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Exploring the Impact of Contextual Variables on the Temporal Variability of Grazing and Risk Avoidance Patterns of Red Deer (*Cervus elaphus*) in an Alpine Environment

Master Thesis – Geo 511

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Summary

The behaviour of red deer (*Cervus elaphus*) is largely determined by a trade-off between foraging and predator avoidance. Predator avoidance frequently manifests itself in the use of both structural and non-structural cover, which conceals the prey from the predator. In a heterogeneous landscape, the spatial distribution and availability of these elements of cover are subject to change over time, especially when migratory movements are considered.

In this thesis, the importance of this trade-off is investigated by linking the space use of red deer in the Lower Engadine valley of Switzerland to contextual variables. To this end, the migration patterns of 16 red deer were first investigated by combining Minimum Convex Polygons (MCPs) and Kernel Density Estimation (KDE), which provided the basis for further inspections. Subsequently the temporal variability of diurnal activity levels were investigated by means of crepuscularity and diurnality indices and linked to the ecology of deer. The temporal variability of the importance of structural and non-structural cover was analysed mainly in relation to forested areas and shrublands, which constitute a crucial habitat characteristic for red deer. Lastly in relation to grazing activity, the spatio-temporal patterns of locations were investigated at core grazing sites and analysed with respect to forage quality and risk avoidance strategies.

Results showed, that the extent of migratory movements of the studied individuals varied greatly, supporting the notion that migration is a phenomenon that should be placed on the resident-migratory continuum rather than classified in a binary fashion. The exploration of annual variations in activity levels showed a distinct preference of crepuscular activity which persisted throughout the year. Diurnal activity showed much greater annual fluctuations, with a general preference of night-time activity in spring, autumn, and winter and a daytime preference in summer months. The possibility of anthropogenic influences on diurnal activity patterns are discussed. The central importance of forested areas and shrublands as elements of cover were largely confirmed, though their importance varies both in the course of the year and at different times of the day. The decrease in preferential selection of forests found in summer months is most likely linked to intensified foraging behaviour in open landscapes and a decrease in human disturbance in mountainous regions. On the other hand, a decrease in preferential selection of shrublands in winter was sought to be related to declining forage availability due to snow cover. Investigation of grazing activity showed that at sites associated with winter home ranges, positions in open landscapes occurred mostly during the hours of darkness, providing indications of human disturbance influencing the behaviour of deer. At such sites associated with summer home ranges, the risk avoidance strategies seem to manifest themselves in an increased distance to hiking trails during the day, as the higher quality forage was of mountain pastures was typically only accessed during the night. Results further suggest that red deer do not seek areas which are invisible from hiking trails during the day.

Acknowledgements

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For his help and support with all aspects relating to remotely sensed data, I am indebted to Dr. Rogier de Jong from the remote sensing department of the University of Zurich. He was kind enough to lend me a helping hand when struggling to find suitable remote sensing data.

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1 Introduction

1.1 Motivation

Despite the red deer being part of the indigenous fauna, its history in the Lower Engadine valley and the Swiss National Park (SNP) is marked by overhunting and seemingly complete eradication in the 19^{th} century followed by periods of regeneration and repopulation following partial or complete hunting bans. However, since the end of the 19^{th} century the population has steadily increased in the entire Canton of Grisons, thanks to emigrant deer from surrounding valleys (Haller 2002). In 2015, the spring population before the annual reproduction in the Canton of Grisons alone reached approximately 16'000 individuals (see Figure 1), not lastly as a consequence of the warm winters with little snow of the past couple of years. These numbers are merely estimations that are based on spotlight counts carried out towards the end of April, cohort analysis and additional methods. Though a large population of red deer may seem desirable from a conservation biologist's perspective, once a certain density level of ungulates is reached, the impact they have on their vegetational environment, both wild and cultivated, is not to be underestimated (Putman 1996). Arguably the most serious damage to forest ecosystems is the damage to the bark of trees, which deer feed on for their rich nutrient, vitamin and water supply. The resulting bark stripping damage leaves trees susceptible to infestations with wood decaying fungi and ultimately alters the structure of the forest (Vospernik 2006). It is typically trees between 7 and 20 years old that are affected most by bark stripping (Mitchell et al. 1977). Whilst bark stripping does occur in the

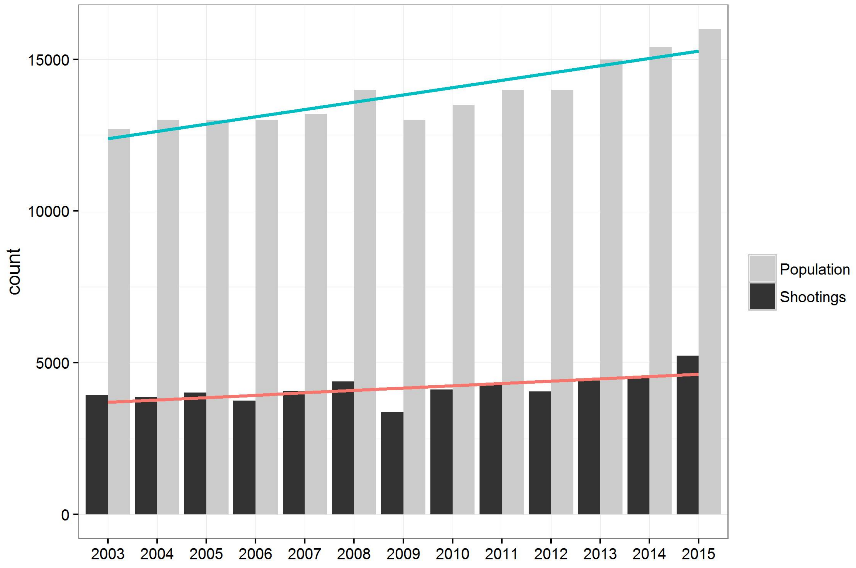

Figure 1: Development of red deer population since 2003 and number of reported shootings in the Canton of Grisons. Based on spotlight counts (Eidgenössische Jagdstatistik).

Canton of Grisons, problems relating to the natural regeneration of woodlands are much more prominent (Suter 2005), as deer also feed on young trees and bushes. Already in the 1970s it was observed, that within the SNP, the optimum number of red deer had been exceeded, which was assumed to be the cause for declining numbers of chamois and roe deer (Voser 1987). This exemplifies the importance of the SNP as a game reserve. Nonetheless efficient management solutions are required as indications have shown that the density of red deer is above the carrying capacity (Wagenknecht 1996, Amt für Jagd und Fischerei 2015). To effectively regulate the red deer population the Office for Hunting and Fisheries of the Canton of Grisons (AJFGR[1]) devises an annual hunting plan, specifying the number of red deer that are to be culled during the hunting season (Jenny et al. 2011). The aim is to harmonize both the preservation of a healthy red deer population in the alpine environment and the conservation of woodlands and agricultural areas. To gain knowledge about the space use of red deer in the Lower Engadine valley and surrounding areas, the SNP and the AJFGR made use of recent technological advances and in a joint effort equipped a number of red deer with GPS collars in the spring of 2015.

The turn of the millennium marked the rise of GPS based biotelemetry methods, which opened up numerous opportunities for researchers in various fields of science (see Tomkiewicz et al. 2010). Particularly in animal ecology, GPS technologies would go on to replace outdated data acquisition methods. Previously, triangulation techniques were applied to derive locations through the use of very high frequency (VHF) tracking (see Georgii 1981; Georgii & Schröder 1983), meaning that the animal was equipped with a transmitter which sent out radio signals for the researcher to detect with radio receivers. The major drawback of this system was that the researcher had to get close enough to the animals to get a location estimation which may in turn have affected the behaviour of the animal (Cagnacci et al. 2010). Further, the natural environment of the animal may not have allowed the researcher to monitor the animal for a prolonged and continuous period of time. With the emergence of GPS technology and in particular the suspension of selective availability – a system applied by the military in the 1990s that degraded the accuracy of GPS locations for non-military purposes (Tomkiewicz et al. 2010) – many of the problems of VHF tracking have been remedied. GPS technology allowed the user to reduce sampling intervals down to seconds and to remove the necessity of the observer to be present while sampling. Positional accuracy and precision are greatly increased and for the first time it became possible to remotely track animals in challenging environments (Hebblewhite & Haydon 2010). Finer temporal resolutions in turn allowed researchers to investigate movement patterns that can only be observed on small temporal scales, such as sudden migrations or flight responses.

However, the other side of the coin is the trade-off researchers now face between high sampling rates and battery life (Frair at al. 2010; Pépin et al. 2004; Walter et al. 2011). Depending on the

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[1] Amt für Jagd und Fischerei Graubünden

questions researchers aim to answer, the sampling rate is set to suit these needs. For instance, if the aim is merely to conduct a home range[2] analysis a coarser sampling rate of a couple of hours should suffice, especially given the multitude of home range estimation techniques that have emerged in the last couple of decades. If, on the other hand, the aim is to detect small scale behavioural patterns that are unique to the studied species, the sampling frequency must be set accordingly, which in turn compromises the length of the sampling period and increases the risk of oversampling at resting sites when the animals remain inactive. Brown et al. (2012) consequently proposed the utilization of what they call accelerometer-informed GPS telemetry. This technique continuously adapts the sampling rate based on the information provided by an accelerometer, allowing for shorter sampling intervals when the accelerometer data indicates that the animal is active and vice versa.

All these considerations relate to studies, where the data collection process has not yet been finalised and can still be influenced by the researcher. The costs of gathering GPS data are still considerably higher than most alternative methods, mainly due to the cost of the collars (Hebblewhite & Haydon 2010). It is therefore worth examining how questions that were not initially posed and would have required a different sampling rate, can be answered using contextual information and simplified assumptions about the activity of an animal. To reduce costs, it could be worthwhile to consider re-evaluating older data to retrieve valuable information and insights for management or conservation strategies in ecology.

What is meant by contextual information is information from various sources that can be attributed to GPS locations. Such sources may include remotely sensed data, data derived from remotely sensed data (e.g. landcover data, digital elevation models, aspect, slope), meteorological data, and data relating to the infrastructure of the study site (e.g. roads, urban areas).

1.2 Research Questions

This thesis focuses on the detection of temporal variation of behavioural aspects of the red deer in a Swiss alpine environment which relate to the main driving forces in the ecology of red deer, namely the need for cover and foraging activity. Specifically, the temporal changes in the importance of various factors relating to the necessity of cover are investigated. The following research questions will be addressed throughout this thesis:

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[2] Definition by Burt (1943, p. 351): 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.'

1. What are patterns and the extent of seasonal migration observed in the individuals studied?
2. How do the seasonal variations in diurnal activity budgets relate to ecology? Are there indications of increased human disturbance?
    a) Can evidence of hunting periods be found in the activity data?
3. Which ecologically meaningful conclusions relating to the driving forces of red deer ecology can be derived from contextual information?
4. Can evidence of predator avoidance be found in the spatio-temporal distribution of locations at potential grazing sites?

To answer research questions 3 and 4, various additional datasets will provide the contextual information. For research question 3, considering the vital importance of woodlands as a habitat characteristic relating both to cover and to the availability of food for red deer in Switzerland, the GPS positions will be analysed mainly in relation to forested areas and the cover that such provide. Research question 4 will focus on locations outside of forested areas (which are assumed to be associated with foraging behaviour) and analysed using contextual information provided by Normalized Difference Vegetation Index (NDVI) and visibility maps.

This thesis can be seen as an extension to the Project Raetikon (Reimoser et al. 2014), a similar project which was carried out close to the research area in the border triangle of Switzerland, Liechtenstein and Austria. The aim was to devise management solutions that consider both impacts of red deer on a regional scale and cross-border movements of red deer.

At this point it must be noted that the increased monetary cost associated with gathering data via GPS biotelemetry, and the time-consuming task of capturing the deer in order to attach the collar implies that fewer animals can be intensively tracked. In this study, 16 individuals were tracked for a little under one year (with the project still ongoing, however). Therefore, statistically significant inferences about the behaviour of the entire population in the study area cannot be drawn from this study. Nonetheless, the methods proposed in this thesis could be transferred to a sister project which is currently being carried out jointly by the Canton of Grisons and the neighbouring Canton of Ticino (Hirschwanderungen im Grenzgebiet Graubünden-Tessin werden untersucht, 2014).

1.3 Thesis Structure

The thesis is structured as follows. Given the interdisciplinary nature of this thesis, I will first review related work on the ecology of the red deer and enlarge upon the most relevant aspects with respect to the need for cover and foraging activity. Subsequently, the methods and concepts of geographic information science will be outlined, referring both to methods which are applied in this thesis as well as alternatives. Chapter 3 deals with the study area and the data used for the analysis, pre-processing steps and the limitations of the data. The methodology is outlined in Chapter 4 with subchapters ordered according to the order of the research questions. Results and discussion are addressed separately for each research question in Chapter 5. Finally, results are synthesised in Chapter 6 by addressing the findings of each chapter and linking to the research questions.

2 Theoretical Background and Related Work

This chapter will first give an overview of red deer ecology with a strong focus on diurnal and seasonal activity cycles. Subsequently, the applied methods and concepts relating to home range estimation and geographic information science will be outlined. Although this thesis does not constitute a home range study per se, some traditional home range and utilization distribution estimators play an important subordinate role in the classification of migration behaviour and the analysis of resource preference. Lastly, insights into the ecological concepts relevant to this study will be provided. Throughout this chapter, related work will be presented and discussed.

2.1 Red Deer Ecology

Given the absence of activity data, it is crucial to understand the ecology of red deer in order to derive information from context variables. The following section provides a summary of the most important aspects of red deer ecology in relation to activity cycles, foraging behaviour and the importance of cover. Red deer (Figure 2) have been the focus of numerous studies in the past decades, though the most important and influential work on red deer ecology, population dynamics, and genetics emanates from a research project on the Isle of Rum, a small island on the west coast of Scotland. Research on the island dates back to 1953 and aided the publication of one of the most extensive books on red deer behaviour and ecology by Clutton-Brock et al. (1982) titled *Red Deer: Behaviour and Ecology of Two Sexes*. This commonly cited work deals with

Figure 2: Red deer stag and hind with young. Fotographed by Hans Lozza, Swiss National Park.

numerous aspects relating to the ecology of red deer and draws up differences between the sexes in relation to activity budgets, rutting behaviour, and grazing patterns. More recently, similar publications have appeared — albeit in a lot less detail — dealing with red deer in central Europe and the Alps specifically, as the habitat characteristics differ greatly from those of the Scottish islands (Bützler 2001; Wagenknecht 1996).

The red deer (*Cervus elaphus*) is among one of the largest wildlife species in central Europe, though their size and weight is a function of climate, altitude, habitat, and racial differences. Within Europe, their size and weight generally increases from west-north-west in east-south-easterly direction. Furthermore, fluctuations occur during the course of a year, with weight reaching a maximum shortly before the rut in mid-September (Mitchell et al. 1977). In Switzerland, adult stags can weigh anywhere between 140 and 220kg, while females weigh around 1.5 times less (Clutton-Brock et al. 1982). The shoulder height and body length can reach up to 150 cm and 210 cm respectively. The reddish-brown summer coat is what gave the red deer its name, though this too is subject to change. In winter the coat is typically brown to grey and hairs are roughly twice as long as those of the summer coat. The change of coat occurs in late April and September. Undoubtedly the most prominent morphological feature of male red deer are their antlers. They start growing in spring and are shed approximately 6 months later. Although their function is not fully understood at this point, it can be said that they serve as a weapon during the rutting season to prove dominance over other male deer and secure a harem (Wagenknecht 1996).

Red deer live in groups, segregated by sex, whereby the degree of segregation varies considerably between populations throughout Europe. The basic unit for female groups consists of a matriarch, her daughter, and their offspring, though the total composition of the groups is somewhat unstable and may change within only a couple of hours. Different groups can share a portion of their home range and merge temporarily (Mitchell et al. 1977). Similarly, stags only spend the first couple of years in groups with their mother, before leaving to join groups of other stags (Clutton-Brock et al. 1982). Obviously, this segregation is suspended during the rutting season which takes place between mid-September and mid-October in the Alps.

2.1.1 Daily Activity Cycle

For the most part, the behaviour of red deer is determined by digestive processes, meaning that a typical day is characterized by repeated cycles consisting of periods of grazing, social interactions, and resting. Grazing typically lasts for anywhere between 30 minutes and 2.5 hours (Wagenknecht 1996; Bützler 2001), and in total accounts for roughly 50% of activity during daytime and around 15 – 30% during night-time, though these numbers are also subject to seasonal variation (Clutton-Brock et al. 1982).

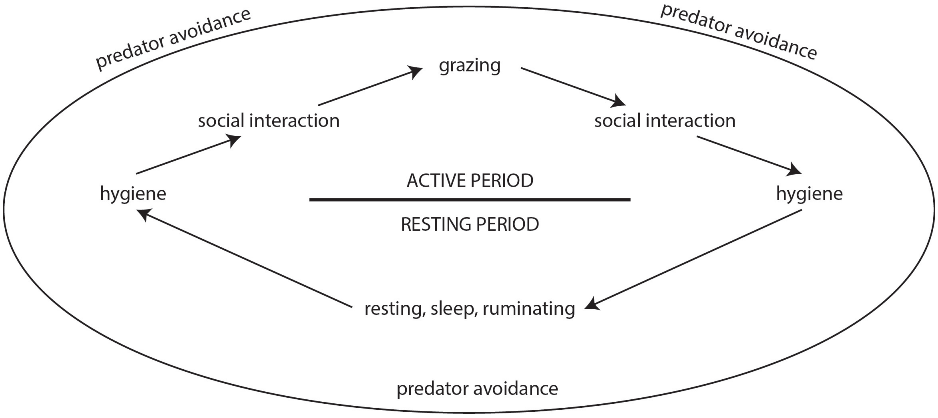

Figure 3: Schematic representation of the activity cycle of red deer (Bützler 2001).

Figure 3 illustrates the activity pattern for red deer which dominates the course of a day. According to Bützler (2001) it begins with grooming and hygiene, followed by social interactions with other members of the herd. Thereafter the herd moves to grazing sites, typically in a single line formation. Once the grazing period is over the cycle is inversed and the herd returns to the resting site, where they maintain social interactions and focus on grooming and hygiene before returning to a state of rest. During resting periods, the actions of the herd are primarily limited to sleeping, dozing and ruminating. Clutton-Brock et al. (1982) found that reed on the island of Rum in Scotland typically fitted around four to six cycles into the daylight hours during summer and around three at night. Hence, resting can account for up to roughly 50% of their annual time budget (Adrados et al. 2008). The necessity to fit multiple grazing bouts into one day at more or less regular intervals stems from the requirement of a constant state in the rumen, which allows for the utilization of foodstuffs by the micro-organisms (Mitchell et al. 1977). Generally, activity (i.e. the length of activity bursts and the number of activity bursts) is highest during the twilight hours for both female and male animals in the alps, resulting in a distinctly bimodal activity pattern (Georgii & Schröder 1983). This crepuscular activity profile has been found in several other ungulate species though interestingly, Ensing et al. (2014) found red deer in Alberta, Canada to prefer diurnal activity while red deer in the Netherlands showed a distinct preference for nocturnal activity. Furthermore, red deer in the Netherlands were most active during the winter months, which is likely due to increased human disturbance in summer. Also, red deer in mountainous regions tend to climb to slightly higher altitudes during the day and return for the night (Merker 1995). This daily variation in elevation is likely caused by increased human activity in the valley and/or harassment by insects during the summer months[3].

Being a flight animal, predator avoidance plays an important role in the behaviour of red deer. Resting places are chosen such that they are in proximity of the main grazing site and offer suffi-

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[3] Personal communication with Hannes Jenny AJFGR, 02.12.2016.

cient cover against sightings by predators and harsh weather conditions (Bützler 2001). Further, Adrados et al. (2008) showed that visibility at resting places exhibited considerable variations between night and day, with concealment during the day exceeding concealment during the night. Predator avoidance also expresses itself in the vigilance behaviour of red deer, which increases as vegetation cover decreases but also as human disturbance increases. Figure 3 clearly demonstrates that the two main drivers of red deer behaviour are food and safety.

2.1.2 Annual Activity Cycle

In order to adapt to the annual variations in environmental factors such as temperature, snow depth and the availability of food, the behaviour and energy metabolism of red deer is subject to great change over the course of the year. As a migratory mammal, red deer in the Alps typically spend the summers in the mountains until the first closed snow cover has formed. To cope with these harsh conditions, they migrate down to lower altitudes and spend the winters in the more sheltered environments in the valleys below the tree line (Mysterud et al. 2011; Jarnemo 2008). This seasonal movement pattern results in the establishment of two distinct home ranges, a summer and a winter home range. The red deer typically frequent the same home ranges each year. This habitual movement pattern is usually transferred from the hinds to their offspring, which ultimately results in high concentrations in certain areas (Voser 1987). It must be noted that not all individuals exhibit this seasonal migration pattern but rather remain resident throughout the year (Reinecke et al. 2014; Schmidt 1993). Georgii & Schröder (1983) examined home ranges for red deer in the Alps and found the distance between summer and winter home ranges to be around 2.5 km on average, though distances of up to 25 km can occur in extreme cases. Furthermore, home range sizes were found to be significantly smaller in winter when compared to summer, though large differences among the individual animals were found. Also, most deer exhibited high home range fidelity as the seasonal home ranges only changed very slightly from year to year.

The answer to the question as to why red deer migrate back up to higher altitudes in summer remains disputed. Mysterud et al. (2011) explored the possibility of migration movements being caused by increased competition in winter home ranges as a result of growing population density. Even predation risk avoidance, despite the frequent absence of any natural predators in the area, has been named as a possible trigger for migration (Mysterud et al. 2011). However, the most commonly cited hypothesis is that the deer seek to feed on the crude protein rich grasslands which has been found to be positively related to altitude in summer and becomes available as the snow melts (Albon & Langvatn 1992). This hypothesis is commonly referred to as the forage maturation hypothesis.

The rutting season starts around mid-September, depending on factors such as photoperiod, odour from the hinds or past experiences (Clutton-Brock et al. 1982). It is the older animals that first move to the rutting ground, which is typically characterized by a more or less open area where deer typically graze (Wagenknecht 1996).

2.1.3 Foraging Behaviour

Throughout the year, the intensity of food intake varies strongly (see Figure 4), depending on the availability of quality forage, the age, and breeding condition of the deer (Mitchell et al. 1977). Especially lactating deer tend to eat more than twice their maintenance requirements (Clutton-Brock et al. 1982). As the snow melts in spring the intensity of food intake increases to a high around June and July, due to the increased energy demands caused by the growth of the foetus and milk production for females and, to a lesser extent, the growth of antlers for males. Concurrently, they build up fat reserves for the tiring rutting season, as grazing is reduced to a minimum during this time and deer lose up to 35% of their body weight (Mitchell et al. 1977). Once the rut is over, the intensity of food intake increases to its annual maximum in preparation for the winter. Further, their metabolism is geared toward storing energy provisions for winter (Wagenknecht 1996), as the snow cover reduces the availability of quality forage and grazing activity is reduced drastically. Arnold et al. (2004) suggested that the reduction of energy expenditure is linked to nocturnal hypometabolism. The reduction of grazing activity is also assumed to be linked to lower digestibility of winter forage. Despite the decrease in available forage in winter months in the alps, the seasonality has been shown to persist, even when forage is abundant. Seasonality seems, therefore to be a function of day length (Mitchell et al. 1977).

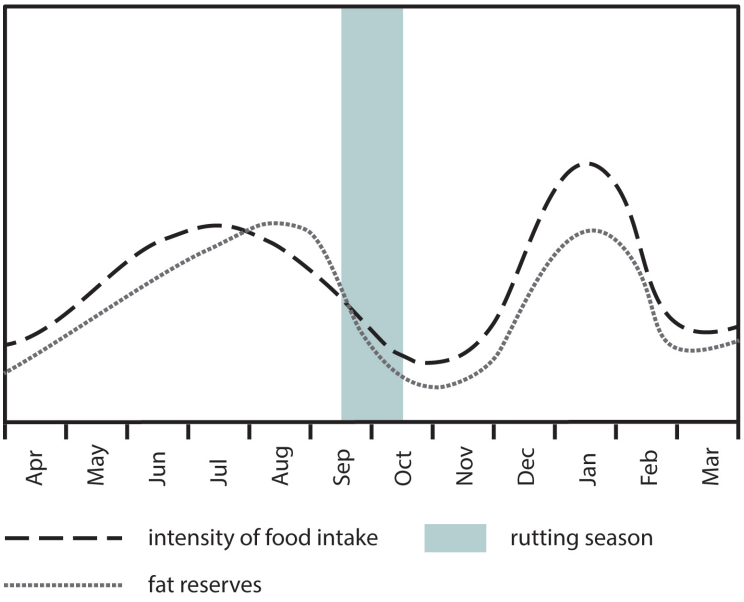

Figure 4: Annual variation of intensity of food intake and fat reserves (adapted from Wagenknecht 1996).

Crude protein is considered to be the key substance related to the growth of red deer and is synthesized through the ingestion of nitrogen rich vegetation. The nitrogen content of a plant can range from anywhere between 0.03 and 7% of dry weight, requiring mature red deer to consume 8-20 kg of nourishment per day, depending on the nutrient content (Mattsen 1980). Gebert & Verheyden-Tixier (2001) showed that the diet of red deer is highly dependent on environmental factors relating to habitat and season by identifying three diet types. While complementary food types such as bark, twigs, forbs, fruits and seeds showed considerable variation throughout the year and between habitat types, an important component of red deer diet, namely grass and sedges, remained relatively constant across seasons.

Red deer are known to frequent different grazing sites within their seasonal home ranges during the course of a day. Those visited during the day are typically forest meadows, grasslands within light forests, or shrublands. Those visited during the night on the other hand are typically associated with higher quality forage and are not necessarily characterized by the availability of cover (Bützler 2001).

2.2 Home Range Analysis and Other Spatial Operations

2.2.1 Minimum Convex Polygon (MCP)

Numerous statistical and mechanistic models for home range estimation have emerged as a result of ever growing data sets in animal ecology. While statistical models are based solely on empirical data, mechanistic models aim to incorporate the nature of the animals use of space and movements in order to assign meaning to the various locations within the home range (Kie et al. 2010). Not belonging to either of these categories, yet still having enjoyed tremendous popularity in home range estimation is the minimum convex polygon (Laver & Kelly 2008).

The derivation of minimum convex polygons (MCP), also known as convex hulls, is arguably the simplest method to estimate home range size. They do not take the underlying density of points into account but merely enclose all locations by connecting all outer locations (see Figure 5), under the constraint, that the internal angles at the nodes must not exceed 180° (thus the name convex polygon). Further, one can define, as a percentage, how many points should be contained by the polygon. Typically, for the definition of home range boundaries and size, the outermost 5-10% percent of relocations are omitted from the computation (Moorcroft & Lewis 2006). This allows, to a certain extent, for the exclusion of what Burt (1943) refers to in his famous definition of a home range as "occasional sallies", i.e. excursions out of the boundaries of the home range which are not considered to be part of the home range. The main advantage of this method is

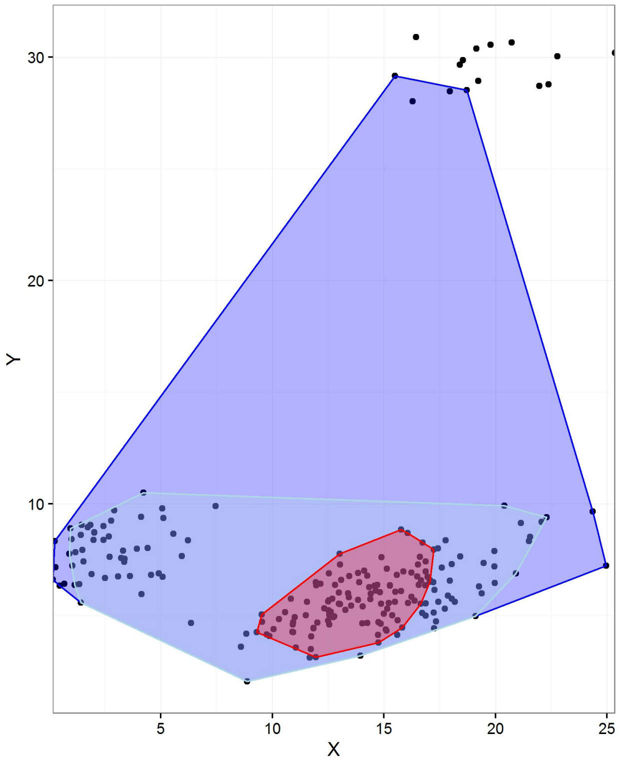

Figure 5: Representation of minimum convex polygon for simulated data. The dark blue area represents the 95% MCP, the light blue area the 80% MCP, and the red area the core home range (50% MCP).

that it allows for a quick and easy definition of home ranges with no *a priori* knowledge of the distribution of locations. Disadvantages include the uninformative nature of the polygons in that they do not allow for any inferences to be drawn about the intensity of space use within the home range, and the sensitivity to outliers (Laver & Kelly 2008). Furthermore, MCPs are highly sensitive to sampling intensity in that low sampling frequencies produce unreliable home range estimates (Kolodzinski et al. 2010). With these considerations in mind, it is unsurprising that Nilsen et al. (2008) advise against the use of MCPs for home range studies where the size of the home range is of primary interest, but argue that MCPs should not be disregarded as tools for deriving meaningful ecological conclusions.

2.2.2 Kernel Density Estimation (KDE)

Kernel density estimation has become one of the most frequently used estimators for utilization distributions in home range analysis and ecology (Fieberg 2007). It has been previously shown that kernel methods can provide more accurate estimations of home range size and shape, not lastly thanks to the 3-dimensional representation of home ranges (see Figure 6), with the z axis corresponding to the density of points in a specific area (Seaman et al. 1999). The computation of a density surface further allows for the extraction of areas corresponding to a given percent-

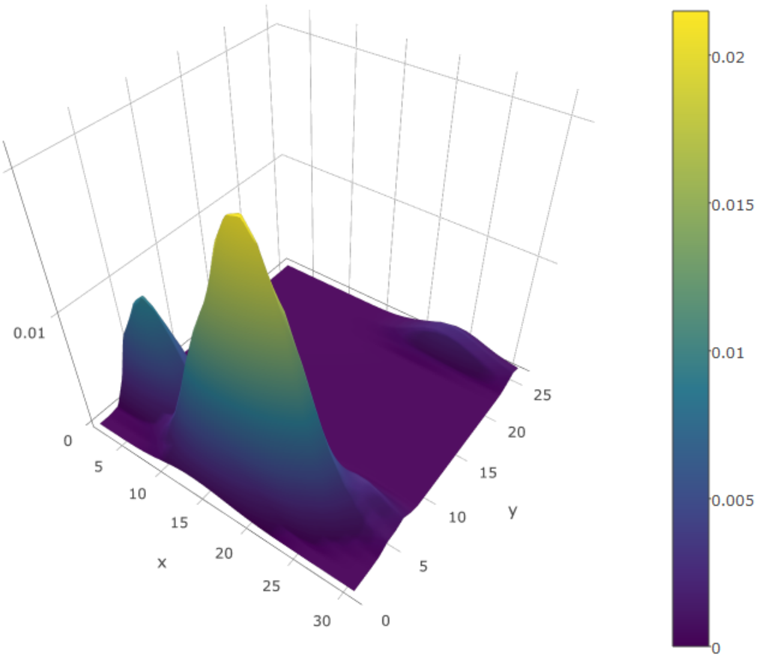

Figure 6: Representation of the Kernel Density Estimation technique. Using the same simulated data as in Figure 5. The surface represents the underlying distribution of points.

age of the total distribution, known as volume contour lines. For instance, to estimate the total home range, it is common practice to use the 95% volume contour line, while for the estimation of core home range areas 50% volume contour lines are seen to best represent areas of intense use, though this may vary between species (Karns et al. 2012). From a biologist's perspective, the core area is thought to be the part of the animal's home range, which is most important to it (Boitani & Fuller 2000). Despite the popularity of KDE, the recent advent of GPS-based telemetry studies has raised concerns relating to the suitability of KDE for the high sampling frequencies that characterize GPS-based telemetry studies when compared to the traditional VHF methods. Several functions have been developed over the years to estimate the optimal smoothing parameter, the most prominent of which include the reference function (h_{ref}) and least-squares cross validation (h_{LSCV})(Gitzen et al. 2006). Both methods aim to simplify the underlying density of points by a smooth surface and inevitably introduce a certain amount of error (Fieberg et al. 2010). While h_{ref} is known to over-smooth the home ranges (Hemson et al. 2005; Walter et al. 2011) h_{LSCV} has been known to fail when the distribution of GPS locations showed a "very tight cluster of points" (Gitzen et al. 2006; Hemson et al. 2005; Kranstauber et al. 2012). Coincidently, this highlights another issue of KDE in biotelemetry. Home ranges, by definition, are constructed of autocorrelated movement (Otis et al. 1999), as animal's movements are not random but can be perceived as patterns of space use or movement (de Solla et al. 2010). In other words, the distance or area which is reachable by an individual is a function of the previous location, resulting in temporally autocorrelated data. The extent of the temporal autocorrelation depends to a large extent on the sampling interval, with smaller sampling intervals resulting in higher temporal autocorrelation. Because KDE assumes independent data, researchers are somewhat divided on how to address the problem of autocorrelation. While one possibility is the subsampling of data, it is often argued that this not only significantly reduces the sample size but also reduces the biological significance of the analysis and further reduce the total daily movement (de Solla et al. 2010; Frair et al. 2010).

