ on the principal components (only the relevant components have been included here). Cells that are highlighted show loadings greater than 0.4.

Variable	Bog	Clearcut	Midage Forest	Old Forest	Young Forest	Minor Road Distance	Minor Road Density	Major Road Distance	Building Distance	Elevation	TRI
PC1	0.297	-0.482	-0.493	-0.489	-0.427	0.062	-0.016	-0.041	0.030	-0.086	-0.024
PC2	-0.471	-0.114	-0.104	-0.108	-0.138	-0.431	-0.230	0.127	-0.007	0.642	-0.236
PC3	0.299	0.059	0.055	0.067	0.057	-0.457	-0.609	-0.469	0.261	-0.169	-0.006
PC4	-0.051	-0.048	0.021	0.039	0.050	0.262	0.331	-0.462	0.549	0.178	-0.514

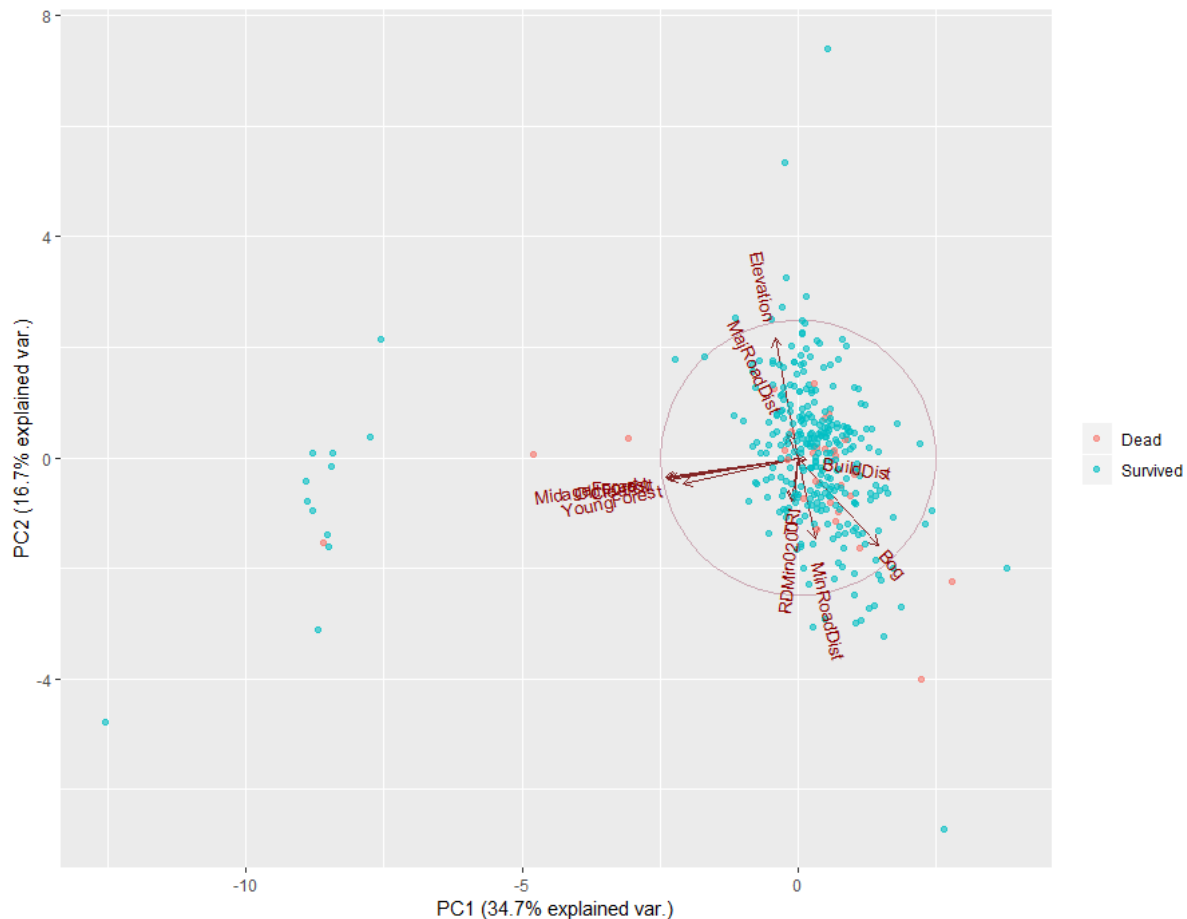


Figure 4.3: PCA biplot, with observations colour-coded by survival-status that hunting season. The first two principle components explaining the greatest amount of variation (51% together) are plotted. There were two points for every bear-year (one before and one after the hunting season began). The correlation circle has been added, and arrows/explanatory variables pointing in similar directions are more correlated with each other than with others in the PCA space. There is no obvious clustering of survivor vs. non-survivor bear-years in the PCA space.

The magnitude of the observed habitat shift was calculated for each individual, along every principal component individually. The magnitude was then averaged for the survivors and non-survivors, and the difference in this average was tested – an overview of the results presented in Table 4.5. There was no significant difference between the two groups in the average difference in shift in the PCA space, for any of the four relevant principal components.

Table 4.5: Results from the Welch two-sample t-test, measuring the distance in the PCA space between two paired observations. The observation pairs were grouped into “survivor” or “non-survivor”, and the mean difference size compared between these two groups.

Component	Mean		df	t	p-value
	Survivor	Non-survivor			
PC1	1.132	1.365	16.5	0.42	0.68
PC2	0.951	0.938	18.8	-0.05	0.95
PC3	0.910	1.252	13.6	0.73	0.48
PC4	0.770	1.343	13.3	1.18	0.26

In short, the average survivor bear *did not* show a marked difference in the magnitude of their habitat shift when compared to the habitat shift of the average non-survivor.

4.4 Habitat-use differences between survivors and non-survivors

Habitat use differed between bears that survived and bears that didn’t during a given bear-year. Increasing distances from minor roads and buildings, and increasing elevation show a *lower* chance of being hunter-killed among bears (all negative relationships in Figure 4.4). On the other hand, increasing TRI, minor road density, and distances from major roads show a *higher* chance of being hunter-killed among bears (all positive relationships in Figure 4.4). However, the confidence intervals are also wider for the two latter variables. Finally, the habitat variable suggests that “bog” and “clearcut” habitat types are more used by non-survivor bear-years, whereas “midage forest” was used relatively little by this group.

For bear behaviour studies, temporal and demographic elements have been shown to be important. In this research, the addition of a temporal and demographic variable (“hunt season” and “age” respectively) did improve model performance in all instances, when compared to the base-model with only spatial variables (M1 in Table 4.6). The best model incorporated these two variables as a double-interaction term (Table 4.6).

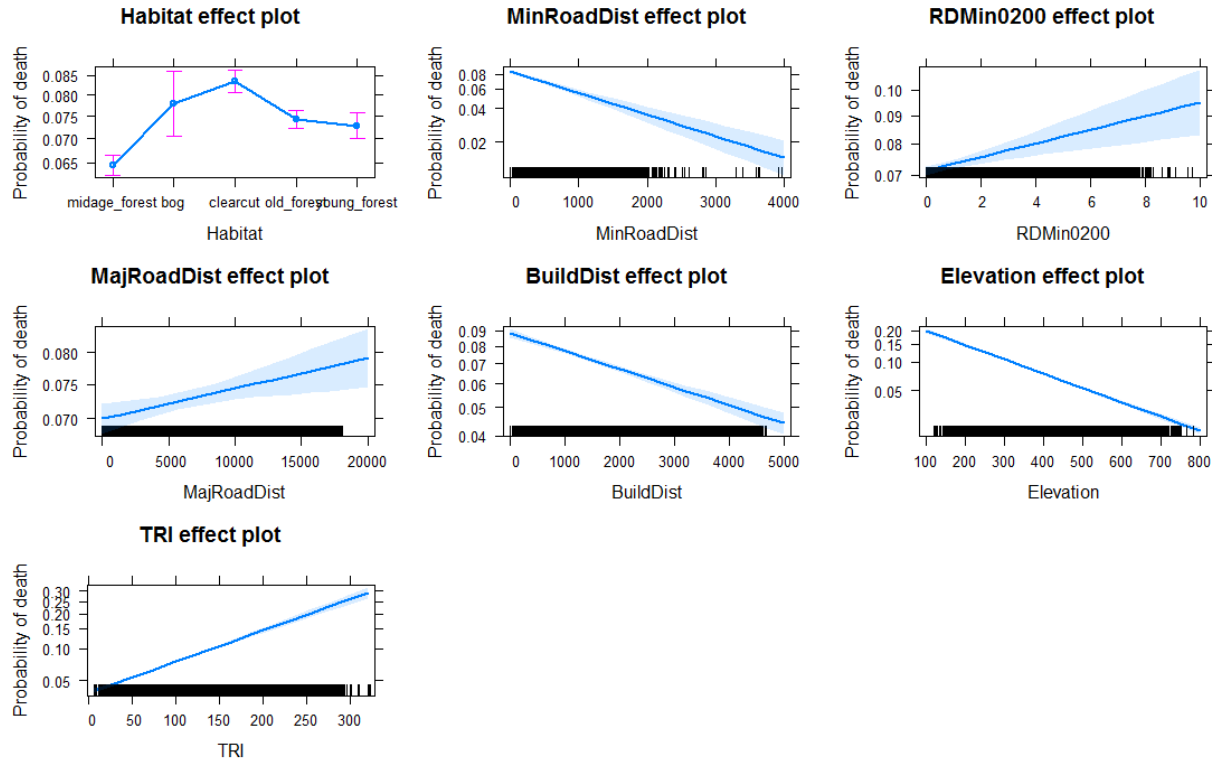


Figure 4.4: Overview of habitat use model, with effects of all spatial variables depicted, unscaled. The y-axis denotes the probability that a given location belongs to a non-survivor bear-year (in the binary logistic regression; non-survivors=1, survivors =0). The x-axis is in the unit of the spatial variable in question. The shorthand labels for the variables mirror those introduced in Table 3.1.

