Univerza *v Ljubljani*
Biotehniška fakulteta

**University of Natural Resources
and Applied Life Sciences, Vienna**

Do wolves affect browsing intensity around red deer feeding sites and wolf dens? Investigating predator- prey dynamics in Dinaric forest ecosystem, Slovenia

Master Thesis

for obtaining the academic degree Master of Science

in Wildlife Ecology and Wildlife Management

Submitted by: Laura HUBER-EUSTACHI
Immatriculation number: 1141867

Institute of Wildlife Biology and Game Management (IWJ)
Department for Integrative Biology and Biodiversity Research

Supervisors:

Dr. Miha Krofel
University of Ljubljana, Biotechnical Faculty
Department of forestry and renewable forest resources

Prof. Klemen Jerina
University of Ljubljana, Biotechnical Faculty
Department of forestry and renewable forest resources

Vienna, March 2016
Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

28. 03. 2016

Date   Signature

Acknowledgements

Abstract

Apex predators such as grey wolves (*Canis lupus*) are recovering in many countries. There is increasing research interest in the impacts they have on terrestrial food webs. Previous studies on such predator-prey dynamics (trophic cascades) were mostly conducted in protected areas and rarely considered potentially important environmental variables. We studied the effects of wolves on the spatial distribution of browsing intensity around red deer (*Cervus elaphus*) supplemental winter feeding sites (SFS) and wolf dens in a human-dominated landscape of Dinaric forest ecosystem in southern Slovenia. On a total of 382 plots we collected browsing data on tree saplings. This data was included together with a comprehensive set of variables in a generalized linear mixed model (GLMM) to explain browsing intensity at the sampling plots. Variables included set of ecological factors, distance from the nearest SFS or wolf den, distances from human disturbances and wolf presence. We predicted lower browsing intensity around SFS with high wolf visiting frequency. However, the best models predicting browsing did not contain the variable wolf, indicating that the presence of wolves does not affect browsing intensity of red deer around SFS in a human dominated landscape of Slovenia. On the other hand, analysis of browsing intensity around wolf dens revealed that browsing decreases with increasing proximity to wolf den sites, as expected by the trophic cascade hypothesis. These results indicate spatially limited influence of wolves on browsing behaviour of red deer and warrant further research on parameters that influence predator effects on red deer behaviour and browsing in human dominated landscapes.

Keywords: behavioural mediated trophic cascade, predator – prey dynamics, *Cervus elaphus*, *Canis lupus*, browsing, supplemental winter feeding, Dinaric forest

1 Introduction

Predator- prey interactions in terrestrial systems are a widely discussed topic. Top-down effects of predators are not only characterized by density changes, but in some cases also by behavioural changes of the prey species. In a three level system with predator, prey and plants the indirect influence of the carnivore on the plants is called a *trophic cascade.* When herbivores change their behaviour by moving to places of lower perceived predation risk that might induce a shift in browsing patterns, as plants are locally released from herbivore control (Schmitz, Beckerman, & O'Brien, 1997).

This change in behaviour and browsing patterns is more obvious in landscapes, where previously exterminated predators return into the ecosystem. As humans became more aware of the ecological importance, the systematic eradication of predators is redeemed and carnivores such as wolves (*Canis lupus*) were protected in many countries or even reintroduced to some regions. As wolves as top predators are returning in many ecosystems, trophic interactions as *trophic cascades* can be observed actually as they develop. Scientific research is reflecting this: up to 2000 only two papers with evidence for trophic cascades involving mammalian herbivores were found in a review (Schmitz, Hambäck, & Beckerman, 2000), while 10 years later numerous publications on this topic have been published, reflecting the increasing interest in studying trophic cascades in terrestrial ecosystems (e.g. Eisenberg, 2010).

Animals may use different strategies to minimize the risk of predation (Lima & Dill, 1990)*.* Depending on the hunting strategy of the predator, ungulates adjust their behaviour with various anti-predatory strategies (Atwood, Gese, & Kunkel, 2009; Barja & Rosellini, 2008; Gervasi et al., 2013; Prokešová, Barančeková, & Homolka, 2006). In this risk avoidance behaviour, habitat heterogeneity plays an important role. It affects the movement patterns of prey species, as risk of predation can be minimized by usage of particular habitat types (Campos & Fedigan, 2014; Gorini et al., 2012; Kittle, Fryxell, Desy, & Hamr, 2008; Lima & Dill, 1990). Recent studies, mostly focusing on wolf-deer interactions, reveal which landscape attributes implement distinctive predation risk and lead to changes in spatial use (Bergman et al., 2006; Creel & Winnie, 2005; Gervasi et al., 2013; Mark Hebblewhite, Merrill, & Mcdonald, 2005; Winnie & Creel, 2007). Other strategies besides changes in landscape use include adjustment of diurnal rhythms (*risk allocation*), aggregation in groups and/or changes in group size (Eisenberg, Hibbs, Ripple, & Salwasser, 2014; Gude, Garrott, Borkowski, & King, 2006) and increasing vigilance level (Creel & Winnie, 2005; Eisenberg et al., 2014; Gervasi et al., 2013; Mark Hebblewhite et al., 2005; Kauffman et al., 2007).

A representative and often cited study case is the reintroduction of wolves after 70 years of absence into the Greater Yellowstone Ecosystem. Triggered by the new predation risk, red deer (*Cervus elaphus*) changed their behavior leading to a behaviorally-mediated trophic cascade induced by the wolves (e.g. Ripple & Beschta, 2003). Riparian areas and their vegetation were released from high browsing pressure, because these areas were more risky for wolf predation due to several reasons, such as reduced visibility and escape impediments. Consequently deer switched their habitat use by moving more frequently to less risky habitats at higher grounds, which offer the possibility to overview terrain and avoid predation (Ripple & Beschta, 2006). This finding illustrates, how predators

create a *landscape of fear* by redistributing herbivores due to landscape characteristics (Fortin et al., 2005).

Trophic cascades in Europe

In Europe the trophic cascade theory has been explored to lesser extent, with the notable exception of studies from the Białowieza Primeval Forest (BPF). *Landscape of fear* at local scale („Patches of fear") in terms of coarse woody debris was investigated for its function as an impediment for escaping prey. The effect of such impediments on the browsing was compared inside and outside of the wolf core area. Indirect predator influences were documented, although these effects were not as visible as in the broader landscapes of North America (Kuijper et al., 2013).

It is important to note that most studies were conducted in protected areas like the Yellowstone National Park and the BFP, where natural processes could differ in important ways to those in human-dominated landscapes and managed ecosystems. For example, in the BFP where the study was conducted there are no settlements, forest or wildlife management or any other human disturbances except for work conducted by scientists and visitors accompanied with guides.

Forests and high deer densities

To our knowledge there is only limited information available on the potential of wolf-triggered trophic cascades in human managed landscapes, which dominate across Europe (Sommerfeld 2015). Differences of managed forests from natural forest ecosystems include tree species composition, soil characteristics, light regime and understorey growth. These characteristics are altered and can in general offer higher carrying capacity for ungulates (Jennings, Brown, & Sheil, 1999). Managed forests generally offer more forage, which in addition to supplemental feeding practices support high ungulate densities in many European countries,- although ungulate numbers are often controlled by hunting. Further the high rates of reduction in large predators in former times also facilitated increased ungulate numbers (Adamič & Jerina, 2010; Côté, Rooney, Tremblay, Dussault, & Waller, 2004; Kuijper, 2011). Such perturbations to deer populations can trigger various ecological consequences. Occurrence and distribution of plants and tree species is altered by browsing when ungulates densities increase (Augustine & McNaughton, 1996; Didion, Kupferschmid, & Bugmann, 2009; Gill & Beardall, 2001). This can obstruct human interests, for example in economic use of forests and agriculture.

Predators in Slovenia

Wolves are opportunistic cursorial predators with a diverse and wide range of prey species. As an apex predator, wolf is the main natural predator of red deer in many regions over the world (Mech, 2003). In Slovenia, the percentage of prey species varies among packs and regions. Cervids represent up to 83% of the wolf diet. The proportion of red deer and roe deer (*Capreolus capreolus*) in wolf diet is dependent on their relative densities in the different regions, but red deer seems to be a preferred prey species in Southern Slovenia (Krofel & Kos, 2010). Other prey species include wild boar (*Sus scrofa*) and small cattle (Majic 2014). Two other large carnivores are present in Slovenia, the Eurasian Lynx (*Lynx lynx*) and the brown bear (*Ursus arctos*), but they rarely hunt red deer: lynx preys mostly on roe deer (79,1 %) while red deer represent only 6,6% of their diet (Krofel, Huber, & Kos, 2011).

Main food sources for brown bear are corn and livestock carrion from supplemental feeding sites; bears rarely hunt wild ungulates (Kavčič et al., 2015).

Supplemental feeding practice in Slovenia

Supplemental feeding of red deer is a common management practice in Slovenia, and supplemental feeding sites (SFS) with varying amounts of supplied food are widespread (see map in the appendix 7.2). The purpose of red deer supplemental feeding is mostly to increase the survivorship of the animals and the hunting success- while decreasing damage to forest through browsing by offering alternative food sources and directing ungulates away from vulnerable plants during wintertime (Jerina, Dajčman, & Adamič, 2008). Other feeding sites, such as baiting places or brown bear feeding sites, are also common in Slovenia. In this study, we focused on SFS, main purpose of which was to feed red deer, especially in winter. Studies on winter supplemental feeding have shown, that the SFS affect spatial distribution of red deer. This leads often to high red deer concentration around the SFS (Jerina, 2012; Jones et al., 2014; Sahlsten et al., 2010; Van Beest, Loe, Mysterud, & Milner, 2010). Research on browsing in relation to distance from the SFS found an increasing browsing impact with decreasing distance to the SFS (Cooper, Owens, Cooper, & Ginnett, 2006; Garrido, Lindqvist, & Kjellander, 2014; Mathisen, Milner, van Beest, & Skarpe, 2014; Sahlsten et al., 2010; Semenič, 2009; Van Beest, Gundersen, Mathisen, Milner, & Skarpe, 2010).

Wolves at supplemental feeding sites

Wolves often focus their hunting on areas of high prey densities (Bergman et al., 2006; Kunkel & Pletscher, 2000; McPhee, Webb, & Merrill, 2012). In Slovenia, wolves were observed to regularly visit and hunt deer around the SFSs in winter (M. Krofel, personal communication). This could be related to higher success of locating potential prey due to higher prey densities at these sites.

The visitation frequency of a predator in a landscape reflects direct predation risk (Fortin et al., 2005). SFS inside or near wolf territories and with a high wolf visitation frequency are areas with higher *direct predation risk* for ungulates. If these SFS are perceived as *risky areas* by the deer, higher predator vigilance leads to a trade-off between the need for foraging, e.g. access to (high energetic) food, and the need to avoid predation risk (Brown, 1999; Creel & Winnie, 2005). Deer could respond to this higher risk by behavioural changes, e.g. spending less time at SFS with frequent wolf visitation or visiting them at time periods of lower predation risk as proposed by the *risk allocation* hypothesis. One of the effects of SFS is higher browsing pressure on the trees around, as deer spent more time at SFS in general. With this study we will test the hypothesis that wolves hunting at SFS results in a lower usage by the red deer, reflected in the reduction of browsing on the trees around and redistribution of browsing with regard to distance to the feeding place.

Wolf dens

Wolf dens are usually located inside the wolf territory, mostly more than 1 km away from its borders, to avoid encounters with other packs (Ciucci & Mech, 1992). The characteristics of dens vary, depending on the landscape and habitat characteristics (Mech, Adams, Meier, Burch, & Dale, 1998; Packard, 2003). An overview of the variety of den sites is given by Mech et. al (1998). The wolf dens investigated in this study were mostly located at rocky places, e.g. in the cavities between the rocks.

Wolf dens and their surroundings represent areas of frequent wolf presence or high wolf use. The avoidance of areas of frequent wolf presence is an ungulate anti-predator strategy (Ripple, Larsen, Renkin, & Smith, 2001). We used telemetry data of several wolf packs in Slovenia to locate the den sites and conducted sampling of browsing intensity to test whether high use by wolves in such areas reduces browsing by deer.