An advancement on KDE is the incorporation of the temporality of tracking data in the approximation of home ranges using Brownian bridges (see Horne et al. 2007). Essentially, home range estimators based on Brownian bridges (e.g. the Brownian bridge movement model) take the elapsed time between two consecutive relocations, the speed of movement (given by a diffusion parameter) and GPS inaccuracy into account to compute the probability of the animal being in a specific area between the two relocations, thus eliminating the effect of autocorrelation. The probability is computed by means of a random walk, resulting in a distinctly bimodal density distribution. Naturally, the probability of an animal being in a specific location is highest at the GPS locations and decreases towards the midway point between the two locations (Buchin et al. 2012). The strength of this new mechanistic approach is that it quantifies the intensity of space use by animals based on its movement paths rather than the density of locations, which lends itself to the characterization and detection of movement corridors or to calculate encounter rates of animals (Kranstauber et al. 2012). In the context of this study, however, I argue that an application of KDE should suffice, given that the focus is much less on the actual movement paths than on the characterization of the locations themselves and their frequency within a given landcover type.

2.2.3 Adding Context to GPS Locations

When embedding GPS locations with context information there are several considerations that need to be taken into account, as outlined by Gschwend (2015). Firstly, the context information can be provided by raster or vector data. While the vector format is commonly used to store categorical data, such as land use, continuous variables are typically stored in raster grids (e.g. digital elevation models). If we are to extract the value of a raster or vector layer, the simplest method is to take the coordinates of the GPS location and treat it as a map pin (see Figure 7, a), meaning that only the value at precisely that location is selected. This may be adequate if the resolution of the grid or vector data is a multiple of the typical GPS error and only the value at a specific point in time is of interest. However, given that a GPS position is only a snapshot in time and the movement of animals between fixes can only be estimated, it may be more realistic to take surrounding pixels into consideration by means of a buffer (b), sector (c), weighting function (d),

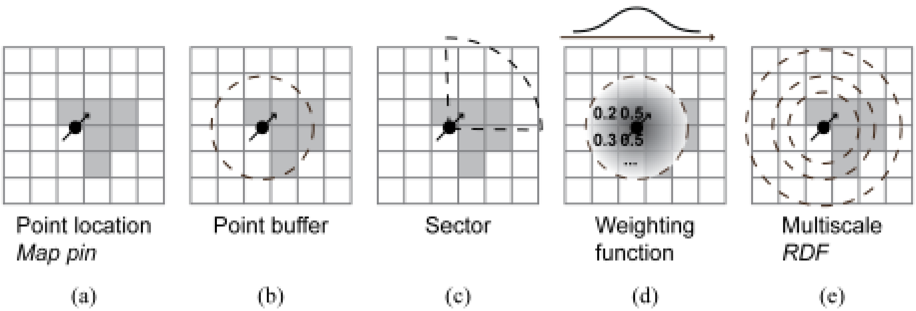

Figure 7: Methods for assigning context information to point locations. Gschwend (2015).

or multiscale rqadial distance functions (e). If we imagine a raster of continuous values, such as a digital elevation model, the point buffer method would take all pixels within a specified radius into account by assigning the average value of all pixels within the buffer to the GPS location. The sector method goes one step further and links the movement direction to the buffer by using only a fraction of the buffer in the direction of travel, given by the previous fix. For the sector method to deliver reliable results, the sampling frequency ought to be small enough to allow for inferences about the actual trajectory of the animal. For certain applications it may be useful to apply a weighting function by making the weighting factor dependent on the distance from the point if the values closest to the point location are assumed to be of greater importance and errors are negligible. Lastly, radial distance functions aim to capture the characteristics of the surrounding environment on multiple spatial scales.

When the contextual information is provided as vector data, much of the above can be applied in an analogous way. For instance, the point location method merely returns the value of the polygon containing that location. The point buffer method would take into account the contribution of the underlying polygons to the buffer and assign the most dominant polygon values to the location.

2.2.4 DBSCAN

DBSCAN (Density-Based Spatial Clustering of Application with Noise) describes an efficient hierarchical clustering method developed by Ester et al. (1996), which is used in this thesis for the detection of potential grazing sites. DBSCAN requires only two input parameters, the *Eps-neighbourhood* and *MinPts*. *Eps* sets a cut off value for similarity in the data while the *MinPts* defines the minimum number of points at which a neighbourhood of points is considered dense. In a first step, the algorithm distinguishes between three types of points. Firstly, a point (p) is considered a core point if its neighbourhood, as defined by *Eps*, contains the minimum required

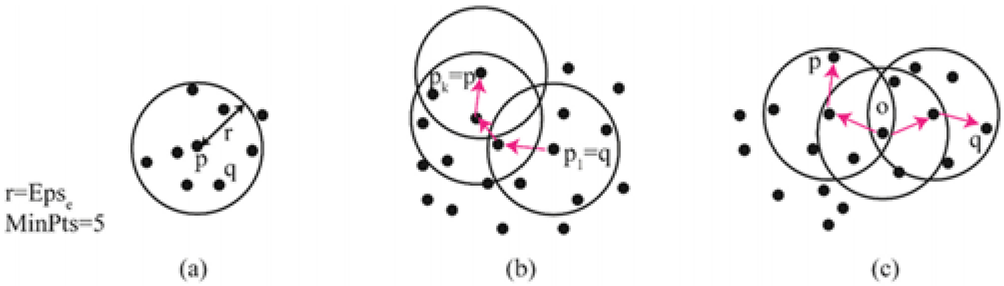

Figure 8: DBSCAN. (a) q is density reachable from p, as it lies within the Eps-neighborhood given by r, (b) p is density reachable from q and (c) p and q are density-connected through o (from Teimouri et al. 2016).

points given by *Minpts* (Figure 8a). In other words, points within the *Eps-neighbourhood* of p are said to be density reachable from p. Similarly, border points (q) are points which contain at least one core point, but less than *MinPts*. Border points must be density reachable from at least one core point but a core point cannot be density reachable from a border point. Lastly, the remaining points are labelled as noise points and represent outliers, i.e. points which do not belong to a cluster (see Figure 8). The resulting clusters can be considered points, which are density-connected.

The most significant advantages of this clustering algorithm include the modest amount of knowledge of input parameters and most importantly the ability to detect clusters of arbitrary shapes. Additionally, not all points are required to be assigned to a cluster thanks to the detection of noise points (Ali et al. 2010).

An adapted DBSCAN algorithm has recently been applied by Teimouri et al. (2016) to detect clusters in both space and time, thus identifying inactive periods in the animal's movement. This technique requires that the sampling interval be small enough to allow for multiple position acquisitions during an inactive period but fails when the sampling interval is greater than the duration of the inactive period.

2.2.5 Viewshed Analysis

Viewshed analysis is a tool which is among the standard operations in most geographic information systems. Its application is manifold, though typically it is used to facilitate decision making based on the factor of visibility (or invisibility) (Fisher 1996).

A binary viewshed computes the area (pixels) that is visible, respectively invisible, from a specified location (Lee 1991). Figure 9 shows a profile representation of a viewshed analysis. The terrain is typically stored in a grid with grid values representing the elevation at each location, though methods based on elevation data stored as triangulated irregular networks do exist (Lee 1991). A line of sight is then drawn between the viewpoints (*observer*) and the midpoint of the surrounding grid cells within a specified radius (*r*). A cell is invisible by the observer if the line

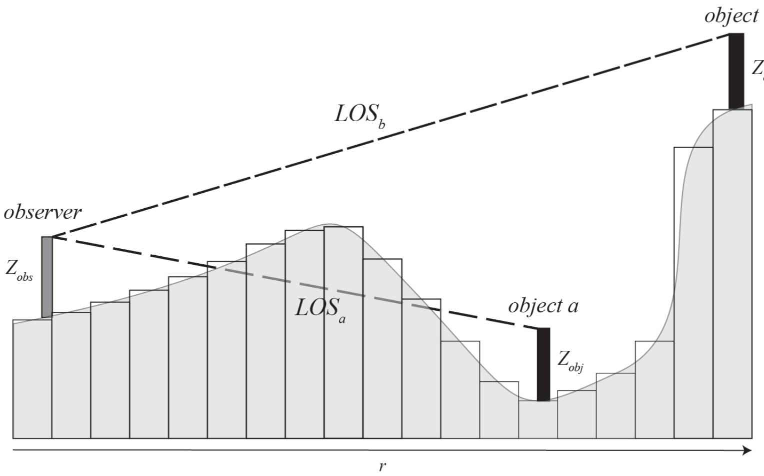

Figure 9: Schematic 2D representation of a viewshed analysis.

of sight is obstructed by the terrain (LOS_a) and visible if there is no obstruction (LOS_b). In other words, a cell is invisible, if the viewing angle of a local horizon between the observer and the cell is greater than the viewing angle of the object itself. Additionally, offset values (Z) can be set for observer and objects to account for observer height and object height. In a three-dimensional setting, the observer is assumed to have sight in every horizontal as well as vertical direction, although these can be limited as well using maximum and minimum azimuth and vertical angles. Maichak & Schuler (2004) recognized the potential of viewsheds for determining optimal census routes by maximizing the total area visible from the routes.

The approximation of topography as a regular grid of given cell size induces a certain amount of error and uncertainty. While uncertainty is not accounted for in the binary viewshed (Ruiz 1997), Fisher (1992) has proposed the incorporation of DEM error in what he calls fuzzy viewsheds. Hereby a specified number of DEMs are created with a certain amount of simulated error added. A binary viewshed analysis is then performed on all the DEMs and resulting grids aggregated to a single visibility map with pixel values indicating how many times the location was visible. Naturally, locations which were obstructed by the simulated error were assigned lower values than such that were not affected.

2.3 Ecological Resources

2.3.1 Classification of Migration

As stated in Section 2.1.2, red deer are commonly known as migratory animals, though the extent to which their seasonal home ranges are disjoint, may vary considerably. The seasonal home ranges can be used to determine whether an individual exhibits migratory behaviour by checking for spatial overlap, though the success rate of correct classification by this method is highly dependent on the choice of seasonal cut-off dates (Cagnacci et al. 2016). Alternatively, a common method used to quantify migration movements is the net squared displacement approach, a measure which describes the displacement (i.e. Euclidean distance) of subsequent relocations from a starting location (see Bunnefeld et al. 2011; Singh et al. 2016). This method allows for the distinction between different modes of movement aside from migration, such as exploratory or dispersal movements, though again, the choice of a starting location is crucial to the successful classification of migration strategies. Furthermore, it is yet unclear how missing fixes affect the result of the net squared displacement method.

Recently, Cagnacci et al. (2016) compared three different methods of characterize these migratory movements by mammalian species, including the two mentioned above and a method based on seasonal clusters. They concluded that regardless of the chosen method, all methods were relatively consistent on the number of individuals classified as migratory on a population level. However, the classification of partial migration was much more inconsistent and varied widely across methods.

2.3.2 Jacobs Index

Originally developed as a quantitative measure of food selection in ecology, the Jacobs index (1974) compares the relative abundance of a resource within a given area to the selection of that resource by an individual. It is calculated as follows:

$$J = \frac{obs - exp}{obs + exp - 2 * (obs * exp)} \tag{1}$$

where *obs* is the fraction of a resource type consumed by an individual and *exp* is the fraction of the same resource in the environment. The resulting index ranges from -1 to 1. Negative values indicating negative or non-preferential selection and positive values indicating positive or preferential selection. Though somewhat outside of its intended use, the Jacobs index has been applied not only to identify positive selection of certain types of food by animals but also to identify preferential selection of specific habitat characteristics by animals (Projekt Raetikon, Reimoser et al. 2014). If the resource of interest is a specific landcover class, then *exp* would be represented by the fraction of that landcover type to the total area and similarly *obs* would correspond to the portion of locations contained by the landcover class.

2.3.3 Ecological Importance of Cover

According to Mysterud & Østbye (1999), cover plays an important role in the selection of habitat areas for ungulates, and includes, by definition, "anything which veils or conceals, shelters or protects (...) and can be both vegetation and topography". Further, they argue that studies examining the influence of cover on the habitat selection and demography have only operationalized a fraction of what is typically considered cover and thus provide a more complete conceptualization of cover. Firstly, a distinction is made between structural and non-structural cover, whereby the structural cover is any tangible structure within the habitat, such as vegetation or topography. On the other hand, non-structural cover primarily comprises factors relating to reduced visibility due to weather conditions or the time of day. Structural cover in particular may also be used to protect the animal from environmental factors. For instance, it has been shown that red deer shifted to areas with increased structural cover (primarily forested areas) when strong winds and low temperatures occurred simultaneously (Schmidt 1993).

Whilst cover does play an important role in concealing the prey from the predators, it must be noted that predators may use the increased cover to their advantage, resulting in increased vigilance behaviour by ungulates in dense vegetation or high grass (Goldsmith 1990). Similarly, structural cover may reduce or increase the ability of prey to escape from predators. Nonetheless, red deer have been shown to choose resting sites with increased structural cover provided by the vegetation (Adrados et al. 2008) and shift habitat preference to forested areas at the onset of hunting seasons (Lone et al. 2015). These findings and the overall importance of forest ecosystems in red deer ecology indicate that concealment by vegetation constitutes a habitat characteristic which is linked to predator avoidance.

2.3.4 NDVI as a Proxy for Forage Quality

The importance of the nitrogen content of plants is of vital importance to herbivores, given the fact that it constitutes a key element in the growth of all organisms. The nitrogen content of plants is determined primarily by its requirements and its environment, though it is subject to significant changes throughout the seasonal and ontogenetic development of the plant. Thus, nitrogen content may range from anywhere between 0.03 to 7% of dry weight, with the highest concentration occurring in young or storage tissues (Mattson 1980). As ungulates typically seek plants which have a high nitrogen content it has been hypothesised that the spring migration of red deer is triggered in part by the search for higher quality, nutrient rich plants following the snow melt in elevated regions (Malnar et al. 2015; Mysterud et al. 2011). When nitrogen levels are at a low during dry seasons and winters, ungulates tend to substitute or supplement their diet, consisting mainly of grass, with wood browse (Mysterud et al. 2011). Nevertheless, some plant species may be avoided entirely due to the presence of substances which have an adverse effect on the rumen micro-flora (Mitchell et al. 1977).

Optical remote sensing techniques provide the potential to efficiently gather information on plant functioning and status over large areas. The functioning and status of vegetation is strongly linked to the productivity of the photosynthetic process, which is a function of chlorophyll content. Fortunately, nitrogen is a key building block of chlorophyll and the enzymes required for photosynthesis, resulting in a strong correlation between chlorophyll and nitrogen content (Clevers & Gitelson 2013).

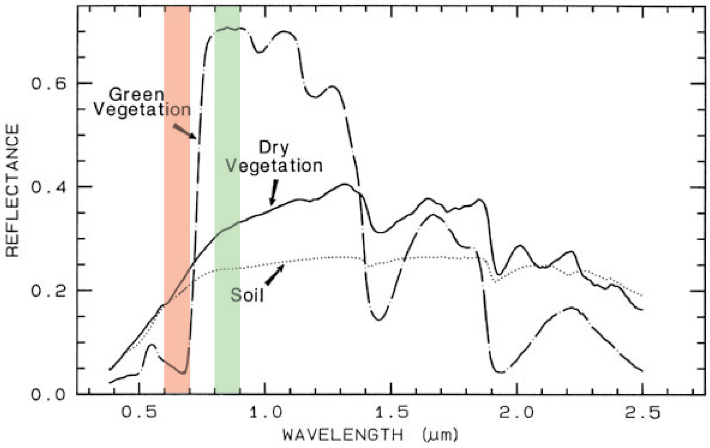

Figure 10: Spectral signature of vegetation and soil. The red and green bars show the RED and NIR regions of the spectrum used to calculated the NDVI (Lillesand & Kiefer 1987).

The NDVI (Normalized Difference Vegetation Index)is calculated using the reflectance of vegetation at the RED and near infrared (NIR) positions of the spectrum (see Equation 2) and essentially measures the height of the red edge. Healthy plants absorb most of the visible light in the red region of the spectrum due to the presence of chlorophyll, resulting in the pronounced absorption feature at around 0.6 - 0.7 μm. On the other hand, the internal cellular structure of the plant is indicated by the NIR region (around 0.8 - 0.9 μm)(see Figure 10). Healthy and dense vegetation generally reflects a large portion of incident near infrared light. Inversely, unhealthy or sparse vegetation absorbs less light at the red position as chlorophyll content declines and also reflects less light in the NIR region, resulting in a less pronounced red edge.

$$NDVI = \frac{NIR - RED}{NIR + RED} \tag{2}$$

The high temporal and spatial resolution of NDVI images derived from Landsat 8 (see Section 3.2.2) allow for a close approximation of the NDVI value at the location of the studied animal at any point in time, given that the images are not affected biased by cloud or snow cover (Pettorelli et al. 2011). Therefore, ecologists have recently moved away from harvest-based methods to investigate relationships between forage quality and quantity and increasingly adopted satellite based methods (Borowik et al. 2013; Pettorelli et al. 2011; Santin-Janin et al. 2009). The vast increase in available data allowed for links between vegetation productivity and availability and the distribution and dynamics of herbivores to be investigated on a larger scale (Borowik et al. 2013). Recent studies have indicated that the NDVI can be used a proxy for forage availability in terms of biomass (Santin-Janin et al. 2009; Ullah et al. 2012) and in terms of forage quality (Ryan et al. 2012). Unfortunately, the suitabilty of remotely sensed vegetation indices does not extend to the estimation of plant productivity on the ground level within forest ecosystems (Borowik et al. 2013).

3 Study Area and Data

3.1 Study Area

3.1.1 Overview

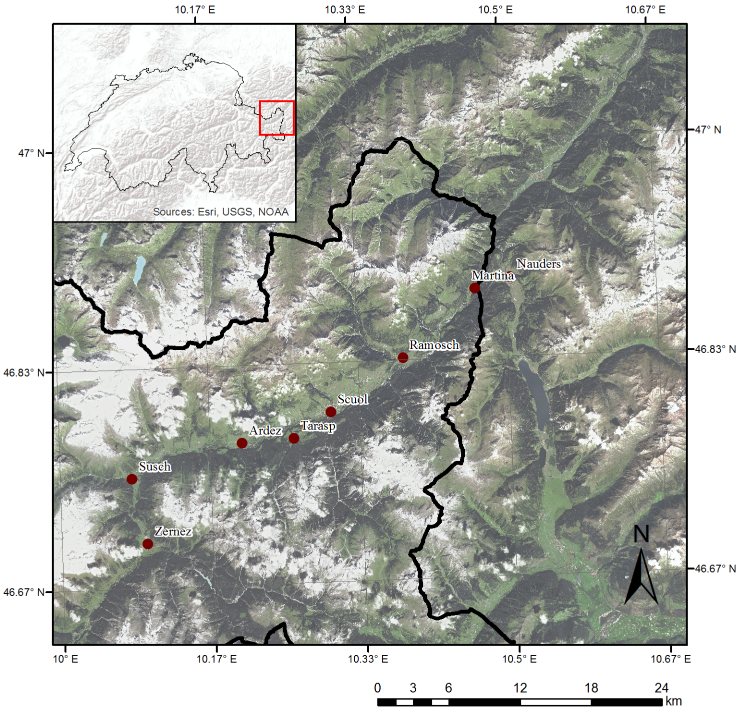

Figure 11: Overview of study area in the Lower Engadine valley.

The study area (Figure 11) lies in the Unterengadin valley and surrounding areas, in the easternmost part of Switzerland between 10°00′ and 10°32′ E and 46°40′ and 47°00′ N. The altitude ranges from around 1000 meters above sea level in the valley floor to the peak of Piz Linard at 3411 meters above sea level. Nestled in the middle of the Alps, the Lower Engadine valley extends in north-easterly direction for approximately 90 km and is influenced by a continental climate. The valley can be considered an inner alpine dry valley, meaning that both the mountains to the South and North provide a rain shadow. Further, the area is subject to strong seasonal change, with average temperatures ranging from -4.1°C in January to 15.3°C in July in the village of Scuol at 1300 m above sea level and from -6°C in January to 9.6°C in August at an altitude of 2400 m above sea level (see Figure 12). These substantial variations in height combined with the seasonality of the climate result in the existence of a wide array of habitat conditions (Haller 2002). The tree line is considerably higher when compared to other regions in the Alps and can be as high as 2300 meters above sea level. Forests are dominated by spruce (*Picea abies*), larch (*Larix decidua*), Scots

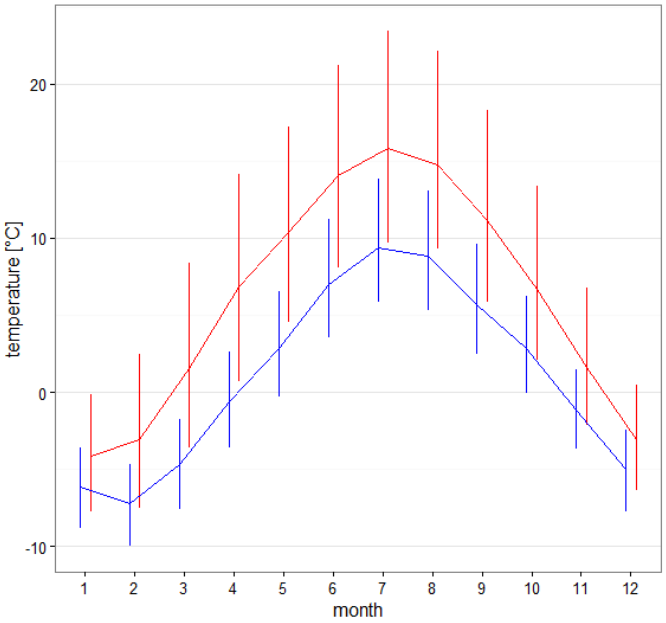

Figure 12: Mean monthly temperature for Motta Naluns meteo station at 2400 m.a.s.l. (blue) and in Scuol at 1300 m.a.s.l. (red). Additionaly the average daily maxima and minima are indicated by the vertical lines.

pine (*Pinus silvestris*) and Swiss pine (*Pinus cembra*), while particularly the shady northern slopes of the valley are forested. Deciduous trees are far less common in the area. Alluvial forests and Swiss mountain pine communities (*Pinus mugo*) are common at higher elevations and are of vital importance to game (Voser 1987).

The Swiss National Park covers an area of 170 km^2 and is located to the Southeast of Zernez on both sides of the Ovenpass. Since its establishment in 1914 agricultural and silvicultural activities as well as hunting have been strictly prohibited in this area. Furthermore, there are numerous game reserves (*Wildschutzgebiete*) and wildlife refuges (*Wildruhezonen*) throughout the valley. The primary role of game reserves is to offer protection from predation by humans (i.e. hunting activities). This offers the red deer safe zones outside of the SNP which in turn ensures an equal distribution of game in the area. As deer move between the game reserves, they are at risk of being shot by hunters during the hunting season. Therefore, the establishment of game reserves outside of the SNP serves as a tool to achieve the quota set by the annual hunting plan and simultaneously allows for the deliberate redistribution of the red deer population (Jenny & Filli 2014). Wildlife refuges, on the other hand, are established to ensure that wildlife is not disturbed during the harsh conditions during winter months and are necessitated by the recreational use of the area by skiers, snowboarders and so forth (Wildruhezonen 2016). The restrictions imposed on humans are therefore only in effect between 20th December and 4th April of each winter.

The Lower Engadine valley is only sparsely populated, with around 8 inhabitants/km^2. Consequently, modifications in the behaviour of red deer due to human disturbances is lower when compared to more densely populated alpine areas (Haller 2002). Despite the sparse population, the valley is a popular region for outdoor activities such as hiking, mountain biking or skiing in winter. A large ski resort extends from the village of Scuol up the southern slope of the valley to around 2800 m.a.s.l. Agricultural activities are largely limited to the valley floor, though grasslands at higher altitudes are used as alpine pastures.

3.1.2 Hunting in the Study Area

To regulate the ever growing population of red deer and avoid the concentration of red deer in large game reserves (e.g. the SNP) in the Canton of Grisons the AJFGR devises an annual hunting plan, specifying the number of red deer that are to be shot during the hunting season, which takes place for around 3 weeks in September and during another couple of days (max. 10) in November or December on selected mornings from 7:30 until 14:00 (see Table 1). During the first phase, which we will call the coarse regulation (*Hochjagd*), calves, lactating hinds, stags with surroyals, and brockets with antlers longer than their ears are protected. The underlying motive for protecting these animals is to convey a sense of security outside of game reserves and wildlife refuges, allowing them to follow the nutrient rich vegetation independent of the protection offered by game reserves and ensuring a better spatial distribution of animals[4]. This, in turn, ensures a less localized distribution of the population in areas, where hunting is prohibited (e.g. the SNP). Dur-

Date	Event
03.09.–13.09.15	1^{st} phase coarse regulation
21.09.–30.09.15	2^{nd} phase coarse regulation
21.11.15	fine regulation 10.1/10.2
22.11.15	fine regulation 10.1/10.2
28.11.15	fine regulation all regions
29.11.15	fine regulation all regions
05.12.15	fine regulation all regions
06.12.15	fine regulation all regions
09.12.15	fine regulation 10.1/10.2
12.12.15	fine regulation all regions
13.12.15	fine regulation all regions
16.12.15	fine regulation 9.1
19.12.15	fine regulation 9.1
20.12.15	fine regulation 9.1

Table 1: Dates of fine regulation hunting in 2015 for each hunting region. Hunting is limited to 7:30 until 14:00

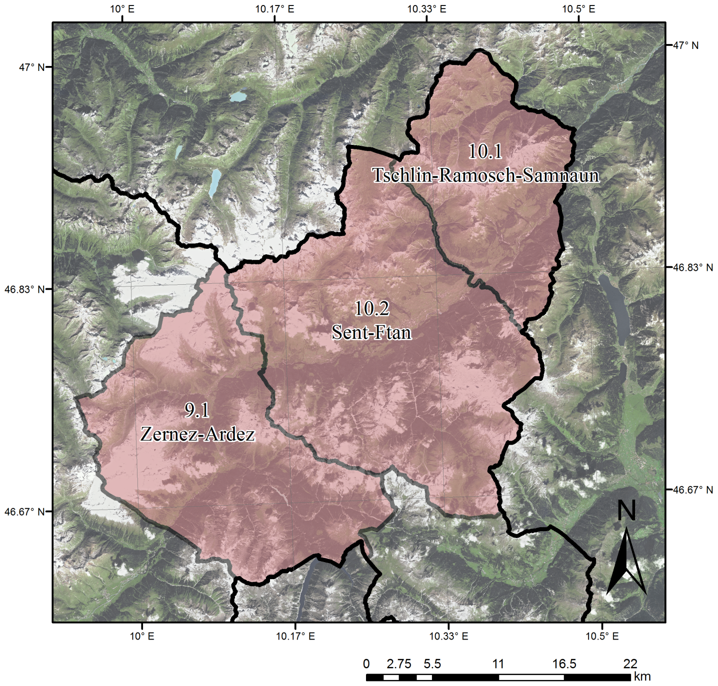

Figure 13: Hunting Regions 9.1, 10.1 and 10.2.

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[4] Personal communication with Hannes Jenny AJFGR, 02.12.2016

ing the second phase, which takes place after the migration to the winter home range (*Sonderjagd*, henceforth the fine regulation hunt), calves and female animals, which were protected during the coarse regulation, are the primary target, depending on whether the quota set by the annual hunting plan was reached during the coarse regulation (Jenny et al. 2011). While the coarse regulation is open to anyone with a permit throughout the entire Canton during the periods specified in Table 1, the fine regulation hunt takes place in selected hunting regions (Figure 13) and depends on the requirement of further regulations in the respective region. Further, only hunters who previously registered for the fine regulation hunt in a specific hunting region are permitted to hunt. The aim of this two-stage approach is to harmonize both the preservation of a healthy red deer population in the alpine environment in terms of their overall condition and in terms of an age structure within the population, which is as close to the natural state as possible. In turn this ought to reduce the damage to woodlands and agricultural areas. A further concern is the preservation of hunting as a cultural heritage in the Canton of Grisons (Jenny et al. 2011).

3.2 Data

3.2.1 GPS Data

The GPS data, provided as .csv files, were gathered in a joint effort by the SNP and the AJFGR. The deer were captured during the winter and early spring of 2014/2015 and equipped with GPS collars by VECTRONIC Aerospace GmbH. The entire data set includes 19 animals (7 males, 12 females) which are distinguishable by their collar ID. Due to the ongoing nature of the collaboration between the SNP and the AJFGR and the tremendous effort related to the capturing of the animals, the start date of the sampling varies between individuals (see Table 2). For most animals, sampling began around mid-March or the beginning of April. However, for two females sampling did not begin until October 2015 and for another stag not until December 2015. It is debatable whether these individuals can be included in the analysis in any meaningful way. The sampling interval is set to 1 hour for 13 individuals and 1.5 hours for the remaining 3, not considering missed fixes or gaps created by filtering of imprecise fixes. Additionally, for individuals h61 and h81, the sampling interval decreased in late November (20.11.15) to alternating bursts of 15 minutes and 1 hour.

The variables stored by the device include the GPS locations in different coordinate systems, including WGS84 and CH1903+, along with the height in meters as recorded by the GPS device. Further, the timestamp of each fix is stored in various time formats (UTC and LTM). For each fix, the dilution of precision (DOP) is stored as an indicator for the precision of the location (Langley 1999). The DOP value relates to the number and position of satellites that are in view without obstruction. Generally speaking, the more satellites are available the higher the accuracy, though an unfavourable constellation of satellites can cause an increase in DOP even when a sufficient number of satellites are available. Lower values indicate increased accuracy and vice versa (Langley 1999). Additionally, for a couple of individuals, 3D error data – as measured in meters – is available, though it is very patchy. Fortunately, the fix type is stored as well. The fix tpye (i.e. 2D or 3D GPS) denotes how many satellites were involved in determining the GPS position, with 4 or more satellites resulting in 3D fix types. This allows for filtering of error prone 2D GPS fixes. At present, no activity data is available as the data recorded by the accelerometer sensor needs to be read from the Collar directly and cannot be accessed remotely. This data will however become available once the deer have either been shot or their collars have been remotely separated. Figure 14 provides an overview of all GPS positions during the study period, colour coded by the individual's collar ID.

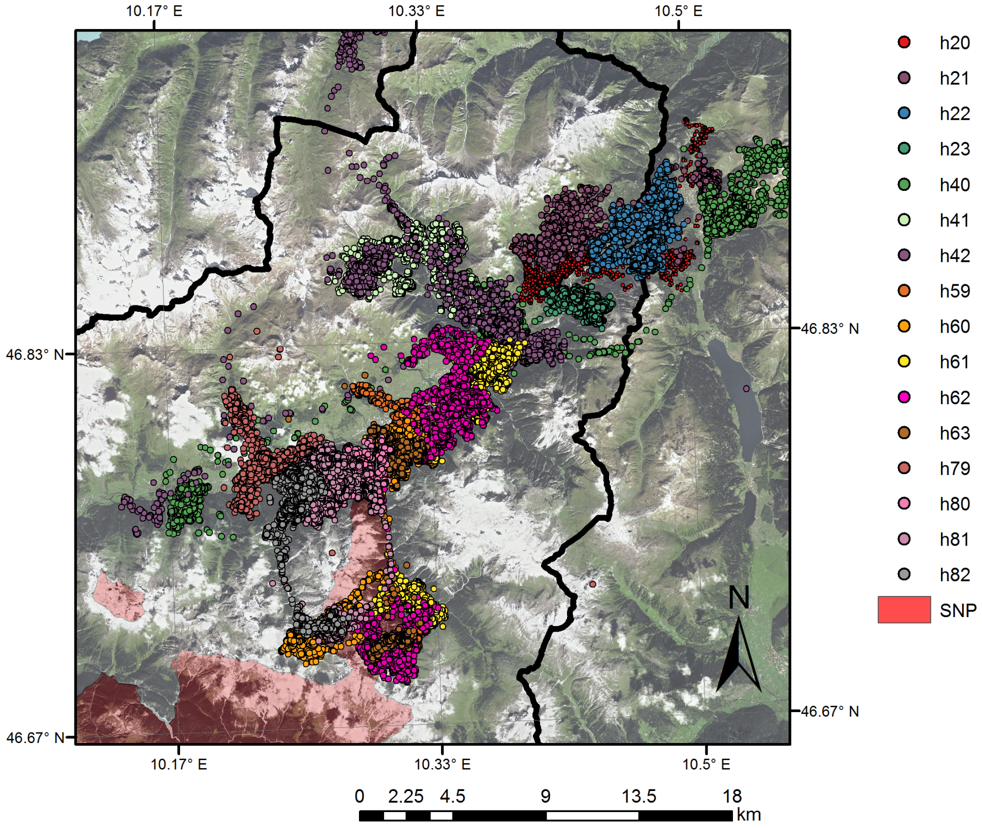

Figure 14: Overview of GPS locations, colour coded by collar ID.

Pre-processing

Failed GPS position acquisitions had previously been filtered by the parties involved in gathering the data, though 2D GSP positions and invalidated 3D GPS positions were still included in the data (see Table 3 for more information). Zweifel-Schielly & Suter (2007) showed that the propor-

Table 2: Percentage of fix types (GPS-2D, GPS-3D, and val. GPS-3D) for the entire data set.

GPS-2D	GPS-3D	val. GPS-3D
5684 (5%)	8407 (7%)	106700 (88%)

tion of 3D positions is prone to relatively large bias due to vegetation cover and the topographical ruggedness that also characterizes the study area of the Unterengadin, but advise against filtering the data of 2D positions for the purpose of conducting home range studies, as it may lead to an undesired loss of information. Similarly, DeCesare et al. (2005) found that a dense forest canopy structure can introduce an error in overall track lengths of up to 27% for extremely short sampling intervals of a couple of seconds. With these considerations in mind and the fact that the focus of this thesis lies on the association of the GPS locations with context information provided by high resolution vector and raster data, only validated 3D positions were used for the analysis. Table 2 shows the proportion of each GPS fix type for the entire data set. Validated GPS positions make up a total of 88% of the data, while 2D GPS and 3D GPS positions account for 12%. Obvious outliers were manually removed from the data. At this point it is important to note that a remaining source of error and bias stems from habitat induced inconsistencies in position acquisition rates, which is especially problematic when comparing positions in open habitats (e.g. pastures) with such in closed habitats (e.g. forests).