Table 4.6: Comparison of candidate models and their performance in AICc terms

#	Model names	K	$\Delta AICc$	AICcw	LL
7	M1 \times age \times season	44	0	1	-50644.42
9	(M1 + season) \times age	24	306.3127	0	-50817.59
6	M1 \times age	22	549.176	0	-50941.02
8	(M1 + age) \times season	24	808.6664	0	-51068.77
4	M1 + age + season	13	877.8228	0	-51114.35
2	M1 + age	12	1130.0287	0	-51241.45
5	M1 \times Season	22	1601.1661	0	-51467.02
3	M1 + Season	12	1673.1367	0	-51513
1	M1	11	1955.8274	0	-51655.35

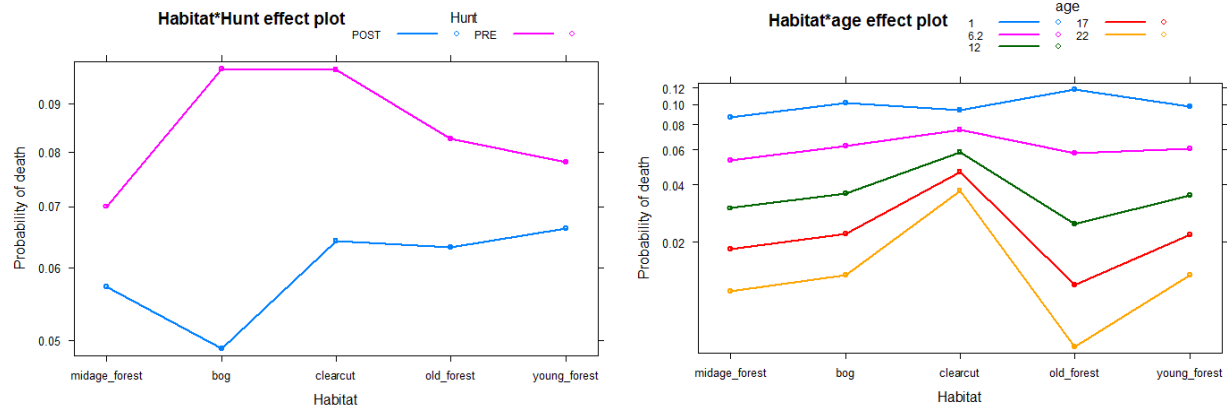


Figure 4.5: Effect of interaction term "Age" (left) and "Hunt Seasonality" (right) on response variable. These effect plots are extracted from the best-performing model with a double-interaction term (Model 7 in Table 4.6). Younger bears are more vulnerable than older bears, regardless of the habitat type (plot on the left). Similarly, habitat type used in the pre-hunt period is a greater determinant of habitat success than during the hunting season (pink line is consistently higher than blue, see plot on right).

Taking a closer look at the additional temporal and demographic elements, we see that in general, older bears show better survival success than younger bears across all spatial variables (Figure 4.5–right and Figure 4.6). It must be noted that the proportion of older bears is quite small (see Figure B.4). Also habitat use in the pre-hunt period seemed to be more determinant of survival success than habitat use after the hunt began (pre-hunt is consistently higher; Figure 4.5–left and Figure 4.7), though again as most bears died in the early days of the hunting season, this could again be biased by less post-hunt data for non-survivors (see Figure 3.3).

When looking at the habitat types in more detail, most risky habitats appear to be bogs and clearcuts (Figure 4.4). However, as Figure 4.5 shows, the most risky habitats vary with age. The flatter shape of the lines for the younger bears suggests that their vulnerability remains high regardless of habitat type. With older bears however, there is clear peak at “clearcut” habitat type, suggesting this is a more vulnerable category than others, and a dip at “old forest”, suggesting this is more of a refuge. The survival of older bears appears more strongly connected to habitat-use than compared to younger bears.

When considering the interaction of “Hunt seasonality” with “Habitat”, the habitat type utilised during the pre-hunt period appeared to be a greater determinant of survival success than during the hunt (Figure 4.5–left). The shape of the pre-hunt habitat use is similar to the overall habitat-use model (Figure 4.4). This could be an artefact by the lower data volume for non-survivor bear-years during the hunting season.

When looking at the other variables, the trend mirrors the general habitat-use model, and the same influence holds true for most of these variables: younger bears are more vulnerable, and habitat use in the pre-hunt period are more reflective of survival chances (see Figure 4.6 and Figure 4.7). The lines consistently lay parallel to each other. However, there are a few exceptions, primarily with the topographic variables. The variables “Elevation” and “TRI” all show a cross-over point with the “Hunt” interaction term. This suggests that at a certain threshold, the opposite holds true – the pre-hunt period is less impactful than during the hunt at high elevations (>520m) and low ruggedness (>70m).

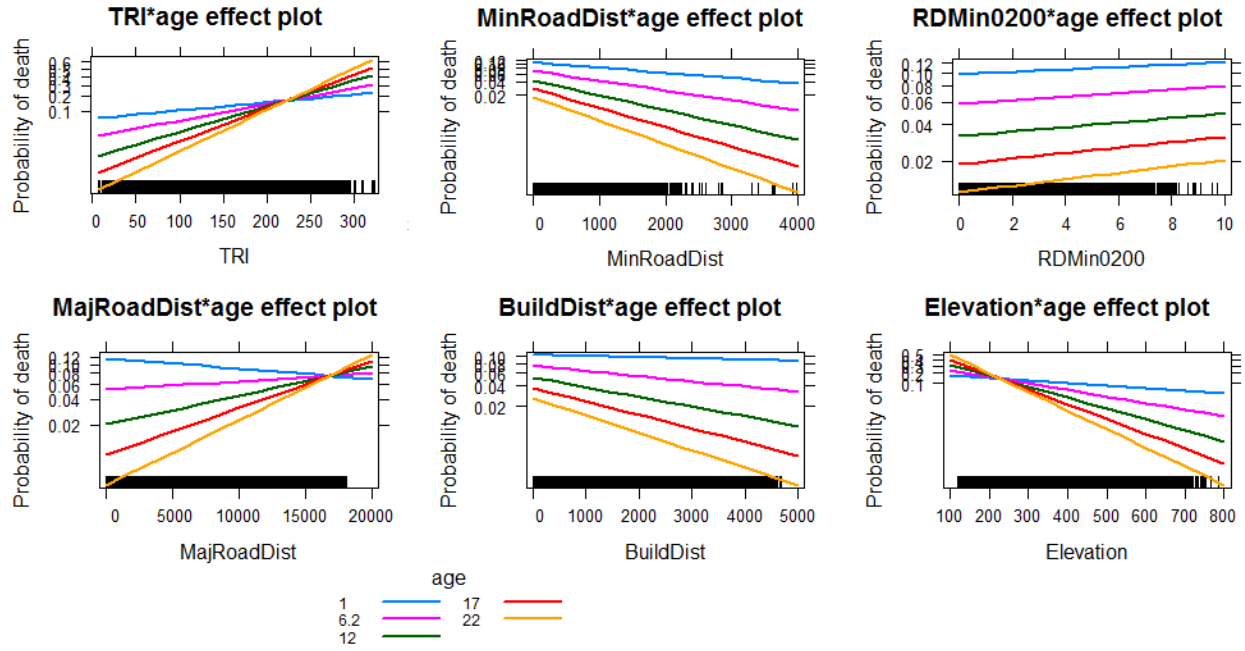


Figure 4.6: Interaction effect of "age" on the anthropogenic and topographic variables

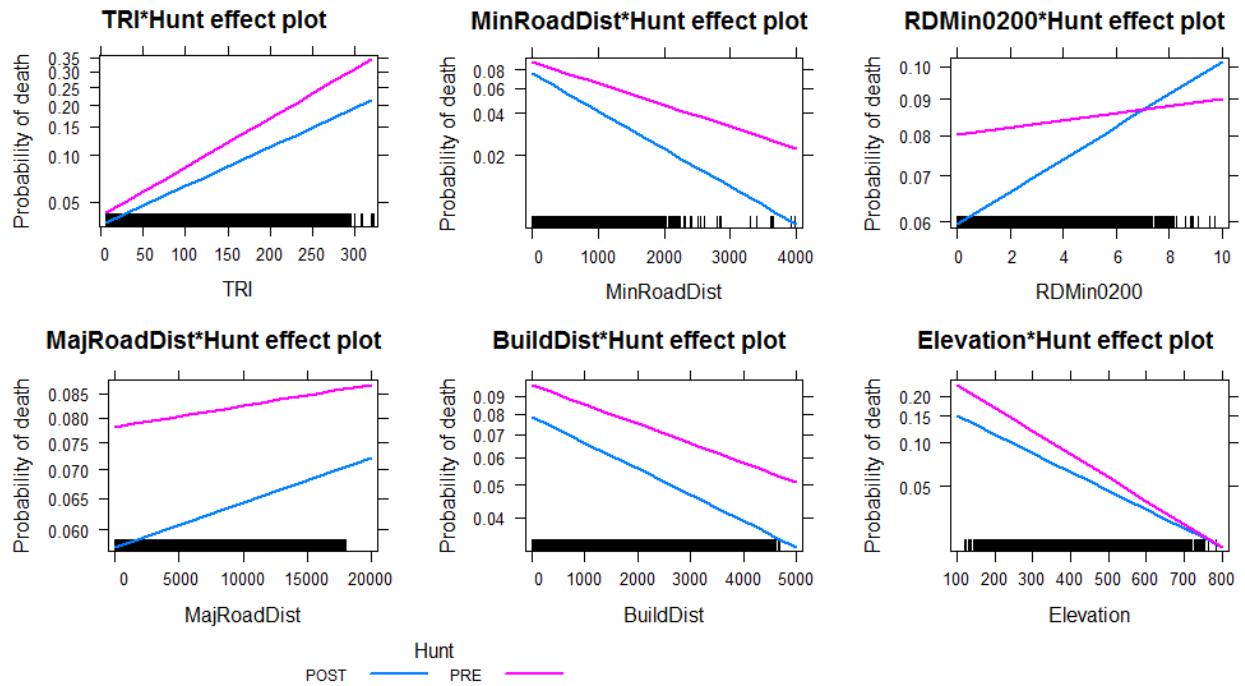


Figure 4.7: Interaction effect of "hunt" on the anthropogenic and topographic variables

5. DISCUSSION & RECOMMENDATIONS

The purpose of this research was to determine what space-use patterns could be identified across individual bears in the hunting season, and how that related to their survival.