Bottom- up and top- down effects on browsing intensity

Earlier findings imply the inclusion of both bottom up and top down effects, as only together they can explain prey species density changes (Krebs et al., 1995). To analyse the effects of wolves on browsing intensity we also included in our analysis several environmental factors that could influence red deer density and habitat selection. Therefore, potential drivers, such as availability of low and high preferred tree species, abiotic values (e.g. *slope*) and variables related to human disturbance (e.g. *distance from settlements*), were also included in the study.

Study aims

The main aim of present study is to investigate presence of wolf-triggered trophic cascade in a human-dominated landscape in Europe.

Simultaneously to this thesis, an additional partner thesis concerning potential wolf-triggered trophic cascades in Southern Slovenia was done (Sommerfeld, 2015), focusing on differences in browsing intensity among areas with low to high wolf abundance using browsing census and forestry data on plots distributed randomly across larger sale. In contrast, this study was conducted in the same study area, but focused only on specific locations in respect to the wolf and red deer presence: winter supplementing feeding sites for deer and wolf den sites.

Our aim is to test, (1) if presence of wolves modulates the red deer browsing around Supplemental Feeding Sites (SFS), and (2) whether there is a decrease in tree browsing around wolf dens with increased wolf use during the summer.

This study will give new insights into food web interactions of wolf and red deer in European, human-dominated landscapes. This will provide a basis for developing management practices and further research especially on winter feeding practice in regions with wolf packs present.

2 Study area and status of wolves

The study area was located in Southern Slovenia in a managed temperate forest ecosystem of the Northern Dinaric Mountains. The forests are logged, ungulate populations are intensively managed through hunting and supplemental feeding, while wolf population is controlled by annual culling permits.

The geomorphological character of this area is shaped by limestone and dolomite with typical karstic structures, such as dolines and caves. The investigated plots range in altitudes from 230 m above sea level up to the highest mountain Snežnik with its 1797 m height. The Alps, the Mediterranean Sea and the Pannonian basin influence the climate in the study area. Temperature annual averages 4- 8 °C, average annual precipitation ranges between 1560 – 2950 mm. The forest cover in whole

Slovenia is over 60%. The forests in the study area are dominated by the west-Dinaric fir-beech association *Omphalodo-Fagetum* (Surina, 2002). For our study of SFS we selected only feeding sites that are within this forest association to get more reliable results.

The average density of humans in the Slovenian part of the Dinaric Mountains is 54 persons/km^2 (Perko and Orožen Adamič 1998). Red deer densities in the study area range from 0 up to 15 animals/ km^2. The mean hunting bag for overall Slovenia between 2004 and 2014 was 4747 shot animals, with the highest bag in 2014 with 5816 (www.stat.si), population size of red deer was estimated about 10 000 – 14 000 animals (Adamič & Jerina, 2010).

In Slovenia wolves have never been exterminated, although they have been substantially reduced in the 20th century. Due to their protection in 1990, the population has been partly recovered in the last decades. In whole Slovenia, 10-12 packs with average pack size of approximately 4 adults are present while most packs live in the southern part of the country (Majic, 2014). The wolf population size is around 40 animals (before reproduction) and is managed by yearly changing numbers in culling permits (Majic, 2014). During the LIFE- project „SloWolf" (2010 – 2013) high quality data concerning pack sizes, ranges, diet and mortality have become available.

The wolf dens included in this study were located by GPS telemetry data of the packs or by howling surveys between 2011 and 2014. We investigated browsing intensity around the dens of five different wolf packs.

3 Material and Methods

3.1 Field data

Browsing data was gathered during summer 2009 and summer 2014. 2009 data was collected by Boris Semenič for his thesis "Studying influence of red deer winter supplemental feeding on place arrangement and damage embracement of forest saplings of Snežnik area".

The same sampling method was used in both years. The method was described in Semenič (2009), who adapted it from former national browsing inventories in Slovenia. We adjusted the procedure for the investigation of wolf dens; the sampling protocols are explained in detail below.

We investigated browsing intensity with increasing distance from 9 wolf dens and 16 SFSs. With the den or SFS as the „central spot" in the middle, a random direction was chosen. In this and the opposite direction (= +180°) browsing intensity was measured. Bias by collecting distance data just from one direction should be diminished by adding the second direction. Originally it was planned to collect distance data from 4 different directions in 90° degree towards each other, as used by Semenič 2009. Time contraints made this impossible, so we reduced data gathering into two directions with sampling plots distributed as described below.

Sampling distances around SFS
Around the SFS, sampling plots were located at the following distances from the SFS:

- 50 m
- 250 m
- 500 m
- 750 m
- 1000 m
- 1500 m

We have chosen these six distances with reference to previous studies measuring browsing intensity around SFS. These particular distances were chosen as they should correspond with local red deer density distributions. We included three plots within 500 m around a SFS, where the density of red deer is significantly higher (Jerina et al., 2008; Semenič, 2009). The three following plots were between 500 and 1500 m from the SFS and were based on estimated declines in the probability of annual use at this distance from the SFS (Jerina et al., 2008).

Sampling distances around wolf dens
Distance plots around wolf dens were chosen similarly to the procedure of the SFS distance plots. We included additional distance at 25 m around the den site, as unlike the SFS which covers larger area, wolf dens are very localized features (typically a small karstic cave). The distances between the sampling plots and the den site were:

- 25 m
- 50 m
- 150 m

- á CC
- ' CCC
- ' á CC

ldw A cek vk ml c c cl s e A n c n kel

smer krmišča

izhodišče

P=1   P=4   P=6   P=9   P=13

3.2 Fixed variables

Besides data about browsing status, several other data was sampled in the field. Additionally to this field data, information from different other sources was used, as our aim was to include a comprehensive range of factors that determine red deer habitat and browsing activity. We used ArcMap 10.1, Esri ArcGis for all manipulation of spatial data.

An overview of the set of analysed variables is given in table 1 and table 2, whereas the justifications for selecting these variables are provided in the next paragraph.

Table 1: Variables used as fixed variables in models analysing browsing around SFS. Further details for each variable (minimal + maximum amount, quantiles) are provided in the appendix 7.3.1

Variable description	abbreviation	type and unit
Response variable		
Browsing status	brows	Binary: 0 or 1
Categorical explanatory variables		
Tree specie preference	group	Binary: "high", "low"
Sapling height	height	Factor, 4 levels: "30", "50", "150", "200"
Snow	snow	Factor, 3 levels: "140-200", "200-280", "280-420"
Frequency of wolves visiting	wolf2	Binary: "0" (absent), "1" (present)
Ownership of hunting ground	hunt	Binary: "local", "state" (= Slovenian Forestry Service)
Continuous explanatory variables		
Canopy closure	canopy	Integer, in %
Slope	slope	Integer (decline in degree)
Forest cover	forestcover	numeric, between 0 - 1
Red deer density	red_dd	numeric (no. of animals per km^2)
Roe deer density	roe_dd	numeric (no. of animals per km^2)
Distance to the nearest forest edge	dist_forestedge	Integer, meter
Distance to the nearest forest road	dist_forestroad	numeric, meter
Distance to the nearest settlement	dist_settlement	numeric, meter
Random effects		
Year of field data sampling	year	Binary: "2009" or "2014"
Identification Number of Feeding Site	SiteID	Factor, 16 levels
Identification Number of sampling plot	PlotID	Factor, 136 levels

Table 2: Variables used as fixed variables in models analysing browsing around wolf dens. Further details for each variable (minimal + maximum amount, quantiles) are provided in the appendix 7.3.2

Variable description	abbreviation	type and unit
Response variable		
Browsing status	brows	Binary: 0 or 1
Categorical explanatory variables		
Tree specie preference	group	Binary: "high", "low"
Sapling height	height	Factor, 4 levels: "30", "50", "150", "200"

Snow	snow	Factor, 5 levels:"60-100", "100-140", "140-200", "200-280", "280-420"
Continuous explanatory variables		
Canopy closure	canopy	Integer, in %
Slope	slope	Integer (decline in degree)
Forest cover	forestcover	numeric, between 0 - 1
Red deer density	red_dd	numeric (no. of animals per km^2)
Roe deer density	roe_dd	numeric (no. of animals per km^2)
Distance to the nearest forest edge	dist_forestedge	Integer, meter
Distance to the nearest forest road	dist_forestroad	numeric, meter
Distance to the nearest settlement	dist_settlement	numeric,
Distance to the nearest red deer feeding site	nxt_SFS	numeric, meter
Random effects		
Identification Number of Den Site	SiteID	Factor, 9 levels
Identification Number of sampling plot	PlotID	Factor, 109 levels

Environmental data

Environmental and other ecological factors sampled at each plot included: the percentage of dead wood, stone and tree stumps inside the sampling plots, exposition, canopy coverage and slope at the plot (see appendix 7.4). For the further analysis, we used *canopy* information and *slope*. These two parameters out of many sampled characteristics of the plot were chosen as they do not require further transformations or investigation, because their influence on habitat and browsing has been shown in previous studies. Furthermore, they were also protocoled in 2009.

The *slope* was recorded by an inclinometer. It implements several biotic information, as it influences habitat properties such as light angle, snow cover and soil nutrition. *Canopy cover* represents the cover of all tree layers, estimated at the plot looking up vertically. This parameter defines habitat quality for saplings through the light regime at the plot and its potential for regeneration or snow interception (see Gerhardt et al. 2014).

Other variables that could potentially affect browsing intensity were selected in respect to the previous studies, especially recommendations made by Gerhardt et al. (2014). We included following parameters: (1) forest cover, (2) percentage of conifers, (3) snow cover, (4) red deer densities and (5) roe deer densities.

The variable *forestcover* was included in addition to "canopy" parameter, which measured small scale canopy cover at the plot. *Forestcover* on the other hand represents mean forest coverage at larger scale (1x1 km). *Percentage of conifers* was included, to take regional differences in percentages of conifers into account, and to consider differences in forest composition. Deer prefer broadleaf trees and their body mass increases when conifer percentage decreases (Jerina, 2006). *Percentage of conifers* data was provided from the database at the 1x1 km grid from the Department of Forestry of the University of Ljubljana (Jerina, unpublished data). For each sampling plot the data of the nearest inventory point was used.

Snow cover provides information on height of snow cover. High snow cover affects energy demands for red deer and its habitat selection and reduces accessibility of plants (Jerina et al. 2008). On the other hand, higher plant parts emerging out of the snow can be reached more easily by the deer (Gerhardt, Arnold, Hackländer, & Hochbichler, 2013). Data on cumulative *snow* cover in height intervals was provided at the 1 km^2 scale by ARSO (Slovenian Environmental Agency). Investigated plots were within a range of 5 different height intervals, with snow heights given in cm (60-100, 100-140, 140- 200, 200-280, 280-420).

The ungulate abundance is a crucial variable when investigating factors determining browsing (Gerhardt et al. 2013). We included data from the two main ungulate species in Slovenia, red deer and roe deer. Roe deer densities were included to avoid neglecting their possible browsing effects-although its browsing patterns are different as roe deer is a concentrate selector feeding type while red deer is an intermediate feeding type (Hofmann, 1989). Densities were calculated from a combination of countrywide removal data (Adamič & Jerina, 2010) and pellet group count (Jerina, 2012), provided at the 1km^2 scale and transformed into a kernel density layer to get smoothed values for every sampling plot.