Table 3: Overview of the 16 individuals including sex, age, the date of the first and last GPS location (fix), the percentage of validated GPS locations and the most frequent sampling interval.

id	CollarID	sex	age	first fix	last fix	fixes	val. fixes	% valid	interval
h20	16962	m	5	14.03.2015	01.03.2016	8223	7624	92.72	1 h
h21	16960	f	10	18.03.2015	01.03.2016	8254	7878	95.44	1 h
h22	16961	m	2	09.04.2015	12.02.2016	7176	6683	93.13	1 h
h23	16959	f	10	22.03.2015	01.03.2016	7925	6840	86.31	1 h
h40	16963	m	10	12.03.2015	01.03.2016	8642	8231	95.24	1 h
h41	16965	f	10	14.03.2015	01.03.2016	8264	7796	94.34	1 h
h42	16964	m	4	17.03.2015	01.03.2016	8564	8013	93.57	1 h
h59	16968	f	5	18.03.2015	01.03.2016	8422	7917	94.0	1 h
h60	16967	m	10	26.03.2015	01.03.2016	8293	7766	93.65	1 h
h61	8710	f	13	09.04.2015	16.02.2016	6337	4203	66.32	1.5 h
h62	9054	m	2	30.04.2015	01.03.2016	5931	5069	85.47	1 h
h63	8871	f	13	22.04.2015	01.03.2016	7472	5924	79.28	1 h
h79	11217	f	10	25.03.2015	16.02.2016	4935	3938	79.80	1.5 h
h80	16966	f	11	17.03.2015	01.03.2016	8426	7462	88.56	1 h
h81	8714	f	5	24.03.2015	16.02.2016	7238	5479	75.70	1.5 h
h82	8875	f	13	08.04.2015	01.03.2016	6689	5877	87.86	1 h

As previously mentioned, the sampling interval increased in late November for the hinds h61 and h81 to 15 minutes and 1 hour for the remainder of the study period. For the remaining individuals, sampling intervals increased to 15 minutes in the period between the 21^{st} and 23^{rd} of November. As the sampling rate determines to which extent the true path of the animal can be approximated, this increased sampling rate in November is likely to introduce a bias that affects movement parameters such as speed, step length or sinuosity. It has previously been shown that an increase in sampling frequency leads to a noticeable increase in speed (Laube & Purves 2011). This problem can be approached by either subsampling the data in order to obtain a more or less constant sampling frequency or by interpolating the positions, for instance by random walk models. I argue that the interpolation of positions may be a pragmatic solution for certain ecological questions, however, when the focus lies on the analysis of movement parameters the interpolation of positions is likely to lead to unpredictable results. Further, given that the increase in sampling rate typically only affected 3 days, the decision to subsample the data during these periods to intervals of a minimum of 55 minutes was made, as intervalls were frequently below the specified sampling interval of 60 minutes. This allows for better comparability of activity values between individuals, especially as the periods affected by the increase coincide with the start of the fine regulation hunt (see Table 1)

3.2.2 Context Information

Vector Data

Landcover data was extracted from the VECTOR25 dataset by Swisstopo. It covers the entire country and includes roughly 8.5 million objects stored either as points, lines, or polygons, with a positional accuracy of 3 - 8 meters. The objects are stored in the Swiss grid reference system (CH1903+ LV95) and the same data is used to generate the 1:25’000 topographic maps by the Swiss mapping agency, swisstopo (Bundesamt für Landestopographie 2007). Most important for the purpose of this thesis is the availability of primary landcover classes including forests, open forests and shrublands. All primary landcover classes are mutually exclusive. Further, shapefiles representing the game reserves, wildlife refuges, hiking trails, and hunting regions were acquired through www.geogr.ch, which operates as part of the administration of the Canton of Grisons.

Raster Data

Using Google Earth Engine, a total of 9 monthly composites were derived from Landsat 8 images from the months of March until November of 2015. The months of January, February and December were not included, as the study site is mostly covered by snow during winter, making NDVI measurements redundant. The revisit time of the Landsat 8 satellite is 16 days, resulting in monthly composites made up of two images, whereby the best pixel (i.e. the pixel with the higher NDVI value) of the two images was used for the composite image. Using band 4 (RED, 0.64–

0.67 μm) and band 5 (NIR, 0.85–0.88 μm) the NDVI was computed, while simultaneously storing cloud score images, i.e. images that assign a value between 0 (no cloud cover) to 100 (mostly cloudy) to each pixel. The spatial resolution of visible (VIS), near infrared (NIR) and short wave infrared (SWIR) bands is 30 meters. The composite derived for August was strongly affected by cloud cover (see Figure 15), especially at higher altitudes. The effect this had on the mean NDVI value of all pixels in the study area was quite considerable, therefore the composites of July and September were linearly interpolated in an attempt to reduce the bias introduced by cloud cover (see Figure 15). The remaining composites, though still slightly affected by cloud cover, were not further manipulated (see Appendix A.4).

Due to the fact that GPS elevation measurements are typically erroneous, a digital terrain model (DTM) was used as a basis for any operation related to elevation, with a spatial resolution of 10 meters. The computation of a cumulative visibility map (i.e. viewshed) was based on a digital surface model (DSM), also with a spatial resolution of 10 meters. Both the DTM and DSM were acquired through swisstopo.

3.2.3 Limitations of the Datasets

Due to the absence of accelerometer sensors and a relatively coarse sampling interval, detecting fine scale movements or movement patterns for red deer remains a difficult task. Laube (2014) argues, that the locations alone do not provide enough information on the activity of the observed animal. The sampling frequency of between 1 and 1.5 hours is arguably too coarse to allow for the identification of the length and number of resting or grazing periods. Further, the relocation movements between the sites associated with resting and grazing behaviour are most likely not detectable at the given sampling rate, especially given the relatively high frequency and short duration of the daily activity cycles (see Section 2.1.1). For instance, grazing periods would, at most, consist of merely 1 or 2 points for grazing bouts of 0.5 – 2.5 hours. With respect to the

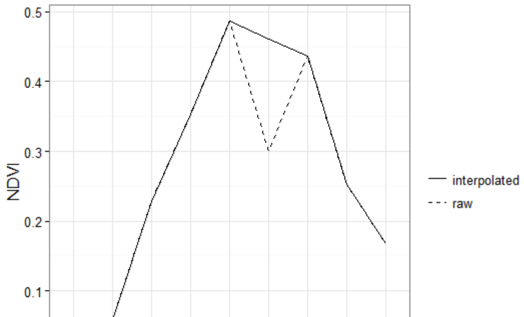

Figure 15: Effect of the linear interpolation of the August NDVI map.

accuracy of the GPS locations, the absence of 2D error estimates and the patchiness of 3D error estimates impedes the handling of inaccuracies and further supports the filtering of positions by invalidated 2D and 3D positions.

With regards to the vector data provided by the VECTOR25 dataset the land cover data does not account for any changes in land cover that occurred since 2006. Furthermore, the mutual exclusiveness does not allow for the recognition of ground vegetation within forested areas, limiting the detection of grazing sites to those located in open areas.

4 Methods

4.1 Classification of Migration Patterns

In order to determine whether the red deer exhibit migratory behaviour between two distinct areas of intensified use, the analysis was based on the extraction of seasonal home ranges, as shown in the flowchart of Figure 16. In a first step, seasonal home ranges were calculated using minimum convex polygons (MCPs) for the months of July and August (summer home range) and January and February (winter home range). 95 percent of all GPS location within these timespans were used. If the resulting home ranges did not overlap, the deer was said to migrate. Inversely, if they did overlap, the deer was classified as resident. However, this simple method is highly susceptible to bias, either from sporadic movements between the home ranges that occur during the times specified or from premature or delayed migration movements. To deal with this Kernel Density Estimation (KDE) was applied to the locations within the same timespans specified above using h_{ref} smoothing function. Core areas of the home range were then defined as the 50 percent volume contour lines, which are indicative of areas of intense utilization. It is important to note that red deer may have multiple core areas, due to the daily cycle of grazing and resting and the movement associated with this behaviour. A distance matrix was then computed between the centroids of the resulting seasonal core areas. Red deer that travelled above a threshold distance of 2500 meters between centroids of seasonal core areas were then also classified as migratory, even if the respective MCPs overlapped (see Figure 16). The choice of the threshold was based on findings by Georgii & Schröder (1983), who, based on VHF tracking, found seasonal home ranges given by MCPs to be, on average, 2.3 km apart for red deer in the Bavarian Alps.

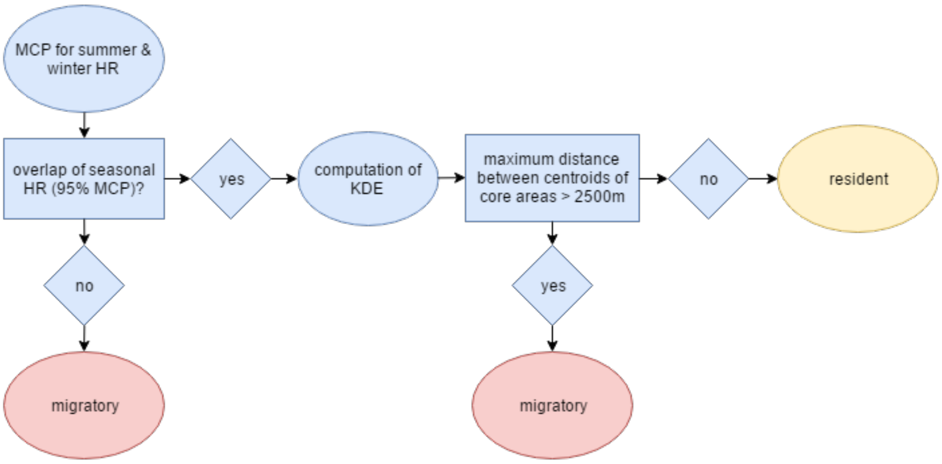

Figure 16: Schematic representation of migration classification.

4.2 Activity Measures

While no activity data was available at the time of this study, Ensing et al. (2014) found the correlation between activity values as provided by accelerometer sensors in GPS collars, which is indicative of head movements, and locomotion speed to be highly significant. Thus, in the absence of accelerometer data, for the analysis of red deer activity the locomotion speed between consecutive fixes was calculated and used as a proxy for activity.

To inspect the variability of activity levels in dependence of the time of day a diurnality index and crepuscularity index were computed (Ensing et al. 2014). For the crepuscularity index, the twilight hours were defined as the period between onset of nautical twilight (i.e. the time when the sun is 12° below the horizon) and sunrise in the morning and sunset and the end of nautical twilight in the evening. To determine whether the activity value occurred during the twilight hours, the period was extended by -1 hour and +0.5 hours, due to the fact that the distance and speed measures of GPS positions were defined as the distance and speed from that location to another. Furthermore, the extension of the timespan serves as a range of tolerance and aims to account for the suboptimal sampling interval.

Equation 3 shows the formula of the **diurnality index** (I_D), where A_D is the sum of activity during the day and A_N is the activity during the night.

$$I_D = \frac{A_D - A_N}{A_D + A_N} \tag{3}$$

Similarly, Equation 4 calculates the **crepuscularity index** (I_C), where the activity during twilight hours (A_T) is related to activity values during non-twilight hours.

$$I_C = \frac{A_T - A_N + A_D}{A_D + A_N + A_D} \tag{4}$$

Both indices result in values between -1 and 1, where -1 and 1 represent nocturnal and diurnal activity, respectively, for the diurnality index and non-crepuscular activity and crepuscular activity, respectively, for the crepuscularity index.

Activity values were aggregated at different temporal scales, ranging from weeks to months to seasons. Additionally, the dates of the fine regulation hunt were further investigated, including the preceding and following 7 days. Further, investigation into changes in activity during the coarse regulation were not investigated due to the concurrence with the rutting season.

4.3 Cover

Point in polygon tests were performed on the GPS locations to determine whether the deer were situated within forested areas, shrublands, game reserves or wildlife refuges. Further, the Euclidean distance to the edge of the forest was calculated, with negative distances indicating positions within the forest. Due to memory constraints in R, the software used for most of the analysis (R Development Core Team 2010), the boundaries of forest polygons were converted into a sequence of points with a spacing of 20 meters. It is important to note that this procedure introduces an error which is proportionally largest for locations close to the forest edge. The seasonal and daily variations in the distance to the forest edge were then analysed, as well as the timing of the maximum distance strayed from the edge for each day. The underlying assumption hereby is that forests, game reserves and wildlife refuges constitute areas of increased structural and/or non-structural cover (see Section 2.3.3). The obstruction of view that the forest provides, was hypothesized to be of greater importance during the day, when the darkness no longer provides the necessary cover. (Additional aspects relating to cover were not inspected. The microclimate that characterizes mountainous regions and the presence of merely 4 meteostations in the general vicinity of the study area, would have required a sophisticated precipitation and wind speed model, which would have exceeded the scope of this thesis.)

Adding Contextual Information

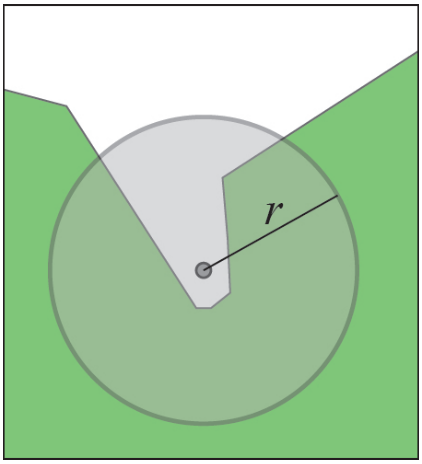

Figure 17: Dominance principle.

Contextual Information was added to point locations by comparing the contribution of areas of different landcover classes to the buffer around the point location (see Figure 17). Whilst the buffer radius is best chosen as the positional error of the GPS location, due to the absence of any 2D error measures (see Section 3.2.3) the value for r was, rather conservatively, set to 20 meters. For instance, a point is said to lie within the forest, if the forest landcover class accounts for more than 50% of the buffer area. Naturally, only locations within 20 meters of the forest edge need to be checked with the dominance principle. Furthermore, it is only possible for a landcover class to contribute more than 50% to the area of the buffer of a GPS location outside of that landcover class if the location is situated inside a concavity of the polygon (Figure 17). The dominance principle was only applied to determine containment by forest and shrubland landcover classes, as these exhibited considerably more concave features when compared to wildlife refuges and game reserves.

4.4 Resource Selection

The preference of a certain landcover type over another was determined by the Jacobs Index (1974). Though the index was developed as an ecological tool for determining the selection of specific food types relative to their abundance, it can easily be applied to landcover data by applying Equation 1. Under the assumption that locations within a deer's home range are uniformly distributed, the percentage of locations within a specific landcover type should be equal to the percentage which that specific landcover type contributes to the home range. A preference can be determined, if values are above 0, meaning that the observed percentage of locations exceeds the expected percentage of locations and selection is positive. Inversely, values of -1 indicate that the resource was not preferred (i.e. negative selection).

To detect seasonal differences in the preference, the index was calculated for the meteorological seasons of spring (01.03.15 - 31.05.15), summer (01.06.15 - 31.08.15), autumn (01.09.15 - 30.11.15) and winter (01.12.15 - 29.02.16) separately. Hereby the expected values (*exp*) corresponded to the contribution of forested areas to the home range of the respective season as given by the area of the 95 % volume contour of the KDE, again using the h_{ref} smoothing function. Observed values (*obs*) were then calculated for each hour as the percentage of locations located within forested areas. This method takes the reduction of forested areas at higher elevations into account and thus provides ecologically meaningful insights for both resident and migratory individuals' preference for forested areas.

The same method was applied to locations within wildlife refuges and game reserves for individuals (n = 12) which spent the entire year within Switzerland as no comparable data of neighbouring countries was available. Further, it must be noted that the validity of these findings may be disputed with regards to preferential resource selection due to the lack of the cognitive capacity of red deer to be aware of the abstract form of cover provided by such areas. That is to say that game reserves and wildlife refuges provide a form of functional cover which is neither structural nor non-structural (see Section 2.3.3) but is much rather embedded in the hunting practices of the area and (to a certain extent) independent of environmental factors or habitat characteristics.

4.5 Main Grazing Site Detection

The detection and characterization of grazing sites was approached in a two-stage approach. First, the detection of main grazing sites was performed considering only locations not contained by forested areas, shrubland or villages, as these were assumed to be related to grazing activity. Furthermore, positions acquired during the rutting season were excluded from the analysis, as

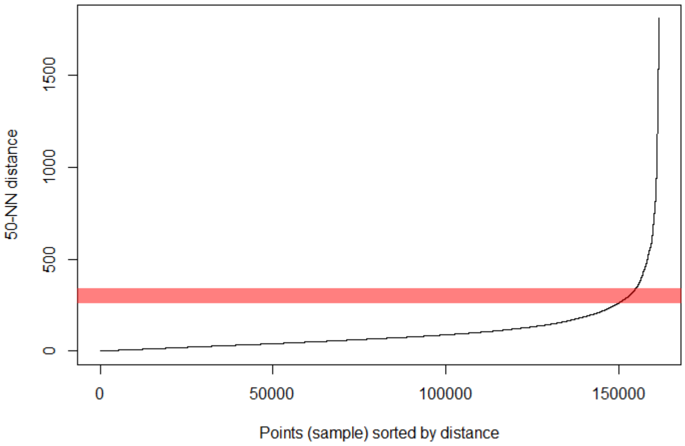

Figure 18: 50-nearest neighbour distance plot.

the decrease in grazing activity and the habitat characteristics of the rutting grounds would have presumably introduced a bias (see Chapter 2). Lastly, only positions exhibiting NDVI values between 0.1 and 0.6 were considered, as values greater than 0.6 indicate an increased influence by canopy structure and values below 0.1 tend to be caused by bare soil or snow (Nemani & Running 1997; Pettorelli et al. 2011). DBSCAN was then performed on the remaining positions. The minimum number of points required was set to 50 while the *Eps-neighbourhood* was chosen by determining the position of the 'knee' in a 50-nearest neighbour distance plot (Figure 18), i.e. the y-position where a sharp change in slope occurs. The choice of a minimum of 50 points relates to the intentional avoidance of small clusters in order to allow for a better comparison of variables between different times of day. Additionally, certain clusters were grouped after visual inspection revealed a temporal overlap (see Figure 19) and spatial proximity of clusters. Once more, KDE was performed with the relocations of each cluster and core areas defined as the 50% volume contour line. These core areas were assumed to be related to intense foraging behaviour due to favourable habitat characteristics. Based on the timestamps of the GPS positions and visual inspection, the clusters were assigned the respective seasonal home range where possible. If the allocation of a specific seasonal home range was not possible due to the resident nature of certain individual's space use patterns or revisitation during different times of the year, the clusters were said to be important throughout the year.

Subsequently, median NDVI, visibility and distance values were investigated at core grazing sites to detect spatio-temporal patterns relating to risk avoidance and foraging activity. Median values were calculated for both day and night for all variables. The choice of median values over mean values stems from the better representation of skewed distributions and the reduction of the influence of outliers.

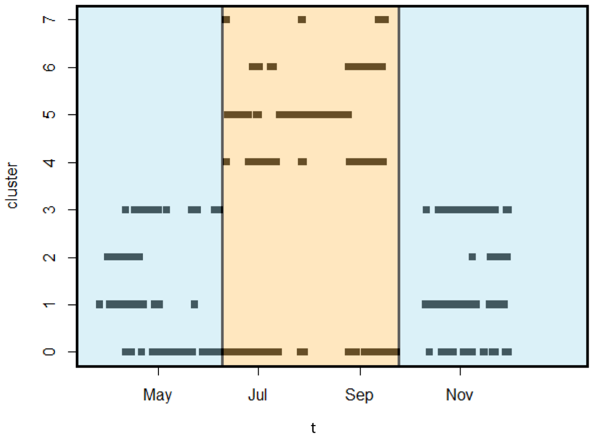

Figure 19: Manual merging of clusters based on temporal overlap/proximity (h60). Timestamps of positions are shown after the initial clustering process. Clusters 1-3 and 4-7 were merged (as shown by the blue and yellow shading) as they exhibited a temporal overlap, resulting in 2 clusters which could be assigned to seasonal home ranges.

Visibility was calculated for the entire study site by deriving a cumulative viewshed model from the DSM with hiking trails used as viewpoints. The decision to use a DSM rather than a DTM to calculate visibility stems from the possibility to detect invisible areas which are concealed by dense vegetation, which the DTM does not allow. Sheltered environments in terms of low visibility by humans were assumed to be of greater importance during the summer months, when most of the deer are located at higher altitudes where cover in the form of forest and other vegetated areas is less available. Due to insufficient memory, the hiking trails were converted to points sampled regularly every 20 meters and only pixels within 1 km of the viewpoints were considered. Observer height (i.e. people) was (conservatively) set to 1.9 m, object height (i.e. deer) to 1.20 m, and the search radius to 1.5 km. The cumulative viewshed sums up the binary viewshed for each viewpoint, resulting in an integer value indicating the number of viewpoints which have an unobstructed line of sight to the pixel in question. Thus, clearly visible areas are assigned a high value while sheltered areas receive a lower value. Finally, visibility values were divided by the distance to hiking trails, with the aim of reducing the probability of high values at locations far from hiking trails.

NDVI values were extracted at the GPS locations from the NDVI layer of the corresponding month. Locations within the forest polygons were not considered for the analysis as this would have led to exceptionally high NDVI values due to the tree canopy. Further, the values were not extracted through bilinear interpolation as this would have led to an increase of values for locations close to the forest. Lastly, it is important to note that only clusters found within Switzerland were considered, due to missing data relating to hiking trails outside of the country and thus missing visibility values. Additionally, .kml files were produced, in order to visually inspect the characteristics of the detected grazing sites.

5 Results and Discussion

5.1 Classification of Migration Patterns

5.1.1 Results

Table 4 shows an overview of the classification of migration behaviour. While ten individuals exhibited overlapping seasonal home ranges (MCP), the additional criterion of a distance larger than 2500m between the centroids of core home range areas (50% KDE) narrowed the number of resident individuals down to three. Of the remaining three individuals, the shortest distance between the centroids of seasonal core areas was 427 meters (h79) and the longest distance 2069 meters (h22). For those individuals that exhibited overlapping seasonal home ranges (MCP), but were later classified as migratory by the second criterion, the distance between the centroids of seasonal core areas ranged from 4185 meters (h41) to 10753 meters (h59). The largest distance was found for h42 with almost 18 kilometres. Interestingly, individuals which were captured and equipped with GPS collars in the same area (as shown by the first numerical digit in the id)

Table 4: Results of classification of migration. Distances between centroids of seasonal home ranges are given as meters and all measures relating to elevation as m.a.s.l.

id	**overlapping seasonal home range?**	**distance between centroids**	**classification**	**mean elevation summer**	**mean elevation winter**	**sd**
h20	yes	2526	migratory	1753	1454	178.7
h21	yes	8247	migratory	1862	1691	161.2
h22	yes	2069	resident	1632	1824	211.2
h23	no	1464	migratory	2041	1200	375.5
h40	no	12560	migratory	2070	1252	336.8
h41	yes	4185	migratory	2211	2091	167.8
h42	no	17716	migratory	1956	1157	400.9
h59	yes	10753	migratory	2183	1441	338.3
h60	yes	11057	migratory	2207	1343	361.1
h61	no	12395	migratory	1905	1294	299.0
h62	no	15353	migratory	2351	1530	402.4
h63	no	10040	migratory	2089	1180	402.2
h79	yes	427	resident	1453	1520	132.4
h80	yes	1697	resident	1550	1678	78.5
h81	yes	8220	migratory	2131	1719	283.6
h82	yes	7043	migratory	1970	1584	298.9
	migratory: 6 resident: 10	mean: 7860 max: 17716 min: 427	migratory: 13 resident: 3			

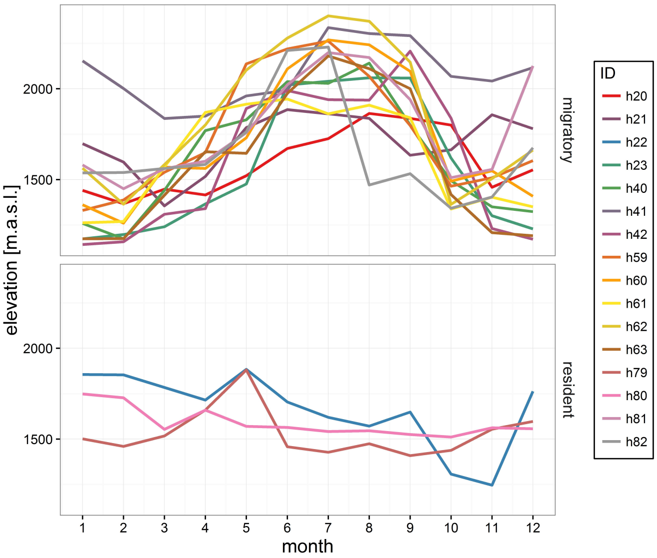

Figure 20: Mean monthly elevation

showed similar space use patterns, especially individuals h61, h62 and h63 (see Appendix A.1 for visualizations).

Additional calculation of the mean elevation (Table 4, Figure 20) per month revealed that individuals classified as migratory exhibited an increased annual variation in elevation, also shown by the standard deviation. Furthermore, Figure 20 shows that for the three resident deer the average monthly elevation never exceeded 2000 m.a.s.l., while for migratory deer, summer home ranges were frequently located above 2000 m.a.s.l. Interestingly, h41 did not exhibit the same annual variation in elevation found for other migratory individuals.

5.1.2 Discussion

There are numerous methods to classify and characterize migratory movements by mammalian species (see Cagnacci et al. 2016). The method proposed above can be seen as an extension to the classification method used in the Raetikon project (Reimoser et al. 2014) where seasonal home ranges, given by MCPs including 100% of all points within the specified temporal ranges for summer and winter, were checked for overlap. Through the introduction of the second criterion the necessity to visually inspect and adjust the result of the classification is obviated as it is less susceptible to false classification due to exploratory movements or delayed or premature migration. Nonetheless, the robustness of the method depends to a high degree on the extent of the temporal shift of migration and the time spent (i.e. the number of GPS locations) in the respective home ranges. If, for instance, an individual was to spend only a fraction of the expected time in the summer home range these positions would not be included by the 50% volume contour lines of the KDE and thus no migratory movement could be detected. Therefore a priori knowledge on the approximate onset of migratory movements is required.

Results showed that complete migration, i.e. the clear separation of seasonal home ranges, can only be observed for 6 individuals, though this depends largely on the choice of temporal ranges chosen for the seasonal home ranges. Nonetheless, visual inspection of the seasonal space use patterns (see Appendix A.1) supports the notion that complete migration is to be viewed as the exception rather than the rule (Cagnacci et al. 2016) and is a common occurrence in areas with high seasonal variation in climate and thus habitat conditions (Malnar et al. 2015). The most distinct migratory behaviour could be observed for individuals h40, h42, h61, and h62, while for h40 and h42 even separate rutting grounds could be identified, belonging to neither summer nor winter home range. Similarly, h23 showed no overlap in seasonal home ranges, though the distance between home ranges was significantly lower than for the other distinctly migratory animals. Among those deer classified as resident, animal h79 showed the most noticeable resident behaviour, with the winter home range being contained by the summer home range (both 95% MCP). While individuals h22 and h80 do actually exhibit a seasonal pattern with respect to the distribution of the GPS locations, the distance between the areas of high utilization, which could be attributed to a season, is too insignificant to classify said individuals as migratory.

The calculation of average elevation in the summer and winter months served both to add additional information to the home ranges as well as a validation strategy. Mean elevation in the winter months was consistently lower than mean elevation in summer months for migratory animals, confirming that summer home ranges are typically located at higher elevations. In contrast, mean elevation for resident individuals was consistently lower in summer when compared to winter, though differences are relatively small. Interestingly h23, the individual which showed no overlap in seasonal home ranges and a distance of merely around 1.5 km between the two home ranges, exhibited over 800 meters difference in elevation between the summer (2041 m.a.s.l.) and winter home range (1200 m.a.s.l.). Furthermore, the standard deviation of all monthly averages revealed that resident individuals typically showed less variation in altitude than those that migrated, with the exception of h20, h21, and h41.

As previously mentioned, no inferences can be made on population level migration behaviour from the small sample size of 16 individuals. Nevertheless, results demonstrate that migration is typically not easily identifiably and subject to a considerable amount of subjectiveness, especially in cases where the migration pattern is not readily identifiable.

5.2 Temporal Variability in Activity Levels

5.2.1 Results

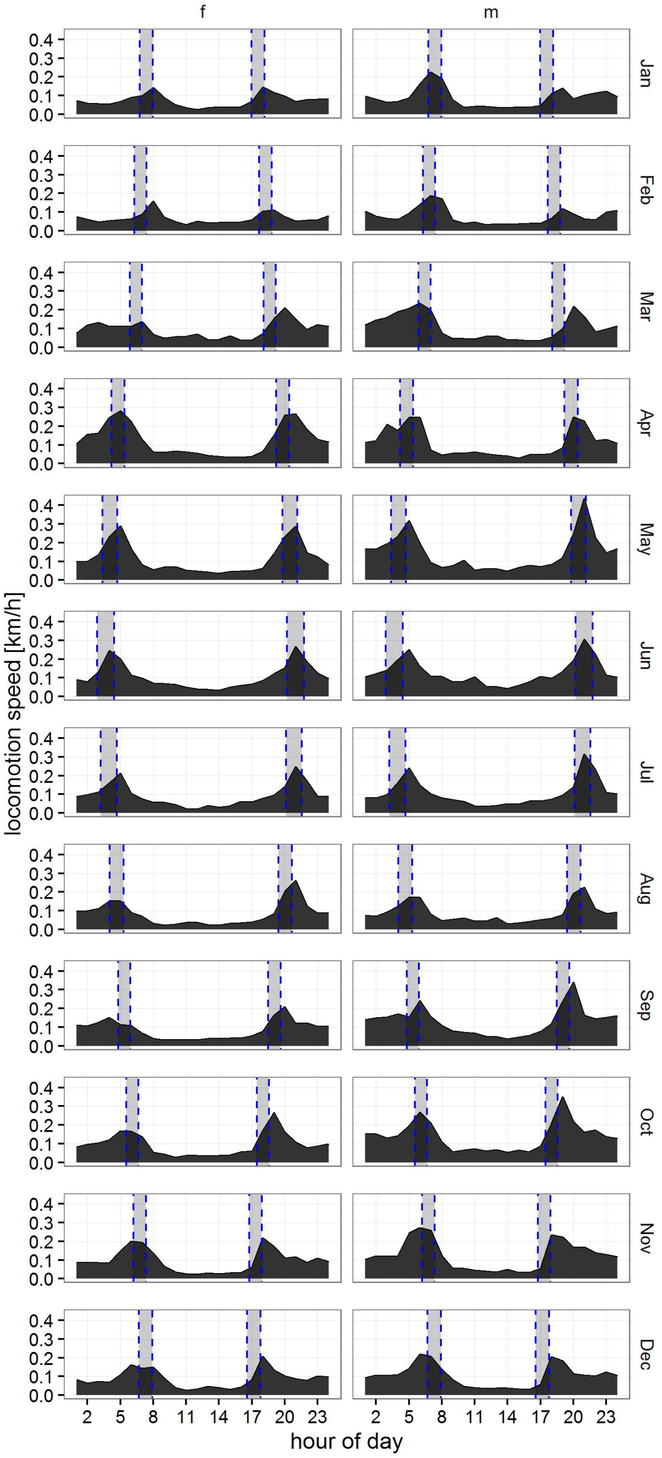

Figure 21: Mean monthly activity (locomotion speed) of male and female red deer. Dark blue dotted lines represent the start of nautical twilight, sunrise, sunset and end of nautical twilight.

A comparison between the activity values of male and female deer (Figure 21) shows a bimodal pattern for both sexes with activity values peaking during, shortly after or before twilight hours. Further, an increase in activity can be observed for male individuals during September and October. This supports the findings by Clutton-Brock et al. (1982), who observed that male deer, in particular so called harem holders, showed an increase of activity during the rutting period and spent up to 15% of the day moving. For hinds this value was considerably lower with only 1-5%. Furthermore, the increased activity values seem to correspond to an increase in foraging activity, as Hester et al. (1996) found the same bimodal pattern upon investigation of the total time spent grazing.

Figures 22a and 22b show the distribution of activity between the day, night, and twilight hours. While Figure 22a shows the contribution of daytime, night-time and twilight activity to total activity, the relative duration of each time of day (day, night, twilight) was taken into account in Figure 22b. In absolute terms, the activity increases during the summer months, while the night-time activity contributes most to total activity during the winter, spring, and autumn months. However, when activity values are inversely weighted by the duration of the respective time of day (Figure 22b), the crepuscularity of the red deer becomes apparent. Throughout the year, activity values are proportionally largest during the twilight hours, while the increase in the daytime activity is still slightly noticeable during the summer months.

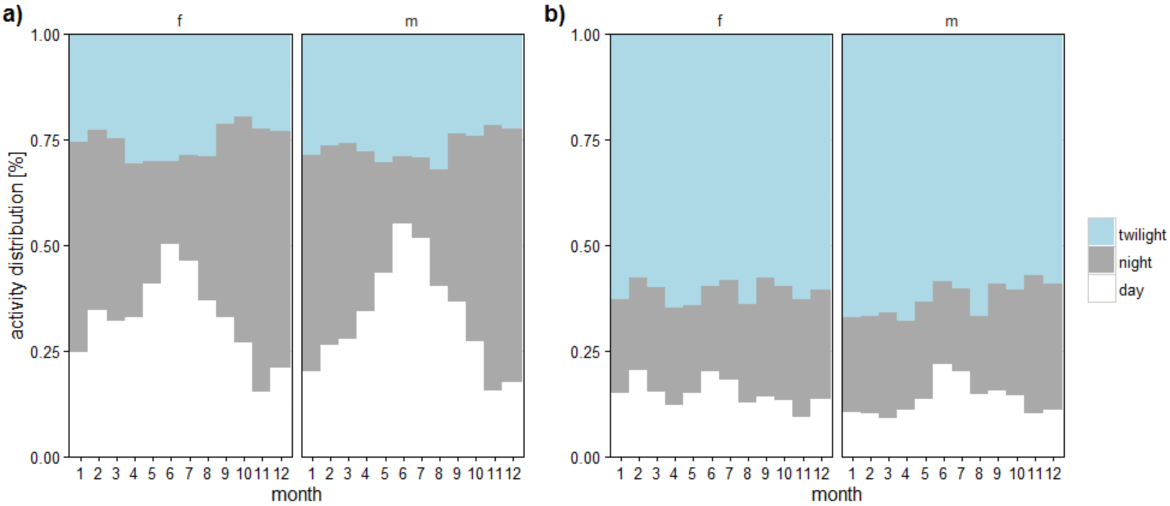

Figure 22: Diurnal distribution of activity. (a) Absolute values; (b) considering the length of respective time of day (day, night, twilight).