Research Question 1 was assessing whether bears were sensitive to the hunting season, and changed habitat-selection behaviour once the hunting season began. A very narrow time-period before and after the hunting season started was looked at, in order to limit as much as possible other seasonal effects that could confound resource selection inferences. The comparison of resource selection functions before and after the hunt began, with this “seasonality” as an interaction term showed that bears *were* indeed sensitive to the hunting season, responding with a change in habitat selection behaviours. This is not surprising, as habitat shifts are just one of the behavioural adaptations large predators exhibit in landscapes where the risk of anthropogenic mortality is high, such as this one (Oriol-Cotterill et al. 2015). The narrow time-period studied here (10 days) highlights how adaptable these bears are in this landscape, and how sensitive they are to the hunting season. When comparing survivor and non-survivor bears, there was no significant difference in the average size of the habitat shift made at the individual-level (Table 4.5), contrary to what was hypothesized (Hypothesis 1). In short, both survivors and non-survivors noticed and responded to the onset of the hunting season by shifting habitat selection.

The success of these habitat shifts varied amongst individuals. This is precisely what Research Question 2 explored, i.e. what space-use patterns contributed to survival success. This was answered by comparing the habitat-use of survivors and non-survivors. When summarised, the results show evidence for three distinct habitat-use “strategies” that a “successful” bear may adopt. These are: 1) the use of locations more inaccessible to hunters; 2) the use of locations that reduce detection by hunters; 3) the use of locations offering human-shield protection from hunters. Each of these strategies will be elaborated individually here.

The use of locations more inaccessible to hunters was one of the hypothesized habitat-use patterns of survivors (Hypothesis 2). These could include locations at great distances from forest trails (termed “minor roads” in this research), or vegetation types that deter hunters from venturing too far, such as bog or marshland habitats. This was observed, where individuals at higher elevations and further away from anthropogenic features (except major roads) show higher chance of survival. There were far fewer observations of the use of bogs, therefore it is difficult to assess whether this habitat type offers more protection from hunters (see the large error bars in Figure 4.4). However, the other results support that the use of locations that act as a deterrent to many hunters better protect some bears from hunting mortality risk.

The use of locations that reduce detection of the bear by hunters was also hypothesized (Hypothesis 2). The results support this. “Clearcut” was the most vulnerable habitat-type – a logical finding when considering how exposed bears would be in such a land-use with zero cover (Figure 4.4). Forest types of varying ages showed much lower vulnerability in contrast – though there was some variation in this pattern with bear-age (see Figure 4.5). One result that is tricky to interpret is that areas of higher ruggedness were related to *greater* hunting vulnerability (Figure 4.4). One would expect that rugged locations are more inaccessible, and should act as a deterrent to hunters. However, as Thurfjell et al. (2017) hypothesises when hunting with rifles ruggedness offers a disadvantage to targeted prey – which

could also be the case for bears here. It could also be a matter of predictability – hunters actively choose rugged locations because they expect bears to be there. This finding is thus a little ambiguous. What would better provide evidence for these two strategies were if an additional vegetation density metric were incorporated into the study, at both human eye-level (regarding visibility) and understory (regarding impenetrability) levels.

The third strategy which was not hypothesized beforehand was the human-shield protection from hunters. This strategy is attributed to the result that increased proximity to major roads is related to *lower* vulnerability for hunting mortality. Brown bears have been shown to use areas close to roads in general. It could be that there are more resources located around major roads, and bears are willing to take a risk and use habitats with a higher foraging reward despite a higher risk (Oriol-Cotterill et al. 2015). Some studies show that this use is not consistent throughout the day, and temporal avoidance may be in effect where these locations are used more at night or when traffic volume is lower (Waller & Servheen 2005; McCown et al. 2009). Other studies show that bear movement behaviour changes dramatically as the bear gets closer to the road, suggesting increased vigilance in a higher-risk area (Roever et al. 2010). However, these studies considered traffic accidents as the primary risk, not hunting mortality. The results here show a clear selection for areas around major roads, which is a novel finding to the author's knowledge (Table 4.2). The use of areas close to roads is not surprising. However, the fact that this increases survival success is evidence that hunters may be avoiding hunting around these areas. It is logical that hunters would avoid areas close to major roads – they may not want to shoot close to major roads for safety issues, and they may be concerned that their dogs or a pursued bear crossing the road may cause an accident. These concerns that likely make hunters avoid major roads are in turn what make successful bears select areas near them – a “*human-shield effect*”. This is a strategy typically explored for prey-animals avoiding other predators (Hebblewhite et al. 2005; Berger 2007; Muhly et al. 2011), but like other predator-prey dynamics, it is not overreaching to extend the same strategy for predators avoiding the human ‘super-predator’. Though the first two strategies show a general spatial avoidance of humans when there is perceived increase in hunting mortality risk, this third strategy shows that bears clearly differentiate between hunters and other humans, and are able to segregate risk types from the same species.

Apart from answering the primary research questions of this study, the results also garnered some other insights on more factors that contribute to bear vulnerability in the hunting season. First, choices made in the pre-hunt period appeared to be a greater determinant of survival success than those choices made once the hunt had begun (see Figure 4.7). This seems counterintuitive, and may be in part because non-survivor bears had very little data once the hunt began, skewing selection estimates (bears are typically killed in the first few days of the hunting season, see Figure 3.3). Nevertheless it does suggest that behaviour before the hunt begins is an important factor for survival during the hunting season. Next, the age of the bear was a relevant factor, as older bears were less likely to get killed than younger bears. Both these factors input as a double-interaction term was the best predictor of survival. Together, this suggests that bears may be learning from previous years, and adjust their habitat selection at that time of year accordingly – as seen in Figure 3.5, most female bears that were shot were very young, and hunters are much less likely to kill an older, well-established bear. However, there are also far fewer of these older well-established bears, a factor which may also be of influence here. Showing how individual bears adjust their behaviour with age would be an interesting next-step, as has been done in studies of other species (Thurfjell et al. 2017).

5.1 Design limitations

Several design choices were made in the modelling of habitat use and habitat selection in this study. First, to estimate available habitat, random locations were generated within a MCP of true bear locations over the entire year. There are two potential issues associated with this method. First, the MCP method of home-range estimation tends to overestimate size, and create a home-range of an unrealistic shape assuming uniform use within the generated polygon (Burgman & Fox 2003). Second, generating points randomly from the annual home-range of a bear does not incorporate the influence of movement constraints, and assumes that all parts of the home-range are available equally to the bear at a given moment in time irrespective of where the bear is currently located (Martin et al. 2008). This is of course not the case, and may be considered a false representation of true habitat “availability” when calculating habitat selection, and overestimate the strength of the habitat selection parameters. This is why the results in section 4.2 must be interpreted with this in mind. By using one of the alternatives discussed in Chapter 2, the “available” habitat may have been better represented. In particular, trajectory-based methods have the added advantage of incorporating movement constraints (Martin et al. 2008). These methods (also called ‘step-selection functions’ or SSFs) give a much more conservative estimate for habitat selection parameters than when habitat availability is based on randomly generated coordinates generated within an MCP. Moving towards SSFs will therefore remove the inherently problematic assumptions MCPs make. These include the assumption that all locations within the home-range are equally available to a bear at any given time, and that that bear has no intrinsic constraints (such as feeding or resting requirements) when moving through the home-range (Martin et al. 2008). Additionally, SSFs may give more insight into behavioural differences between survivors and non-survivors, as the scale applied is more realistic to the individual decision-making scale, and information such as step-length is also available (Roever et al. 2010). Step-length can be used as a marker of vigilance or hunter pursuit, and therefore incorporating this will provide additional depth to the research. Though MCPs are fast and insightful for exploratory analysis, using SSFs will overcome some of the assumptions MCPs make.

The scale of choice for habitat selection at the individual level was the annual home-range. This is a logical choice of scale, but it could be argued that a smaller seasonal home-range, i.e. a subset of the annual home-range would have been more appropriate, given the small temporal window (10 days) in which my analyses were conducted. It may have better depicted available “Habitat” to the bear that season. However, the issue here is that when selecting a seasonal home-range scale it is impossible to disentangle how much of home-range establishment is driven by resource availability, and how much is driven by seeking refugia from hunters. This problem disappears when the annual home-range scale is considered. It is clear that the design choices made influence estimates of availability greatly. Again, SSFs will not face this problem.

Another shortcoming is the manual updating of the land-cover map from the reference year 2000. The only land-cover change that can be incorporated in this study since 2000 is the change of forest classes into clear-cut areas, as the location and date of clear-cut events was known. Using only this data to update the land-cover raster assumes that there were no other land-use changes within the study-area, and gives a somewhat crude overview of true land-cover. Fine-scale changes such as growth of urban areas, farmlands, and even ecosystem shifts or forest encroachment cannot be incorporated with this method of updating, and therefore there could be some inaccuracies present. It would be preferable to have a land classification map created on an annual basis just before the hunting season begins, to more accurately ascribe habitat types to bear-locations specific to that time period.