Additional variables that affect landscape use of deer and wolves included *distance to forest road, distance to settlement, distance from forest edge* and *distance to the next feeding site*.
The variable *distance to forestroad* was included as roads represent potential disturbance by humans, are often avoided by deer, and affect the home range size of red deer (Fortin et al., 2005; Gerhardt et al., 2013; Jerina, 2012; John, 1995; Rogala et al., 2011; Rost & Bailey, 1979). The same was shown for settlements (Jerina, 2012), which were included by the variable *distance to settlement*. Also wolves avoid major roads and settlements (Kaartinen, Kojola, & Colpaert, 2005). This can in turn affect deer, which can increase their use of areas closer to human settlements in order to avoid predators (Beschta & Ripple, 2007; M. Hebblewhite et al., 2005).
The *distance from forest edge* provides information about forage possibilities in open areas, which is an important variable in red deer movement and browsing analysis (Gerhardt et al., 2013; Lung & Childress, 2007). On the other hand, open areas and forest edge also represent higher risk for red deer (Kunkel & Pletscher, 2001): Open areas provide no hiding cover, and wolves in Canada preferred linear structures like forest edges for hunting (McPhee et al., 2012).
The variable *distance to the next feeding* site gives the distance to the nearest supplemental feeding site for red deer from every sampling plot, because feeding sites are predicted to affect habitat selection and browsing intensities, as explained in the introduction.

Distances of every plot to the nearest (1) feeding site, (2) forest road, (3) settlement and (4) forest edge were calculated with the use of "spatial analysis" toolbox of ArcGis.
For (1 – 3) The tool "near" was used. For (4) which is a raster layer, the tool "extract values to point" was used. The shapefile of forest roads was created by combining several layers with road information from the database at the Surveying and Mapping Authority of the Republic of Slovenia (http://www.gu.gov.si/en/). All roads that can be driven by vehicles were included. A layer with settlement information was obtained from the same data base. A layer with feeding sites suitable for red deer was provided by the Department of Forestry at the Biotechnical Faculty, University Ljubljana (Jerina, 2012). Distance from forest edge was calculated from raster layer (positive values inside

forest, negative outside) provided by the Department of Forestry at the Biotechnical Faculty (Jerina 2012).

Ownership of hunting ground

In Slovenia hunting grounds are managed by Slovenia Forest Service (so called special purpose hunting grounds) or local hunting clubs. Hunting and supplemental feeding customs over the last 10 - 20 years in special purpose hunting grounds and hunting grounds managed by local clubs were not equal. The variable *ownership of hunting ground* should represent the complex impact of human management on forest and wildlife.

The management aims of special purpose hunting grounds managed by the Slovenia Forest Service represent the official aims of the state, that implies "sustainable management of wild animals" and "protection of rare and endangered animal species" in which sense wolves and bears are tolerated, studied and managed, international conservation programs are supported and monitoring data is sampled (Slovenian Forest Service, 2005). The amounts of fodder at the supplemental feeding sites are generally higher at these special purpose hunting grounds (M. Krofel, personal communication). This variable is only used in the SFS analysis, as feeding sides are located on both hunting ground - categories. The investigated wolf dens are all on state hunting grounds, so that no differentiation between hunting ground ownership type is required in the den analysis.

Wolf data at feeding sites

For every feeding site the relative wolf visiting frequency was determined as a binary variable, derived from wolf visiting frequency.

0/ low wolf presence

- absent/rare : no permanent territorial pack , n= 3

- low visitation frequency of the feeding site, n=5

1/ high wolf presence

- intermediate visitation frequency, n= 5

- high visitation frequency, n= 3

This ranking was done according to the wolf monitoring programme conducted by the Biotechnical Faculty and Slovenia Forest Service within EU Life project SLOWOLF between 2010 and 2013, which was based on howling surveys, snow-tracking, telemetry and non-invasive genetics. For feeding sites inside stable wolf territories, GPS telemetry data and sign data was used to estimate relative visitation frequency.

Wolf data at den sites

The 10 wolf dens from five different wolf packs were located by telemetry and / or howling surveys. Each den was used by pups for a minimum of 14 days in period between May and September.

3.3 Data preparation and statistical analysis

Exclusion of sampled data

For analysis of the tree species sampled, one species (*Betula pubescens)* occurred only twice and was therefore excluded from further analysis. Other species were grouped together for the analysis, namely *Fraxinus excelsior* and *Fraxinus ornus* as *Fraxinus* sp*., Acer pseudoplatanos* and *Acer plataniodes* into *Acer* sp.

One den site (D4) had to be excluded, as it was located in marshlands. As at this site only few trees were found and most plots where unreachable, we decided to exclude this site from the analysis, which was further justified by its different environmental parameters compared to all the other sites. Due to the random direction of plots in relation to the SFS/ den, some sampling plots were inside meadows or at the edge of settlements. These plots were out sorted or skipped directly in the field, as they did not represent the investigated forest ecosystem and measuring browsing of domesticated animals was not the aim.

Transforming browsing categories into binary variable

As browsing intensity "1" stands for not- or just slightly browsed, and browsing intensities "2" and "3" stand for more intensive browsing we transformed this information into binary data. This allows getting a more contrast differences. The obtained field data on browsing intensities was transformed by converting browsing intensity "1" into "non- browsed" (=0) and counting browsing intensities 2 and 3 together for "browsed" (=1).

Tree species distribution and grouping

Trees were grouped by their palatability. Browsing intensity is high wherever preferred tree species are concerned (Jerina, 2006; Mysterud, Askilsrud, Loe, & Veiberg, 2010; Semenič, 2009). The first aim was to create 3 groups of deer browsing preference (low, intermediate, high) and focus on the intermediate class, as this is supposed to show changes in browsing the best (Klopcic, Jerina, & Boncina, 2009; Mysterud et al., 2010).

The grouping simplifies the subsequent analysis and prevents from spending levels of freedom for each of the 13 collected tree species. The grouping analysis was done by two approaches, to control and see if the two different ways come to the same result. If results would be different, further investigation would be needed.

For statistical analysis the open source program R (R Core Team, 2014) was used. The significance level for hypothesis testing was set to p=0.05.

First and most common approach was grouping tree species palatability according to Jacob's selectivity Index (Jacobs, 1974). A disadvantage of this method is, that it accounts for selectivity at every plot but does not distinguish between tree height classes. For this reason, we also used a second approach, which allowed finer analyses of differences between height classes.
Therefore a generalized linear model was formed with the browsing as dependent binary variable and the tree species, height and SFS/ DEN as independent variables with logit link family. To avoid an overrated effect caused by the high amounts of species in height class <30, we used weighting to balance the samples of different height classes. Browsed trees in the height class <30 cm were

17

weighted by 0,23 (the ratio of counts of that height class and the counts of the other three height classes) while higher trees were weighted with 1.

Groups of preference were formed after regarding both approaches.

Data examination

Browsing data and all variables were visually examined with pairplots and histograms with the functions described in Zuur 2009 (panel.cor, panel.smooth2). To check for collinearity among the explanatory variables spearman rank correlation was used, because the fixed variables were not normally distributed. If two variables with correlation higher than 0.6 were found, the less important variable was removed from the analysis. To test for multicollinearity the variation inflation factor (VIF) of the variable was calculated after Zuur 2009. If VIF > 3 the correlation was supposed to be high, and variables were further investigated to find the reasons for multicollinearity.

Generalized Linear Mixed Model for SFS

We analysed browsing using generalized linear mixed models (GLMM) with binomial error structure and logit link function which is implemented in the `glmer` function in R package lme4 (Bates, D., Maechler, M., Bolker, B., Walker, 2013), using Laplace approximation for parameter estimates. This approach was chosen, because of the possibility to combine a general linear model and mixed effects components, and account on both for random and fixed effects (Zuur et al., 2009).

For the GLMM all continuous variables were standardized by the `scale` function (implemented R package `stats`, version 3.1.0, R Core Team), which subtracts the means and divides by the standard deviation (Zuur 2009).

Wolf presence could affect overall level of browsing and local distribution of browsing around feeding places. Therefore we included main effects of variable *wolf* and its interaction *with distance to SFS* in analysis.

The dependent variable was the binary browsing. Random factors were the year of data gathering (n=2), feeding site ID (n=16) and plots (=278). *PlotID* was nested inside *SiteID*, which was nested inside *year*. This nesting was needed to treat the data in a respective manner: On Plot level, trees at the same plot had the same plot-specific variables (e.g. *slope*, *canopy*, distances). The sampling plots themselves were referring to the associated SFS (e.g. data on hunting club owner and wolf visiting frequency). The sampled data concerning browsing around SFS was sampled in two different years, so both sampling plot and SFS were nested inside *year,* to account for random differences in between 2009 and 2014.

Akaikes's information Criteria (AIC) was used to find the best model, by AIC minimisation via stepwise backwards selection from the saturated model (the model including all variables). This procedure was calculated by the `drop1` function implemented in the lme4 package (Bates, D., Maechler, M., Bolker, B., Walker, 2013). All models with ΔAIC<3 were considered in the set of most informative models for explaining browsing variation, ranked in descending order.

Generalized Linear Mixed Model for den sites

The procedure of this analysis was similar as described for the SFS analysis. The ID of every den site (*SiteID*), was used as a random factor, as well the ID of every sampling plot (*PlotID*). *PlotIDs* were

nested inside *SiteIDs,* to account for different characteristics of the dens, as year of use, duration of use and by which wolf pack the den was used. Because all data was collected in the same year, the random factor *year* was not needed.

4 Results

In total, browsing data in 382 plots from a total of 10579 trees was analysed (overview of the sampled plots per year and the data structure is provided in appendix 7.1).

4.1 Tree species distribution and preference

Both Jacob's Selectivity Index and the coefficients in the GLM revealed that trees should be grouped in two categories of browsing preference. The GLM coefficients of the tree species were clustered in one group of preferred tree species and a wider scattered group of low preference.

Highly preferred were 8 tree species with 7100 tree counts, less preferred 4 species with 3419 tree counts.

Table 3: Number of counted tree saplings per tree species in 4 different height classes, grey background: low browsing preference

	0-30 cm	30-50 cm	50-150 cm	150-200 cm
Abies alba	733	39	38	1
Acer sp.	5071	296	93	1
Carpinus betulus	158	33	13	1
Fagus sylvatica	1266	400	413	69
Fraxinus sp.	264	68	45	8
Ostrya carpinifolia	90	22	32	11
Populus sp.	10	14	34	0
Picea abies	220	83	94	5
Sorbus aria	44	8	12	0
Sorbus aucuparia	412	61	32	0
Tilia sp.	20	2	0	0
Ulmus sp.	223	44	14	1

4.2 GLMM Supplemental Feeding Sites

Spearman correlation analysis revealed that variables were not highly correlated (≥ 0.6) and Variance Inflation Factor for all variables was < 2.5.

We built several models. In the end we decided for two initial sets of models: one with all variables as main variables [ModM] and one additionally containing the interaction of *wolf* and *distance to the next feeding site* [ModI].

Table 4: Composition of the two saturated Models: including Main effects (ModM) and additional an interaction (ModI), AIC= Akaike's Information Criteria, (1 | SiteID/Plot_ID) = random nested effects.

Model	Formula	AIC
ModM	brows ~ g + height + slope + nxt_SFS + wolf2 + canopy + forestcover + dist_forestedge + dist_settlement + dist_forestroad + snow + red_dd + roe_dd +	9173.6

	hunt + (1 | SiteID/PlotID)	
ModI	brows ~ g + height + slope + nxt_SFS + wolf2 + nxt_SFS:wolf2 + canopy + forestcover + dist_forestedge + dist_settlement + dist_forestroad + snow + red_dd + hunt + (1 | SiteID/Plot_ID)	`9172.4`

We decided to leave the random effect *year* outside of the saturated models (before, Site ID and Plot ID were nested inside year), as the proportion of variance explained by this variable was very low. As well, AIC for the model with the variable *year* was higher [9175.6] than without it, indicating that the model without year has better power to explain the data.

Model ModI with interaction

Model ModI, the second initial model, did not contain the variable *roe deer,* as it seemed to be a confounding variable in the (following) process of model selection by variable dropping. When dropping the variable snow out it was changing the p – value from no significance into high significance - indicating some underlying multicollinearity that we have not detected beforehand. For the model formula, see table 4.

The stepwise reduction of variables in ModI dropped the interaction out in the 4th step, that it afterwards resembled the other initial Model, ModM.

Model ModM with main effects

The stepwise AIC selection of ModM in backwards direction (starting with the model containing all variables and reducing them stepwise) revealed three models within the ΔAIC < 3. The best fitting model contained the variables of *tree preference group, tree height, forestcover, distance to the next settlement, snow, red deer density* and *hunting ground owner* (Table **5**). Models with good results contained additional the variable *distance to forest road* (ModM6), and the *distance to the next SFS* (ModM5). The binary variable of wolf presence, *wolf2*, was dropped out already in the first step.