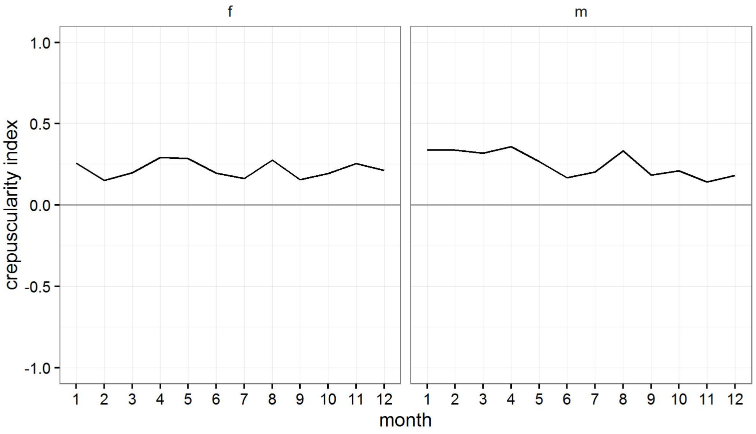

Figure 23: Crepuscularity Index. Activity during the twilight hours. Negative values indicate increased activity outside of the twilight hours while positive values indicate increased activity during twilight hours.

Daytime activity is lowest during the winter, spring, and autumn. Differences between male and female deer serve merely as an indication for possible differences in annual activity patterns, as the small sample size does not lend itself to statistically significant conclusions.

The crepuscpularity index (Figure 23) confirms that the deer are most active during the twilight hours throughout the entire year, with a slight decrease in the summer months. These results are in accordance with findings by Ensing et al. (2014), who compared the crepuscular and diurnal activity between two populations at different latitudes. The increase of diurnal activity in during summer months presumably stems from a decrease in night-time activity as the crepuscular activity levels remained rather constant throughout the year. Contrary to the findings by Ensing et al. (2014), who found red deer to be either nocturnal or diurnal, red deer in the Lower Engadine valley show both diurnal activity patterns in winter months as well as nocturnal patterns in spring and autumn (Figure 24).

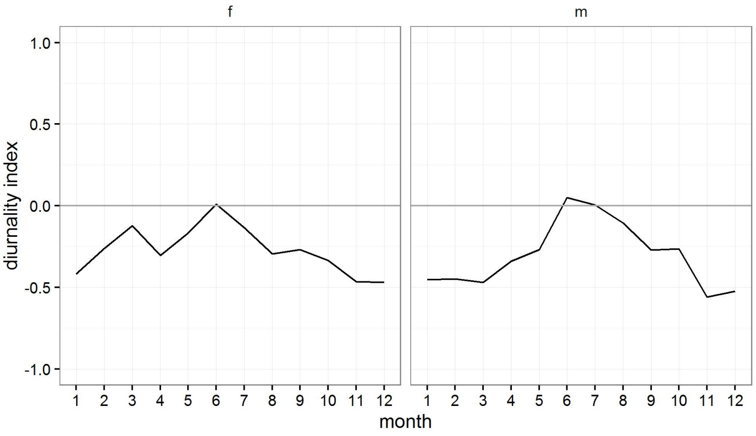

Figure 24: Diurnality index. Negative values indicate increased activity during the night (preference of nocturnal activity) while positive values indicate increased activity during the day (preference of diurnal activity).

Figure 25 shows boxplots of the average speed per individual aggregated by month. Noticeable is the increase in activity during the night in the colder winter and spring months when compared to daytime activity. In fact, daytime activity across all individuals only exceeds night-time activity in June and July. Additionally, there is a noticeable peak in night-time activity during the months of November and December, especially for resident individuals. On the one hand, this increase coincides with the timing of migration to the winter home range in the valley floor, though given that the most noticeable increase is observable for resident individuals suggests that the reason for the increase may be best sought in the fine regulation hunt which begins in late November (see Section 3.1.1). The avoidance of predation during this period may have caused the deer to shift their activity into the night. Furthermore, there is an increase in monthly activity during the month of May, which coincides with the migration to summer home ranges.

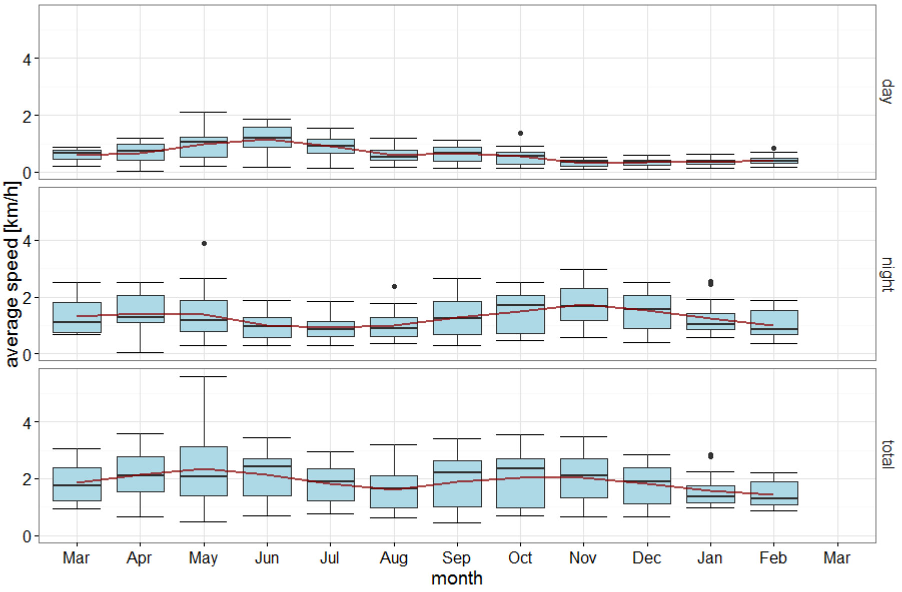

Figure 25: Mean monthly activity values for all individuals during the day, night, and in total. The red line indicates the average accross all individuals.

Investigation into overall weekly activity values and the activity during the fine regulation hunt, including the preceding and following 7 days as a reference, showed no noticeable increase in activity values. The expected marked increase during days of fine regulation hunting did not materialize, though certain patterns can be inferred. Further, considering the proportion of location within forested areas, no patterns are recognizable that deviate from the prevailing preference of forested areas during the day found in Section 5.3.

5.2.2 Discussion

Results of activity patterns demonstrated a distinct bimodal activity distribution for daily activity which persisted throughout the year. Peaks were found to be typically associated with twilight hours, shortly before or thereafter. Findings are consistent with observations by Hofmann & Nievergelt (1972), who were able to show that red deer in same area tended to leave their resting places in forested areas around 6 – 8 o'clock in the morning and returned roughly around 18 – 19 o'clock. This suggests, that the increase in activity during twilight hours is mainly associated with movements between resting places and grazing sites. The tendency of crepuscular activity was additionally confirmed by the analysis of the amount of activity in relation to the respective time of day. On average, crepuscular activity levels were higher than the combined activity levels during the night and day (as shown by the crepuscularity index) throughout the entire year and remained relatively constant. The comparison of activity levels between daytime and night-time hours, excluding the twilight hours (diurnality index), revealed that red deer, on average, were more active during the night than during the day. However, an increase in the index value is observable during the summer months, resulting from an increase in daytime activity at the cost of night-time activity. Additionally, a small peak in daytime activity is observable for hinds, which may be associated with an increase in foraging activity, as they tend to require more nutrition for the growth of the foetus and milk production (see Section 2.1.3).

Results are in accordance with findings by Georgii (1981) and Georgii & Schröder (1983), who carried out similar research using VHF techniques for red deer in the Bavarian Alps. Activity peaks were consistently found to coincide with twilight hours throughout the year, indicating that activity cycles are strongly linked to a circadian clock. Previous research into the extent to which human disturbance, hunting or the presence of natural predators influenced the daily activity distribution of red deer revealed that in areas where such influence is reduced, the bimodal activity distribution is less apparent, if not completely removed (Kamler et al. 2007). Therefore, it is likely that the preference of crepuscular activity is, at least in part, caused by hunting and human disturbance in the study area. For both male and female deer, a slight increase in crepuscular activity is observable in August. While this may be attributable to increased foraging activity in preparation for the tiring rutting period, the possibility that the peaks were caused by an unfavourable constellation of sampling intervals and the relative duration, start and end of twilight periods cannot be fully ruled out. An inspection of the crepuscularity index on the individual level revealed that index values do show a certain degree of fluctuations throughout the year, though no distinct pattern was observable. Values are relatively constant and ranged between –0.38 (h63) and 0.53 (h20). Additionally, whether the individual red deer showed migration or resident behaviour did not seem to influence crepuscularity index values, though the small sample size does not permit any conclusive statements. Due to the relatively short duration of twilight periods, it is conceivable that an increase in sampling frequency would lead to more conclusive results and would allow for the derivation of ecologically meaningful insights.

Interestingly, the decrease in nocturnal activity in summer months and the strong preference of night-time activity during the colder months is somewhat counter-intuitive. One would expect red deer to be more active during the late afternoon in winter, given that that is typically the warmest part of the day (Kamler et al. 2007). Furthermore, it has previously been shown that red deer show nocturnal hypometabolism as part of their overwintering strategy (Arnold et al. 2004), meaning that energy expenditure is significantly reduced during the night and early morning hours. Since it has been suggested that, in addition to hunting, the exposure to human recreational activity is perceived as a predation risk by red deer (Jayakody et al. 2008), it is likely that the shift towards increased nocturnal activity is caused by an increase in anthropogenic disturbances in the valley floor. On an individual level, individuals h40, h59, h62, h63 and h81 show the most distinct unimodal distribution of diurnality index values, with maximum values occurring during summer months (see Appendix A.2 for visualisations). Interestingly, of these individuals, all except h40 spent the summer either in or close to the SNP, indicating that red deer are aware of the safety provided by the hunting ban in the park. In contrast h21 exhibited a preference for nocturnal activity in July and August which can be explained by the proximity of the summer home range to the village of Tschlin in the valley floor. Furthermore, the most distinctly resident individual, h79, showed a consistent preference for nocturnal activity, which suggests that the increased human activity in the valley floor causes the main activity period to shift into the night. A similar behaviour can be observed for h80, though the remaining resident individual (h22) does not exhibit such a strong preference of nocturnal activity, most likely due to the habitat characteristics of its home ranges, which consist mostly of forested areas.

Total monthly activity values (Figure 25) support the nocturnal tendencies of red deer in the area discovered by the diurnality index. Overall, nocturnal activity contributed more to total activity than did diurnal activity, except from the months of June and July where diurnal activity exceeded nocturnal activity. Further, there is a noticeable increase in total monthly activity beginning in May, which is most likely associated with an increase in foraging activity as the snow cover melts. This will accommodate the increased energy demands caused by the relatively low availability of forage during the winter, the production of milk and growths of the foetus for hinds, and to a certain extent the growth of antlers for males (see Section 2.1.3). Most noticeably, Figure 25 revealed a large increase in average locomotion speed in November. According to the annual variation in the intensity of food intake outlined by Wagenknecht (1996) in Section 2.1.3, this increase is unlikely to have been caused solely by an increase in foraging activity. Further, a slight increase in activity values in September and October can be observed. While a closer inspection of this period may have yielded interesting results with regards to behavioural responses during the coarse regulation hunting period, the temporal overlap of this period with the rutting season would have made the interpretation of results a difficult task.

The aggregation of locomotion speeds on a weekly basis (see Appendix A.2) demonstrated that the activity peak in November cannot be attributed to an increase in activity in a single week. Therefore, all the dates of the fine regulation hunting period were further investigated with the aim of detecting responses to hunting pressure in the average locomotion speeds of the red deer. Results showed no distinct pattern of an increase or decrease in activity during the days of fine regulation hunting. Furthermore, the proportion of fixes within forested areas seemed to be largely unaffected by the hunting activity. While slight indications of behavioural responses to hunting pressure can be observed, it would be naive to claim predator avoidance to be the sole reason, without further investigation. Nonetheless, the absence of any change in resource selection (i.e. forest areas) is in accordance with findings by Cleveland et al. (2012), who found that hunting pressure did not alter resource selection, though movement rates, as measured by first passage time, were significantly higher during hunting periods. This indicates that the locomotion speed is not crucial when measuring the response to hunting pressure, but rather the combination of various movement parameters, which are implicit in the calculation first passage time.

5.3 Cover

5.3.1 Results

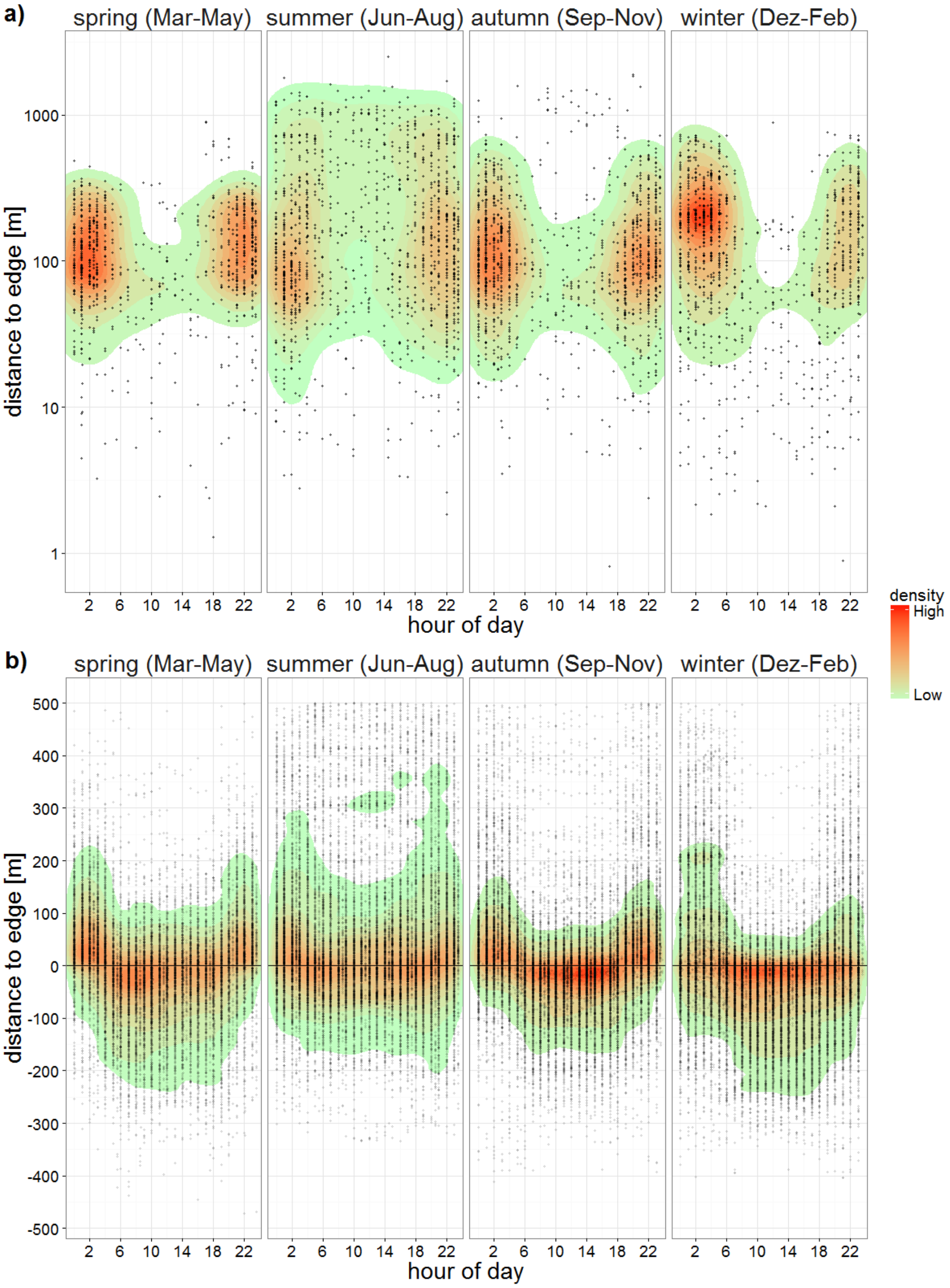

Figure 26: Timing of the daily maximum distance from the forest edge (a) and distance of all locations from forest (b). Each point represents the time and distance from the edge of the forest. The coloured surface represents the density of the underlying point distributions and allows for the identification of frequent distances at any point in time.

The time of the maximum distance from forested areas (as shown in Figure 26a) indicates that deer stray the farthest from the forest during the night and twilight hours throughout the year. The most distinct bimodal distribution can be observed during the winter months, with only a handful of maximum distances occurring during the day. Maximum distances also occur more frequently during the day in summer months, though the densest time can still be found during hours of darkness.

Similarly, by plotting the time and distance of each point to the edge of the forest, with negative values representing locations within the forest (Figure 26b), a u-shaped distribution becomes apparent. Negative values thus occur most frequently during the day, while positive values cluster around the hours of darkness. Furthermore, the densest areas are typically between -100 and 100 meters from the edge of the forest. The u-shaped distribution persists throughout the year, though it is more pronounced during spring, winter and autumn months. During the summer, the density of points close to the edge of the forest decreases. Especially dense areas do not seem to follow the same u-shaped distribution.

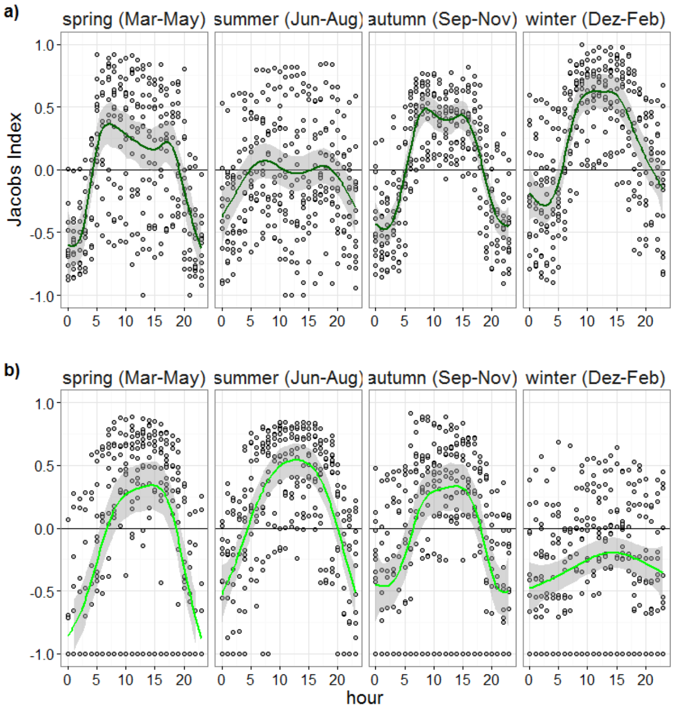

Figure 27: Jacobs index (1973). Temporal variation in preference of forested areas (a) and shrublands (b) for all individuals. Positive values indicate preferential resource selection. Green lines show the fitted local regression (LOESS) and the grey area the 95% confidence interval.

In order to remove the effect of variations in the contribution of forested areas to the habitat of red deer the Jacobs Index was computed based on seasonal home ranges. The computation of the Jacobs Index (1973) revealed a distinct preference of forested areas (Figure 27a) during the day for spring, autumn, and winter, with values rising above 0 around 5 o'clock in the morning (LMT) and dropping below 0 around 8 o'clock in the evening (LMT). Preference values never exceeded 0.5 throughout the year. For autumn and winter the distributions is distinctly unimodal, while a slight bimodal tendency is noticeable for all seasons except winter, with a minor decrease in index values around mid-day. For summer, the same unimodal distribution can be observed, though the fitting of the local regression suggests that there is no distinct preference of forested areas during the summer months, as values rarely rise above 0.

Similarly, a unimodal distribution can be observed for shrublands (Figure 27b), though the season of least preferential selection can be found in winter. Furthermore, perfect negative selection (values of -1) occurs a lot more frequently than for forested areas, meaning that despite shrublands contributing to the 95% volume contour line of the seasonal KDE, no locations were found to lie within these areas.

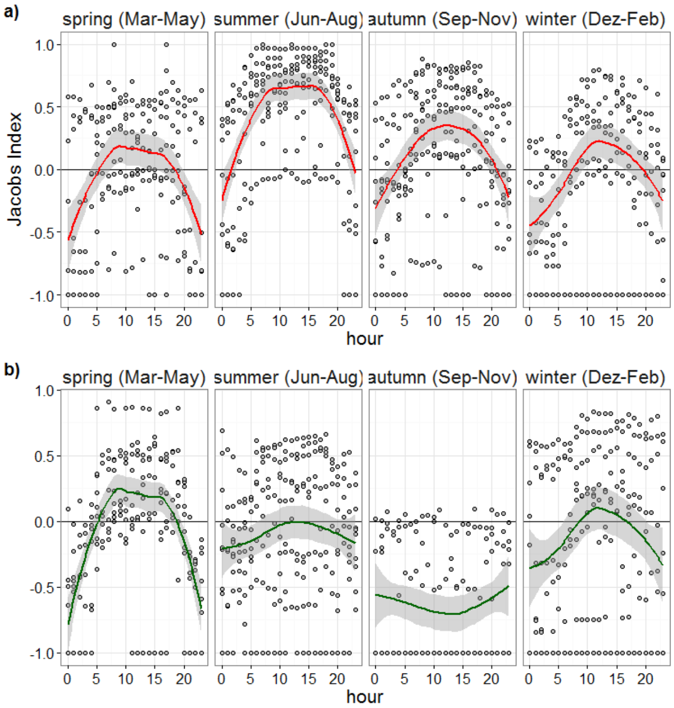

Figure 28: Jacobs index (1973). Temporal variation in preference of game reserves (a) and wildlife refuges (b) for all individuals. Positive values indicate preferential resource selection. Green lines show the fitted local regression (LOESS) and the grey area the 95% confidence interval.

Preferential use of wildlife refuges and game reserves (Figure 28) showed a similar unimodal distribution during the course of the day, with preferences reaching the highest values during the daylight hours. In general, the positive resource selection of game reserves was higher than for wildlife refuges. For game reserves, index values frequently rose above 0.5 during the day in summer months. For wildlife refuges, the index revealed less clear patterns, especially during summer and autumn. Values of -1 occurred almost throughout the entire day, indicating that although a wildlife refuge was available in the respective seasonal home range, the deer did not make use of it in all cases. The highest values occurred during spring and winter months for wildlife refuges.

5.3.2 Discussion

The possibility of combining contextual information and in-depth knowledge about the ecology of red deer in order to make up for suboptimal sampling frequencies for the detection of behavioural patterns relating to foraging activity and cover was explored in the section above. Naturally, such investigations involve a considerable amount of interpretative evaluation, which is why the plausibility of findings will be supported with literature where possible.

Investigation of distances of GPS locations to the edge of the forest revealed that the darkness allows the red deer to stray farther from the edge of the forest than during the day, resulting in the distinctive bimodal pattern, with peaks typically occurring shortly before dawn and after dusk and only few positions occurring during the daylight hours. This supports evidence found by Adrados et al. (2008) that the use of structural cover prevailed during the day, while visibility during the night showed greater variability. Ultimately, findings support the notion that red deer habitat selection is influenced primarily by a trade-off between foraging activity and the necessity of cover. The investigation of the annual variability of interactions with forest ecosystems revealed that during summer the bimodal distribution of maximum daily distances was less pronounced. While this may be attributable to increased foraging activity in preparation for the rutting season (see Section 2.1.3), it is possible that the decrease in human disturbance at higher altitudes allows the red deer to graze during the day, which would explain the increase in daytime activity (see Section 5.2.1). While the exact cause cannot be unequivocally determined without ground-based observations, the increase of positions outside of the forest during the day and the more frequent occurrence of maximum distance outside of forested areas supports the notion that red deer increase their foraging activity in summer. However, it is important to consider the decrease in forested areas at higher altitudes, as this is likely to lead to a decrease of locations within the forest. A comparison of altitude and the proportion of locations outside of forested areas revealed a positive correlation (r = 0.49). Therefore the proportional contribution of forested areas must be considered in order to determine, whether the increase in locations in open landscapes is a function of altitude or a function of decreased preference due to increased foraging activity.

The analysis of the temporal variation of the Jacobs Index clearly showed that the red deer in this study exhibited positive selection of forested habitats during the hours of daylight in spring, autumn, and winter. However, during summer months no positive selection of woodlands could be determined. These results contrast strongly with findings by Godvik et al. (2009), who found that red deer in Norway show a preference for forested habitats during the summer and winter but less so in spring and autumn. Nonetheless, the negative selection of forested areas supports the hypothesis that the increase of positions in open habitats during the summer months is linked to intensified foraging behaviour at times of low anthropogenic disturbance and not caused merely by the decrease of forested areas in elevated regions. Overall, the increased preference of forest habitats during hours of daylight is most likely linked to the avoidance of human disturbance, especially in winter months. While previous studies have found red deer to be most active during the warmer part of the day in winter for reasons relating to energy conservation (Kamler et al. 2007), the results of the preferential resource selection and activity measures indicate that the red deer in the Lower Engadine valley seem to shift their main active period into the night, where the darkness provides the necessary cover. The same analysis for shrublands, which constitutes an ideal habitat for red deer, revealed very similar results, while the most noticeable change occurred in winter, with values frequently dropping below 0, even throughout the day. The reasons for this negative selection may be the increased visibility, which is more likely to be avoided due to increased anthropogenic disturbance in the valley floor. Furthermore, the decrease in vegetation canopy, which in turn affects the depth of the snow pack, has been shown to have an adverse effect on the energy expenditures for locomotion and may further reduce the availability of forage (Beier & McCulloch 1990; Malnar et al. 2015; Schmidt 1993). At this point it must be noted that the classification of landcover types presumably introduced a certain amount of uncertainty, as distinguishing between forest and shrublands is not an easy task. Nonetheless, results indicate that the seasonal importance of the two landcover classes does differ rather strongly.

The analysis of possible positive selection of wildlife refuges and game reserves surprisingly revealed a very similar unimodal distribution, with the lowest values on average occurring during the night, and rising to a maximum during the day. The lower values observable for wildlife refuges during summer months is in accordance with the intended function of such areas. Given that they serve to protect the animals against human disturbance (see Section 3.1.1), especially in winter, they are typically located at lower elevations than are game reserves. The higher index values for wildlife refuges in winter and spring suggest that the animals do take advantage of the non-structural cover provided by the restriction of human activities in wildlife refuges. The considerably high index values for game reserves in summer are most likely influenced, in part, by the establishment of summer home ranges in and around the SNP, although other individuals did frequent other game reserves in the Lower Engadine valley.

However, the causality of this positive selection by red deer is not entirely clear. Both game reserves and wildlife refuges are typically established, where favourable habitat characteristics can be found[5], therefore it seems unsurprising that a positive selection can be detected. How-

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[5] Personal communication with Hannes Jenny AJFGR, 02.12.2016

ever, given that the same unimodal distribution can be found with low values during the night indicates that there is an element of security red deer associate with these areas. Merely the fact that of the 12 individuals analysed, 8 set up their summer home range in and around the Swiss National Park underlines the importance of game reserves as an element of non-structural cover. Furthermore, given that only 20% of the total area of game reserves are covered by forest it seems unlikely that the preference of such areas can be solely attributed to the cover provided by dense vegetation, though this effect cannot be entirely ruled out. Burcham et al. (1999) found evidence supporting the notion that red deer are aware of the cover provided by game reserves by observing an increase in the utilization of private land refuges where hunting is banned.

At this point it must be noted that the computation of home ranges on a smaller temporal scale (e.g. months instead of seasons) for the determination of expected values may have led to different index values, though it was assumed that the computation of KDE for seasonal home ranges would exclude any large effect of potential exploratory movements.

5.4 Grazing Site Detection

5.4.1 Results

A total of 27 potential grazing sites were detected by the DBSCAN algorithm (see Appendix A.3 for detailed visualisations), though the number of locations contained by them varied considerably. Furthermore, one of the detected sites was removed because the inspection of .kml files showed locations of that cluster to be located within a forest aisle consisting mainly of scree (cluster number 2, h80). A comparison of the produced .kml files showed that grazing sites in the valley floor were frequently located in agricultural areas, while those in elevated regions were characterized by heterogenic landscapes with alpine pastures interspersed with bushes, rocks, and debris.

Figure 29 shows the visibility at grazing sites (a) and the proportion of fixes during the night (b) for clusters associated with summer (n = 11) and winter home ranges (n = 14). Visibility values were generally higher at grazing sites associated with winter home ranges than at such associated with summer home ranges. Similarly, on average the proportion of fixes during the night was higher at winter grazing sites and additionally showed a lot less variation (as indicated by the error bars).

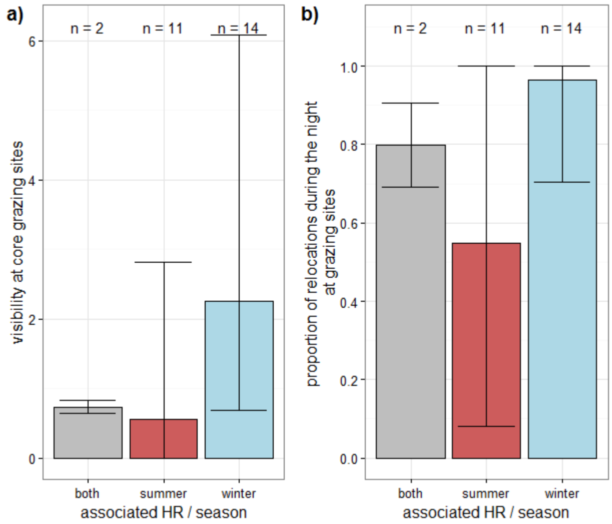

Figure 29: Visibility and proportion of GPS locations acquired during the night for grazing sites associated with summer and winter home ranges. The error bars show minimum and maximum values.

The additional analysis of differences in visibility, NDVI and distances to hiking trails was limited to grazing sites associated with summer home ranges, given the absence of any significant amount of positions during the day at grazing sites in winter home ranges. Furthermore, the low portion of fixes during the day within core areas of grazing sites associated with summer home ranges for individuals h23, h61, h80, and h81 led to their exclusion. As mentioned in Section 4.5, this analysis was limited to positions located within Switzerland. A total of 6 potential grazing sites remained and were further analysed with respect to variations in NDVI values, visibility values and distance to hiking trails between the hours of dailylight and darkness. Specifically, this included clusters found for individuals h41, h59, h60, h62, h63, and h82 (see Table 4).

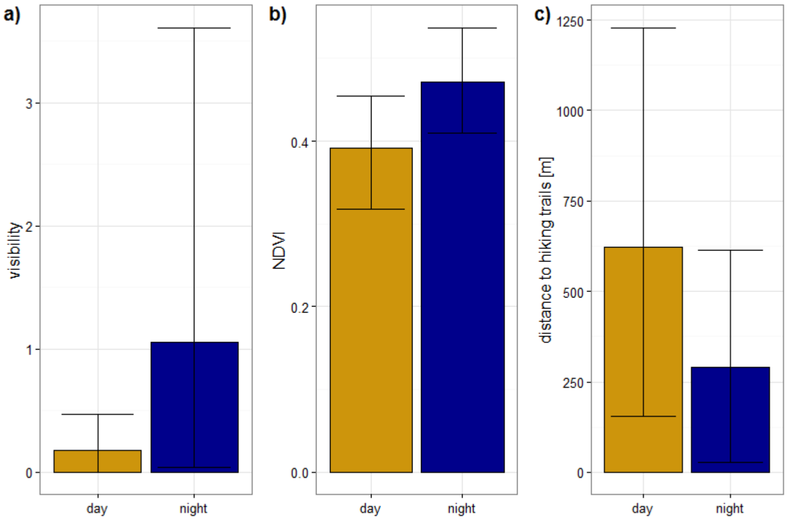

Figure 30: Comparison of Visibility, NDVI, and distance to hiking trails for grazing sites associated with summer home ranges where comparable number of relocations during the night and day were found (Table 5). The error bars show minimum and maximum values.