The raster layers used were of different cell sizes, and were not resampled to obtain an equal resolution. This introduces a bias, as variables with a finer-resolution are more accurately represented. The topographic variables were less accurate than the other variables in this study. Though a standard practice in spatial-data pre-processing, I was hesitant to lose any fine-scale information by resampling variables to coarser resolutions (Dixon & Earls 2009). This was a particular concern for categorical data such as land-cover type as this can vary greatly at the fine-scale. For this study primarily concerned with understanding space-use of ‘smart’ bears, some key details and nuance may be missed by resampling to a coarser level. For this reason, the original resolution of all raster layers was used and values extracted to the point-locations without resampling. In order to evaluate how much of a concern information loss due to resampling is, all variables in Table 3.1 can be resampled to the 50x50m resolution of the topographic variables, and the analysis can be redone, comparing the results here and assessing any differences.

The relevance and importance of the spatial dimension in habitat selection has been made clear. However, the temporal dimension in this study could be further strengthened. Only “hunt seasonality” was incorporated as the temporal element (which significantly influencing selection) – this is arguably inadequate when considering the effect the time-of-day can have on bear habitat selection (Moe et al. 2007). The same population of bears have been shown to *shift* foraging behaviours to more crepuscular and nocturnal hours when hunting risk is high, as hunters are typically only active in the day (Hertel et al. 2016). Not including this variable is a shortcoming and may have offered more insight here. Opting for a SSF will in part add a temporal dimension, as the available resources will be limited by the accessibility (as limited by movement speed) from the current location. However, as this study is concerned with the space-use patterns influencing survival success, an obvious next step would be to conduct a survival analysis. These analyses model time-to-event (in this case, death of a bear during the hunting season) and explore what factors contribute to this. A study done on white-tailed deer (*Odocoileus virginianus*) surviving the hunting season is a good example of this, and also highlights the factors contributing to the longevity of individuals (Delgiudice et al. 2006). Additionally, landscape of coexistence theory claims that in high-risk landscapes, a temporal avoidance of humans may also be a strategy used in order to utilise high-resource areas at a safer time of day (Beckmann & Berger 2003; Oriol-Cotterill et al. 2015). How this differs between survivors and non-survivors with hunting onset is another angle that can be further explored.

5.2 Recommendations

Reducing the limitations of this study has been discussed thus far. However, this study has provided some topical preliminary insight on bear “strategies” that need deeper exploration in order to validate the results seen here. In order to do this, I will propose some research suggestions here.

Two of the proposed space-use strategies that bears could be adopting are the “using locations more impenetrable to humans” and the “using locations of low visibility”. In order to assess these strategies, more information on vegetation density is required, as the habitat-type variable used here is suggestive of these strategies, but more quantitative results is desired. Ideally, vegetation density variables should be constructed at the ground level (for assessing impenetrability), and at human eye-level (for assessing detectability). In order to construct density variables for a study-area of this size, the use of airborne LiDAR information would be suitable, as it is able to penetrate through the canopy and show levels of vegetation, and also provide information on understory density (Campbell et al. 2017, 2018). Additionally, airborne LiDAR information can be used to estimate ground wetness, and assuming marshlands and wetter terrains are a deterrent for hunters, ground wetness can be incorporated as an

additional variable to test this strategy (Langlois et al. 2017). Conducting airborne LiDAR measurements is however expensive, and a cheap and simple alternative (though not as accurate or fine-scale) is the use of freely-available multispectral satellite imagery, and deriving vegetation indices as a proxy for vegetation density. The drawback here is that density at different levels cannot be ascertained in the same way that would be possible with LiDAR information. Martinuzzi et al. (2009) show that space-borne LiDAR can also be used to estimate forest understory with resolution up to 20m – and for far-moving large predators like brown bears, this should suffice.

The final strategy proposed is that successful bears avoid hunting by using the “protection offered by the “human shield” effect”. This strategy is based on the assumption that hunters are less-likely to hunt around major roads and other areas of high human density. To test this assumption, modelling hunter-distribution in the study-area would be a key step. As RSFs have been constructed for bears, similar RSFs could be constructed for humans by equipping hunters with GPS navigators and tracking their movement when hunting bears. From this information, constructing a hunter-distribution variable and incorporating this into the bear-survival models would better validate or invalidate the proposed strategy of human-shield effect. It would also be useful in follow-up research that better incorporates the temporal dimension (like SSFs or survival analyses).

Finally, there are a couple of general follow-up studies that ought to be conducted to assess how generalizable these results are. First, the robustness of models has not been tested, nor validated. This was in part because the non-survivor bear-year data was considerably smaller than the survivor bear-year data, and partitioning it for robustness testing was not desired. However, the models can be validated by testing on unseen data, such as the hunting seasons that have followed since 2016. Next, studying the lone-males and comparing them to the results of the lone-females obtained here is useful in testing how much of the strategies are sex-dependent. The mortality distribution map (Figure 4.1) suggested that there may be some sexual differences, and other intrinsic differences support the case that the sexes ought to be considered separately initially (Martin et al. 2008). Having said that, now that there is some preliminary insight on the females, the natural next-step would be to consider how much can be generalised to the population level.

6. CONCLUSION

Predators adapt behaviours when a high risk of anthropogenic mortality is perceived, and this is no different for brown bears in the wood production forests of central Sweden. Brown bears here were shown to shift their habitat-selection behaviour significantly in a very short time-frame before and after the hunting season began, showing that most bears here are sensitive to the start of the hunting season. This shift was not always successful, and the differences between habitat use of survivors and non-survivors highlight which behaviours contribute to increased vulnerability. Three distinct space-use “strategies” were gleaned from this comparison. The first strategy is that bears select areas where humans are likely not to venture due to their low accessibility and/or impenetrability. Second, bears select locations offering more cover, where their detection by hunters is reduced. Finally, due to issues of safety, hunters may avoid areas around busy roads, and bears that strategically use these areas during the hunting season are offered protection from a human-shield effect. This third strategy demonstrates that certain successful bears are able to differentiate the different types of anthropogenic mortality risk. Though they do not show a particular selection or avoidance of major roads before the hunting season, they show a strong selection for these areas once the hunt has begun. Bears here trade-off increased risk for traffic accidents during this key season because of how acute the hunting risk is at that time of year. This differentiation of risk and a human-shield effect against other humans is a novel finding in bear habitat-selection studies and is valuable in demonstrating the sensitivity and adaptability of this population to the annual hunting season.

Apart from these spatial insights, temporal and demographic factors were also great determinants of survival success. Older bears were less-likely to be shot, suggesting the influence of learning from preceding hunting seasons. Pre-hunt behaviour is also a big determinant of success. It is the pre-emptive habitat selection behaviours that are more likely to predict success than adaptability once the hunt has already begun. In mixed-use landscapes with high human disturbance, temporal avoidance strategies too can help carnivores avoid risk.

The results here are novel in that they highlight how not only avoidance of humans, but a differentiation of hunters from other humans is an important precursor of survival success in a landscape such as this one where hunting has such an efficient and narrow temporal window. This preliminary insight can be strengthened with the addition of parameters on vegetation density and hunter distribution. Further highlighting the temporal domain (with survival analyses and SSFs) will provide more information on vigilance behaviour and any changes that may exist in activity periods between survivors and non-survivors.

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REFERENCES

- Ascione A, Cinque A, Miccadei E, Villani F, Berti C. 2008. The Plio-Quaternary uplift of the Apennine chain: new data from the analysis of topography and river valleys in Central Italy. *Geomorphology* **102**:105–118.
- Athreya V, Odden M, Linnell JDC, Krishnaswamy J, Karanth KU. 2014. A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. *Oryx*:1–7.
- Balme GA, Slotow R, Hunter LTB. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. *Animal Conservation* **13**:315–323.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**:1–48.
- Beckmann JP, Berger J. 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *Journal of Zoology (London)* **261**:207–212.
- Berger J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* **3**:620–623.
- Bischof R, Bonenfant C, Rivrud IM, Zedrosser A, Friebe A, Coulson T, Mysterud A, Swenson JE. 2018. Regulated hunting re-shapes the life history of brown bears. *Nature Ecology and Evolution* **2**:116–123. Springer US.
- Bischof R, Fujita R, Zedrosser A, Swenson JE. 2008. Hunting Patterns, Ban on Baiting, and Harvest Demographics of Brown Bears in Sweden. *Journal of Wildlife Management* **72**:79–88.
- Bischof R, Swenson JE, Yoccoz NG, Mysterud A, Gimenez O. 2009. The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology* **78**:656–665.
- Bjørneraas K, Van Moorter B, Rolandsen CM, Herfindal I. 2010. Screening Global Positioning System Location Data for Errors Using Animal Movement Characteristics. *Journal of Wildlife Management* **74**:1361–1366.
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA. 2002. Evaluating resource selection functions. *Ecological Modelling* **157**:281–300.
- Burgman MA, Fox JC. 2003. Bias in species range estimates from minimum convex polygons: implications for conservation and options for improved planning. *Animal Conservation* **6**:19–28.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference : a practical information-theoretic approach. Springer.
- Burt WH. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**:346–352.
- Campbell MJ, Dennison PE, Butler BW. 2017. A LiDAR-based analysis of the effects of slope, vegetation density, and ground surface roughness on travel rates for wildland firefighter escape route mapping. *International Journal of Wildland Fire* **26**:884–895.