Table 5: Ranked generalized mixed models in SFS analysis after model selection. AIC= Akaike's Information Criteria, ΔAIC = difference in AIC, (1 | SiteID/Plot_ID) = random nested effects. Bold font is indicating variables that were dropped out in the process of AIC minimisation. Variable descriptions see Table 1-

Model	Formula	AIC	ΔAIC
ModM7	brows ~ g + height + forestcover + dist_settlement + snow + red_dd + hunt + (1 | SiteID/Plot_ID)	9163.0	0.00
ModM6	brows ~ g + height + forestcover + dist_settlement + **dist_forestroad** + snow + red_dd + hunt + (1 | SiteID/Plot_ID)	9164.3	1.38
ModM5	brows ~ g + height + **nxt_SFS** + forestcover + dist_settlement + **dist_forestroad** + snow + red_dd + hunt + (1 | SiteID/Plot_ID)	9165.7	2.79

All variables of the final selected Model were significant, except for percentage of *forestcover* and *red deer density*, which were just slightly significant. The output of ModM7 (table 6) showed, that browsing depends on the plant species' browsing preference, with increasing browsing if attractive plants were present. The tree heights between 30 - 50 cm and 50 – 150 cm were browsed more

21

intensively than saplings of the baseline category of under 30 cm height class. Trees between 150-200 cm height were also more heavily browsed compared to saplings under 30 cm. Among the other categorical variables, *snow* heights above the baseline level of 140 – 200 cm had a negative influence on browsing intensity. The category of the hunting club revealed that plots on hunting grounds owned by the Slovenian Forestry Service were more intensively browsed (Fig. **1**).

Regarding continuous variables (Fig. **2**), the browsing intensity decreases with increasing forestcover, whereas at higher distance to the nearest settlement browsing increases and high red deer densities increases browsing intensity at the sampling plot. Regarding the two other models within ΔAIC, browsing intensity is increasing with higher distance to forest roads (ModM6) and decreasing distance to supplemental feeding sites (ModM5).

With the results of the Model selection we can conclude, that in our analysis the frequency of wolves visiting a SFS has no influence at all on browsing around SFS.

Table 6: Output Model M7: Fixed variables, regression coefficients, standard errors, z-values and p-values of the Model M7. Reference classes for categorical variables are "group high" for browsing preference in tree species grouping, "30 - 60 cm" for tree height class, „140 – 200 cm" for snow height interval and "local hunting club" for hunting ground owner (see Table 1 for variable descriptions). Asterisks indicate levels of significance.

Variable	Estimate	Standard error	z-value	p-value	Signif.code
Intercept	0.27782	0.23015	1.207	0.22730	
group low	-1.76781	0.07432	-23.872	<0.001	***
height 50	0.69969	0.09727	7.193	<0.001	***
height 150	0.91320	0.11746	7.774	<0.001	***
height 200	0.17907	0.30749	0.582	0.56033	
forestcover	-0.14993	0.08129	-1.844	0.06512	.
dist_settlement	0.23146	0.07126	3.248	0.00116	**
snow 200-280	-0.55541	0.21662	-2.564	0.01035	*
snow280-420	-0.34311	0.27468	-1.249	0.21162	
red_dd	0.12568	0.06690	1.879	0.06030	.
hunt state	0.43887	0.14167	3.098	0.00195	**
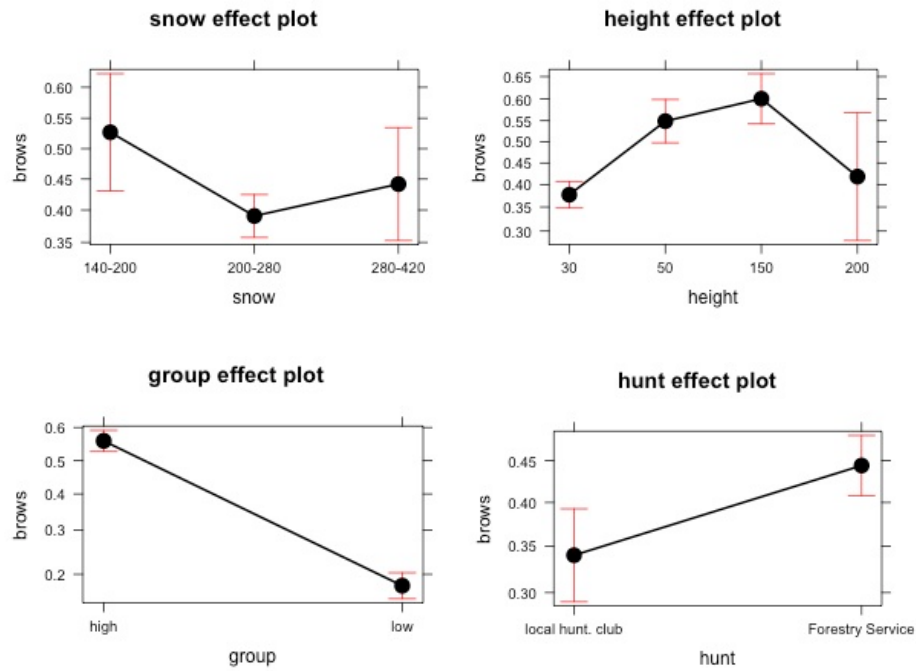
Fig 1: Effect of categorical fixed variables contained in Model M7 on browsing intensity, whiskers show confidence intervals. The figure was built with the `plot (Effect)` function of the „effects" package (Fox, 2003),
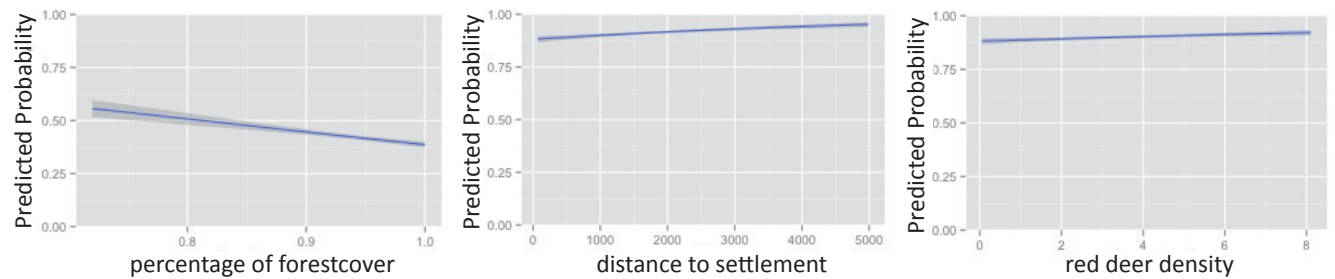

Fig 2: predicted probability plots of continuous fixed variables contained in Model M7, grey bands show confidence intervals. The figure was built with the `sjp.glmer` function of the „sjPlot" package (Lüdecke, 2016)

4.3 GLMM Den Sites

In preliminary analysis of data we noticed that the den with site ID *Den02* had outliers in many variables. *Den02* was located on the mountain Snežnik, and was not comparable with the other den sites in respect of *percentage of conifers* and *distance to the next feeding site*, *settlement*, *forest edge* and *forest road*. All plots recorded in distance to *Den02* were therefore excluded from further analysis. After that reduction of data, spearman correlation matrix revealed a negative correlation between roe deer and red deer [-0.6], therefor the *roe deer* variable was excluded from further analysis.

Table 7: Saturated model den analysis. AIC= Akaike's Information Criteria, (1 | SiteID/Plot_ID) = random nested effects.

Model	Formula	AIC
ModDen	brows ~ g + height + slope + canopy + dist_forestedge + dist_forestroad + dist_settlement+ perc_conifers + nxt_SFS + dist_DEN + snow + red_dd + (1 | SiteID/Plot_ID)	2639.1

After stepwise model selection from the saturated model (Table **7**) via AIC, the most parsimonious model and the remaining "good" models (**Δ**AIC < 3) contained the variables tree preference group, tree height, slope, canopy, distance to forestedge, distance to forestroad, distance to den site, red deer density, percentage of conifers and distance to settlement (Table **8**).

Of the final model ModDen4, all variables except from *slope*, *canopy* and *distance from forestedge* were significant.

Table 8: Ranked generalized mixed models in SFS analysis after model selection. AIC= Akaike's Information Criteria, ΔAIC = difference in AIC , (1 | SiteID/Plot_ID) = random nested effects. Bold font is indicating variables that were dropped out in the process of AIC minimisation. For variable description see Table 2.

Model	Formula	AIC	ΔAIC
ModDen4	brows ~ g + height + slope + canopy + dist_forestedge + dist_forestroad + dist_DEN + red_dd + (1 | SiteID/Plot_ID)	2634.7	0.00
ModDen3	brows ~ g + height + slope + canopy + dist_forestedge + dist_forestroad + **perc_conifers** + dist_DEN + red_dd + (1 | SiteID/Plot_ID)	2635.5	0.8
ModDen2	brows ~ g + height + slope + canopy + dist_forestedge + **dist_settlement** + dist_forestroad + perc_conifers + dist_DEN + red_dd + (1 | SiteID/Plot_ID)	2636.1	1.4
ModDen1	brows ~ g + height + slope + canopy + dist_forestedge + **dist_settlement** + dist_forestroad + **perc_conifers** + **nxt_SFS** + dist_DEN + red_dd + (1 | SiteID/Plot_ID)	2637.1	2.4

Regarding categorical variables (Fig. **3**), the presence of preferred tree species had a positive effect on browsing intensity. Concerning tree heights, trees between 30-50 cm and 50-150 cm height were

browsed more than the baseline tree height category with saplings <30 cm height, whereas trees within 150-200 cm height were less browsed than the baseline category.

Concerning continuous variables (Fig. **4**), browsing intensity was decreasing with increasing slope, increasing canopy and increasing red deer density. Whereas browsing intensity increased with increasing distance from the wolf den and higher distance from the outer forestedge. Regarding the other models within ΔAIC, browsing intensity was increasing with decreasing distance to settlements and decreasing percentage of conifers. Browsing also appeared to be slightly increasing [Estimate = 0.12] with increasing distance to SFS.

To draw a conclusion, with this analysis we were able to show a decrease in browsing around wolf dens. We can thus accept our second hypothesis.

Table 9: Fixed variables, regression coefficients, standard errors, z-values and p-values of the Model ModelDen4. Asterisks indicate levels of significance. Reference classes for categorical variables are "group high" for browsing preference in tree species grouping, "30 - 60 cm" for tree height class (see Table 1 for variable descriptions).