Table 5: Visibility, NDVI, and distance to hiking trails at core grazing sites of individuals h41, h59, h60, h62, h63 and h82 for locations during the day and during the night.

		day			night		
n pts	**id**	**visibility**	**NDVI**	**distance to trails**	**visibility**	**NDVI**	**distance to trails**
486	**h41**	0.155	0.454	664.084	0.152	0.521	613.313
483	**h59**	0.473	0.435	153.981	1.100	0.479	74.570
633	**h60**	0.175	0.318	641.787	0.458	0.452	491.098
638	**h62**	0.003	0.409	1228.770	0.037	0.426	471.930
174	**h63**	0.035	0.418	739.531	0.989	0.537	63.320
480	**h82**	0.252	0.318	304.276	3.610	0.410	28.413

Results showed that for the above-mentioned individuals, visibility and NDVI values were, on average, higher during the night compared to daytime values, though considerable variations were found between individuals, especially with regards to visibility and distance values. Inversely, the distance to hiking trails was larger during the day than during the night. Figure 31 shows the spatial distribution of points in within the grazing site associated with the summer home range of h82. For visualization purposes, alpha shapes (see Edelsbrunner et al. 1983; Pateiro-López & Rodriguez-Casal 2010) were used to delineate the entire cluster found with the DBSCAN algorithm. On an individual level, visibility values during the night were found to be similar or considerably higher when compared to daytime values. When visibility values were

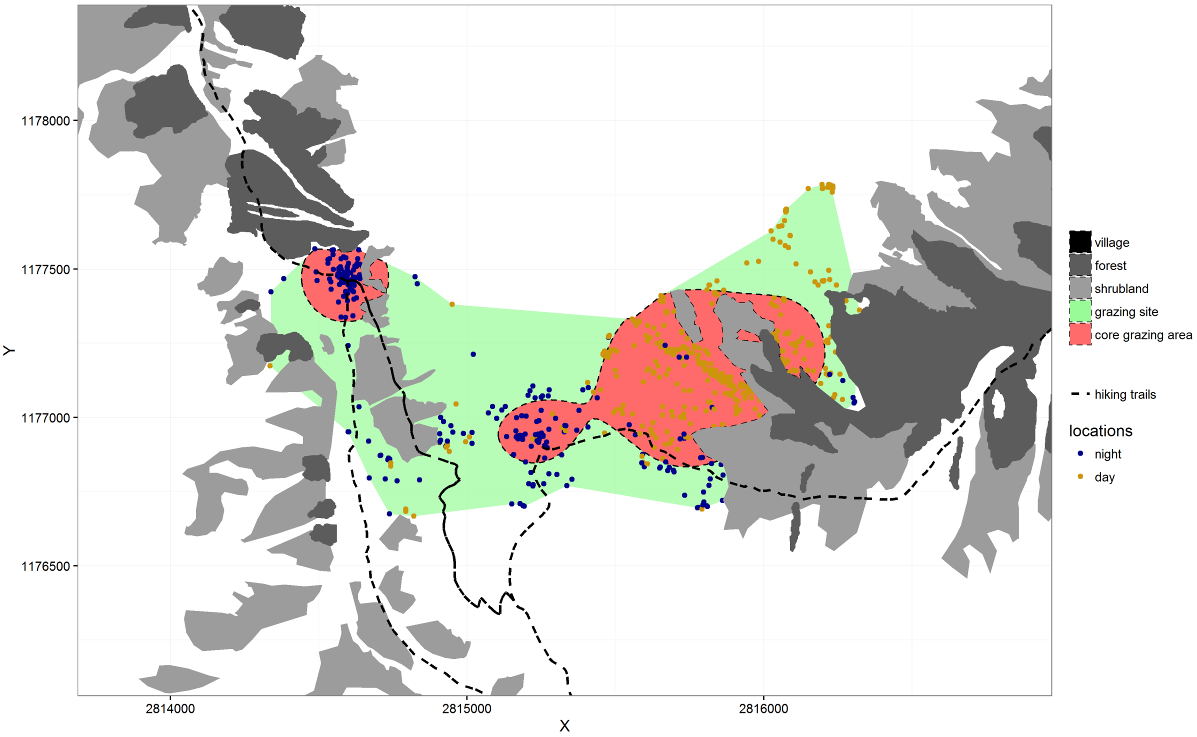

Figure 31: Grazing site associated with the summer home range of individual h82. The green area delineates the grazing site by means of alpha shapes and includes all points of the cluster. Red areas represent areas of intense use, i.e. the 50% volume contour line of KDE (h_{ref}).

noticeably higher during the night (h82, h63), the distance to hiking trails was also noticeably higher. On the other hand, when no large change in visibility was observable between day and night, the distance to hiking trails remained relatively constant too. NDVI values were consistently larger during the night.

5.4.2 Discussion

Overall, the characterization of locations associated with grazing sites revealed the importance of the darkness as an element of cover for red deer in the Lower Engadine valley. Especially when the deer reside in the valley floor, the increase of locations in open areas during the hours of darkness is remarkable (Figure 29). The simultaneous increase of visibility values at locations within grazing sites during winter most likely stems from the increased density of hiking trails in the valley floor and less from the topographic characteristics of the area. This notion is further strengthened by the fact that the red deer generally spend a greater amount of time inside forested areas during this time. I therefore argue that the hiking trails can be used as a proxy for the increased human disturbance overall, which is naturally higher in the valley floor where there is a higher density of anthropogenic influence. To compensate for the increased visibility and disturbance at grazing sites in the valley floor it can be deduced that the deer tend to shift their grazing activity into the night, as shown by the proportion of locations during the night in winter areas. These findings are in accordance with the results of the temporal variability of activity patterns (see Section 5.2), which showed that the red deer in the Unterengadin valley are most active during the darkness in winter. This pattern is recognizable for almost all individuals. While the lowest proportion of fixes during the night in winter was found for individual h63 (0.7), inspection of the visibility values showed that the median visibility value of locations within the core grazing site was considerably lower during the day (0.1) than during the night (3.6), suggesting that the animal either increased its distance from hiking trails or made use of topographic cover during the day. This demonstrates the trade-off between cover and the need to graze once more. The reduction of predation risk by seeking forested areas as cover seems to be of greater importance during the hours of daylight, while the darkness provides the necessary cover desired to graze in close proximity to inhabited areas.

Of those grazing sites, which were characterized by a significant number of relocations during the daytime (see Table 5), the consistently larger distance to hiking trails and lower visibility values show that the red deer prefer areas farther from human disturbance during the day. It is worth noting that the marked decreases in visibility values are most likely linked to an increase in distance to hiking trails, as this distance was used to weight the visibility values in the computation of the visibility map. The largest differences in visibility occur, when difference between locations during the night and during the day are exceptionally large. Further, it is crucial to keep in mind that the analysis of visibility is based on an abstraction of the topographic characteristics and is to a large degree dependent on the grid size of the DSM. Small topographic features, which may be used as structural cover (Mysterud & Østbye 1999) are thus less likely to be detected. While positions close to hiking trails do occur during the day, they are less common, leading to the conclusion that red deer tend to avoid grazing sites in proximity of hiking trails during the day. Supporting these findings, Pépin et al. (1996) observed that the Pyrenean chamois typically moved more frequently and remained more vigilant when close to hiking trails, indicating that the hiking trails are perceived as a source of human disturbance by ungulates.

With respect to the NDVI values within the core of grazing sites that exhibited a noticeable spatio-temporal distribution, values during the night were consistently higher compared to locations during the day, indicating that under the cover of darkness, red deer are able to seek the nutrient rich vegetation otherwise unavailable due to the susceptibility to human disturbance at those locations. This tendency was also uncovered for white-tailed deer (*Odocoileus viranianus*) by Armstrong et al. (1983) and Beier & McCulloch (1990). The most recognizable diurnal variation in grazing site locations can be observed for h82 (see Figure 31). The grazing site frequently visited during the night to the northeast of the daytime grazing site was found to be located within alpine pastures. Overall, results showed that despite the 30 meter resolution of the Landsat images and the heterogeneous nature of the landscape at higher altitudes, the trade-off between higher quality forage and cover can be clearly demonstrated by using the NDVI as a proxy for forage quality. Furthermore, the suitability of hiking trails as a proxy for human disturbance is demonstrated for red deer in the alpine environment. Yet, it must be noted that the large variation in the size (i.e. the number of locations within the clusters) of the detected grazing sites, suggests that the diet of red deer does vary considerably. This has been found to be the case in previous studies (see Christianson & Creel 2008; Gebert & Verheyden-Tixier 2001). For instance, relatively small clusters were found for h61, h23, and h80 in clusters associated with summer home ranges.

6 Synthesis

An issue that is oftentimes associated with movement data collected using both VHF and GPS technologies is what is commonly referred to as the semantic gap (Laube 2014) in computational movement analysis (CMA). It addresses the difficulty of deducing knowledge from the low-level movement data about what the observed animal was doing at any point in time. Much of the focus in CMA is directed at at the development of methods to close this gap. Increasingly, additional information is captured during the data acquisition process, such as accelerometer data or data relating to the physiology of the studied species (Cagnacci et al. 2010). However, when such data is missing, the validation of results relies mostly of previous findings, expert knowledge and interpretive evaluation.

6.1 Insights and Contributions

The analysis of **migration patterns and the extent of the migration** (Research Question 1) showed that whilst the red deer is regarded as a migratory mammal, the manifestation of this phenomenon does show considerable intraspecific variations, especially with regards to the distance between seasonal home ranges. The patterns found ranged anywhere between completely resident individuals to such exhibiting disjoint seasonal home ranges. Additionally, certain deer exhibited rutting grounds outside of their seasonal home ranges. Considering the role of this method as an extension to the Raetikon project (Reimoser et al. 2014), I can conclude that the necessity to visually inspect the results of the classification is partially removed, due to the inclusion of a density based criterion. This is exemplified by the drastic reduction of individuals classified as resident after the second criterion.

With respect to the **seasonal variations in diurnal activity budgets** (Research Question 2) and how they reflect the ecology of red deer, results demonstrated the influence of light intensity on the activity of red deer. The activity maxima consistently occurred during the twilight hours throughout the day. Variations in diurnal activity showed a strong seasonal pattern, with red deer preferring diurnal typically activity in summer and nocturnal activity for the remainder of the year. Mean monthly activity values showed indications of the intensified foraging activity following the winter while the increase of diurnal activity in summer was assumed to be linked to a decrease in human disturbance at elevated regions. Further indications for anthropogenic influences were found although no strong evidence of hunting activities was detected.

The embedding of locations with **contextual information** (Research Question 3) provided by forests and shrublands provided valuable insights in to the role of such areas as safe havens, especially during the day. The temporality and magnitude of preferential selection of these two investigated land cover types confirms the importance of both structural and non-structural cover in habitat selection. Furthermore, results support the red deer management strategies that are in effect in the area by the identification of preferential selection of wildlife refuges and game reserves.

Lastly, through the analysis of **spatio-temporal patterns at grazing sites** (Research Question 4) the trade-off that red deer face was exemplified. Locations during the day were frequently associated with lower quality forage whilst areas of higher quality forage and higher human disturbance were typically visited during the night. This implies that predator avoidance, even given the absence of any natural predator in the study area, is still a crucial driving force in the behaviour of red deer, Further, the applicability of remotely sensed data in ecological studies was largely confirmed.

6.2 Limitations

The findings of this study are largely limited to the Lower Engadine valley and the 16 individuals investigated. Therefore, inferences about the entire population or populations of neighbouring valleys are not feasible. Additionally, the absence of accelerometer data and the use of locomotion speed as a proxy for activity inevitably introduces a bias, as speed is ultimately a function of the sampling rate.

The detection of grazing sites was largely based on the assumption that preferred or nutritional vegetation would lead to an accumulation of locations over time. While this assumption is supported by the literature, the possibility of other factors leading to a dense cluster of points in open landscapes cannot be fully excluded. Further, considering the importance of shrublands in red deer habitat selection, the unsuitability of detecting ground vegetation within this land cover type using remotely sensed data (especially NDVI) somewhat impeded the detection of important grazing sites. Nonetheless, limiting the investigation to grazing sites located within open landscapes aided the validity of the results concerning the trade-off between grazing activity and risk avoidance, as deer are more susceptible to predation and disturbance in open landscapes.

Regarding all results involving home range estimators it is worth mentioning, that the choice of estimator may lead to different results, though expert knowledge suggests that the application of KDE yields plausible results for the methods used throughout this thesis. The reliance on expert knowledge to validate results leads over to another limitation of this study.

As stated by Laube (2014) the validation of results remains a difficult task and much of the derived information relies on interpretation of findings based on the knowledge of previous studies on the behaviour of red deer. Efforts of bridging this semantic gap are moving in the direction of acquiring additional data to support or augment results of CMA studies. This thesis has shown, that with limited data on the actual movement paths of the animal, meaningful ecological conclusions can still be derived by embedding locations with contextual information.

6.3 Outlook

As the collars are gradually retrieved, accelerometer data will become available for the individuals studied in this thesis. The newly gained data could then be used to re-evaluate the results of this study and provide valuable insights into activity bursts, and grazing and resting periods. Furthermore, with newly emerging techniques of pattern recognition in movement data (see Gurarie et al. 2016) additional knowledge could be gained relating to the space use and ecology of red deer in the Lower Engadine valley, particularly on finer temporal scales.

The choice of a finer temporal scale (e.g. weeks) with regards to preferential resource selection of specific landcover types may reveal further behavioural mannerisms, especially considering the hunting periods. Perhaps resource selection could even be extended beyond the analysis of containment to other topological relationship.

Additionally, the investigation of data collected in the sister project TIGRA (Hirschwanderungen im Grenzgebiet Graubünden-Tessin werden untersucht, 2014) could reveal indications for differences in behaviour between the two populations.

Lastly, migration movements (or lack thereof), which constitute an integral part of red deer ecology, require further attention. Especially inquiries into the extent to which environmental factors such as snow cover, temperature and plant greenness influence the timing of migration have not yet been addressed in the study area to my knowledge.

7 References

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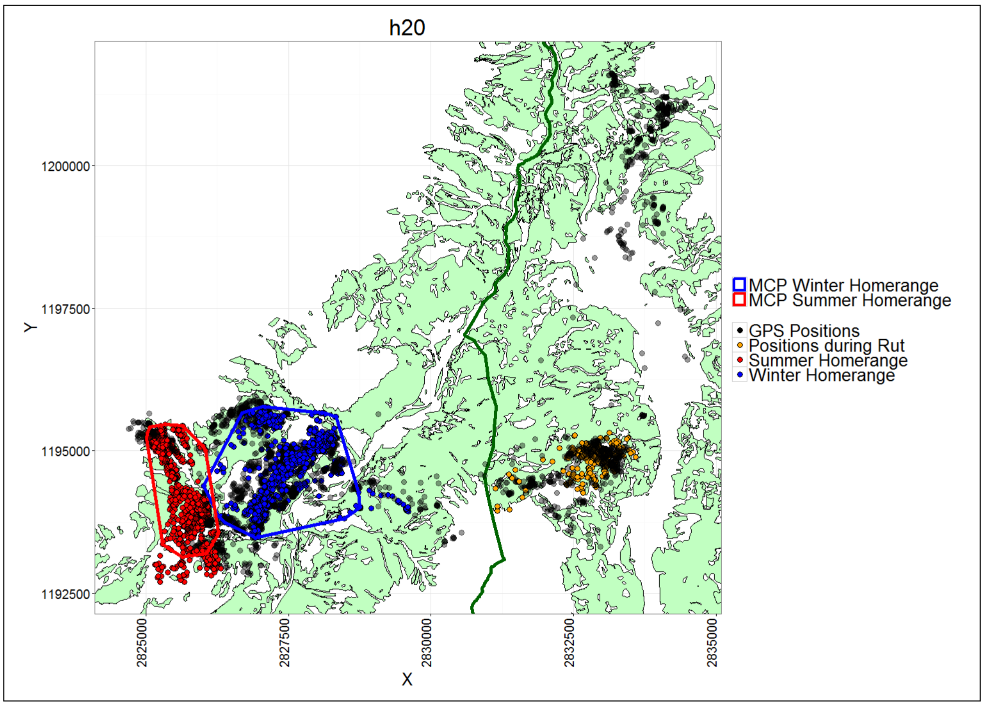
8 Appendix

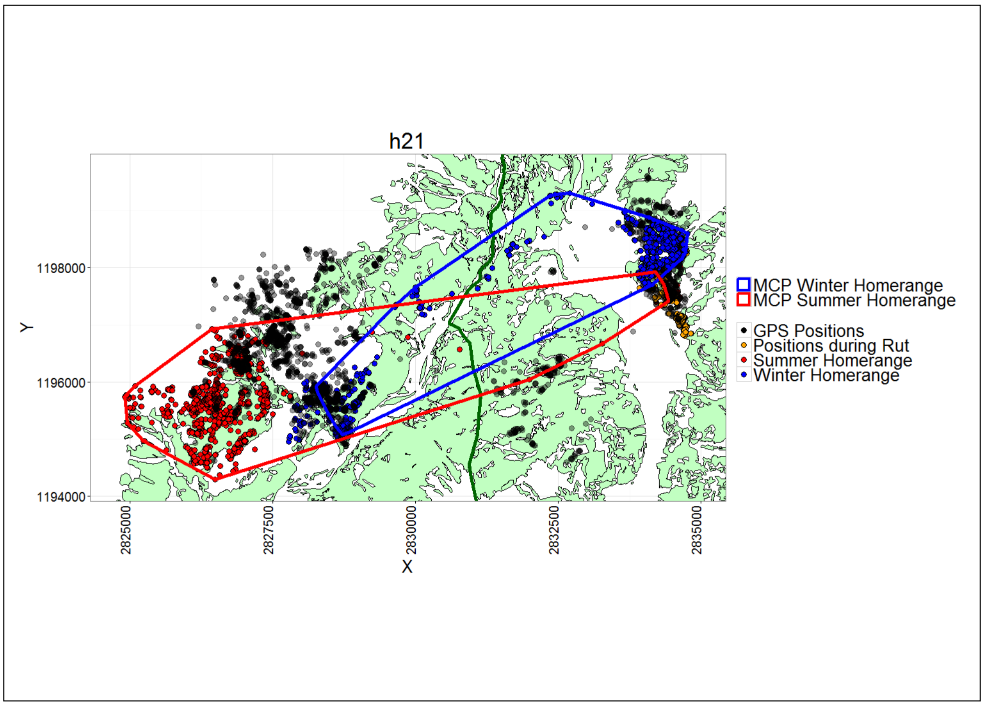
The subsections of the appendix appear in the same order as they are referenced in the text and use the same section titles.

A.1 Classification of Migration Patterns

The following maps show the seasonal space use of the 16 red deer in the study area. Red points indicate the points used to determine the summer home range (July and August) and blue points indicate points used to determine the winter home range (January and February). The colours of the resulting MCPs (95%) are coloured accordingly. Points associated with the rutting season (24.09.15-10.10.15) are orange. The thick green line and red shaded area present in certain maps represent the Swiss border and Swiss National Park respectively. Green areas represent forested areas.

These maps show the classification of migration after the first criterion of overlapping seasonal home ranges, as determined by MCPs. The ID of each individual can be found in the map title.