- Campbell MJ, Dennison PE, Hudak AT, Parham LM, Butler BW. 2018. Quantifying understory vegetation density using small-footprint airborne lidar. *Remote Sensing of Environment* **215**:330–342. Elsevier.
- Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, David C, Orme L, Purvis A. 2005. Multiple Causes of High Extinction Risk in Large Mammal Species. *Science* **309**:1239–1241.
- Castley JG, Knight MH, Mills MGL, Thouless C. 2002. Estimation of the lion (*Panthera leo*) population in the southwestern Kgalagadi Transfrontier Park using a capture- recapture survey. *African Zoology* **37**:27–34.
- Ciuti S, Muhly TB, Paton DG, Mcdevitt AD, Musiani M, Boyce MS. 2012. Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B — Biological Sciences* **279**:4407–4416.
- Dahle B, Swenson JE. 2003. Home ranges in adult Scandinavian brown bears (*Ursus arctos*): effect of mass, sex, reproductive category, population density and habitat type. *Journal of Zoology* **260**:329–335.
- Darimont CT, Fox CH, Bryan HM, Reimchen TE. 2015. The unique ecology of human predators. *Science* **349**:858–860.
- Davidson Z, Valeix M, Loveridge AJ, Hunt JE, Johnson PJ, Madzikanda H, Macdonald DW. 2012. Environmental determinants of habitat and kill site selection in a large carnivore: scale matters. *Journal of Mammalogy* **93**:677–685.
- Delgiudice GD, Fieberg J, Riggs MR, Powell MC, Pan W. 2006. A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management* **70**:1556–1568.
- Delgiudice GD, Riggs MR, Joly P, Pan W. 2002. Winter Severity, Survival, and Cause-Specific Mortality of Female White-Tailed Deer in North-Central Minnesota. *The Journal of Wildlife Management* **66**:698–717.
- Dixon B, Earls J. 2009. Resample or not?! Effects of resolution of DEMs in watershed modeling. *Hydrological Processes* **23**:1714–1724.
- Dorresteijn I, Hanspach J, Kecskés A, Latková H, Mezey Z, Sugár S, von Wehrden H, Fischer J. 2014. Human-carnivore coexistence in a traditional rural landscape. *Landscape Ecology* **29**:1145–1155.
- Elfström M, Swenson JE, Ball JP. 2008. Selection of denning habitats by Scandinavian brown bears *Ursus arctos*. *Wildlife Biology* **14**:176–187.
- Estes JA et al. 2011. Trophic Downgrading of Planet Earth. *Science* **333**:301–306.
- Fox J, Weisberg S, Friendly M, Hong J, Andersen R, Firth D, Taylor S, R Core Team. 2018. effects: Effect Displays for Linear, Generalized Linear, and Other Models. CRAN.
- Frank SC, Leclerc M, Pelletier F, Rosell F, Swenson JE, Bischof R, Kindberg J, Hans GE, Hagen SB, Zedrosser A. 2018. Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *Journal of Animal Ecology* **87**:247–258.
- Gosselin J, Leclerc M, Zedrosser A, Steyaert SMJG, Swenson JE, Pelletier F. 2017. Hunting promotes sexual conflict in brown bears. *Journal of Animal Ecology* **86**:35–42.

- Gula R, Theuerkauf J. 2013. The need for standardization in wildlife science: home range estimators as an example. *European Journal of Wildlife Research* **59**:713–718.
- Hebblewhite M, White CA, Nietvelt CG, McKenzie JA, Hurd TE, Fryxell JM, Bayley SE, Paquet PC. 2005. Human Activity Mediates a Trophic Cascade Caused by Wolves. *Ecology* **86**:2135–2144.
- Herrero S. 1972. Aspects of Evolution and Adaptation in American Black Bears (*Ursus americanus* Pallas) and Brown and Grizzly Bears (*U. arctos* Linné.) of North America. *Bears: Their Biology and Management* **2**:221–231.
- Hertel AG, Zedrosser A, Mysterud A, Støen O-G, Steyaert SMJG, Swenson JE. 2016. Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? *Oecologia* **182**:1019–1029.
- Jacques CN, Jenks J, Siever JD, Roddy DE, Lindzey FG. 2010. Survival of Pronghorns in Western South Dakota. *Journal of Wildlife Management* **71**:737–743.
- Jaeger JAG, Soukup T, Madriñán LF, Schwick C, Kienast F. 2011. Landscape Fragmentation in Europe. Page Joint EEA-FOEN Report. Copenhagen.
- Johnson BK, Kern JW, Wisdom MJ, Findholt SL, Kie JG. 2000. Resource Selection and Spatial Separation of Mule Deer and Elk during Spring. *Journal of Wildlife Management* **64**:685–697.
- Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS. 2006. Resource Selection Functions Based on Use–Availability Data: Theoretical Motivation and Evaluation Methods. *Journal of Wildlife Management* **70**:347–357.
- Johnson DH. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology* **61**:65–71.
- Kaiser HF. 1960. The Application of Electronic Computers to Factor Analysis. *Educational and Psychological Measurement* **20**:141–151. Sage PublicationsSage CA: Thousand Oaks, CA.
- Kansky R, Kidd M, Knight AT. 2014. Meta-analysis of attitudes toward damage-causing mammalian wildlife. *Conservation Biology* **28**:924–938.
- Kindberg J, Swenson JE. 2014. Björnstammens storlek i Sverige 2013-länsvisa skattningar och trender. Stockholm, Sweden, in Swedish.
- Kittle AM, Watson AC, Kumara PHSC, Sadanayake SDKC, Fernando TSP. 2014. Notes on the diet and habitat selection of the Sri Lankan leopard *Panthera pardus kotiya* (mammalia: felidae) in the central highlands of Sri Lanka. *Journal of Threatened Taxa* **6**:6214–6221.
- Kooij B. 2015. A Spatial Temporal Analysis Method to Detect Brown Bear (*Ursus Arctos*) Home Range Change. Wageningen University and Research Centre.
- Kuijper DPJ, Sahlén E, Elmhagen B, Chamaillé-Jammes S, Sand H, Lone K, Cromsigt JPGM. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B — Biological Sciences* **283**:20161625. The Royal Society.
- Langlois MN, Richardson MC, Price JS. 2017. Delineation of peatland lag boundaries from airborne LiDAR. *Journal of Geophysical Research: Biogeosciences* **122**:2191–2205. Wiley-Blackwell.
- Lantmäteriet. 2016. Product description: GSD-Elevation data, grid 50+ nh. Available from

<https://www.lantmateriet.se/sv/Kartor-och-geografisk-information/Hojddata/GSD-Hojddata-grid-50-/> (accessed November 8, 2018).

- Leclerc M, Frank SC, Zedrosser A, Swenson JE, Pelletier F. 2017. Hunting promotes spatial reorganization and sexually selected infanticide. *Scientific Reports* **7**:1–6.
- Leclerc M, Vander Wal E, Zedrosser A, Swenson JE, Kindberg J, Pelletier F. 2016. Quantifying consistent individual differences in habitat selection. *Oecologia* **180**:697–705.
- Lodberg-Holm HK. 2015. When the hunter becomes the hunted: Impacts of hunting on the foraging behavior of the brown bear (*Ursus arctos*) in Sweden. Norwegian University of Life Sciences.
- Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW. 2007. The impact of sport-hunting on the population dynamics of an African lion population in a protected area. *Biological Conservation* **134**:548–558.
- Loveridge AJ, Valeix M, Elliot NB, Macdonald DW. 2017. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. *Journal of Applied Ecology* **54**:815–825.
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. *Resource Selection By Animals: Statistical Design and Analysis for Field Studies* Second. Kluwer Academic Publishers, Dordrecht.
- Martin J, Basille M, Moorter B Van, Kindberg J, Allainé D, Swenson JE. 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology* **88**:875–883.
- Martin J, Calenge C, Quenette P-Y, Allainé D. 2008. Importance of movement constraints in habitat selection studies. *Ecological Modelling* **213**:257–262.
- Martinuzzi S, Vierling LA, Gould WA, Falkowski MJ, Evans JS, Hudak AT, Vierling KT. 2009. Mapping snags and understory shrubs for a LiDAR-based assessment of wildlife habitat suitability. *Remote Sensing of Environment* **113**:2533–2546.
- Mazerolle MJ. 2017. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). CRAN.
- McCown JW, Kubilis P, Eason TH, Scheick BK. 2009. Effect of traffic volume on American black bears in central Florida. *International Association for Bear Research and Management* **20**:39–46.
- Moe TF, Kindberg J, Jansson I, Swenson AE. 2007. Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (*Ursus arctos*). *Canadian Journal of Zoology* **85**:518–525.
- Morrison CD, Boyce MS, Nielsen SE, Bacon MM. 2014. Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity. *Journal of Wildlife Management* **78**:1394–1403.
- Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M. 2011. Human Activity Helps Prey Win the Predator-Prey Space Race. *PLoS ONE* **6**:e17050.
- Nielsen SE, Herrero S, Boyce MS, Mace RD, Benn B, Gibeau ML, Jevons S. 2004a. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation* **120**:101–113.