Variable	Estimate	Standard error	z-value	p-value	Signif.code
Intercept	-0.36561	0.10548	-3.466	<0.001	***
group low	-1.88436	0.16152	-11.666	<0.001	***
height 50	0.58887	0.18758	3.139	0.0016	**
height 150	1.13343	0.24165	4.690	<0.001	***
height 200	-0.80528	0.61839	-1.302	0.1928	
slope	-0.14791	0.09704	-1.524	0.1274	
canopy	-0.13946	0.09580	-1.456	0.1454	
dist_forestedge	0.14590	0.09627	1.516	0.1296	
dist_forestroad	0.21676	0.10705	2.025	0.0429	*
dist_DEN	0.24135	0.10768	2.241	0.0250	*
red_dd	-0.50763	0.11342	-4.476	<0.001	***
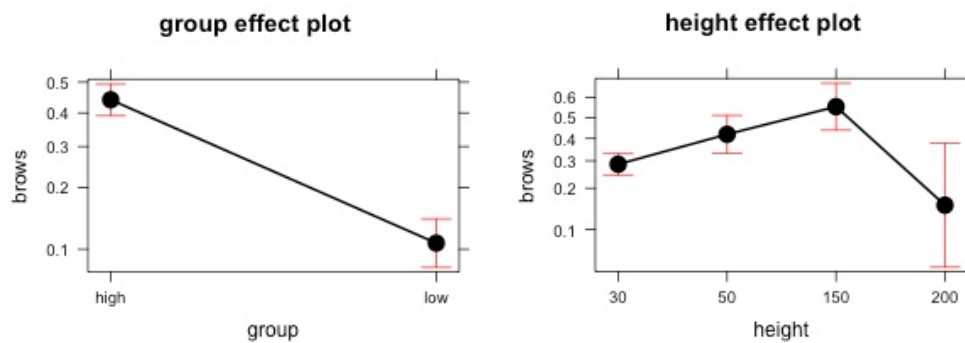
Fig 3: Effects plot for categorized fixed variable of the final model ModelDen4. The figures were built with the „effects" package (Fox, 2003). **Whiskers show confidence intervals.**

Fig. 4: Predicted Probabilities of the browsing variable in relation to continuous variables of the final ModelDen4. Plotted with the function `sjp.glmer` of the package sjPlot (Lüdecke, 2016)**. Grey bands show the standard error of probabilities. For variable abbreviations see Table 2.**

5 Discussion

Analysis SFS

Our data indicates that wolf presence does not have any influence on the browsing intensity around SFS. The variable presence of wolves had less explanatory power than other factors, such as distances (e.g. *distan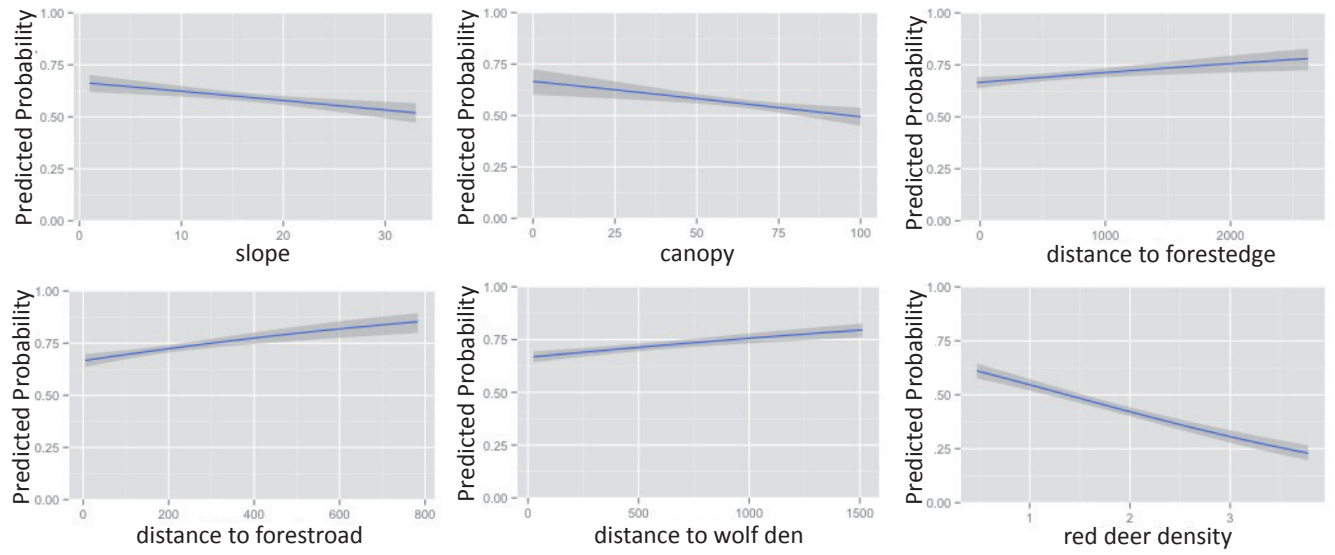ce to settlements* as significant variable) or management (e.g. the variable *hunt*, which implements hunting/ fostering strategies). Abiotic factors such as *snow* height and percentage of *forestcover* were also influencing browsing intensity and complement the results of various studies (e.g. Gerhardt et al., 2013).

With increasing *distance to the next feeding site*, which was included in the third best model, browsing showed a negative trend, which is in line with findings of earlier studies (Cooper et al., 2006; Garrido et al., 2014; Mathisen et al., 2014; Sahlsten et al., 2010; Van Beest, Gundersen, et al., 2010). However in our study, decrease in browsing with increasing distance was not significant, maybe because of the high density and variability of SFS in the study region.

Indices for terrestrial trophic cascades were found in several studies conducted in broad and protected landscapes such as Yellowstone National Park and have taken into account just a few tree species (*Populus* sp. *Populus tremuloides* and *Salix* sp.), different habitat types, high and low wolf-use areas and estimated red deer densities by pellet counts (Ripple & Beschta, 2003, 2006; Ripple et al., 2001; Ripple & Larsen, 2000) .

These studied landscapes differed from our study area as they consist of broad open areas and patches of forests, showing heterogeneity on a large scale (Schmidt & Kuijper, 2015), while our study area consisted of homogenous, highly productive forests, with just few elements of heterogeneity, e.g. clearings at SFS, forest gaps, clear cuts, roads. Changes in browsing due to behaviourally mediated trophic cascades might be much more existent and detectable in broad and heterogenic landscapes: The open forage area with a wide view and fleeing opportunity (Holmes & Laundré, 2006) and distributed patches of dense vegetation, functioning as hiding cover (Creel & Winnie, 2005). The changes in landscape use and in browsing should be easier to measure, due to the clear structures. Furthermore, the human control, which is mostly absent in these listed examples, perhaps diminishes trophic effects. This will be investigated in more depth in the general discussion paragraph below.

Our first result, which shows that wolves have no indirect influence on plants, is in line with other studies in this ecosystem. The parallel conducted thesis about general browsing in Southern Slovenia comparing presence and absence of wolves revealed even higher browsing rates in the wolf core areas than in areas of lower wolf usage (Sommerfeld, 2015).

Our study has shown that other factors are more important than predator presence. That was also identified by several other studies. When studying moose (*Alces alces*) in south Sweden, researchers did not find a significant effect of wolves on prey species behaviour, while they included factors like habitat parameters or human disturbance which have been included in our study as well (Nicholson, Milleret, Månsson, & Sand, 2014). In Ontario, moose and deer resource selection was more influenced by abiotic factors such as snow, rather than by direct and indirect wolf predation risk (Kittle et al., 2008).

Wolf visiting frequency had no influence on browsing around SFS in our study – this could also be showing that, when facing the trade-off between high energetic food supply during winter feeding and the risk of predation, red deer is choosing the food. As it was already presented in earlier studies, supplemental feeding sites play an important role in habitat selection and life history of red deer in Slovenia (Jerina, 2012), and the "beneficial" effects of feeding might be weighted higher in red deer ayes than the potential risk of predation. This is underlined by observations of red deer returning to a supplemental feeding site, just a day after wolves killed a red deer at this site (M. Krofel, personal communication).

Analysis wolf dens

Our analysis of ungulate browsing around wolf dens showed that browsing near a wolf den is lower than further away from the den. The increased wolf habitat use around a den during summer and the year round presence in their territory causes elevated predation risk. The lower browsing near wolf dens can be explained by risk avoiding behaviour of prey species (Lima & Dill, 1990). Our results showed that wolves have an influence on browsing on a small scale. Staying away from core wolf areas (e.g. wolf dens), was also shown for calving caribou (Mech 2003, p. 136) and moose (Kunkel & Pletscher, 2000).

This local patch with low browsing intensity due to high predation risk constitutes an interesting finding and is in line with other studies. As in Yellowstone National Park, where at places with higher predation risk, browsing was lower, or in Europe, where lower browsing at small scaled *patches of fear* (Kuijper et al., 2013) was found. Our findings are on a very local scale though sparse due to wolf specific biology (1 den per pack territory), and imply that just a tiny portion of landscape is conceived as *landscape of fear* due to the presence of wolves, as illustrated by our results concerning browsing around SFS.

Distance to forestroad had a positive effect on browsing, as found also in other literature (Fortin et al., 2005; Jerina, 2012; John, 1995; Rogala et al., 2011; Rost & Bailey, 1979). Whereas *distance to settlement* had a negative effect on browsing- this result, although not significant, could be underlined by studies that found red deer moving closer to settlements to avoid wolf predation (Beschta & Ripple, 2007; M. Hebblewhite et al., 2005).

Browsing intensity was found to be increasing with increasing *distance from the forest edge*. Jerina et. al (2008) showed also increased browsing with a maximum at 600-800 m from the forestedge. Contrary to this finding, other studies suggest an attractive function of forest edges as they are often adjacent to alternative food sources as meadows and crops (for a summary, see Gerhardt et al., 2013). However, the human hunting pressure is supposed to be higher in these open areas (Adamič & Jerina, 2010) as it is in human interest to mitigate damages on agriculture. Outer forest edges also constitute higher wolf predation risks for red deer (Bergman et al., 2006).

Contrary to our previous finding in the SFS analysis, in den analysis browsing intensity was slightly increasing with greater *distance to the nearest feeding site*. This result could be an artefact of other random factors connected with the area of the nearest feeding site, such as roads and human disturbance. It could perhaps also indicate that around these feeding sites, which are located inside or near wolf territories, less browsing occurs due to higher wolf predation- as we wanted to show with our previous SFS analysis. But to make any conclusions, this result requires further investigation

with a higher sample size.

A significant result of our analysis shows a negative relationship of browsing intensity and red deer density. In contrast, is it widely established that higher deer densities have a greater impact on vegetation (see also Gerhardt et al., 2013). Similarly, in our SFS analysis, deer density was positively correlated with browsing intensity. Why did we find the opposite around den sites?

One explanation could be that the density data may not be up to date. Deer densities possibly shifted and were lower in this study's sampling year 2014. The deer numbers per km^2 were calculated based on removal data and pellet count data from the year 2009. The wolf population is monitored since 2010, and dens included in this study were used by wolves between 2011 and 2014. Wolves have been present in our study area in Southern Slovenia since decades and were never totally eliminated (Adamič, Jerina, Zafran, & Marinčič, 2004). A strong shift in deer dynamics in the last five years due to wolf presence could explain our result; however, this seems unlikely as the deer had time to adapt to the wolf presence.

On the other hand, wolves do not necessarily use the same den site in consecutive years, hence there wouldn't be a strong need for deer to permanently shift movement patterns by avoiding these areas in general.

If deer density calculation was appropriate, then the assumption that high deer densities implement high browsing has to be revised. A decrease in food intake or foraging time in these risky areas (Winnie & Creel, 2007) could be an explanation for this low. Higher deer densities could be found there due to landscapes attributes such as a dense shrub layer or other forms of hiding cover, which are favoured to diminish wolf predation (Creel & Winnie, 2005; Kunkel & Pletscher, 2000), while distance from human disturbances may also be a factor. Deer could use these habitats for these aspects, but change to nearby habitats for foraging.

As Slovenia offers a very detailed data base for environmental and management data, and telemetry studies of red deer delivered high quality space use data, more investigation of this result could provide more in-depth insights.

Limitations of the study

Wolf presence had no impact on browsing around SFS in our study. One reason for this could be that the 16 investigated SFS were in different conditions, some were well-cared for and large in size, others small and without driveable forest roads. A study with a larger sample size of comparable SFS in non- wolf and in wolf areas might reveal a more precise result.

As expected, browsing around wolf dens was significantly lower. The low sample size of wolf dens in this study allows only a limited inference, as our findings could be affected by more complex circumstances. A potentially relevant factor that we did not include in this study is the selection of den sites by wolves. Trapp et. al (2008) found that besides other factors, such as canopy and hiding coverage, woody debris is an important habitat attribute determining location of denning places in Canada, and we know from Kujiper (2013) that these escape impediments are also avoided by red deer. In our study landscape, distance from sources of human disturbance other than our variables roads and settlements might have also be an influence (e.g. logging and other forest operations, seasonal disturbances such as off road vacationists, mushroom pickers). Furthermore, environmental

factors, such as soil conditions, camouflage or micro and macro relief at the nearer distances to wolf dens, which we did not include in our analysis, may have an influence. Habitat parameters, which are favoured by wolves, could be avoided by red deer. This means that not only predator density is the explanation for less browsing around wolf dens but also less favourable habitat conditions, as risky landscape features.