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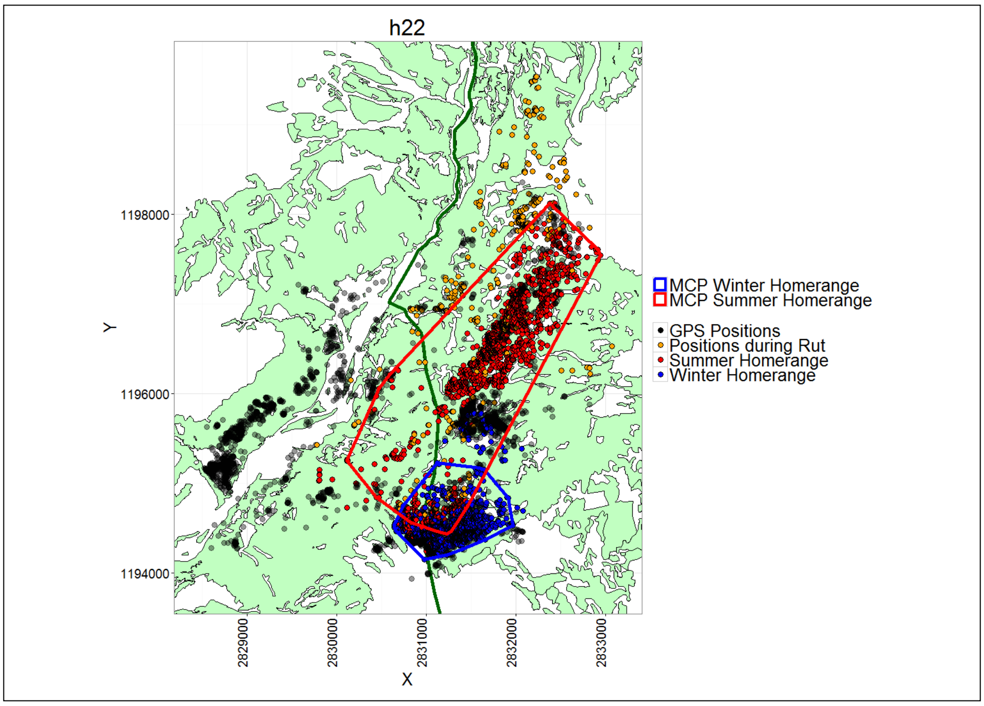
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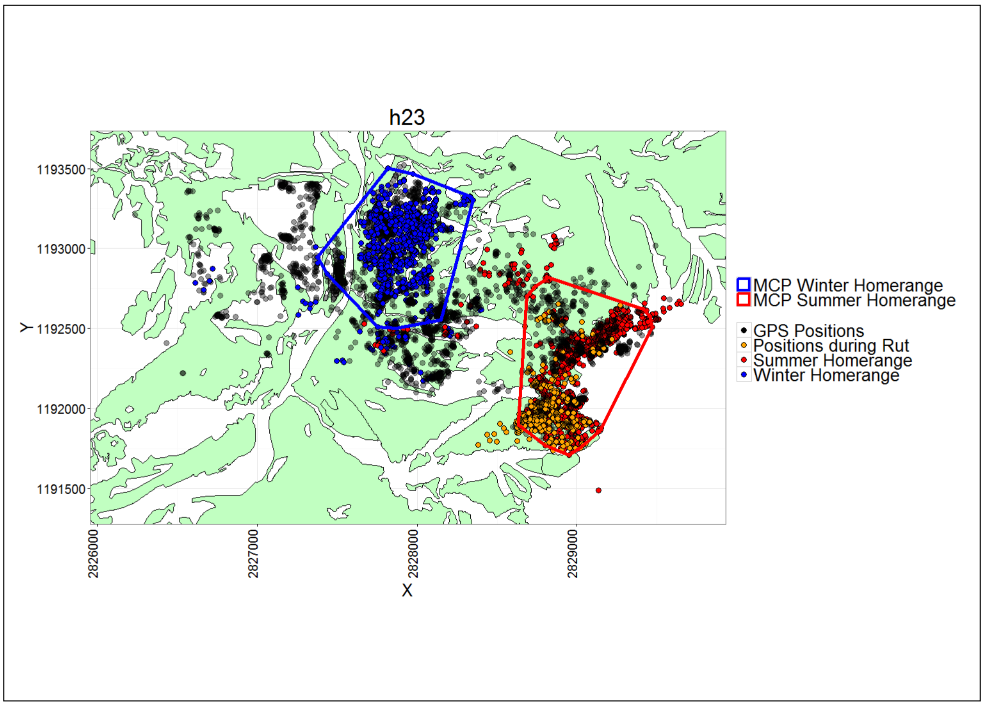
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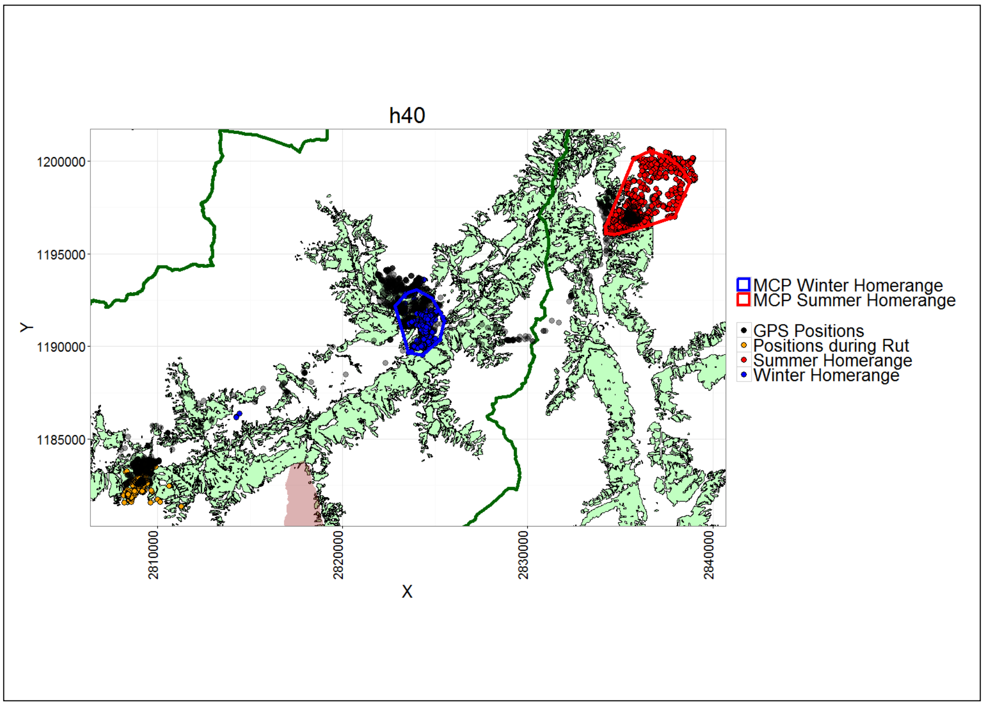
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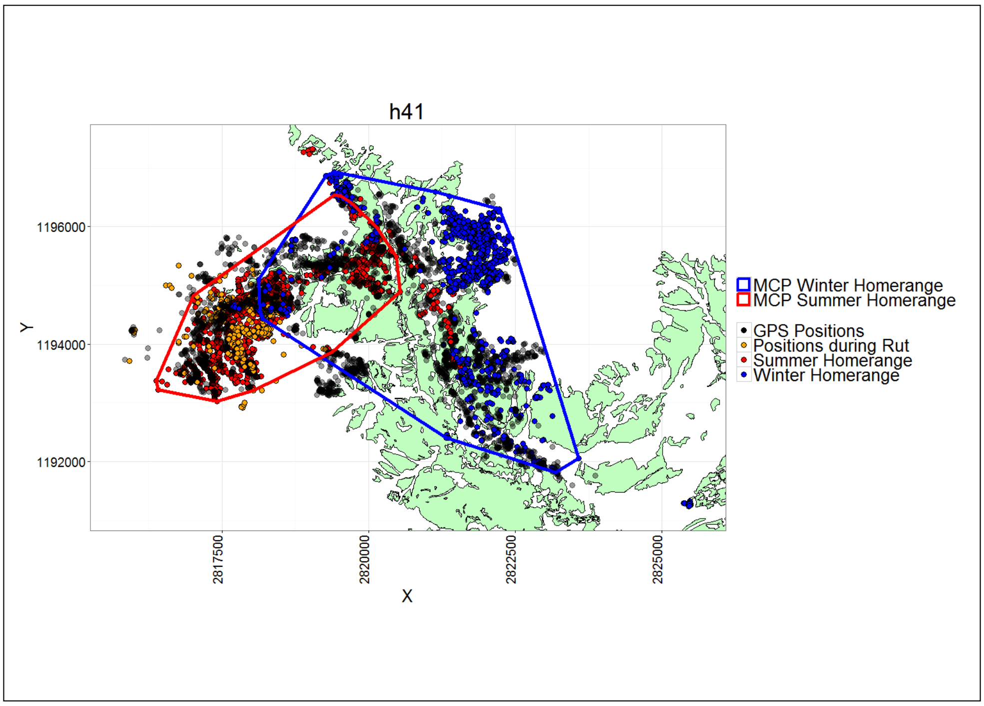
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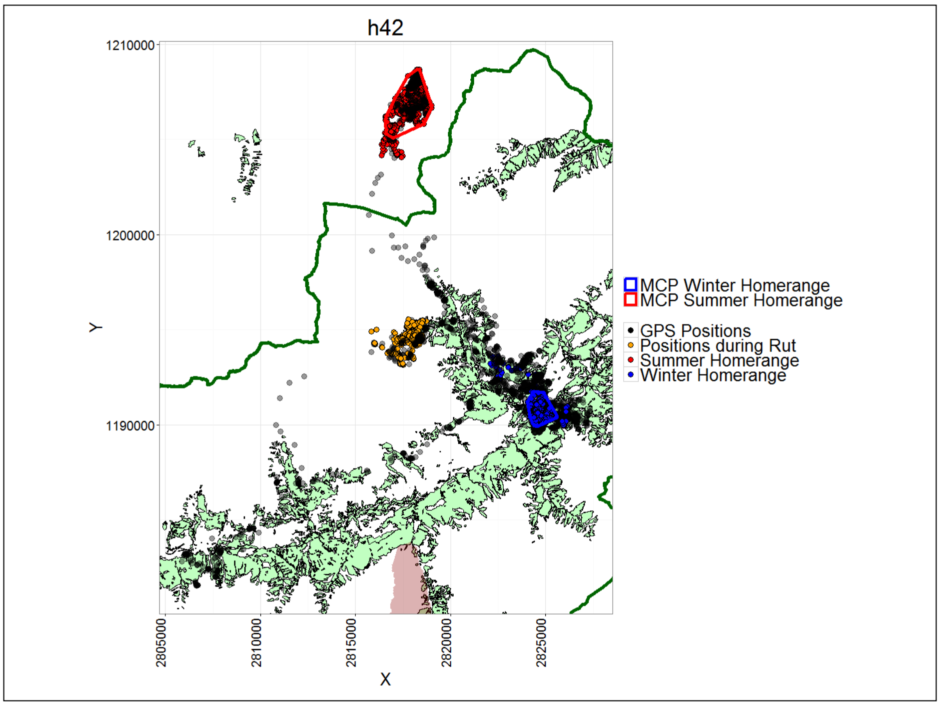
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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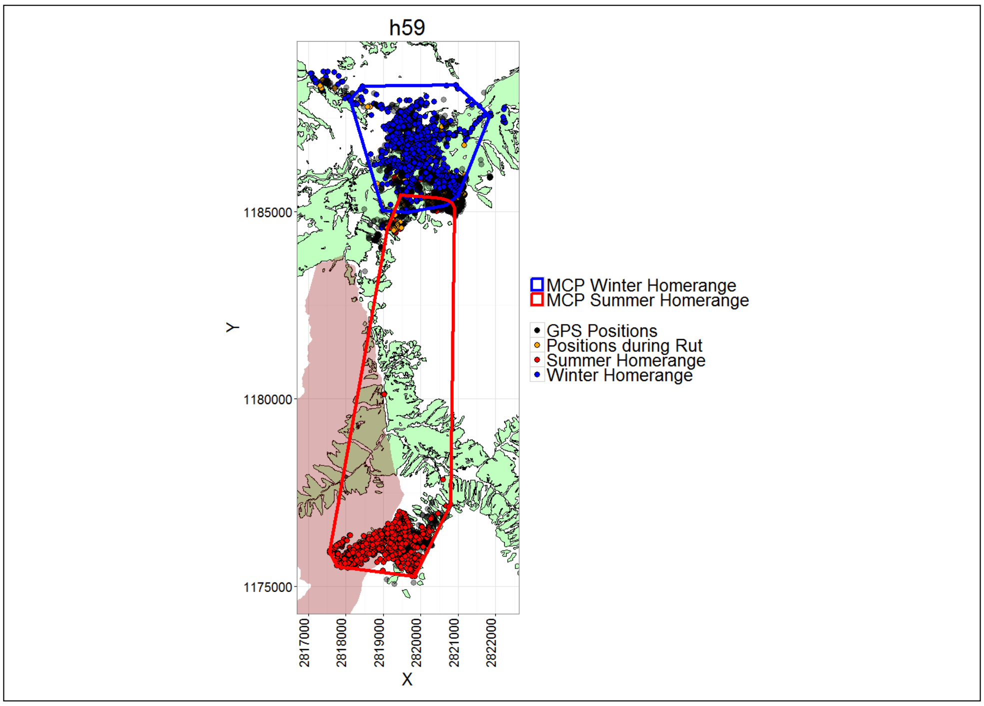
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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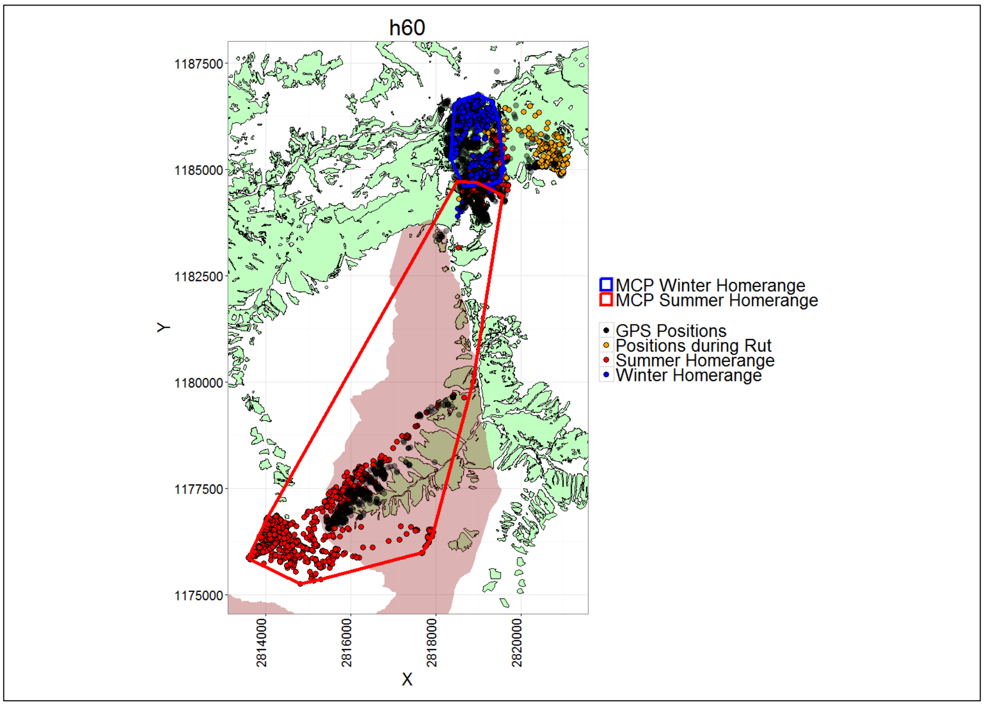
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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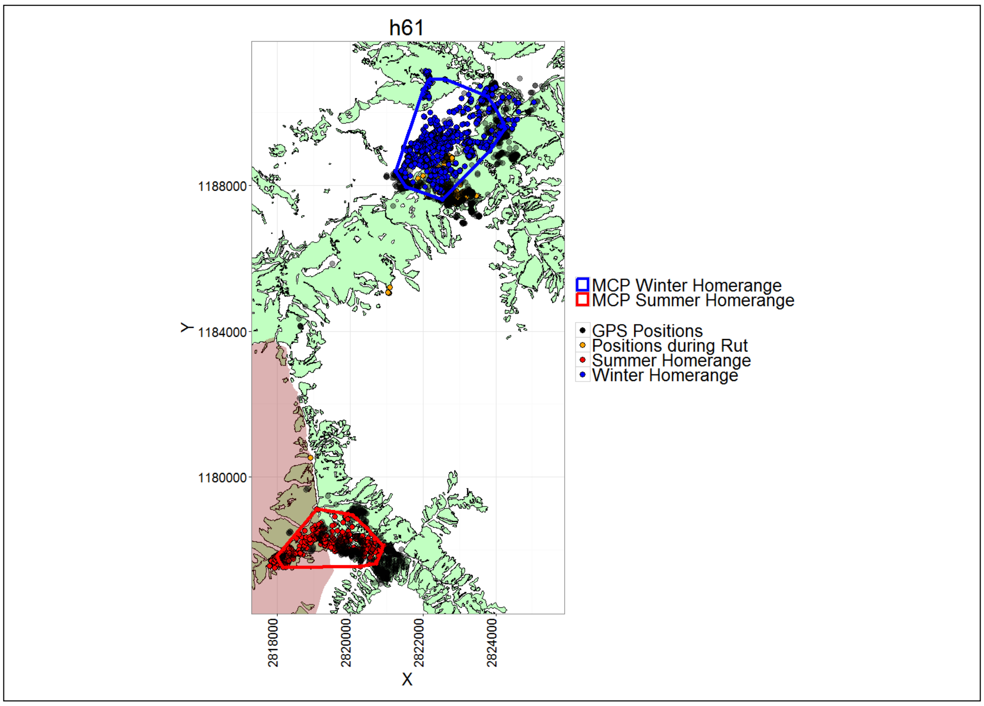
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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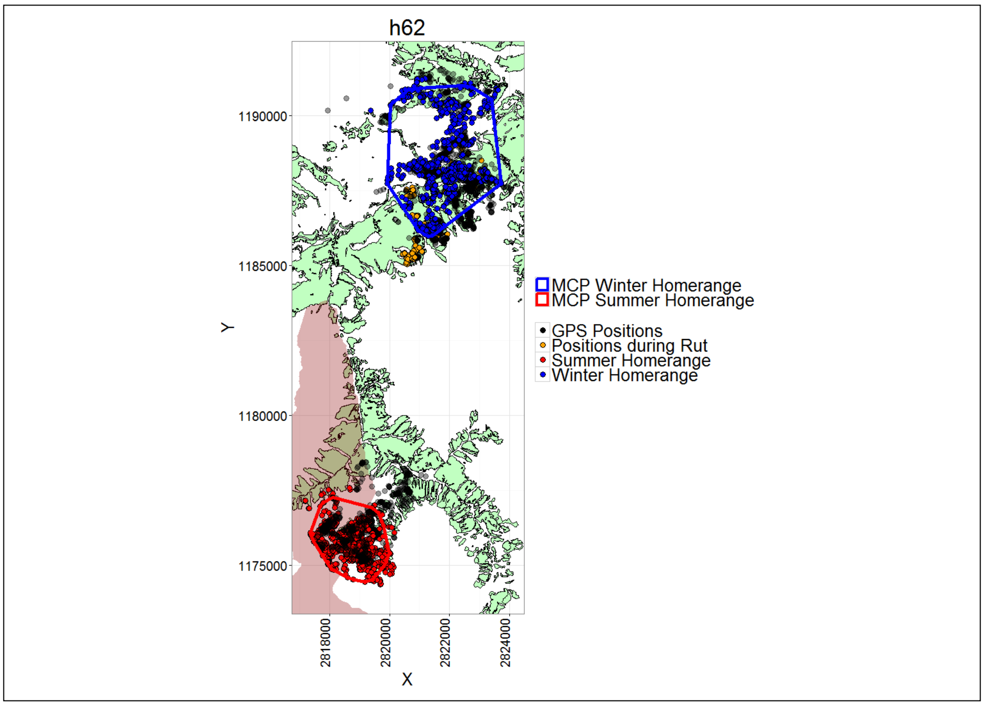
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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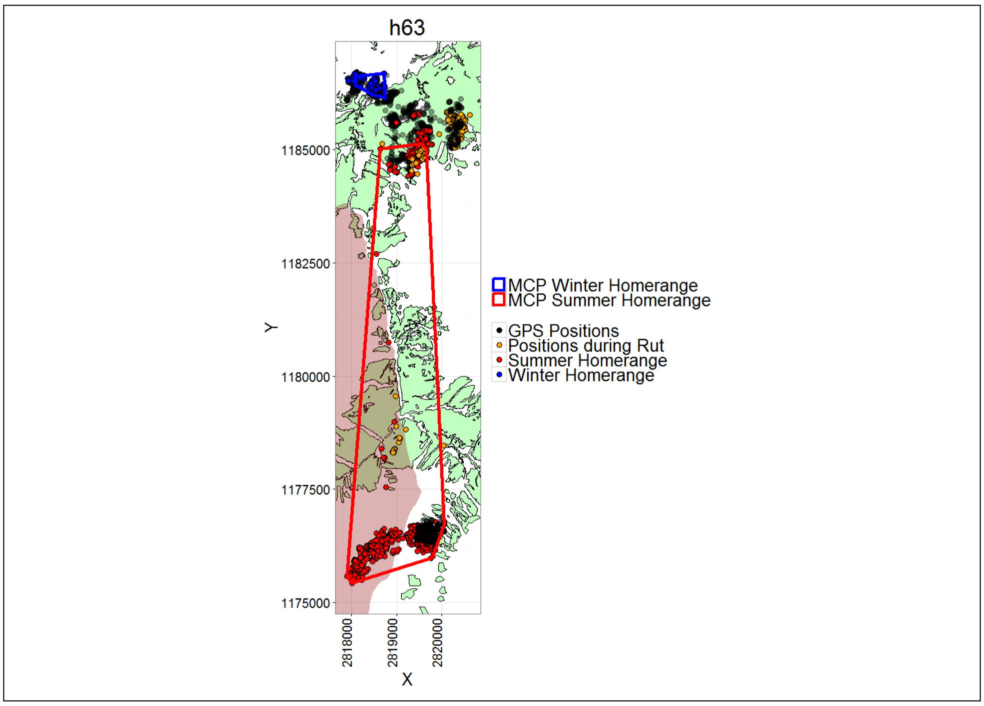
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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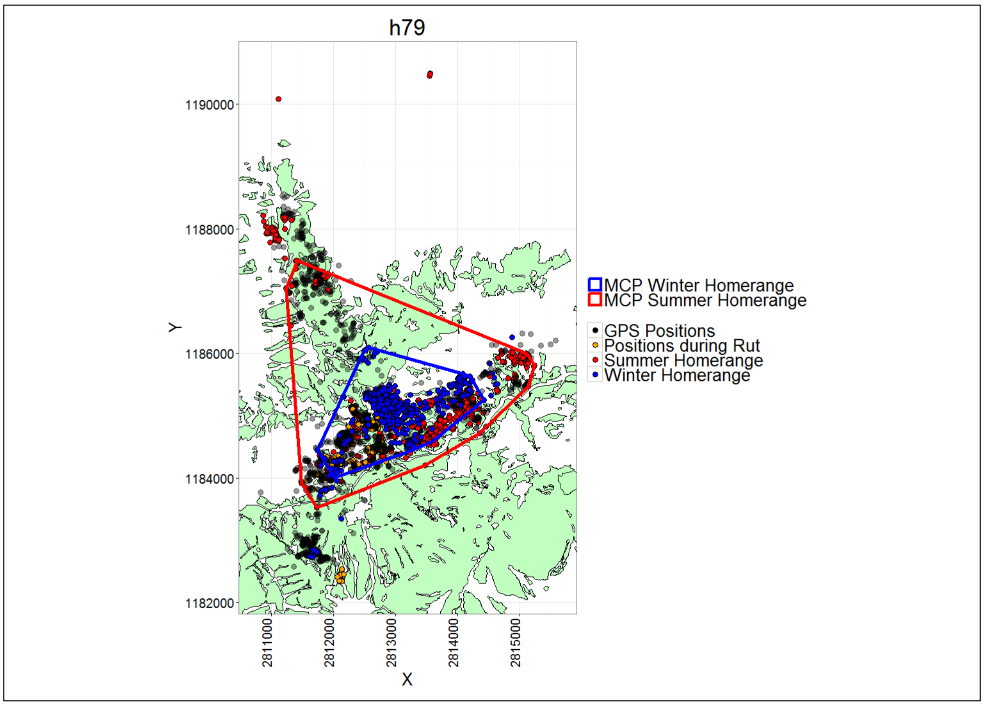
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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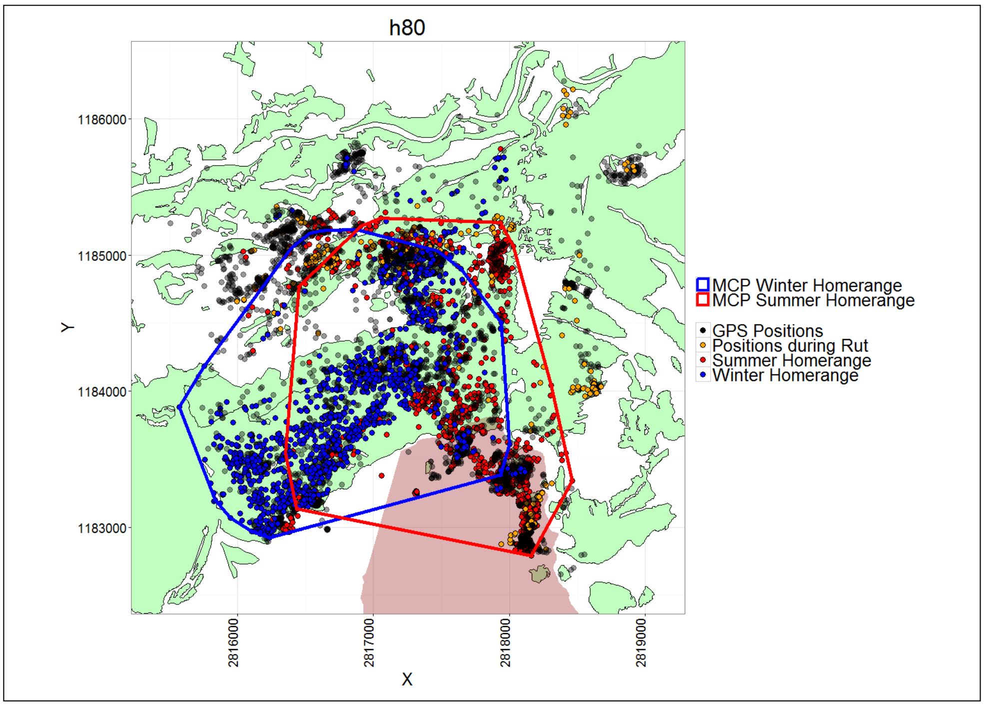
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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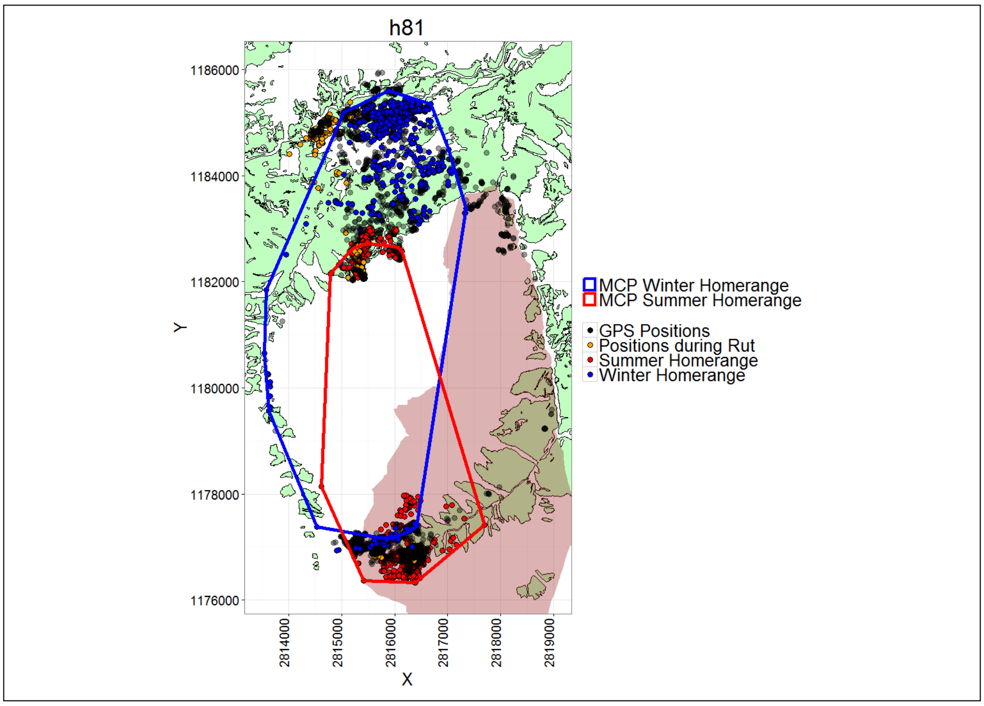
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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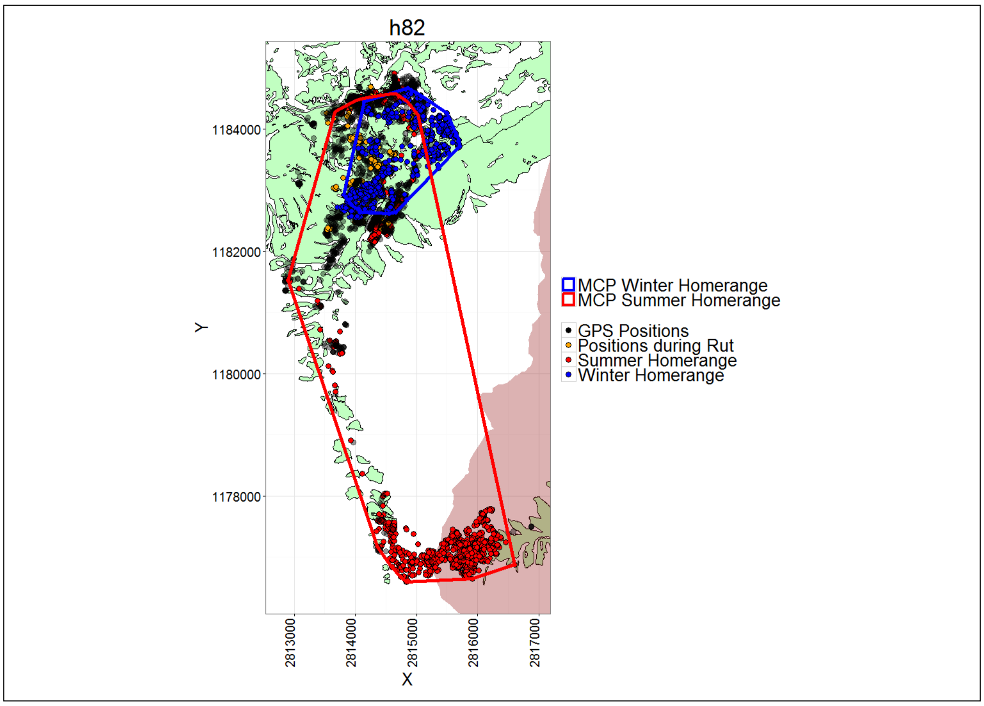
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange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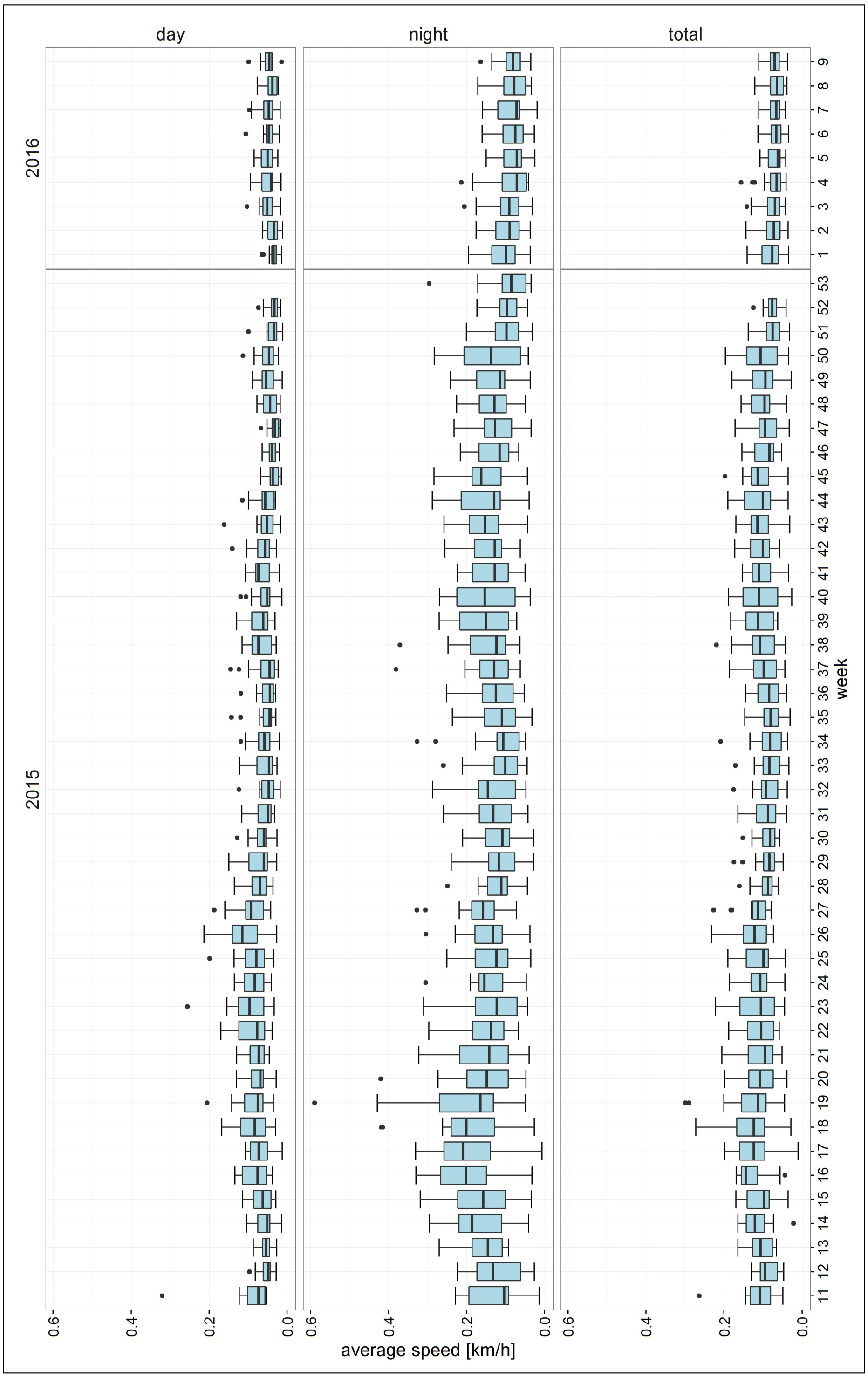
X
MCP Winter Homerange
MCP Summer Homerange
GPS Positions
Positions during Rut
Summer Homerange
Winter Homerange

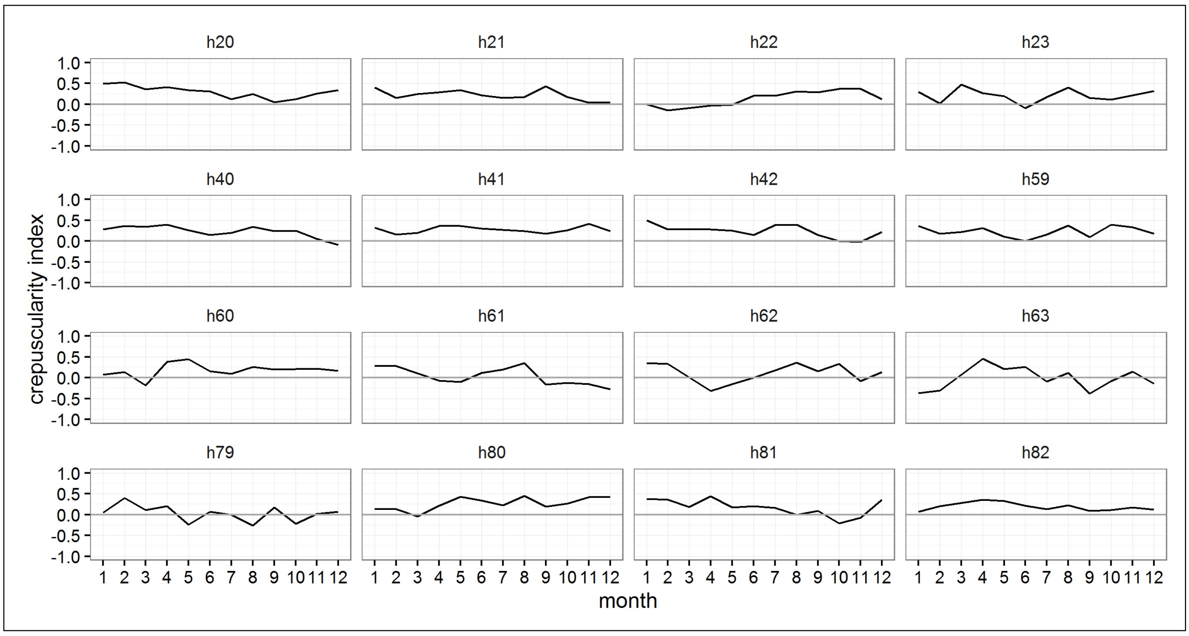
A.2 Temporal Variability in Activity Measures

The following figures provide insights into the behaviour on an individual level and are used in the discussion of results on the temporal variability of activity levels.

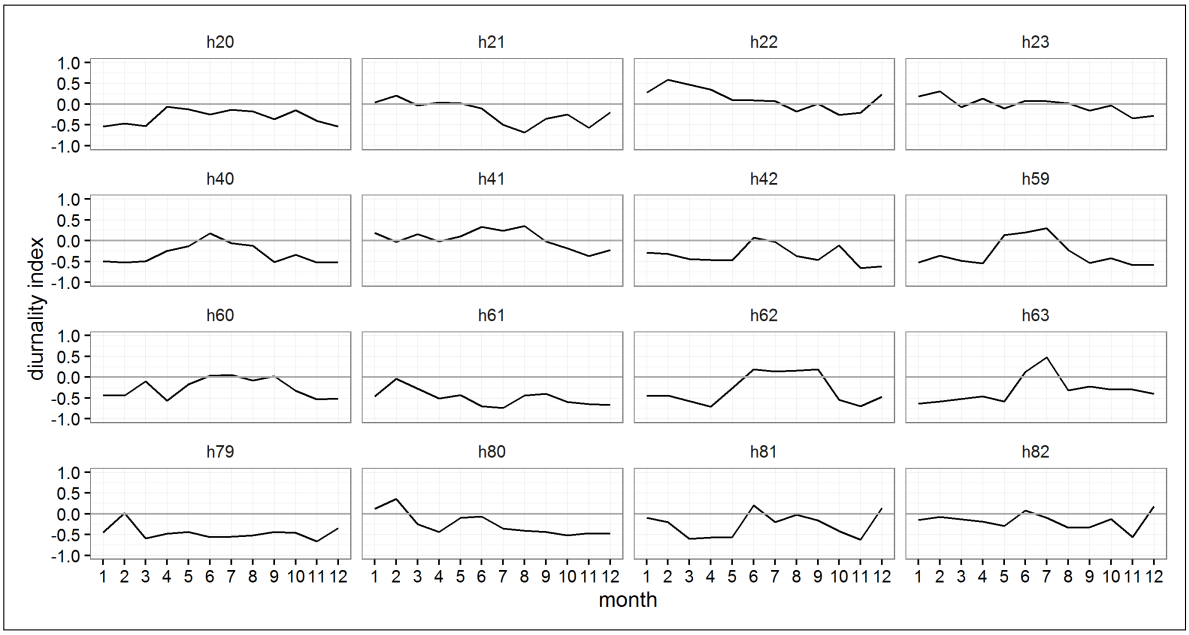


Boxplots of activity (locomotion speed) aggregated by week. Weeks represent 7 day periods starting on January 1 of each year and not calendar weeks.

crepuscularity index for all individuals



diurnality index for all individuals



A.3 Grazing Site Detection

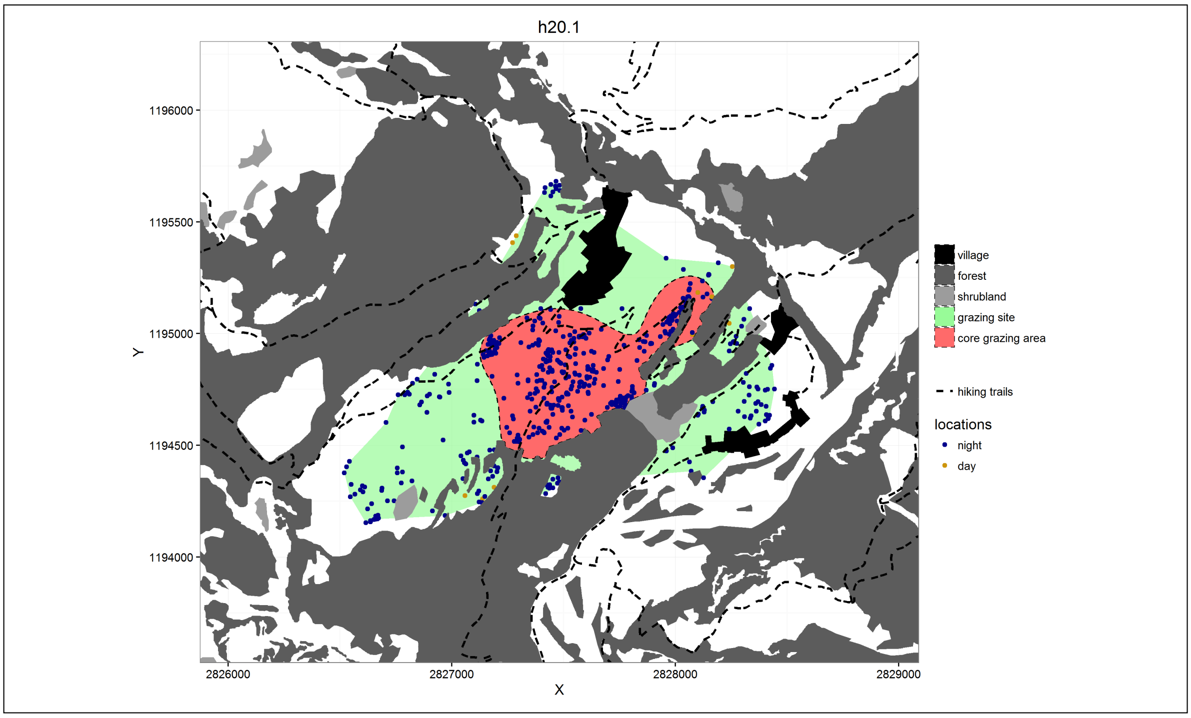
The following section provides a detailed overview of the results of the detection of grazing sites and their characterization with respect to median NDVI, visibility and distance values. Detailed maps include the entire cluster delineated as alpha shapes, the core grazing site (KDE, 50% volume contour line), hiking trails, as well as forests, shrublands and villages. Image titles show the animal ID with the first decimal place corresponding to the number of the cluster.

Table 6: Median NDVI, visibility and distance values for all grazing sites.

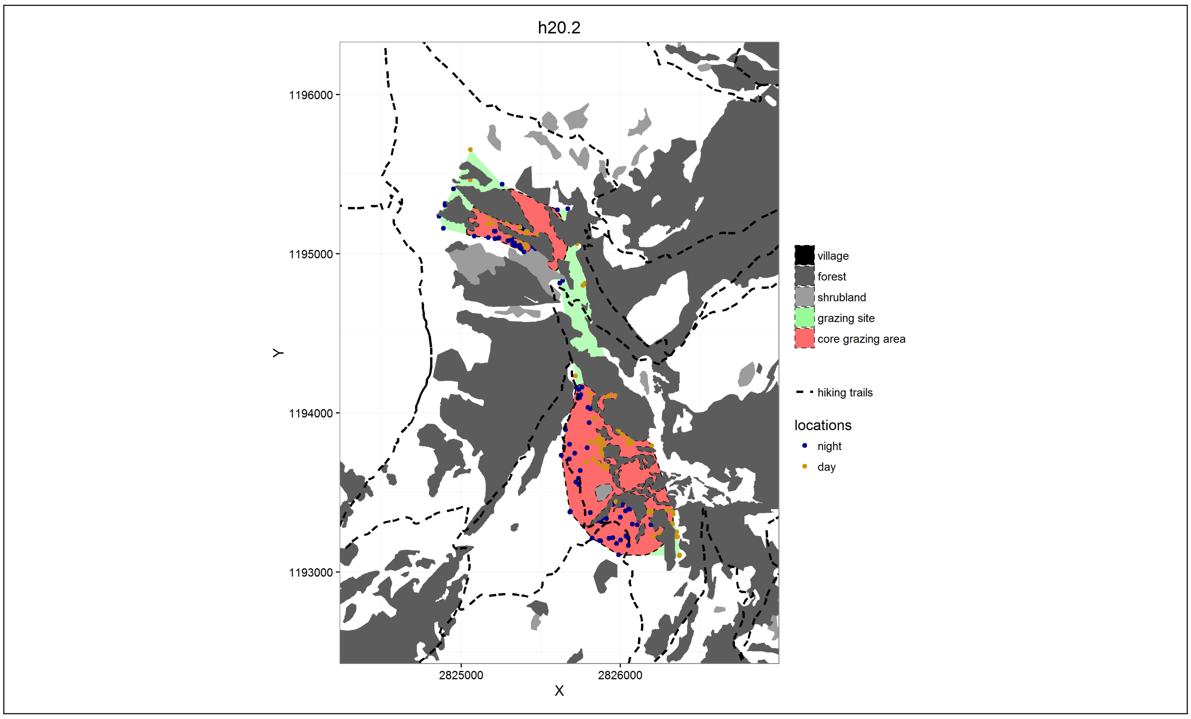
			day			night				
id	**cluster**	**fixes**	**NDVI**	**visibility**	**distance to trails [m]**	**NDVI**	**visibility**	**distance to trails [m]**	**proportion of locations during the night**	**associated home range/season**
h20	1	347	0.377	3.057	48.845	0.471	3.252	49.730	99.1%	winter
	2	160	0.496	0.181	228.102	0.545	0.703	108.739	50.6%	summer
h21	1	567	0.425	0.194	260.527	0.417	1.041	103.288	69.3%	multiple
h22	1	140	-	-	-	0.538	1.311	138.288	100.0%	multiple
h23	1	348	0.185	1.606	90.774	0.389	3.021	58.361	98.3%	winter
	2	93	0.426	-	1124.668	0.510	0.000	1163.675	98.9%	summer
h40	1	353	0.311	0.002	171.394	0.472	2.163	82.003	94.3%	winter
h41	1	218	0.368	0.526	244.488	0.361	1.315	120.462	89.0%	winter
	2	486	0.454	0.155	664.084	0.521	0.152	613.313	50.0%	summer
h42	1	420	-	-	-	0.393	1.504	141.385	100.0%	winter
h59	1	200	-	-	-	0.432	6.078	83.480	100.0%	winter
	2	483	0.435	0.473	153.981	0.479	1.100	74.570	62.3%	summer
h60	1	307	-	-	-	0.342	1.870	58.344	100.0%	winter
	2	633	0.318	0.175	641.787	0.452	0.458	491.098	42.0%	summer
h61	1	88	-	-	-	0.357	1.057	112.698	100.0%	winter
	2	43	0.411	0.313	192.457	0.268	2.912	38.530	90.7%	summer
h62	1	638	0.409	0.003	1228.770	0.426	0.037	471.930	23.2%	summer
	2	155	-	-	-	0.458	0.687	179.534	100.0%	winter
h63	1	172	0.482	0.115	502.685	0.400	3.595	38.200	70.3%	winter
	2	174	0.418	0.035	739.531	0.537	0.989	63.320	58.0%	summer
h79	1	310	0.527	0.437	186.531	0.428	0.926	147.950	90.6%	multiple
h80	1	258	0.182	1.630	72.261	0.438	3.579	36.012	98.8%	winter
	2	64	0.402	0.253	374.775	0.296	0.241	334.227	9.4%	summer
h81	1	212	-	-	-	0.392	4.472	39.841	100.0%	winter
	2	241	0.522	1.005	46.243	0.524	1.245	57.800	86.3%	summer
h82	1	299	0.529	0.208	289.876	0.499	1.112	140.807	99.0%	winter
	2	480	0.318	0.252	304.276	0.410	3.610	28.413	32.3%	summer

