Migration Behavior Analysis of Red Deer (Cervus elaphus) and the Influence of Environmental Covariates on Migration Timing

GEO 511 Master's Thesis

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Summary

The red deer *(Cervus elaphus)* is a common ungulate in Switzerland, Austria and Italy. The different characteristics like a high climatic variability and various anthropogenic influences of these areas make it difficult to predict the movement of red deer. This thesis aims to analyze red deer migratory behavior concerning propensity and distance in eight different study areas. Furthermore, the timing of migration in spring and autumn is investigated in relation to environmental covariates.

First, the migration pattern of 346 red deer were analyzed using MigrO, a QGIS plug-in based on the SeqScan algorithm. Defined criteria were applied to classify the red deer trajectories into migratory, resident, and disperser individuals. For the following analysis, the focus lied on the migratory and resident red deer. Next, the home range size (HRS), altitude, distance and timing were analyzed for all populations. These parameters are all outputs of MigrO. The results for all parameters of the eight study areas were then compared. Furthermore, intersexual differences were looked at. Influences of environmental factors such as snow, vegetation and temperature on migration timing were then investigated with the Cox Proportional Hazard Model. For snow, the Normalized Difference Snow Index (NDSI) was used, provided by MODIS Aqua. Vegetation was predicted by the Normalized Difference Vegetation Index (NDVI) supplied by MODIS Terra and for temperature data, the Land Surface Temperature (LST) by MODIS Aqua was used.

The different results for the migration probability per study site showed that red deer behavior is dependent on various environmental factors (i.e. weather conditions and topology) and anthropogenic influences like hunting, supplementary forage and human made barriers. In addition, only moderate intersexual differences were observed for the behavior. Moreover, few red deer individuals (females and males) traveled to rutting grounds outside of their seasonal home ranges.

Resident animals show a larger covered HRS than migratory individuals. Consequently, resident individuals likely roam larger areas within one larger annual range, while migratory animals fulfill their needs in two spatially separated smaller ranges. Stags cover a larger HRS than hinds and generally also have their home ranges at lower altitudes than female red deer. Generally, all migratory individuals traveled to lower elevations during winter and migrated to higher altitudes in summer. The traveled distances between the home ranges were evenly distributed between hinds and stags. Only on the study site in Tyrol, where supplementary feeding has a long tradition in winter, the traveled distances are significantly lower than compared to the other study sites, suggesting the effects of supplementary feeding in altering migration behavior. The spring migration starts earlier for stags than hinds, whereas in autumn the stags migrate all at once in a short time. This is assumed to be in relation to the rut or an event like for example the end of hunting or changing weather conditions.

The results of the Cox Proportional Hazard Model show that the timing of spring migration is assumed to be determined by changes in vegetation and temperature, while the determinant driver for the autumn migration is snow and vegetation.

Overall, the results show plastic responses of red deer to environmental and anthropogenic drivers. Differences in the studied populations show that various factors influence the migration behavior of red deer which need still more research to fully understand the mechanism.

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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.

29.06.2022

Ursula Fellmann

Date

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1. Introduction

1.1 Motivation

The red deer *(Cervus elaphus)* was considered extinct in Switzerland around the middle of the 19th century after it had already successively decreased in population for the previous 200 years. The reasons for this were the free, often unregulated hunting with increasingly effective weapons, the miserable climatic conditions during the Little Ice Age, the general overexploitation of the habitat by the growing population, but also foreign troops and last but not least conflicts with food and wood production (Haller et al. 2002; Jenny et al. 2011). However, starting from small remnant populations in neighboring countries and supported by releases, the red deer began to reclaim its habitat in Switzerland already towards the end of the 19th century (Righetti 1995). From 1872 on, red deer migrated back from Vorarlberg and the Principality of Liechtenstein, as well as from North and South Tyrol, into the canton of Grisons and was officially hunted again from 1905 onwards (Jenny et al. 2011).

More recently, a new hunting law was implemented in 1989 in the whole canton of Grisons, which supported a sustainable regulation of the red deer population. This hunting law requires an annual hunting plan based on wildlife monitoring (Jenny et al. 2011). Furthermore, from 1990 onwards, partial and complete hunting bans in no-hunting zones (Eidg. Jagdbanngebiete) and cantonal game reserves (kantonale Wildschutzgebiete) additionally support the red deer population and guarantee a good dispersion of the animals (see Appendix A1) (Haller et al. 2002). Since the new laws were implemented, the red deer population in Switzerland has continued to increase, as can be seen in Figure 1. The same also applies to the cantons Ticino, Grisons, and Valais (Jenny & Filli 2014).