In this study, we accounted for several variables that represent environmental and spatial effects – more factors were incorporated than in most previous studies. Still there might be additional factors that influence use of space and browsing of red deer, especially in human dominated landscapes with its artificial attributes. Other attractive places with deer clustering are sources of minerals, such as salt licks (Dussault et al., 2007; Paakkonen, Nieminen, Roininen, & Mustonen, 2014), which were also widespread in the study region. We included only the outer forest edges, which are different from internal forest edges along the roads, clear-cuts or forest gaps inside the forest. Such forest edges provide nearby coverage and red deer are known to preferably feed in these landscape elements (Kuijper et al., 2009; Reimoser & Gossow, 1996).

The small-scale landscape structures could also be taken into account, for example karstic structures such as dolinas (small karstic valleys). These structures are characteristic in the area and may function as escape impediments, constituting higher predation risk, as was shown for lynx predation in Slovenia (Krofel, Potočnik, & Kos, 2007).
Including such habitat structures would be in line with research done in Białowieża, where browsing around woody debris in its function as escape impediments was investigated (Kuijper et al., 2013). The influence of dead wood representing escape impediments may also be considered in our study area, although big dead tree trunks are seldom found lying around in these economically used forest stands.

Another factor that we did not consider in the analysis is the predation risk by other predators, such as lynx, even though red deer forms just 6% in lynx diet (Krofel et al., 2011). The lynx presence may cause *perceived predation risk* on which red deer has to react differently: Safe habitats in relations to cursorial predators such as wolves (e.g. cover) implement higher predation risks concerning stalking predators as lynx (Schmidt & Kuijper, 2015). That was also shown for cougars (*Puma concolor*) and wolves (Atwood et al., 2009).

This second predator with a different hunting behaviour than wolves creates, in addition to human hunters, a complex multi- predator landscape of fear (Lone et al., 2014). Multiple predators can diminish effects of single predator-prey interactions (Atwood et al., 2009; Gervasi et al., 2013) as risk avoidance has to deal with a high complexity. When facing two predators with different hunting strategies, distinctive risk prevention for each predator might be necessary. This was for example shown in roe deer facing both lynx and human predation (Lone et al., 2014) where lynx predation risk increased with understorey cover, whereas risk of being shot by human hunters decreased with less visibility, e.g. understorey cover.

General discussion
Unlike the protected areas investigated in most previous studies on trophic cascades, our region is human-dominated. The influence of human presence and disturbance on trophic interrelations is

found to reduce top- down effects and to strengthen bottom up processes (Muhly et al., 2013). However, as the interactions of bottom-up and top-down effects are very complex and poorly understood to date, Eisenberg (2013) has recommended shifting the emphasis from the trophic cascade term to "food web studies".

We studied influences of apex predators at locations of artificial (human) bottom-up factors, as SFS stands for food availability and influences the habitat and local densities of red deer. This illustrates how complex human dominated environments are and how careful studies and interpretations of research findings in multicausal environments have to be. Multicausality (e.g. different and complex influences by humans and multipredator assemblage) makes simple answers inappropriate. This was already shown by assessments on the existence of trophic cascades for Yellowstone and Isle Royale (Peterson, Vucetich, Bump, & Smith, 2014).

For both red deer and wolves, humans are not only a source of disturbance already perceived as predation risk (Frid & Dill, 2002), but due to their hunting activity seen as a kind of "super predator" (Gervasi et al., 2013). Red deer responses to human- predation risk were already shown to be stronger than to wolf – predation risk (Proffitt, Grigg, Hamlin, & Garrott, 2009). White, Olmsted, & Kay (1998) even proposed to include humans in a four levelled trophic cascade as the apex predator.

Wolf and red deer populations cannot evolve and distribute naturally in our study area, as roads cut through the landscape and densely settled regions offer limited habitat. The amount of SFS feeding is managed, and deer numbers are primarily determined by hunting. The wolf population is quite low in Slovenia and kept at this level by wolf culling management practice, which is problematic for the stability of the wolf packs in a population currently consisting of ca. 40 individuals (Jelenčič, Skrbinšek, & Trontelj, 2013). Especially in regard to pack dynamics it is important to conserve stable packs (Rutledge et al., 2010), whilst maintaining ecological effective densities. Taking all the human activities into account, and without the possibility of increasing ecological influences of wolves, the beneficial effects of wolves on the ecosystem will never be comparable to those in National Parks (Mech, 2012; Soulé, Estes, Berger, & Martinez Del Rio, 2003). Ultimately, bottom-up influences and top- down influences are human controlled in the investigated landscape. The landscape changes caused by humans are known to be fundamental drivers that influence species and ecosystems all over the world (Houghton, 1994), and human influences cannot be explained by ecological principles alone (Peterson et al., 2014). Improvement of management strategies of forests, supplemental feeding sites and red deer, might lead more effectively to less economic losses through browsing, as behavioural effects induced by wolves.

Further investigations should preferably consider small-scale elements of risks for deer in the landscapes, including also predation by other predators besides wolves, as well as landscapes of fear created by human hunters. The landscape use of wolves and their hunting strategies in human dominated regions in such studies would enhance our knowledge of human- wolf- red deer - plant food webs in Europe. Thereby we might also achieve a better understanding of our role in the ecosystem.

6 References

Adamič, M., & Jerina, K. (2010). Ungulate management in europe in the 21st century: Slovenia. In M. Apollonio, R. Andersen, & R. Putman (Eds.), *European ungulates and their management in the 21st century*.

Adamič, M., Jerina, K., Zafran, J., & Marinčič, A. (2004). Izhodišča za oblikovanje strategije ohranitvenega upravljanja s populacijo volka (Canis lupus) v Sloveniji (Starting point for conservation strategies and wolf population management (Canis lupus) in Slovenia).

Atwood, T. C., Gese, E. M., & Kunkel, K. E. (2009). Spatial Partitioning of Predation Risk in a Multiple Predator-Multiple Prey System. *Journal Of Wildlife Management*, *73*(6), 876–884. doi:10.2193/2008-325

Augustine, D. J. ., & McNaughton, S. J. (1996). Ungulate effects on the functional species composition of plant communities. *The Journal of Wildlife Management*, *62*(4), 1165–1183. doi:10.2307/3801981

Barja, I., & Rosellini, S. (2008). Does habitat type modify group size in roe deer and red deer under predation risk by Iberian wolves? *Canadian Journal of Zoology*, *86*(3), 170–176. doi:10.1139/Z07-129

Bates, D., Maechler, M., Bolker, B., Walker, S. (2013). lme4: Linear Mixed-Effects Models Using Eigen and S4.

Bergman, E. J., Garrott, R. A., Creel, S., Borkowski, J. J., Jaffe, R., & Watson, F. G. R. (2006). Assessment of Prey Vulnerability through Analysis of Wolf Movements and Kill sites. *Ecological Applications*, *16*(1), 273–284. doi:10.1890/04-1532

Beschta, R. L., & Ripple, W. J. (2007). Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research*, *37*, 1873–1885. doi:10.1139/X07-017

Brown, J. S. (1999). Vigilance , patch use and habitat selection : Foraging under predation risk. *Evolutionary Ecology Research*, (1990), 49–71.

Campos, F. a., & Fedigan, L. M. (2014). Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology*, *25*, 477–486. doi:10.1093/beheco/aru005

Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago: University of Chicago Press.

Ciucci, P., & Mech, D. L. (1992). Selection of Wolf Dens in Relation to Winter Territories in Northeastern Minnesota. *Journal of Mammalogy*, *73*(4), 899–905. doi:10.2307/1382214

Cooper, S. M., Owens, M. K., Cooper, R. M., & Ginnett, T. F. (2006). Effect of supplemental feeding on spatial distribution and browse utilization by white-tailed deer in semi-arid rangeland. *Journal of Arid Environments*, *66*(4), 716–726. doi:10.1016/j.jaridenv.2005.11.015

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological Impacts of Deer Overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 113–147. doi:10.1146/annurev.ecolsys.35.021103.105725

Creel, S., & Winnie, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour*, *69*(5), 1181–1189. doi:10.1016/j.anbehav.2004.07.022

Didion, M., Kupferschmid, a. D., & Bugmann, H. (2009). Long-term effects of ungulate browsing on forest composition and structure. *Forest Ecology and Management*, *258*, S44–S55. doi:10.1016/j.foreco.2009.06.006

Dussault, C., Ouellet, J. P., Laurian, C., Courtois, R., Poulin, M., & Breton, L. (2007). Moose Movement Rates Along Highways and Crossing Probability Models. *Journal of Wildlife Management*, *71*(7), 2338. doi:10.2193/2006-499

Eisenberg, C. (2010). *Wolf's Tooth : Keystone Predators, Trophic Cascades, and Biodiversity*. Washington: Island Press.

Eisenberg, C., Hibbs, D. E., Ripple, W. J., & Salwasser, H. (2014). Context dependence of elk (Cervus elaphus) vigilance and wolf (Canis lupus) predation risk. *Canadian Journal of Zoology*, *92*(February), 727–736. doi:10.1139/cjz-2014-0049

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*(5), 1320–1330.

Fox, J. (2003). Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, *8*(15), 1–27.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Ecology and Society*, *6*(1), 11–26. doi:ARTN 11

Garrido, P., Lindqvist, S., & Kjellander, P. (2014). Natural forage composition decreases deer browsing on Picea abies around supplemental feeding sites. *Scandinavian Journal of Forest Research*, (March 2015), 1–9. doi:10.1080/02827581.2014.903993

Gerhardt, P., Arnold, J. M., Hackländer, K., & Hochbichler, E. (2013). Determinants of deer impact in European forests - A systematic literature analysis. *Forest Ecology and Management*, *310*, 173–186. doi:10.1016/j.foreco.2013.08.030

Gervasi, V., Sand, H., Zimmermann, B., Mattisson, J., Wabakken, P., & Linnell, J. D. C. (2013). Decomposing risk: landscape structure and wolf behavior generate different predation patterns in two sympatric ungulates. *Ecological Applications*, *23*(7), 1722–34. doi:10.1890/12-1615.1

Gill, R. M. A., & Beardall, V. (2001). The impact of deer on woodlands: The effects of browsing and seed dispersal on vegetation structure and composition. *Forestry*, *74*(3), 209–218. doi:10.1093/forestry/74.3.209

Gorini, L., Linell, J. D. C., May, R., Panzacchi, M., Boitani, L., Morten, O., & Nilsen, E. B. (2012). Habitat heterogeneity and mammalian predator-prey interactions. *Mammal Review*, *42*(1), 55–77. doi:10.1111/j.1365-2907.2011.00189.x

Gude, J. A., Garrott, R. A., Borkowski, J. J., & King, F. (2006). Prey risk allocation in a grazing ecosystem. *Ecological Applications*, *16*(1), 285–298. doi:10.1890/04-0623

Hebblewhite, M., Merrill, E. H., & Mcdonald, T. L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf- elk - predator- prey system. *Oikos*, *1*(February), 101–111.

Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., … Paquet, P. C. (2005). Human activity mediates a trophic cascade caused by wolves. *Ecology*, *86*. doi:10.1890/04-1269

Hofmann, R. R. (1989). Adaptation steps of ecophysiological Evolutionary of ruminants : and diversification view of their digestive system. *Oecologia*, *78*(4), 443–457.

Holmes, B. R., & Laundré, J. W. (2006). Use of open, edge and forest areas by pumas Puma concolor in winter: are pumas foraging optimally? *Wildlife Biology*, *12*(2), 201–209. doi:10.2981/0909-6396(2006)12[201:UOOEAF]2.0.CO;2

Houghton, R. A. (1994). The worldwide extent of land-use change: In the last few centuries, and particularly in the last several decades, effects of land-use change have become global.

BioScience, *44*(5), 305–313.

Jelenčič, M., Skrbinšek, T., & Trontelj, P. (2013). *Preliminary study of wolf packs stability based on genetic data Culling of wolves in Slovenia*. Ljubljana.