- Nielsen SE, Munro RHM, Bainbridge EL, Stenhouse GB, Boyce MS. 2004b. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management* **199**:67–82.
- Nowak S, Mysłajek RW. 2016. Wolf recovery and population dynamics in Western Poland, 2001–2012. *Mammal Research* **61**:83–98.
- Noyes JH, Johnson BK, Bryant LD, Findholt SL, Thomas JW. 1996. Effects of Bull Age on Conception Dates and Pregnancy Rates of Cow Elk. *Journal of Wildlife Management* **60**:508–517.
- Ordiz A, Kindberg J, Saebø S, Swenson JE, Støen O-G. 2014. Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation* **173**:1–9.
- Ordiz A, Støen O-G, Delibes M, Swenson JE. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* **166**:59–67.
- Ordiz A, Støen O-G, Saebø S, Kindberg J, Delibes M, Swenson JE. 2012. Do bears know they are being hunted? *Biological Conservation* **152**:21–28.
- Oriol-Cotterill A, Valeix M, Frank LG, Riginos C, Macdonald DW. 2015. Landscapes of Coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos* **124**:1263–1273.
- Purvis A, Gittleman JL, Cowlishaw G, Mace GM. 2000. Predicting Extinction Risk in Declining Species. *Proceedings: Biological Sciences* **267**:1947–1952.
- Riley SJ, DeGloria SD, Elliot R. 1999. A Terrain Ruggedness Index that Quantifies Topographic Heterogeneity. *Intermountain Journal of Sciences* **5**:23–27.
- Roever CL, Boyce MS, Stenhouse GB. 2008. Grizzly bears and forestry I: Road vegetation and placement as an attractant to grizzly bears. *Forest Ecology and Management* **256**:1253–1261.
- Roever CL, Boyce MS, Stenhouse GB. 2010. Grizzly bear movements relative to roads: Application of step selection functions. *Ecography* **33**:1113–1122.
- Salmerón R, García CB, García JB. 2018. Variance Inflation Factor and Condition Number in multiple linear regression. *Journal of Statistical Computation and Simulation* **88**:2365–2384.
- Sánchez MCM, Cushman SA, Saura S. 2013. Scale dependence in habitat selection: the case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). *International Journal of Geographical Information Science*.
- Schwartz CC et al. 2003. Reproductive maturation and senescence in the female brown bear. *Ursus* **14**:109–119.
- Schwartz CC, Haroldson MA, White GC, Harris RB, Cherry S, Keating KA, Moody D, Servheen C. 2006. Temporal, Spatial, and Environmental Influences on the Demographics of Grizzly Bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* **161**:1–68.
- Slovenian Bears: Wildlife Photography Tours. 2015. [image]. Available from <http://slovenianbears.com/it/photography/> (accessed September 25, 2018).
- Statistics Sweden. 2000. Markanvändning enligt Svenska MarktäckeData (SMD). Available from <https://www.scb.se/hitta-statistik/statistik-efter-amne/miljo/markanvandning/markanvandning->

enligt-svenska-marktackedata-smd/ (accessed July 9, 2018).

- Steiniger S, Hunter AJS. 2013. A scaled line-based kernel density estimator for the retrieval of utilization distributions and home ranges from GPS movement tracks. *Ecological Informatics* **13**:1–8.
- Steyaert SMJG, Støen O-G, Elfström M, Karlsson J, Lammeren R Van, Bokdam J, Zedrosser A, Brunberg S, Swenson JE. 2011. Resource selection by sympatric free-ranging dairy cattle and brown bears *Ursus arctos*. *Wildlife Biology* **17**:389–403.
- Steyaert SMJG, Zedrosser A, Elfström M, Ordiz A, Leclerc M, Frank SC, Kindberg J, Støen O-G, Brunberg S, Swenson JE. 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. *Wildlife Biology* **22**:144–152.
- Stillfried M, Belant JL, Svoboda NJ, Beyer DE, Kramer-Schadt S. 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural Processes* **120**:30–39.
- Swenson JE, Jansson A, Riig R, Sandegren F. 1999. Bears and ants: myrmecophagy by brown bears in central Scandinavia. *Canadian Journal of Zoology* **77**:551–561.
- Swenson JE, Schneider M, Zedrosser A, Söderberg A, Franzén R, Kindberg J. 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildlife Biology* **1**:wlb.00251.
- Swenson JE, Wabakken P, Sandegren F, Bjarvall A, Franzen R, Soderberg A. 1995. The near extinction and recover of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. *Wildlife Biology* **1**:11–25.
- Thurfjell H, Ciuti S, Boyce MS. 2017. Learning from the mistakes of others: How female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PLoS ONE* **12**:e0178082.
- Tilman D, Fargione J, Wolff B, D ’antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting Agriculturally Driven Global Environmental Change. *Science* **292**:281–284.
- Treves A, Karanth KU. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* **17**:1491–1499.
- Van de Walle J, Pigeon G, Zedrosser A, Swenson JE, Pelletier F. 2018. Hunting regulation favors slow life histories in a large carnivore. *Nature Communications* **9**:1100. Nature Publishing Group.
- Waller JS, Servheen C. 2005. Effects of Transportation Infrastructure on Grizzly Bears in Northwestern Montana. *Journal of Wildlife Management* **69**:985–1000.
- Woodroffe R. 2000. Predators and people: using human densities to interpret declines of large carnivores. *Animal Conservation* **3**:165–173.
- Woodroffe R, Ginsberg JR. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. *Science* **280**:2126–2128.

APPENDIX A: VARIABLE SELECTION – SUPPLEMENTARY INFORMATION

Table A.1: $\Delta AICc$ values for the different anthropogenic density rasters

<i>Density Variable</i>	<i>Processing Window</i>	<i>K</i>	<i>$\Delta AICc$</i>	<i>AICcw</i>	<i>LL</i>
Major Road Density	0500	5	0	1.0E+00	-263404
	0400	5	144.3713	4.5E-32	-263476
	1000	5	344.7975	1.3E-75	-263576
	0300	5	363.3625	1.3E-79	-263585
	0200	5	719.3387	6.3E-157	-263763
	1500	5	775.9821	3.2E-169	-263792
	5000	5	1035.308	1.5E-225	-263921
	3000	5	1045.2884	1.0E-227	-263926
	4000	5	1105.8122	7.5E-241	-263957
	2000	5	1132.5289	1.2E-246	-263970
	0100	5	1494.051	0.0E+00	-264151
	0050	5	2261.1699	0.0E+00	-264534
Minor Road Density	0200	5	0	1.0E+00	-260171
	0100	5	171.3349	6.2E-38	-260257
	5000	5	9724.9097	0.0E+00	-265034
	4000	5	9741.3602	0.0E+00	-265042
	3000	5	9754.1181	0.0E+00	-265048
	2000	5	9745.9268	0.0E+00	-265044
	1500	5	9626.3618	0.0E+00	-264984
	1000	5	8723.8367	0.0E+00	-264533
	0500	5	5212.6318	0.0E+00	-262777
	0400	5	3680.6172	0.0E+00	-262011
	0300	5	1890.8078	0.0E+00	-261117
	0050	5	3413.2094	0.0E+00	-261878
Building Density	0300	5	0	1.0E+00	-263297
	0400	5	45.98319	1.0E-10	-263320
	0500	5	159.85299	1.9E-35	-263377
	0200	5	435.79557	2.3E-95	-263515
	1000	5	1354.8954	6.1E-295	-263975
	5000	5	3456.6148	0.0E+00	-265026
	4000	5	3229.0886	0.0E+00	-264912
	3000	5	2804.7831	0.0E+00	-264700
	2000	5	2467.6713	0.0E+00	-264531
	1500	5	1948.6312	0.0E+00	-264272
	0100	5	1526.2432	0.0E+00	-264060
	0050	5	2433.0185	0.0E+00	-264514

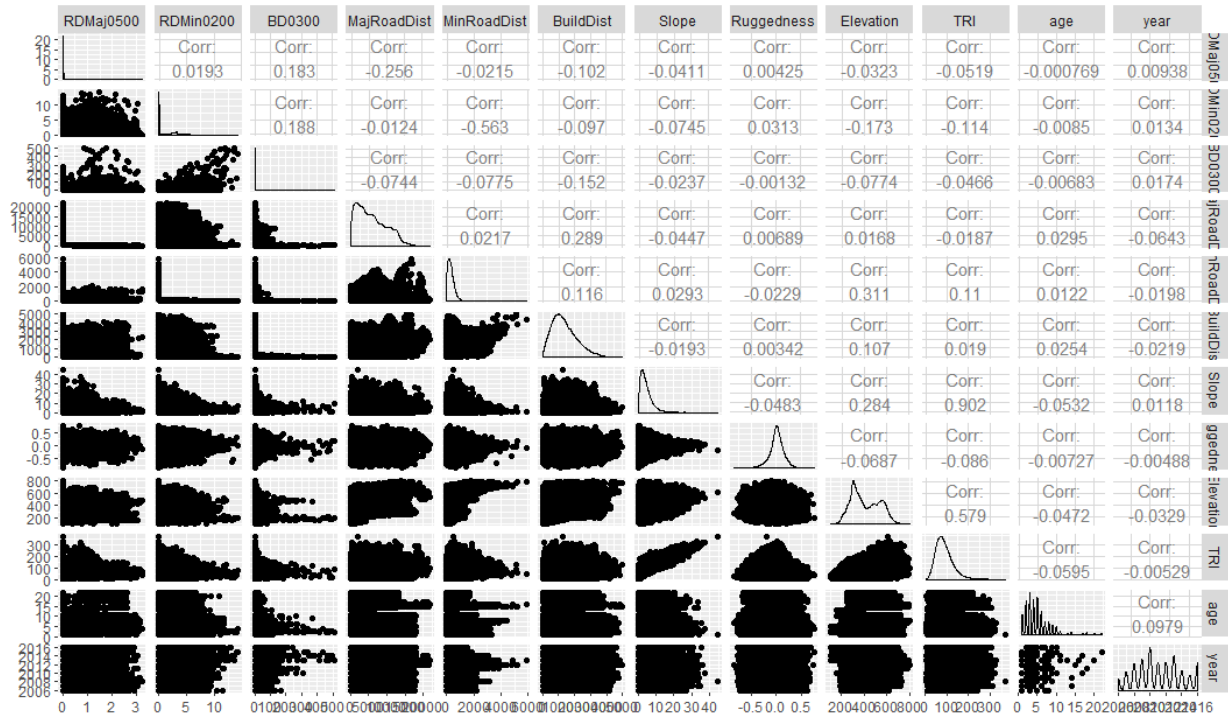


Figure A.1: Correlation of all pairs of variables. TRI was strongly correlated with Slope, and moderately correlated with Elevation.