Individual h20

winter

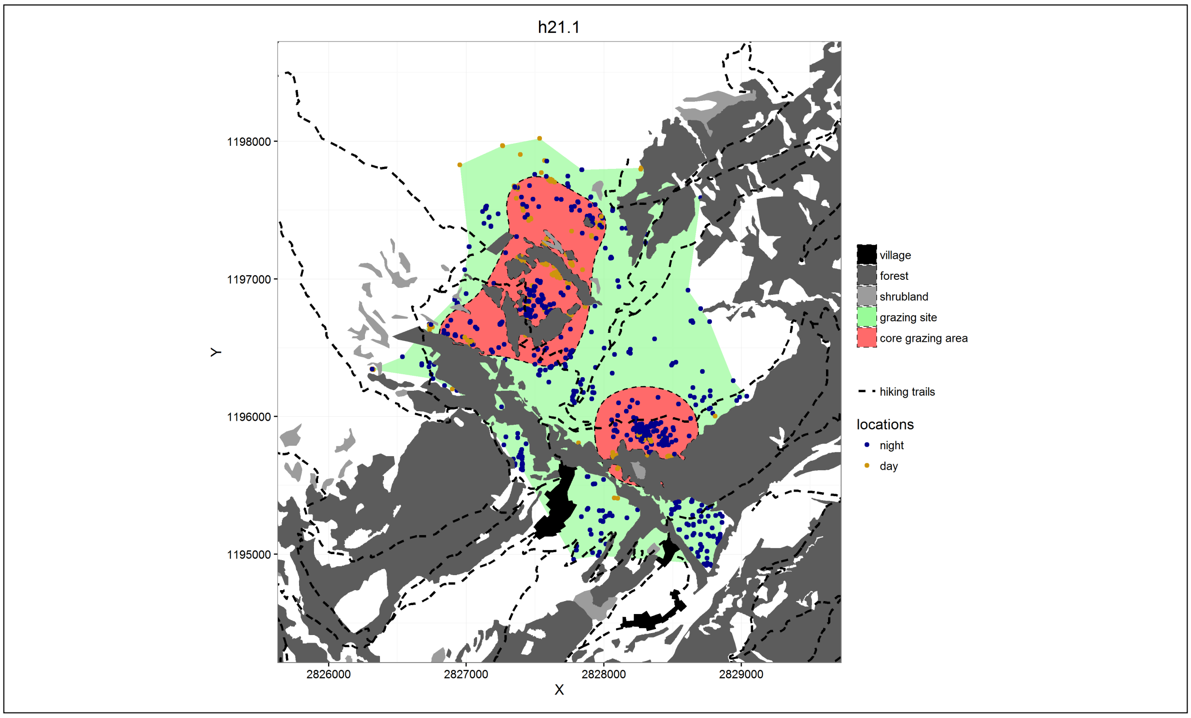


summer



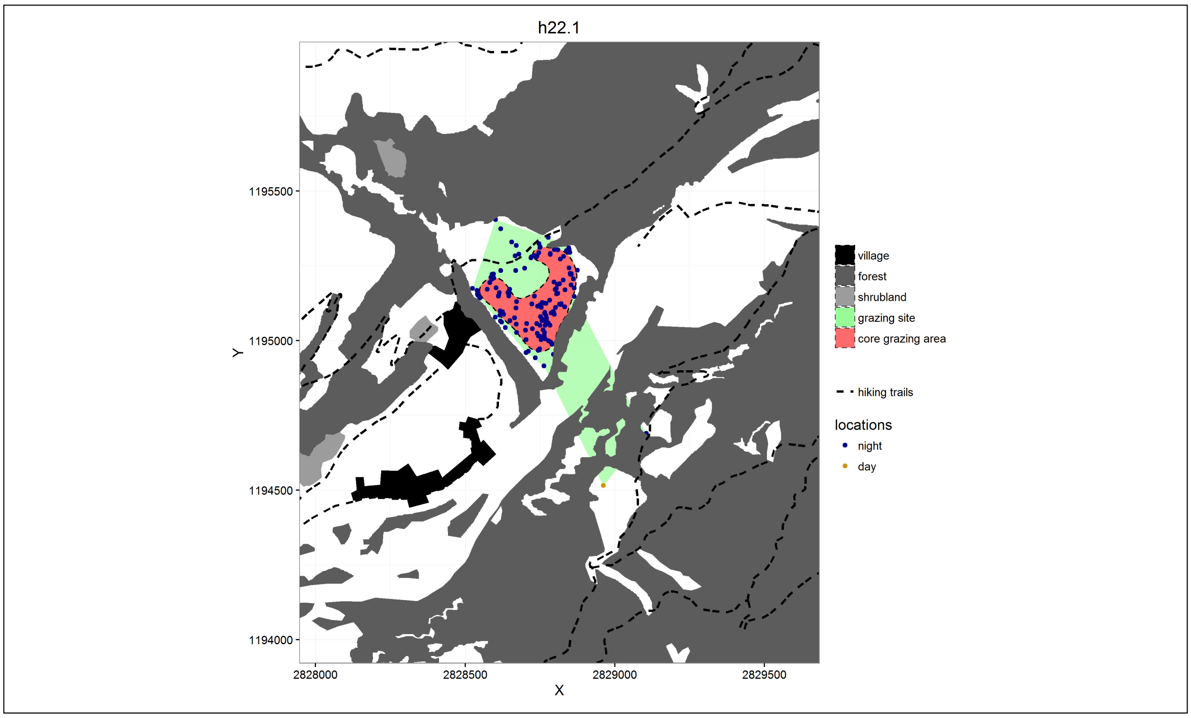
Individual h21

multiple seasons



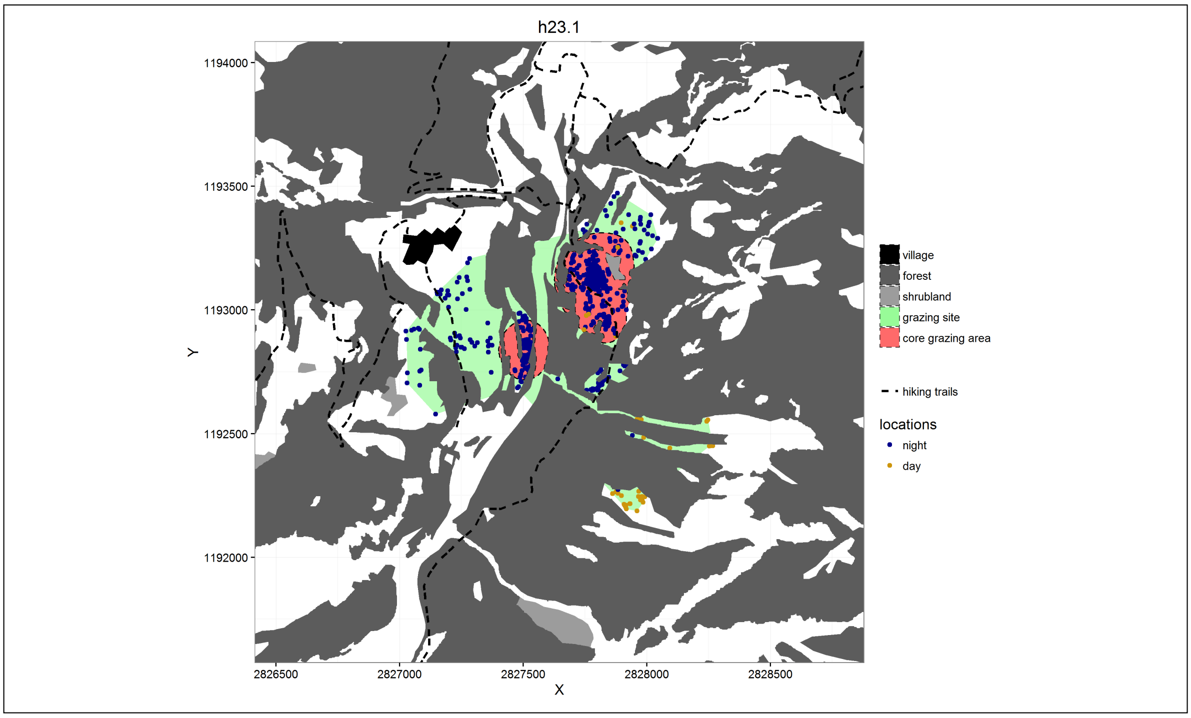
Individual h22

multiple seasons

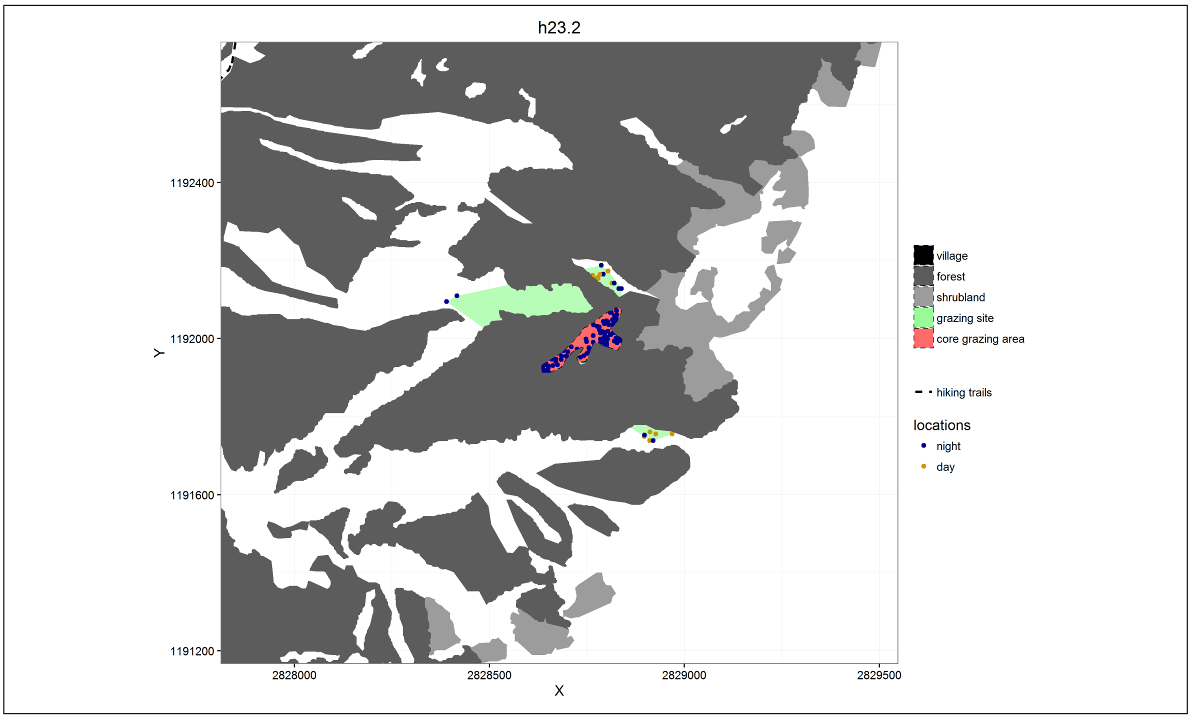


Individual h23

winter

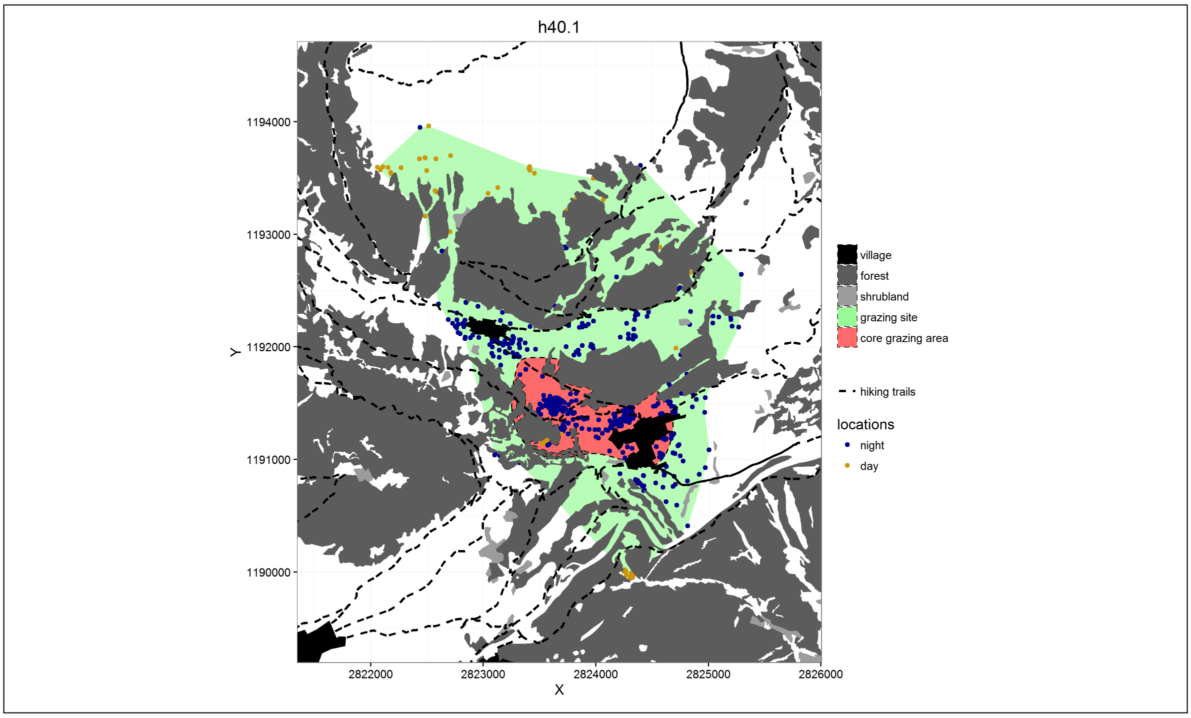


summer



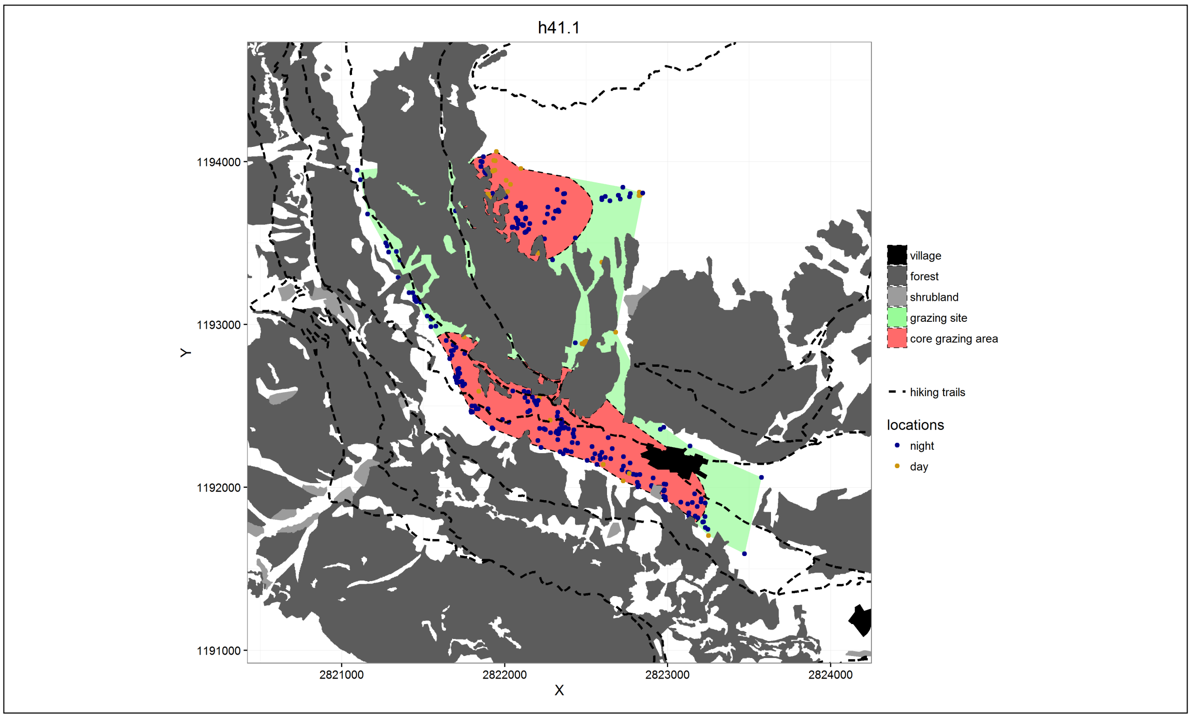
Individual h40

winter

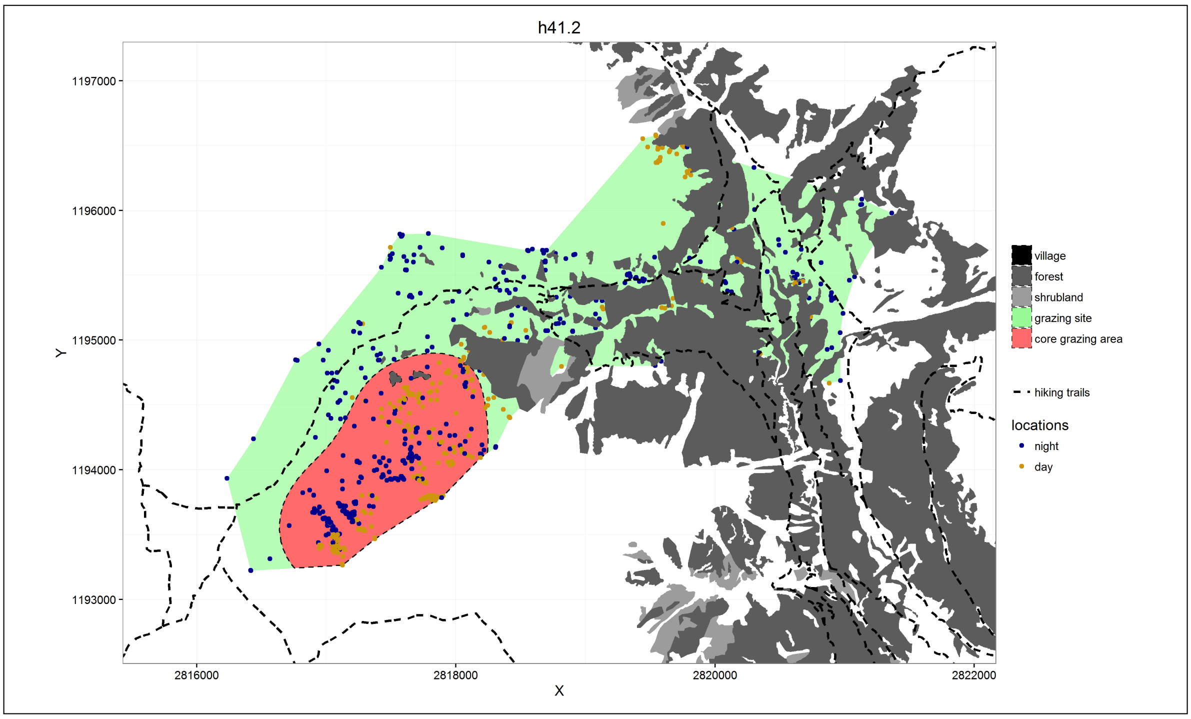


Individual h41

winter

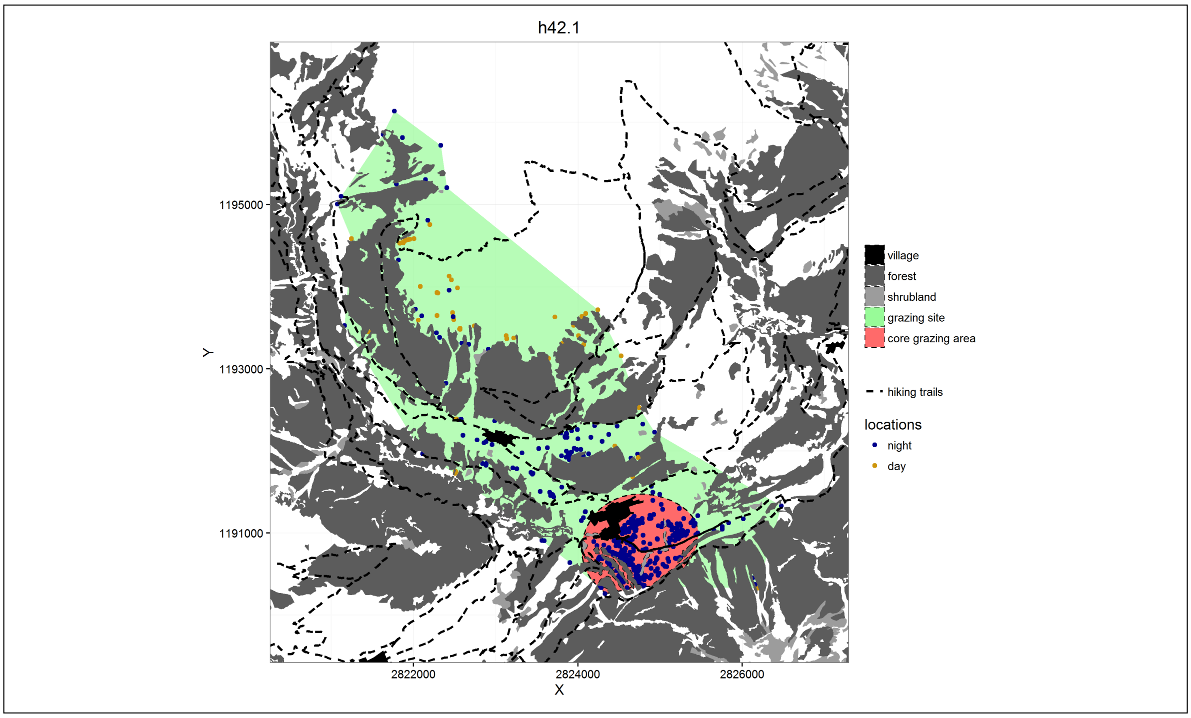


summer



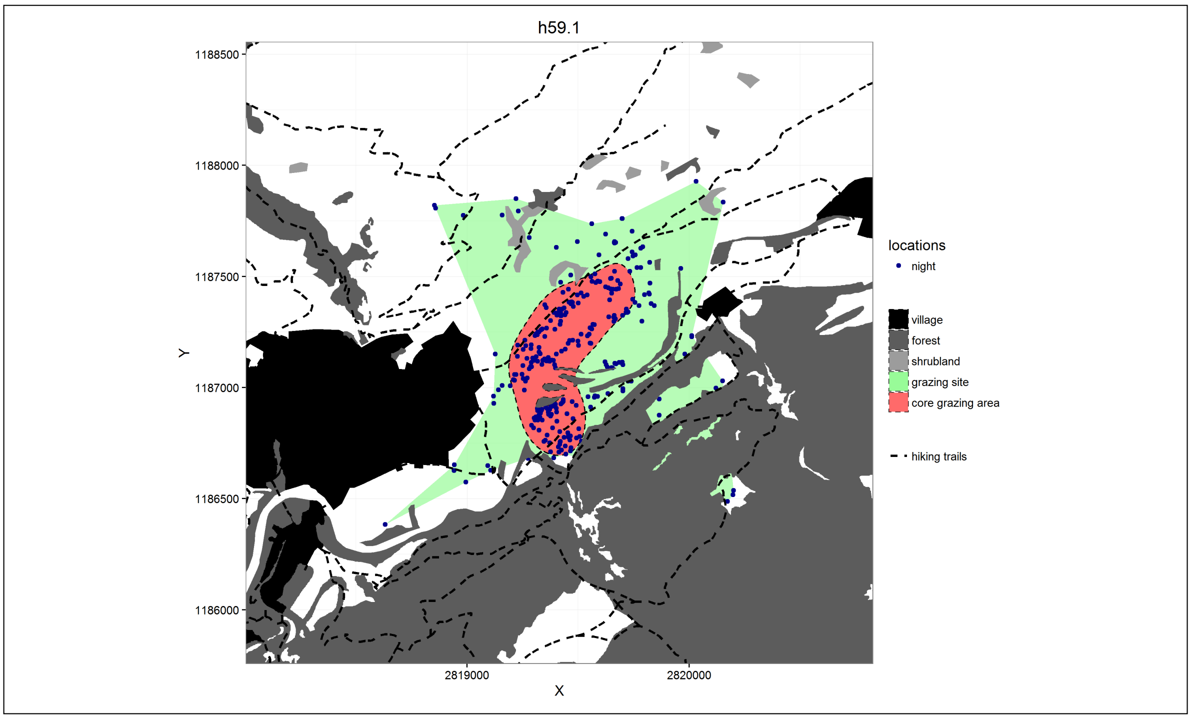
Individual h42

winter

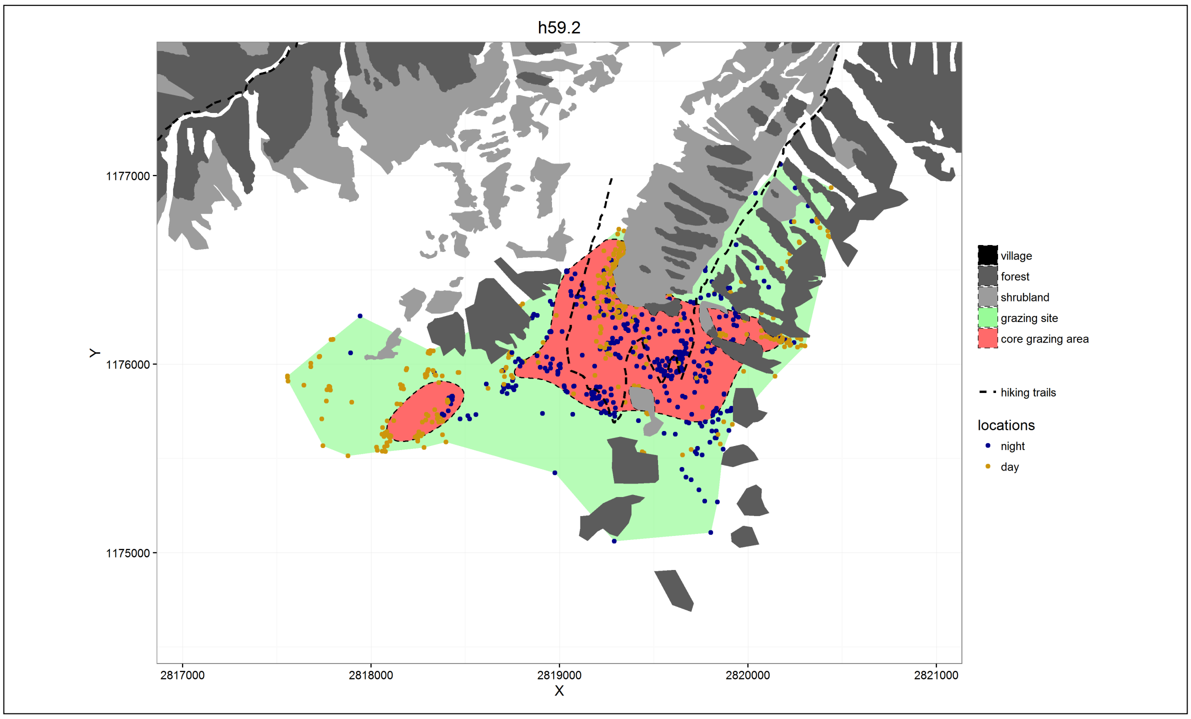


Individual h59

winter

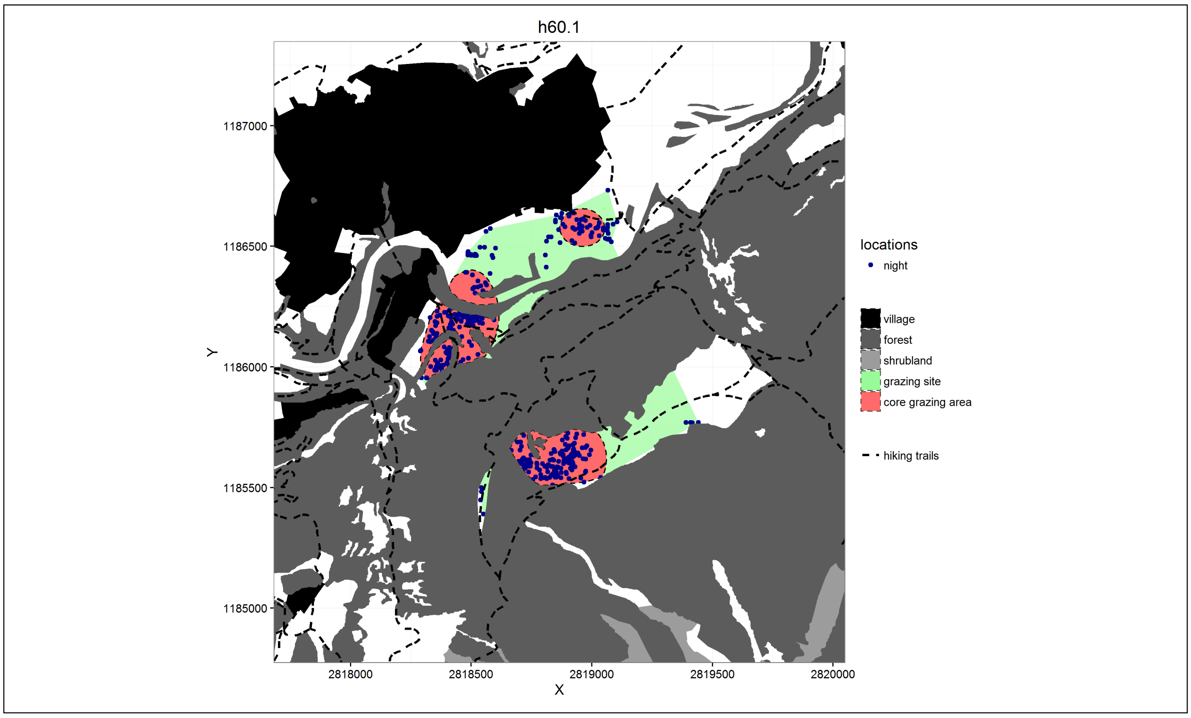


summer

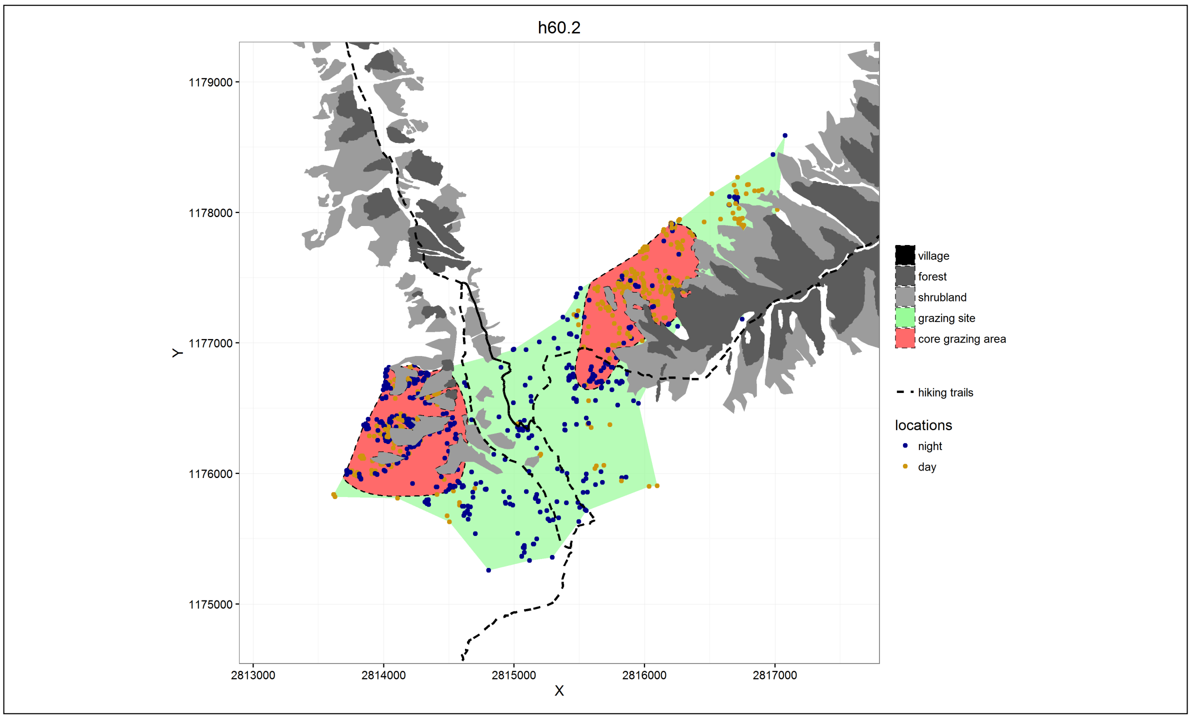


Individual h60

winter

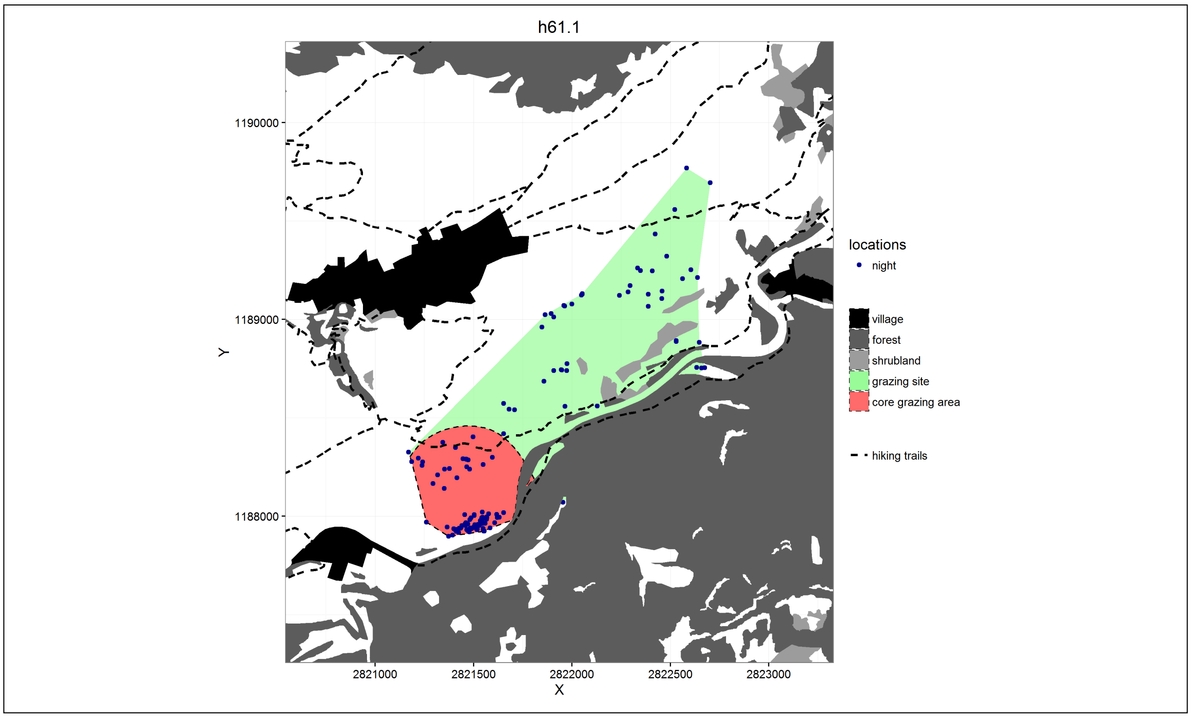


summer

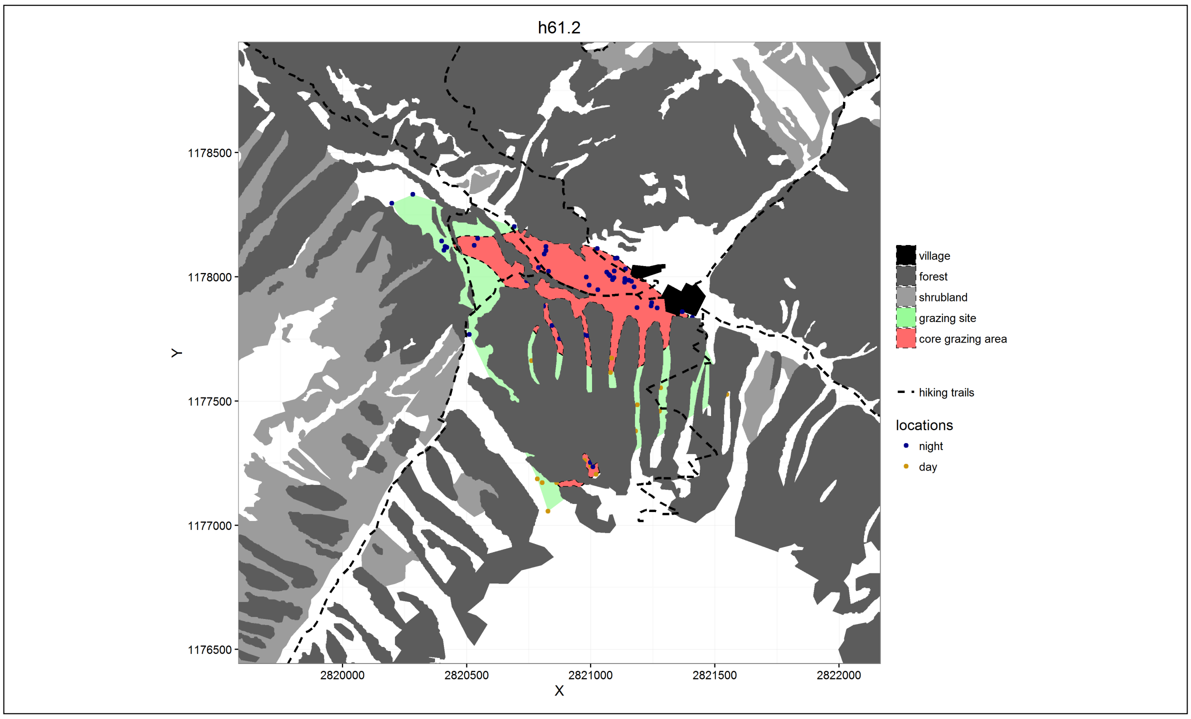