Jennings, S. B., Brown, N. D., & Sheil, D. (1999). Assessing forest canopies and understorey illumination : canopy closure , canopy cover and other measures. *Forestry*, *72*(1), 59–73. doi:10.1093/forestry/72.1.59

Jerina, K. (2006). *Spatial distribution, home range and body mass of red deer (Cervus elaphus L.) in regard to environmental factors*.

Jerina, K. (2012). Roads and supplemental feeding affect home-range size of Slovenian red deer more than natural factors. *Journal of Mammalogy*, *93*(4), 1139–1148. doi:10.1644/11-MAMM-A-136.1

Jerina, K., Dajčman, M., & Adamič, M. (2008). Red deer (Cervus elaphus) bark stripping on spruce with regard to spatial distribution of supplemental feeding places elaphus) glede na prostorsko razporeditev krmišč INTRODUCTION AND PURPOSE OF THE STUDY. *Zbornik Gozdarstva in Lesarstva*, *86*, 33 – 43.

John, R. A. S. (1995). *Aspen Stand Recruitment and Ungulate Impacts: Gardiner Ranger District, Gardiner, Montana*. University of Montana.

Jones, J. D., Kauffman, M. J., Monteith, K. L., Scurlock, B. M., Albeke, S. E., & Cross, P. C. (2014). Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications*, *24*(7), 1–34. doi:10.1890/13-2092.1

Kaartinen, S., Kojola, I., & Colpaert, a. (2005). Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici*, *42*(5), 523–532.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters*, *10*(8), 690–700. doi:10.1111/j.1461-0248.2007.01059.x

Kavčič, I., Adamič, M., Kaczensky, P., Krofel, M., Kobal, M., & Jerina, K. (2015). Fast food bears: brown bear diet in a human-dominated landscape with intensive supplemental feeding. *Wildlife Biology*, *21*(1), 1–8. doi:http://dx.doi.org/10.2981/wlb.00013

Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, *157*(1), 163–175. doi:10.1007/s00442-008-1051-9

Klopcic, M., Jerina, K., & Boncina, A. (2009). Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? *European Journal of Forest Research*, *129*(3), 277–288. doi:10.1007/s10342-009-0325-z

Krebs, C. J., Bountin, S., Boonstra, R., Sinclair, A. R. E., Smith, J. N. M., Dale, M. R. T., … Turkington, R. (1995). Impact of Food and Predation on the Snowshoe Hare Cycle. *Science*, *269*(5226), 1112–1115.

Krofel, M., Huber, D., & Kos, I. (2011). Diet of Eurasian lynx Lynx lynx in the northern Dinaric Mountains (Slovenia and Croatia). *Acta Theriologica*, *56*(4), 315–322. doi:10.1007/s13364-011-0032-2

Krofel, M., & Kos, I. (2010). Analiza vsebine iztrebkov volka (Canis lupus) v Sloveniji (Scat analysis of grey wolves (Canis lupus) in Slovenia). *Acta Silvae et Ligni*, *91*, 85–88.

Krofel, M., Potočnik, H., & Kos, I. (2007). Topographical and vegetational characteristics of lynx kill sites in Slovenian Dinaric Mountains. *Natura Sloveniae*, *9*(1), 25–36.

Kuijper, D. P. J. (2011). Lack of natural control mechanisms increases wildlife–forestry conflict in

managed temperate European forest systems. *European Journal of Forest Research*, *130*(6), 895–909. doi:10.1007/s10342-011-0523-3

Kuijper, D. P. J., Cromsigt, J. P. G. M., Churski, M., Adam, B., Jedrzejewska, B., & Jedrzejewski, W. (2009). Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management*, *258*, 1528–1535. doi:10.1016/j.foreco.2009.07.010

Kuijper, D. P. J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., & Jędrzejewska, B. (2013). Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography*, *36*(12), 1263–1275. doi:10.1111/j.1600-0587.2013.00266.x

Kunkel, K. E., & Pletscher, D. H. (2000). Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology*, *78*, 150–157. doi:10.1139/z99-181

Kunkel, K. E., & Pletscher, D. H. (2001). Winter Hunting Patterns of Wolves in and Near Glacier National Park, Montana. *Journal of Wildlife Management*, *65*(3), 520–530. doi:10.2307/3803105

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*, 619– 640.

Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J., & Mysterud, A. (2014). Living and dying in a multi-predator landscape of fear: Roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*, *123*, 641–651. doi:10.1111/j.1600-0706.2013.00938.x

Lüdecke, D. (2016). Data Visualization for Statistics in Social Science.

Lung, M. a., & Childress, M. J. (2007). The influence of conspecifics and predation risk on the vigilance of elk (Cervus elaphus) in Yellowstone National Park. *Behavioral Ecology*, *18*(1), 12–20. doi:10.1093/beheco/arl066

Majic, A. (2014). FINAL Report SloWolf.

Mathisen, K. M., Milner, J. M., van Beest, F. M., & Skarpe, C. (2014). Long-term effects of supplementary feeding of moose on browsing impact at a landscape scale. *Forest Ecology and Management*, *314*, 104–111. doi:10.1016/j.foreco.2013.11.037

McPhee, H. M., Webb, N. F., & Merrill, E. H. (2012). Hierarchial predation: wolf (Canis lupus) selection along hunt paths and at kill sites. *Canadian Journal of Zoology*, *90*(5), 555–563. doi:10.1139/z2012-021

Mech, D. L. (2003). *Wolves : Behavior, ecology, and conservation*. Univ. of Chicago Press.

Mech, D. L. (2012). Is science in danger of sanctifying the wolf ? *Biological Conservation*, *150*(1), 143–149. doi:10.1016/j.biocon.2012.03.003

Mech, D. L., Adams, L. G., Meier, T. J., Burch, J. W., & Dale, B. W. (1998). *The Wolves of Denali*. Minneapolis: University of Minnesota Press.

Muhly, T. B., Hebblewhite, M., Paton, D., Pitt, J. a, Boyce, M. S., & Musiani, M. (2013). Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PloS One*, *8*(5), e64311. doi:10.1371/journal.pone.0064311

Mysterud, A., Askilsrud, H., Loe, L. E., & Veiberg, V. (2010). Spatial patterns of accumulated browsing and its relevance for management of red deer Cervus elaphus. *Wildlife Biology*, *16*(2), 162–172. doi:10.2981/09-043

Nicholson, K. L., Milleret, C., Månsson, J., & Sand, H. (2014). Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. *Oecologia*, *176*(1), 69–80. doi:10.1007/s00442-014-3004-9

Paakkonen, T., Nieminen, P., Roininen, H., & Mustonen, A.-M. (2014). Salt licks do not increase local densities of the deer ked, Lipoptena cervi, an abundant ectoparasite of cervids. *Medical and Veterinary Entomology*, *28*(3), 307–13. doi:10.1111/mve.12030

Packard, J. M. (2003). Wolf Behavior: Reproductive, Social, and Intelligent. In L. D. Mech & L. Boitani (Eds.), *Wolves. Behavior, Ecology, and Conservation* (pp. 35–65). Chicago: University of Chicago Press.

Peterson, R. O., Vucetich, J. A., Bump, J. M., & Smith, D. W. (2014). Trophic Cascades in a Multicausal World : Isle Royale and Yellowstone. doi:10.1146/annurev-ecolsys-120213-091634

Proffitt, K. M., Grigg, J. L., Hamlin, K. L., & Garrott, R. A. (2009). Contrasting Effects of Wolves and Human Hunters on Elk Behavioral Responses to Predation Risk. *Journal of Wildlife Management*, *73*(3), 345–356. doi:10.2193/2008-210

Prokešová, J., Barančeková, M., & Homolka, M. (2006). Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest. *Folia Zoologica*, *55*(1), 1–14.

R Core Team. (2014). R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing.

Reimoser, F., & Gossow, H. (1996). Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *Forest Ecology and Management*, *88*(1-2), 107–119. doi:10.1016/S0378-1127(96)03816-9

Ripple, W. J., & Beschta, R. L. (2003). Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*, *184*(1-3), 299–313. doi:10.1016/S0378-1127(03)00154-3

Ripple, W. J., & Beschta, R. L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management*, *230*(1-3), 96–106. doi:10.1016/j.foreco.2006.04.023

Ripple, W. J., & Larsen, E. J. (2000). Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation*, *95*, 361–370. doi:10.1016/S0006-3207(00)00014-8

Ripple, W. J., Larsen, E. J., Renkin, R. a., & Smith, D. W. (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, *102*, 227–234. doi:10.1016/S0006-3207(01)00107-0

Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J., & Musiani, M. (2011). Human Activity Differentially Redistributes Large Mammals in the Canadian Rockies National Parks, *16*(3).

Rost, G. R., & Bailey, J. a. (1979). Distribution of Mule Deer and Elk in Relation To Roads. *Journal of Wildlife Management*, *43*(3), 634–641. doi:10.2307/3808741

Rutledge, L. Y., Patterson, B. R., Mills, K. J., Loveless, K. M., Murray, D. L., & White, B. N. (2010). Protection from harvesting restores the natural social structure of eastern wolf packs. *Biological Conservation*, *143*(2), 332–339. doi:10.1016/j.biocon.2009.10.017

Sahlsten, J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., & Dettki, H. (2010). Can supplementary feeding be used to redistribute moose Alces alces? *Wildlife Biology*, *16*(1), 85–92. doi:10.2981/08-085

Schmidt, K., & Kuijper, D. P. J. (2015). A "death trap" in the landscape of fear. *Mammal Research*, *60*(4), 275–284. doi:10.1007/s13364-015-0229-x

Schmitz, O. J., Beckerman, A. P., & O'Brien, K. M. (1997). Behaviorally Mediated Trophic Cascades : Effects of Predation Risk on Food Web Interactions. *Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions*, *78*(5), 1388–1399.

Schmitz, O. J., Hambäck, P. a., & Beckerman, A. P. (2000). Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. *The American Naturalist*, *155*, 141–153. doi:10.1086/303311

Semenič, B. (2009). Studying influence of red deer winter supplemental feeding on place arrangement and damage embracement of forest saplings of Snežnik area.

Sommerfeld, A. (2015). *Is there evidence for wolf-triggered trophic cascades in Dinaric forest ecosystem?* University of Life Sciences.

Soulé, M. E., Estes, J. a., Berger, J., & Martinez Del Rio, C. (2003). Ecological Effectiveness: Conservation Goals for Interactive Species. *Conservation Biology*, *17*(5), 1238–1250. doi:10.1046/j.1523-1739.2003.01599.x

Surina, B. (2002). Phytogeographical differentiation in the Dinaric of the western part of the Illyrian floral province, *61*(2), 145–178.

Van Beest, F. M., Gundersen, H., Mathisen, K. M., Milner, J. M., & Skarpe, C. (2010). Long-term browsing impact around diversionary feeding stations for moose in Southern Norway. *Forest Ecology and Management*, *259*(10), 1900–1911. doi:10.1016/j.foreco.2010.02.002

Van Beest, F. M., Loe, L. E., Mysterud, A., & Milner, J. M. (2010). Comparative Space Use and Habitat Selection of Moose Around Feeding Stations. *Journal of Wildlife Management*, *74*(2), 219–227. doi:10.2193/2009-109

White, C. A., Olmsted, C. E., & Kay, C. E. (1998). Aspen, elk, and fire in the Rocky Mountain national parks of North America. *Wildlife Society Bulletin*, *26*(3), 449–462.