Table A.2: Comparing the two terrain roughness indices performance in AICc terms

<i>Terrain Roughness</i>	<i>K</i>	<i>ΔAICc</i>	<i>AICcw</i>	<i>LL</i>
TRI	2	755844.4	0.00	-377920.2
Ruggedness	2	770167.2	14322.87	-385081.6

Table A.3: Table with Variance Inflation Factors of final selection of variables. As all are low (below 5), collinearity is assumed to be low and therefore do not confound the results when included.

<i>Variables</i>	<i>VIF</i>
RDMaj0500	1.11012
RDMin0200	1.4475
BD0300	1.100818
MajRoadDist	1.175101
MinRoadDist	1.558348
BuildDist	1.154872
TRI	1.526199
Elevation	1.681074
age	1.015158
year	1.017554

APPENDIX B: HABITAT SELECTION SHIFT WITH SEASONALITY – SUPPLEMENTARY INFORMATION

Table B.1: Parameter estimates of the spatial variables in the population-level model, with the hunt-seasonality as an interaction term. These results are summarised in Table 4.1.

Variable	PRE				POST			
	Estimate	Std. Error	z-value	p-value	Estimate	Std. Error	z-value	p-value
Habitat: Bog	0.139	0.050	2.8	0.005	-1.332	0.052	-25.5	< 2e-16
Habitat: Clearcut	-0.081	0.058	-1.4	0.165	1.755	0.041	42.6	< 2e-16
Habitat: Young Forest	-0.119	0.058	-2.1	0.039	1.870	0.041	46.0	< 2e-16
Habitat: Midage Forest	-0.127	0.053	-2.4	0.017	1.364	0.038	35.9	< 2e-16
Habitat: Old Forest	-0.186	0.054	-3.4	0.001	1.462	0.039	37.8	< 2e-16
Elevation	-0.047	0.020	-2.3	0.021	-0.226	0.016	-13.7	< 2e-16
Slope	0.013	0.036	0.4	0.717	-0.112	0.026	-4.4	1.14E-05
Ruggedness	-0.007	0.011	-0.6	0.531	0.067	0.008	8.6	< 2e-16
TRI	-0.018	0.044	-0.4	0.676	0.521	0.030	17.1	< 2e-16
MajRoadDist	-0.009	0.012	-0.7	0.464	0.391	0.010	40.2	< 2e-16
MinRoadDist	-0.020	0.014	-1.4	0.169	0.037	0.010	3.8	1.48E-04
RDMin0200	-0.004	0.014	-0.3	0.801	-0.336	0.010	-34.8	< 2e-16
BuildDist	0.036	0.012	3.1	0.002	0.164	0.009	19.3	< 2e-16

The effect-plot for these variables and the hunt-interaction term is visualised in Figure B.1.

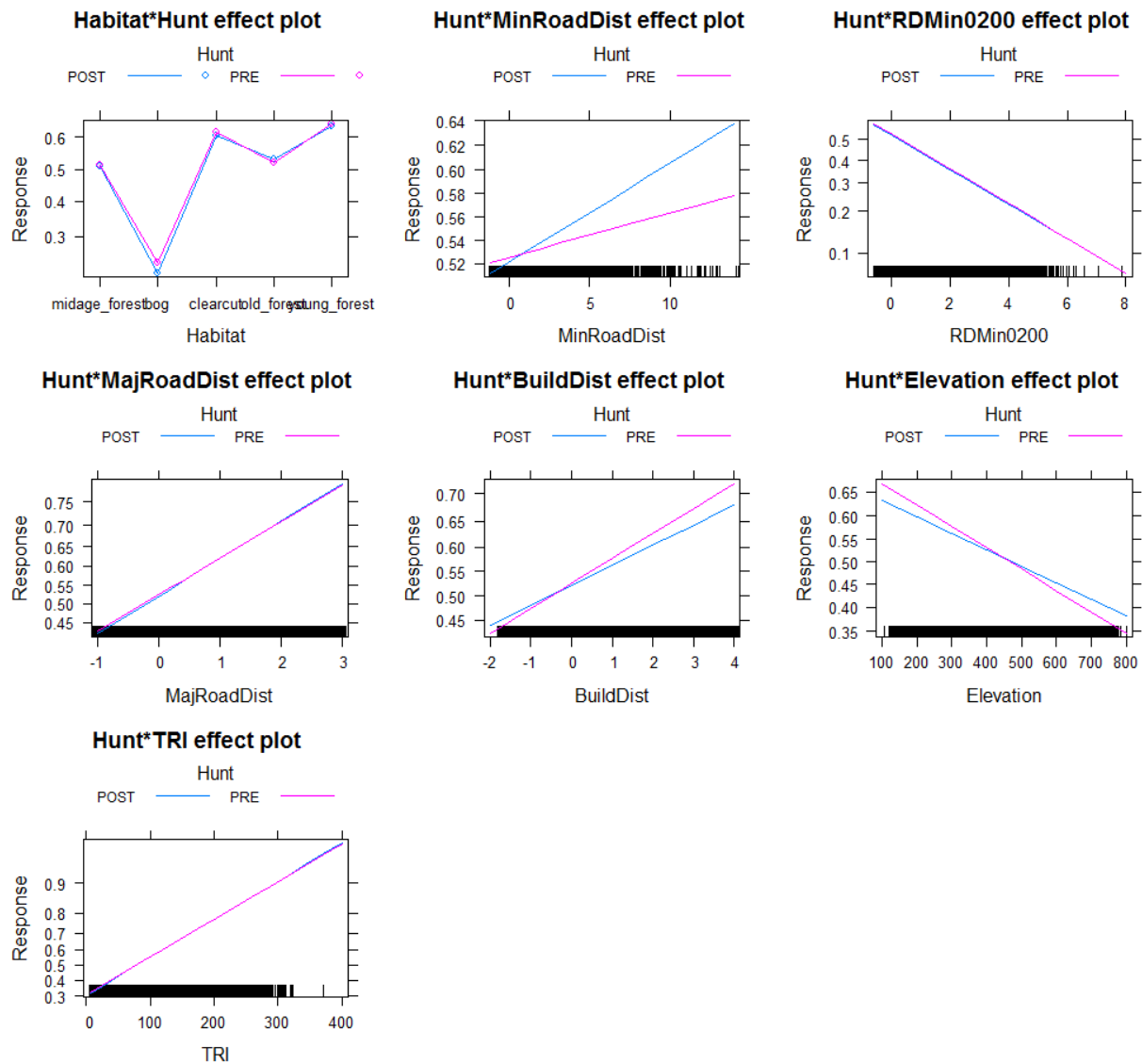


Figure B.1: Effect plot for population-level model (16th - 25th August, all variables scaled)

For the following trend-plots of odds ratio, the two extreme outliers “W0825_2015” and “W0620_2015” were removed in order to better see the trend in the other bear-years. Both these excluded bear-years were non-survivors who were shot on the first day of the hunt – the limited data from the post-hunt commencement period meant that the selection was exaggerated, and the odds-ratio values thus very high for these bear-years. In order to visualise variation in the other bear-years, these have been removed from visualisation. The purple line depicts the selection trend shown by the population-level model (see section 3.4.2), while the red line shows the trend shown by the median bear-year. Mean was not selected as this was heavily influenced by the aforementioned outliers. As the range of odds-ratio values was extremely high, the log-values of the odds-ratios have been plotted here.