Individual h61

winter

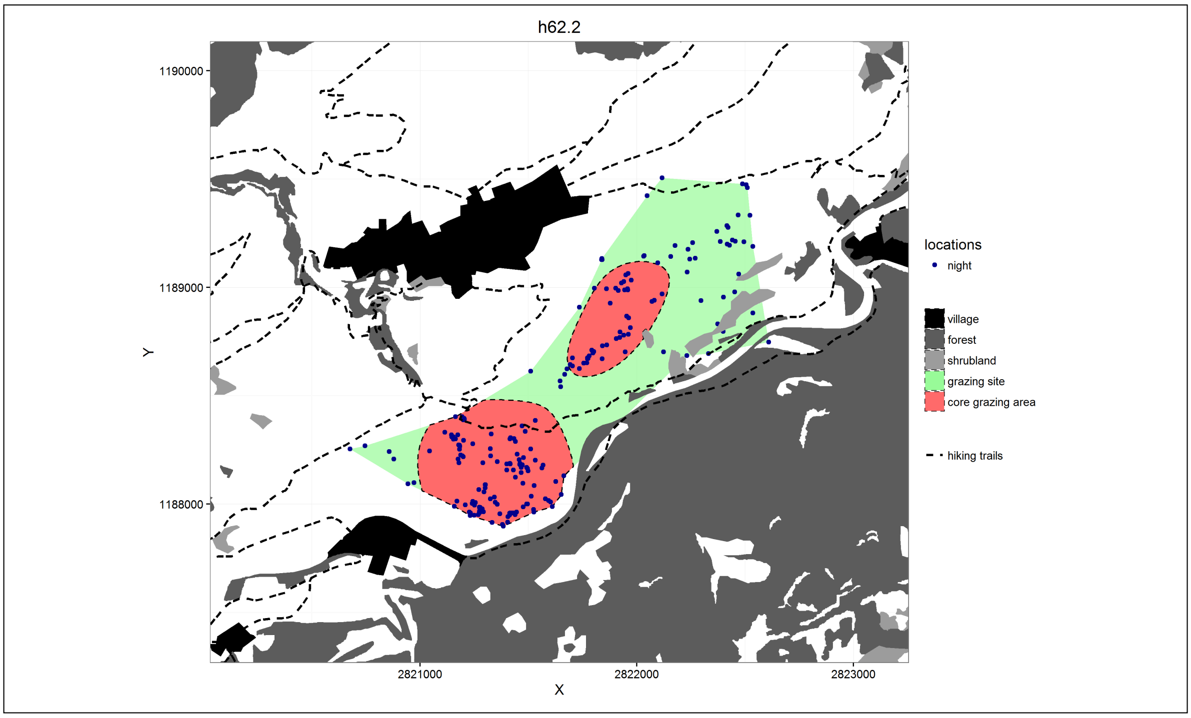


summer

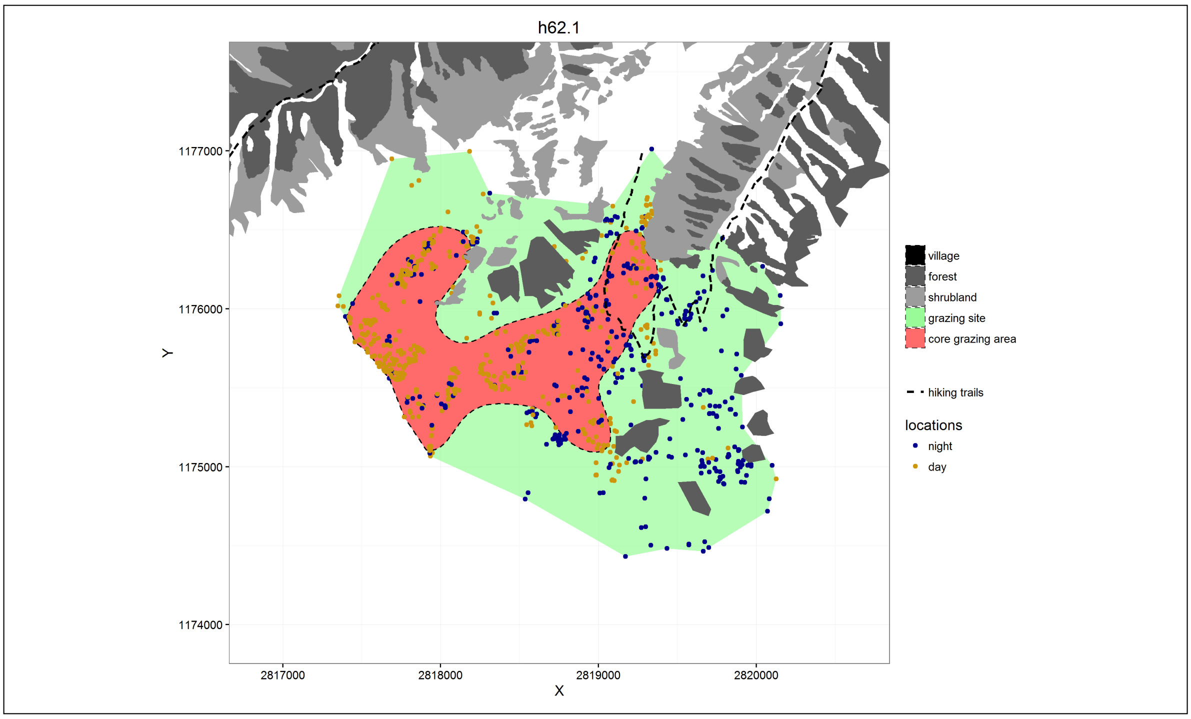


Individual h62

winter

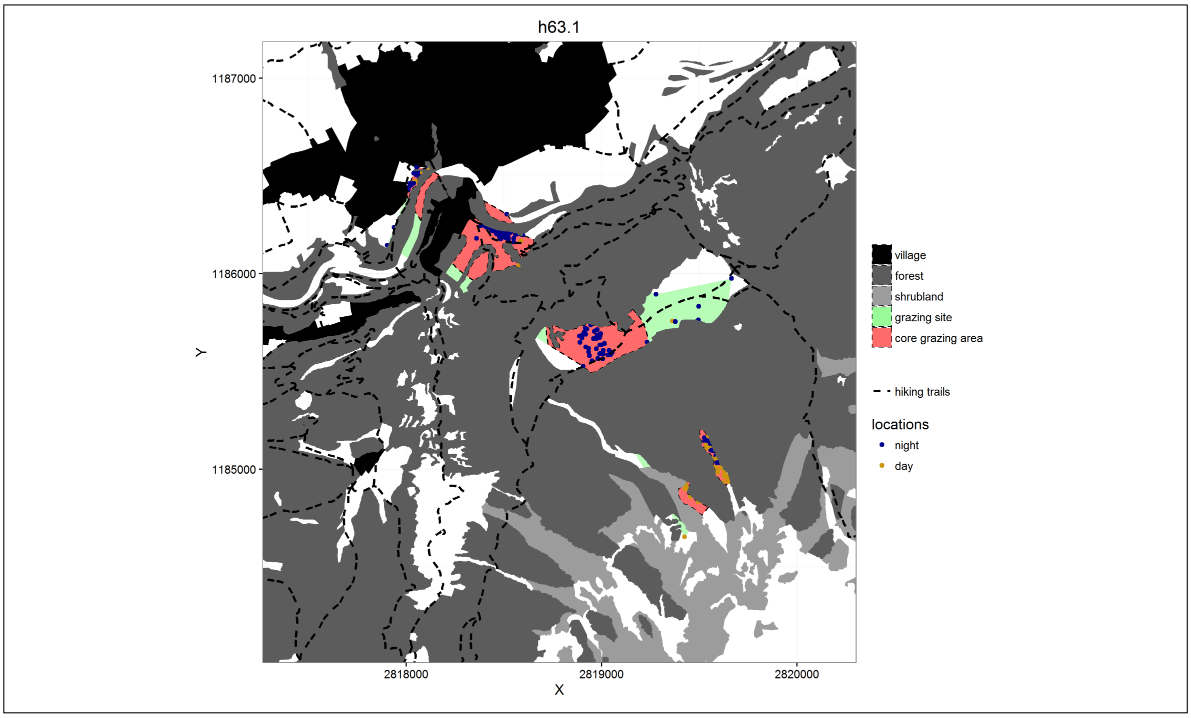


summer

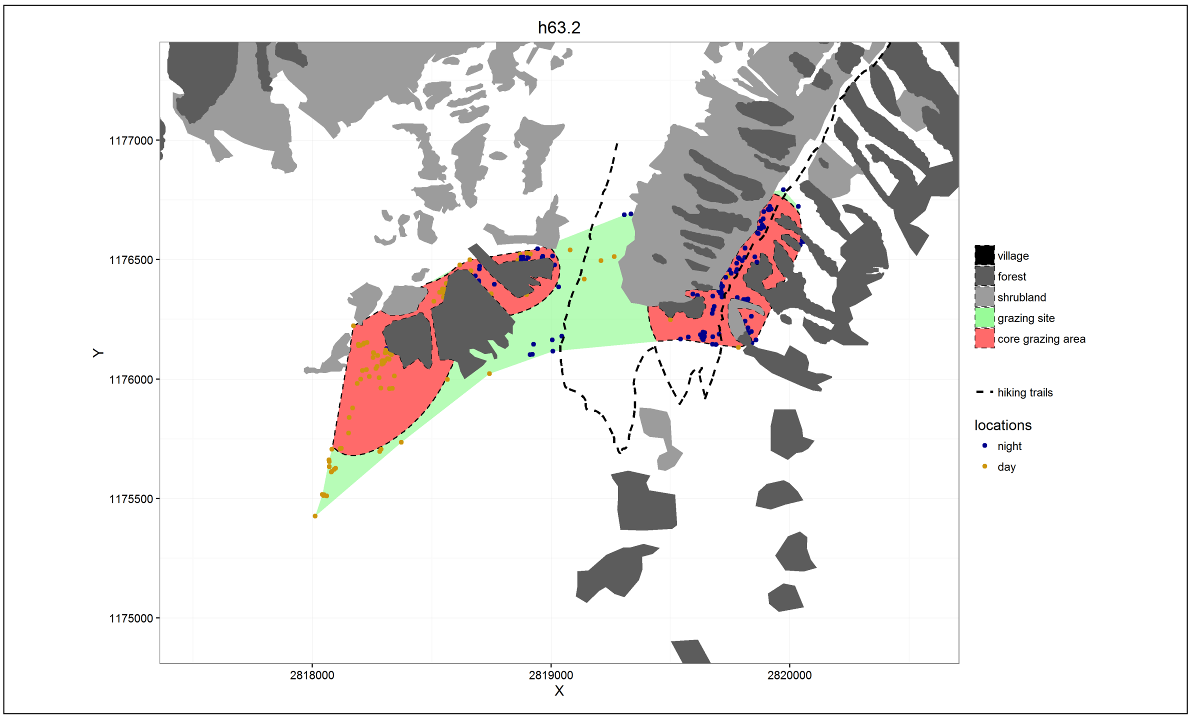


Individual h63

winter

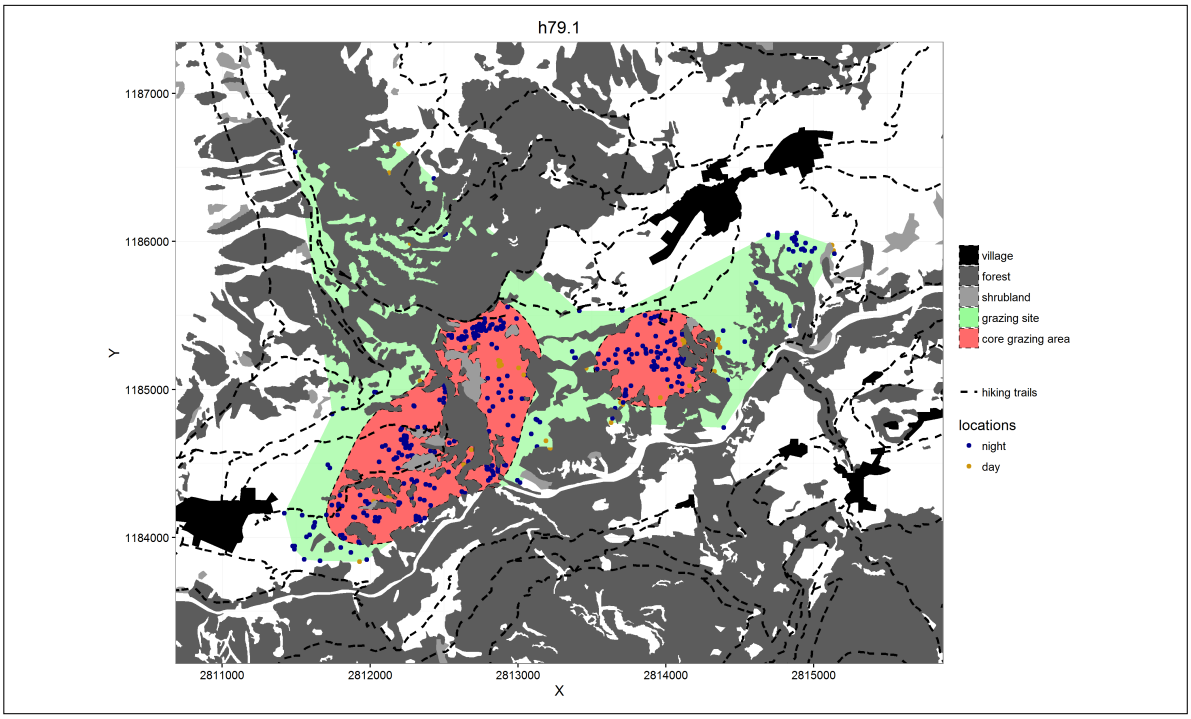


summer



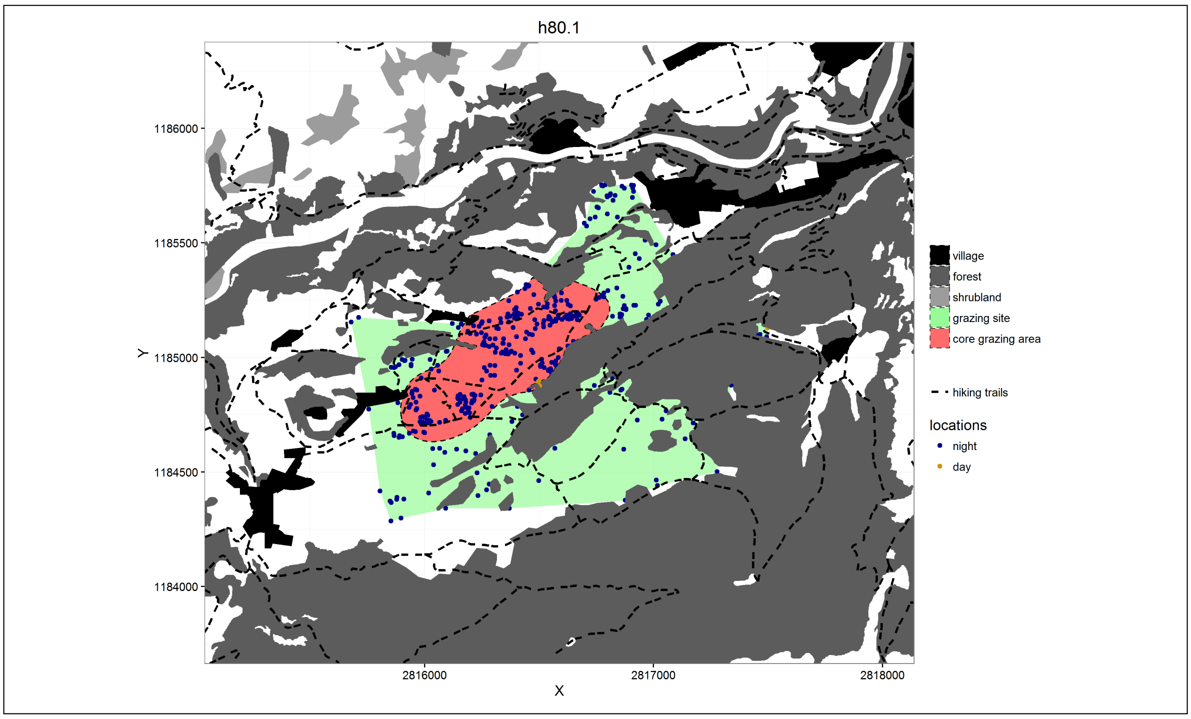
Individual h79

summer/winter



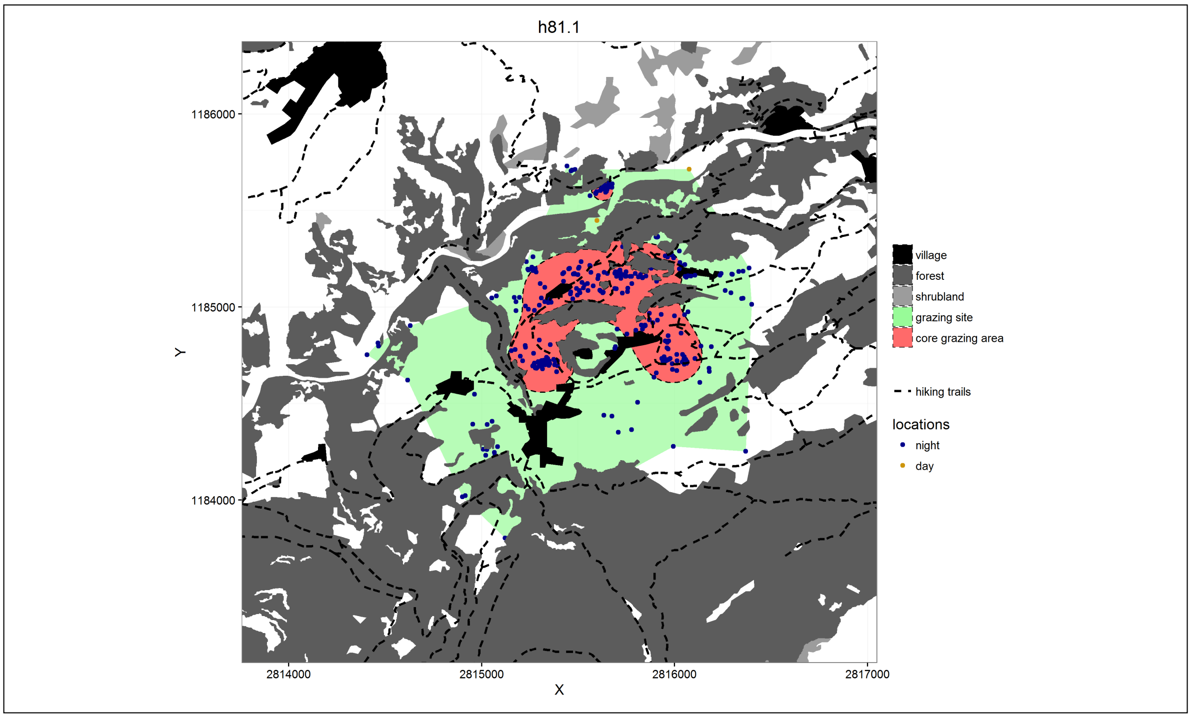
Individual h80

winter

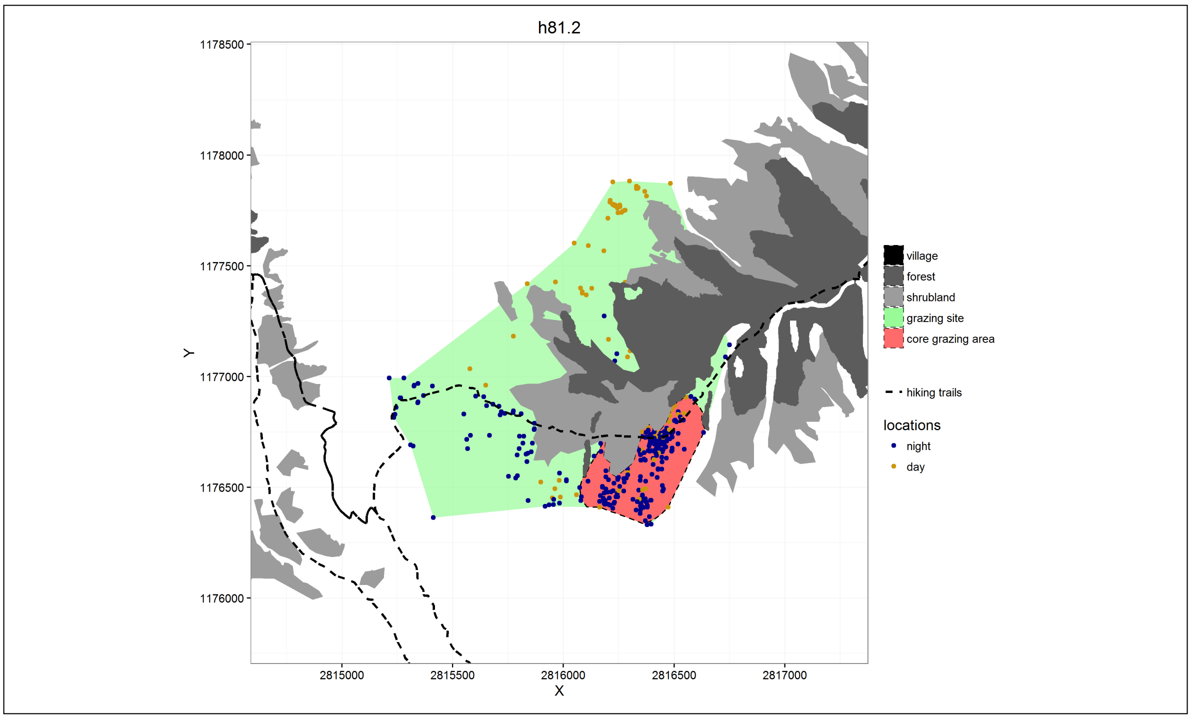


Individual h81

winter

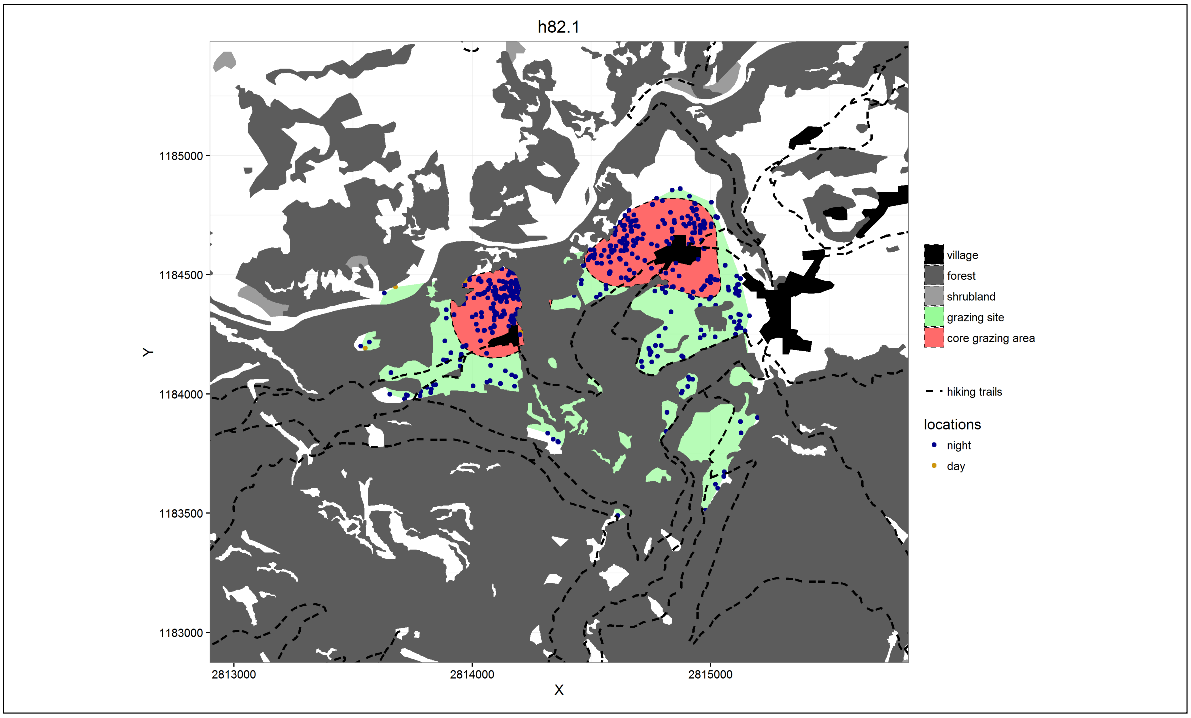


summer

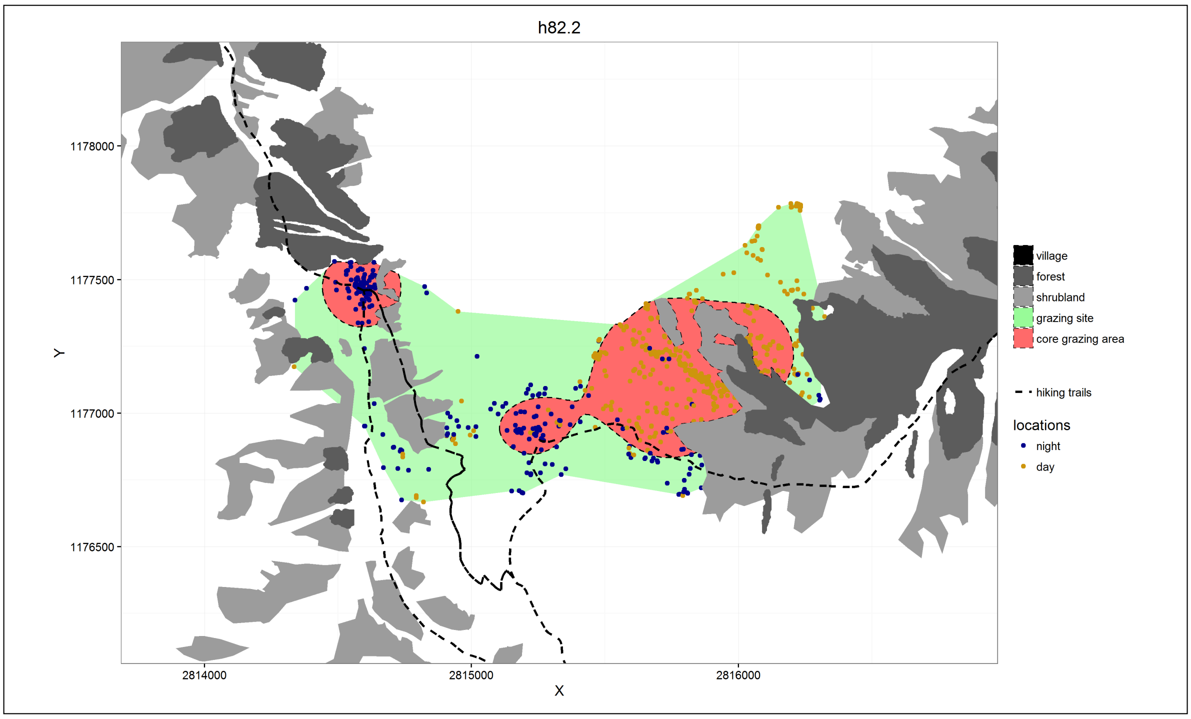


Individual h82

winter

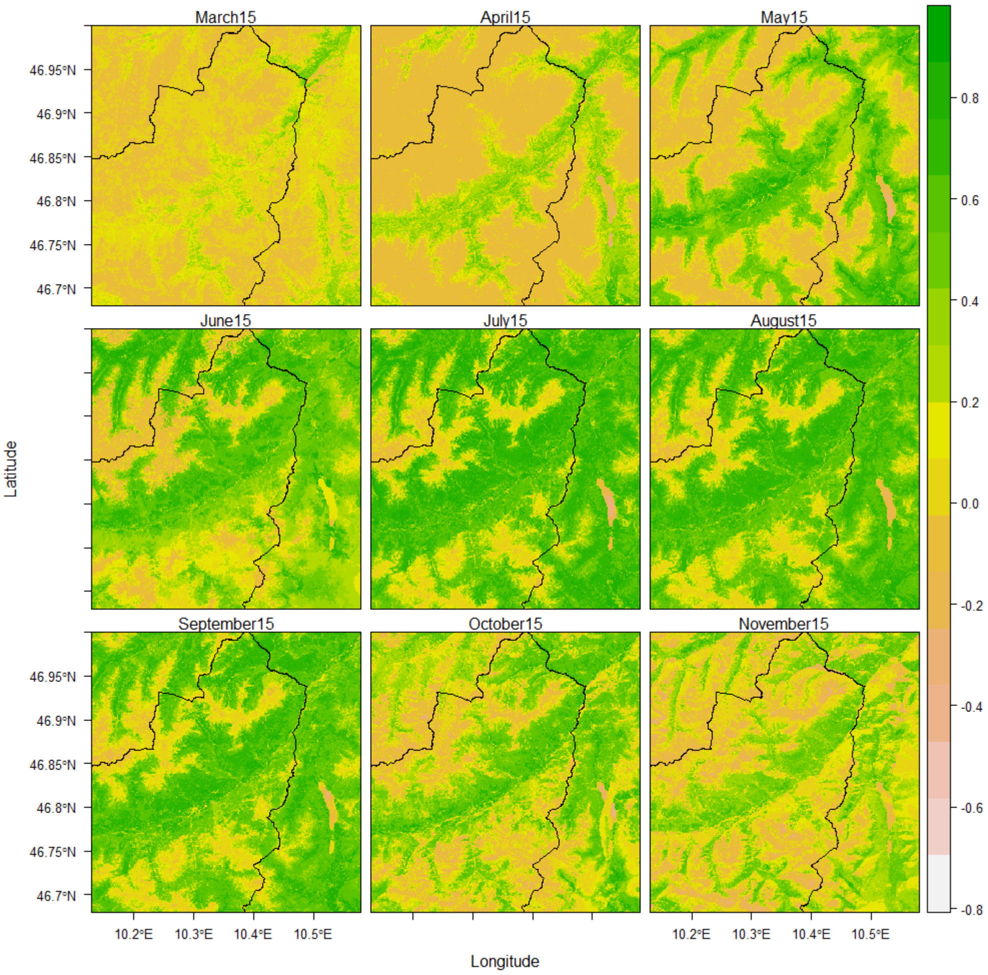


summer



A.4 NDVI composites

Landsat 8 NDVI composites derived for the months between March and November.



Personal Declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

James Patrick	Date