Winnie, J., & Creel, S. (2007). Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Animal Behaviour*, *73*(1), 215–225. doi:10.1016/j.anbehav.2006.07.007

Zuur, A. F., Walker, N. J., Ieno, E. N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer. doi:10.1007/978-0-387-87458-6 e-ISBN

Online sources:

Statistical Office of the Republic of Slovenia :http://www.stat.si/StatWeb/en/home (23.01.15)

Surveying and Mapping Authority of the Republic of Slovenia : http://www.gu.gov.si/en/ (23.11.2014)

7 Appendix

7.1 Overview Structure of Data and Distances
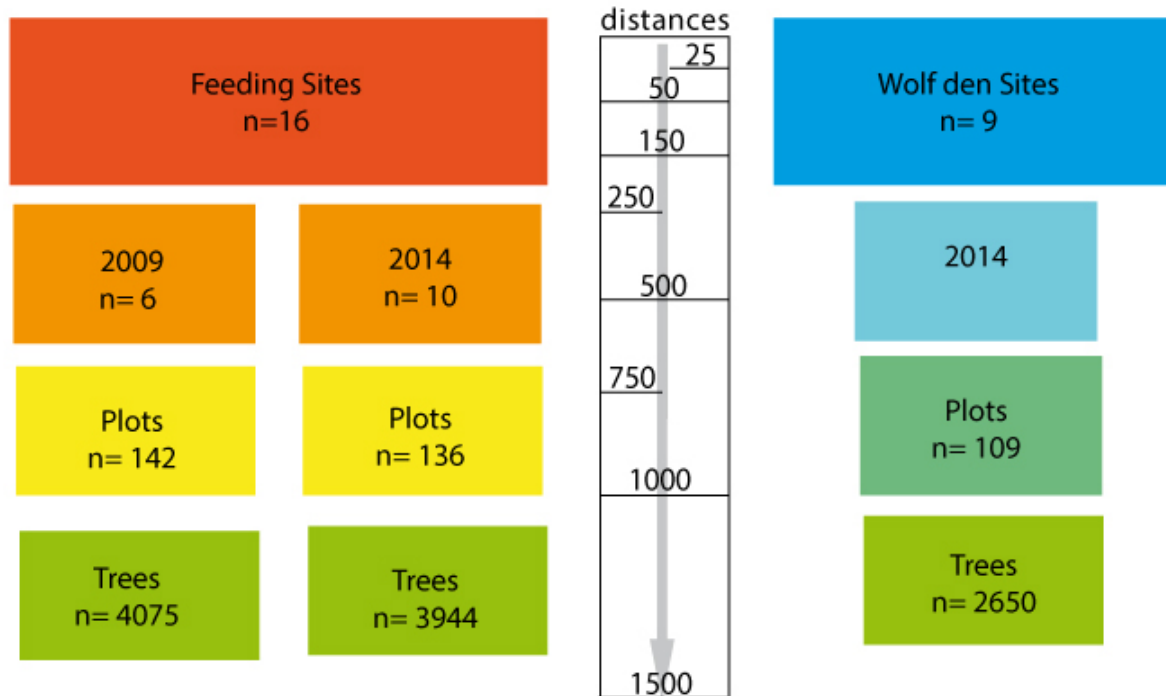
Plots, hunting grounds and feeding sites in South Slovenia

N

Legend

- ▸ SFS Plots 2014
- ● SFS Plots 2009
- ● Den Plots 2014
- ▸ All Red Deer SFS

hunting ground

Overview entire Slovenia
yellow= investigated regions

0 2,5 5   10   15   20
Kilometers
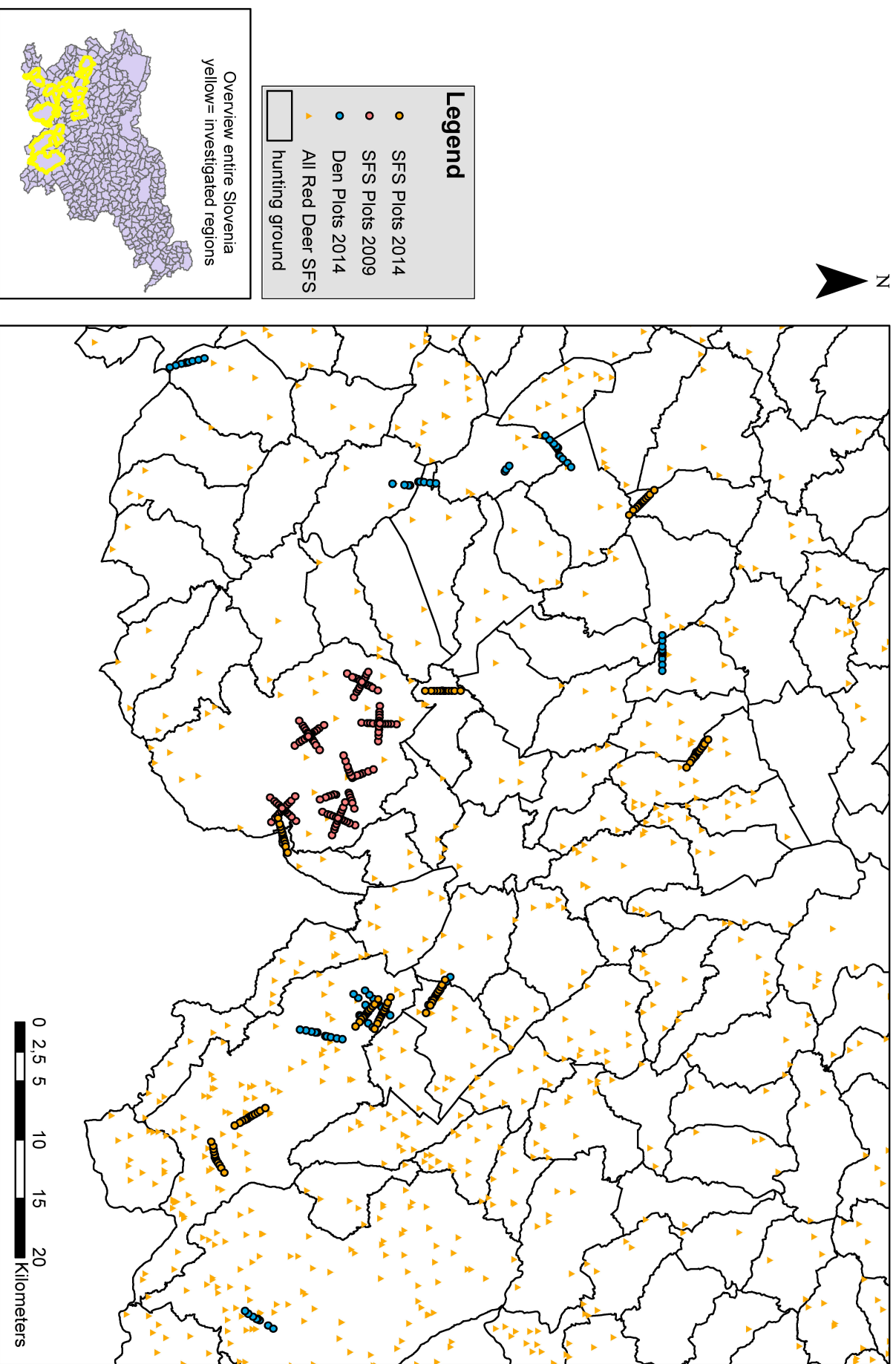
7.3 Overview variables

7.3.1 Summary of variables used in feeding sites analysis

```
      canopy              slope          dist_forestedge   dist_forestroad
 Min.   : 20.00     Min.    : 0.00    Min.    : -35.0    Min.    :   3.58
 1st Qu.: 60.00     1st Qu.: 8.00     1st Qu.: 150.0     1st Qu.:  68.86
 Median : 70.00     Median :15.00     Median : 416.0     Median :145.88
 Mean   : 70.89     Mean   :14.03     Mean    : 473.9    Mean    :199.79
 3rd Qu.: 90.00     3rd Qu.:20.00     3rd Qu.: 691.0     3rd Qu.:287.32
 Max.   :100.00     Max.    :37.00    Max.    :2004.0    Max.    :937.84


   dist_settlement     forestcover       perc_conifers         snow
 Min.   :   70.21   Min.    :0.7200    Min.    :0.1000    140-200:  841
 1st Qu.:1020.72    1st Qu.:0.9100     1st Qu.:0.5500     200-280:6204
 Median :1763.42    Median :0.9700     Median :0.6700     280-420:  809
 Mean   :1955.01    Mean    :0.9411    Mean    :0.6358
 3rd Qu.:2693.64    3rd Qu.:0.9900     3rd Qu.:0.7400
 Max.   :4986.71    Max.    :1.0000    Max.    :0.9500


      red_dd             roe_dd            nxt_SFS
 Min.   :0.0597    Min.    : 0.309    Min.    :  31.72
 1st Qu.:2.0635    1st Qu.: 4.554     1st Qu.: 249.74
 Median :3.3745    Median : 8.345     Median : 510.66
 Mean   :3.6173    Mean    :10.154    Mean    : 645.26
 3rd Qu.:5.0083    3rd Qu.:12.698     3rd Qu.: 999.66
 Max.   :8.0984    Max.    :38.975    Max.    :1999.68


 g          year       hunt          wolf2
 h:5163    9 :4038     local:2484    0:3623
 l:2691    14:3816     state:5370    1:4231
```

7.3.2 Summary of variables used in den sites analysis

```
       slope              canopy          dist_forestedge   dist_forestroad
 Min.   : 1.00    Min.   :  0.00    Min.   : -50.0    Min.   :    4.98
 1st Qu.:11.00    1st Qu.: 50.00    1st Qu.: 182.0    1st Qu.:  89.32
 Median :15.00    Median : 70.00    Median : 403.0    Median : 165.23
 Mean   :16.48    Mean   : 61.15    Mean   : 599.1    Mean   : 239.81
 3rd Qu.:21.00    3rd Qu.: 80.00    3rd Qu.: 760.0    3rd Qu.: 358.53
 Max.   :33.00    Max.   :100.00    Max.   :2620.0    Max.   :1007.27


 dist_settlement    forestcover       perc_conifers        dist_DEN
 Min.   : 358.1    Min.   :0.6756    Min.   :0.000    Min.   :   24.31
 1st Qu.:1007.4    1st Qu.:0.8325    1st Qu.:0.310    1st Qu.:   50.23
 Median :1369.6    Median :0.9558    Median :0.480    Median :  151.10
 Mean   :1687.1    Mean   :0.9027    Mean   :0.442    Mean   :  535.97
 3rd Qu.:2343.0    3rd Qu.:0.9864    3rd Qu.:0.600    3rd Qu.: 1000.20
 Max.   :3184.2    Max.   :0.9977    Max.   :0.740    Max.   : 1534.97


 snow             roe_dd           red_dd           nxt_SFS
 100-140:  20    Min.   : 0.570    Min.   :0.4740    Min.   :   64.36
 140-200: 128    1st Qu.: 3.560    1st Qu.:0.9427    1st Qu.:  516.77
 200-280:1781    Median : 4.330    Median :1.5817    Median :  651.82
 280-420: 261    Mean   : 8.814    Mean   :1.8797    Mean   :  865.71
 60-100 : 138    3rd Qu.: 8.200    3rd Qu.:2.5218    3rd Qu.: 1031.46
                 Max.   :51.720    Max.   :3.7783    Max.   : 2941.07


  group
 high:1651
 low : 677
```

7.4 Browsing Census Sheet

CODE (Site-Transect-Distance): ……………………………… □ wolf den* □ feeding site

Researcher(s)…………………………………………… Date…………………………………

Terrain:……………………………………………………………………….……………

Surface measured (no. of repetitions)………… Incline(°)…… Exposition…………

% plot surface cover by: classes: 0 1 2 3 4 5 10 20 30 40 50 60 70 80 90 100%

Herbaceous plants: ……% Rocks: ……% Large trees and roots: ……% Dead wood: ……%

Canopy cover: visual estimate: ……% Photo-ID:…………

Remarks:……………………………………………………………………………………

Observed signs of presence: □ wolf □ red deer □ roe deer □ bear

Tree species	BI	Germs	<30cm	30-50cm	50-150cm	150-200cm	% plot surface covered with saplings
Fagus sylvatica	1						
	2						
	3						
Abies alba	1						
	2						
	3						
Picea abies	1						
	2						
	3						
Acer pseudoplatanus	1						
	2						
	3						
Sorbus aucuparia	1						
	2						
	3						
Shrubs	1						
	2						
	3						
	1						
	2						
	3						
	1						
	2						
	3						

BI – Browsing intensity: * measure visibility at wolf dens

1: max. 10% shoots damaged, bur NOT damaged terminal shoot

2: max. 50% shoots damaged and/or damaged terminal shoot

3: >50% shoots damaged and damaged terminal shoot