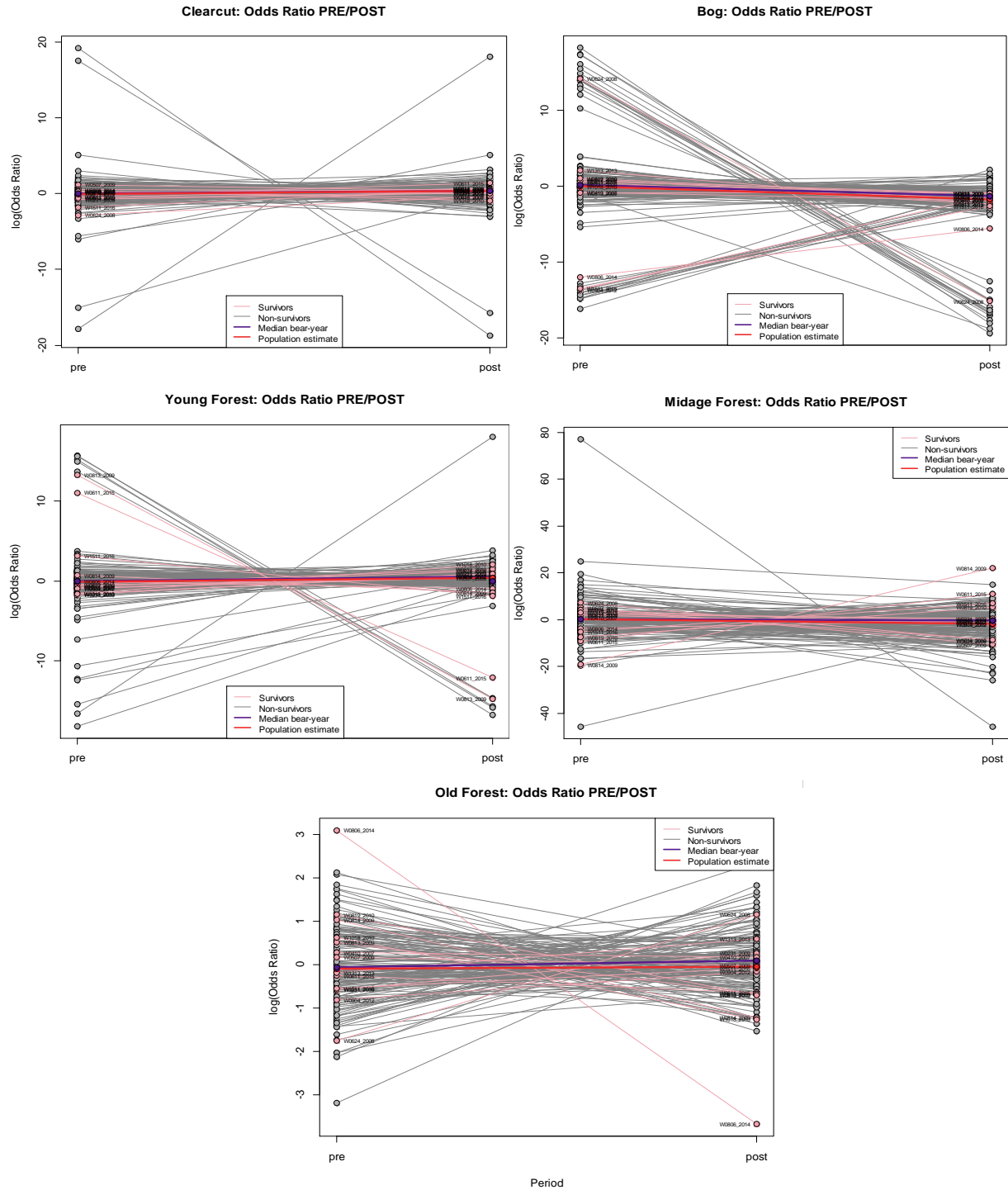


Figure B.2: Odds-ratio plots of habitat types. “Pre” and “Post” denote the odds-ratio values of this variable before and after the hunt began. Note the logarithmic scale for the odds-ratios on the y-axis. Non-survivors are marked in light pink (n=14), and labelled in these plots.

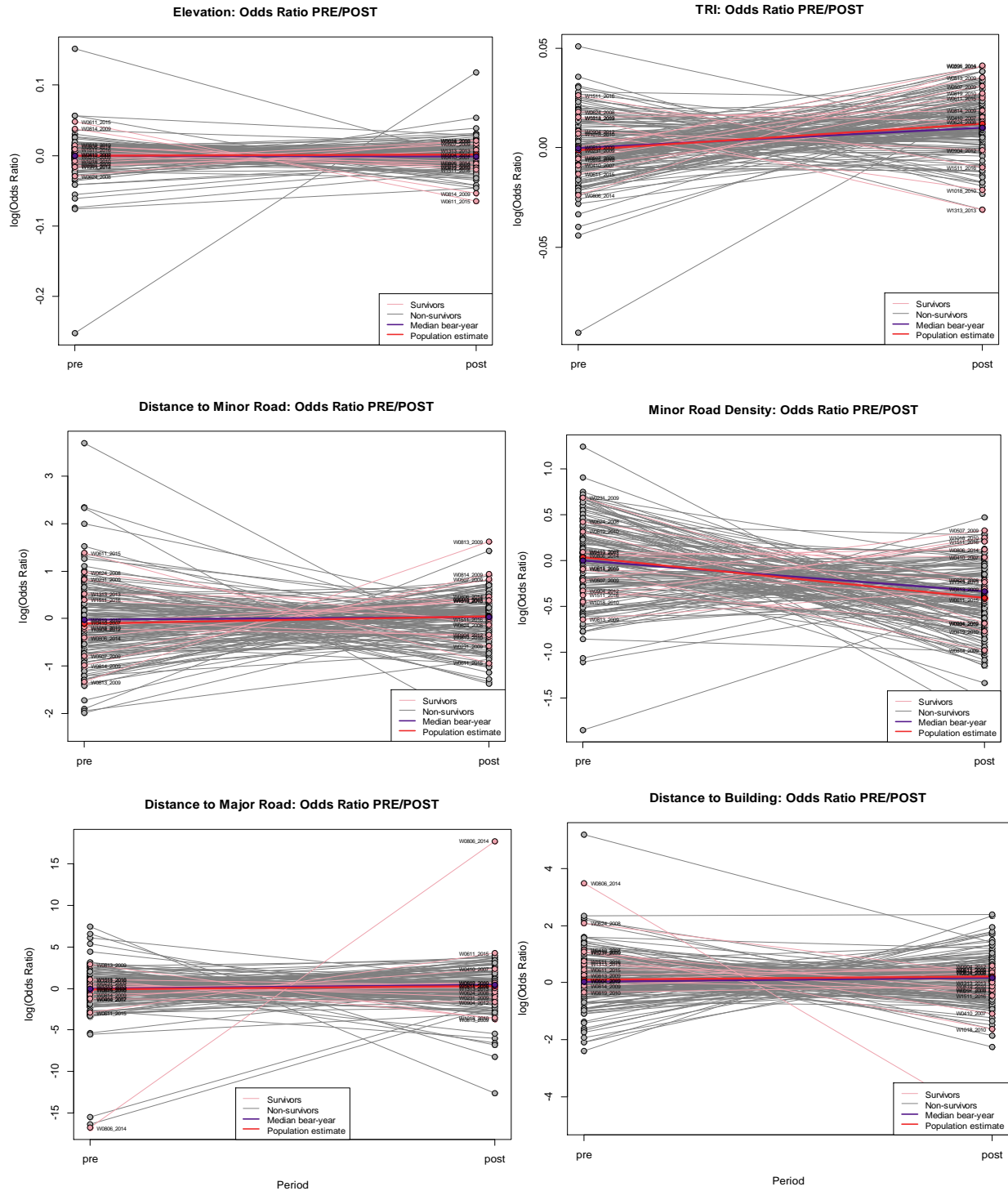


Figure B.3: Odds-ratio plots of topographic and anthropogenic variables. “Pre” and “Post” denote the odds-ratio values of this variable before and after the hunt began. Note the logarithmic scale for the odds-ratios on the y-axis. Non-survivors are marked in light pink (n=14), and labelled in these plots.

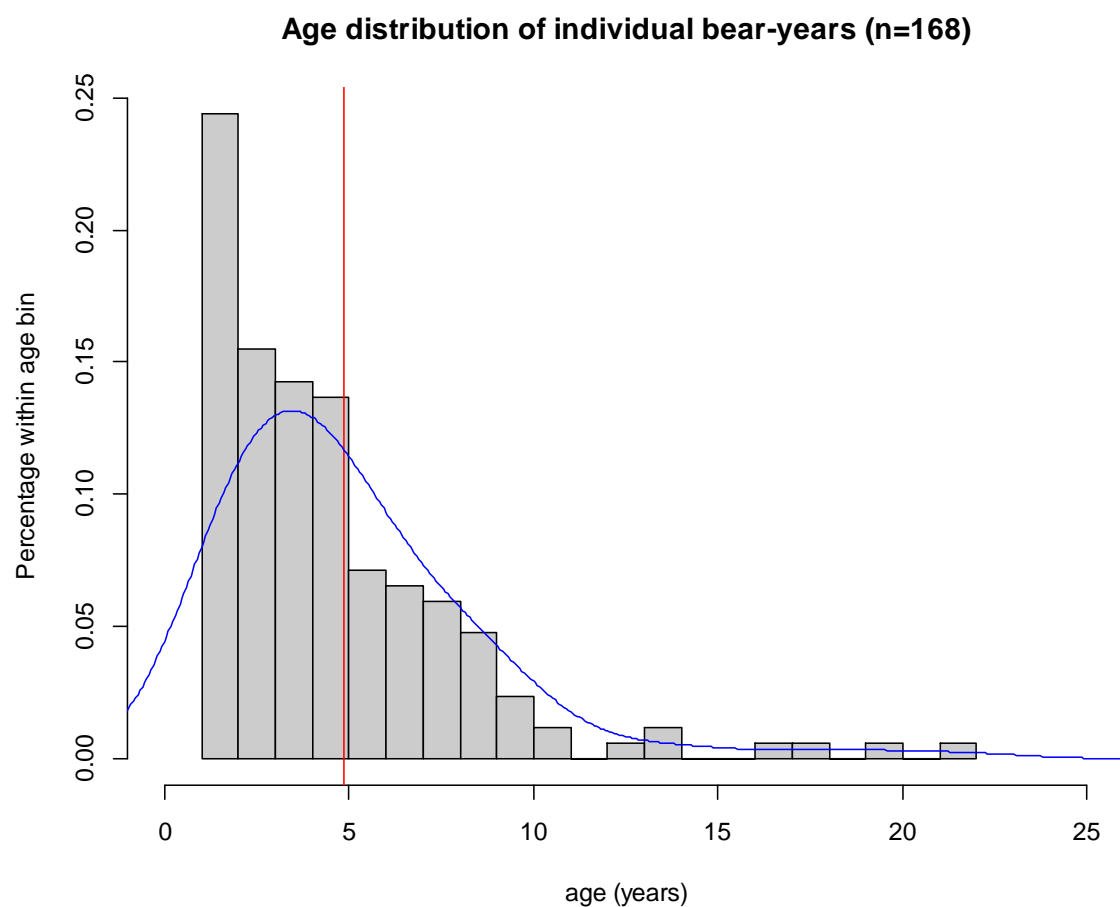


Figure B.4: Age distribution of all individual lone-female bear-years. The horizontal red-line shows the mean bear-year (4.9 years) and the blue line shows the smoothed density curve. The left-skew of this distribution shows that most bear-years considered are from young bears, and very few live over 10 years of age.