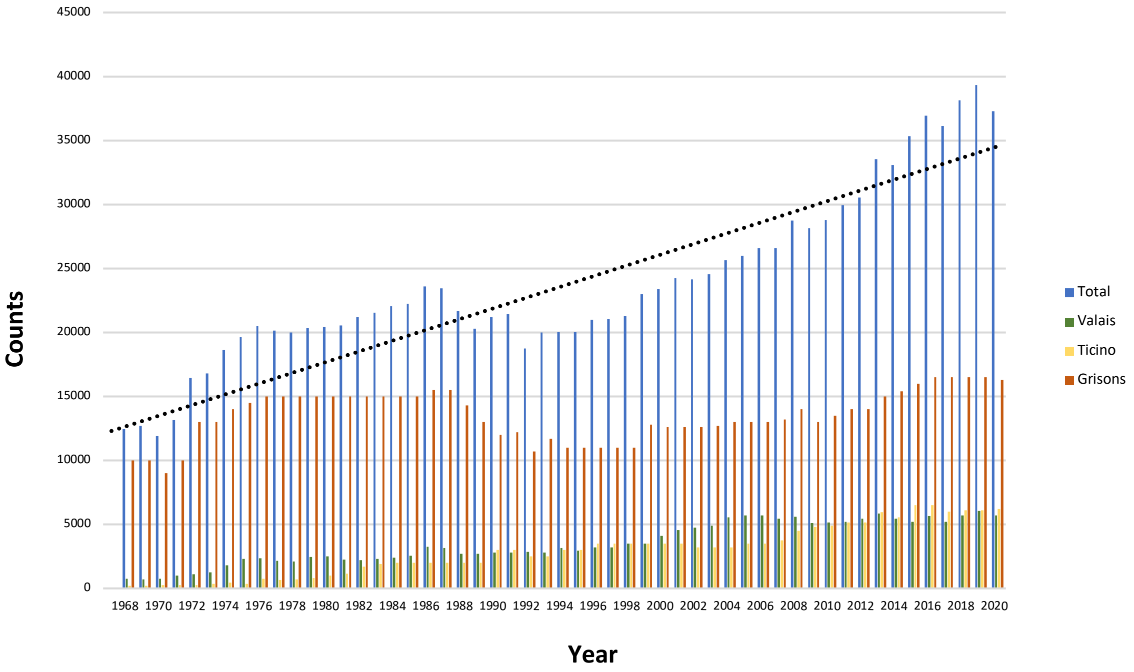

***Figure 1**: Development of the red deer population in Switzerland from 1968 to 2020 compared to the cantons of Valais, Ticino, and Grisons based on observation estimates (Bundesamt für Umwelt, 2022).*

Taking the development of red deer dispersal to date as an indicator, it can be assumed that this ungulate species will also recolonize the last, undeveloped habitats in the Alps and Pre-Alps, the Jura and the lowlands in the coming decades, especially since the conservation of local populations of native wildlife such as red deer is positioned in Swiss law (Baumann and Imesch 2010). For the affected cantons, particularly in the intensively human-used Central Plateau, the challenge will be to ensure adequate protection of the red deer populations, taking into account negative impacts on forestry and agricultural crops (Ruhlé and Juesy 2006; Willisch et al. 2019).

In commercially forested areas red deer can cause considerable conflicts between forestry interests and wildlife management since it can severely damage the growth of plants, and trees by feeding on germinating seedlings or tree fruit whereby the availability of new seeds is reduced. In addition, browsing and bark stripping makes trees vulnerable to windshear and diseases like fungal attacks. Agriculture concerns crops and pastures suffer damage by browsing red deer.

Furthermore, costs that are aimed at reducing the damage through prophylactic measures have to be taken into account as well (Godvik et al. 2009; Kiffner et al. 2008; Mitchell et al. 1977). However, thanks to the revised hunting regulation of 1986 and ongoing research on red deer and other ungulates, conflicts in most areas could be reduced. The hunting regulation of 1986 removed the maternal and juvenile protection status, for the additional hunt in November and December, which is necessary to regulate or reduce the red deer population. Therefore, young and female animals are hunted specifically in the additional hunt, thus the fine regulation is carried out according to the regional needs. (Haller et al. 2002; Jenny et al. 2011).

Modern concepts of wildlife management focus on the species and include habitat protection, securing the necessary resources (such as security and food), coexistence with other wildlife, resolving conflicts with land users, protecting the animals from human disturbances, and species-appropriate hunting activities. All the above-mentioned measures must be optimally coordinated with each other. Simple recipes often fail because they do not sufficiently consider the most important basis, namely the biology of the game species. In the case of the red deer, it is the size, the space-grasping mobility, the above-average learning ability and the passing on of what has been learned about traditions as well as the high rate of reproduction. The high reproductive performance of red deer populations requires consistent annual hunting.

As the largest ungulate species in Switzerland, red deer depend on fertile areas during the growing season. The density and the quality of the summer stand determine the condition and constitution of the individual animals. In winter, the red deer reduces activity in order to use its reserves economically. Besides food, security is a very important resource for the red deer throughout the year. In winter, safety and rest are especially important to be able to use the innate energy-saving mechanisms such as reduction of metabolism, the possibility of reducing body temperature (Arnold et al. 2004) and passive warming in the sun (Jenny et al. 2011).

However, not all conflicts are caused by economic or environmental harm. Nowadays, not only hunting regulations but also human outdoor activities are exerting pressure on wild-living animals. As a result, a conflict developed between human recreation and tourism on the one hand, and wildlife management on the other (Löttker et al. 2009). The above-mentioned facts demonstrate that maintaining a healthy population size through sustainable management systems requires a detailed analysis of red deer ecology in relation to human activities and ecological resources. The findings of such research can also be utilized to objectively analyze new management practices and problems in the public debate and possibly limit emotional responses. This will be required in order to control the red deer populations and reduce confrontations to a minimum.

Red deer show migratory behavior. Dingle and Drake (2007) proposed that the term migration (as applied to animals) evokes three distinct but overlapping concepts: (1) a type of locomotory activity that is notably persistent, undistracted, and straightened out; (2) relocation of the animal on a much larger scale, and involving movement of much longer duration, than those arising in its normal daily activities; and (3) a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable and unfavorable. However, in practice, the distinction is usually blurred. Red deer exhibit partial migration, where only a part of the population migrates while the other remains in the same area year-round. Seasonal migration between low-elevation winter grounds and high-elevation summer ranges is a common pattern among temperate ungulates (Mysterud et al. 2011). Plant phenology (Albon and Langvatn 1992; Bischof et al. 2012), predator avoidance (Fryxell and Sinclair 1988), and reduced parasite pressure are all factors that influence spring migration (Qviller et al. 2013). Snow has for a long time been mentioned as the ultimate driver of autumn migration (Mysterud et al. 2011).

When wildlife crosses administrative boundaries on a regular basis, as is the case with migratory populations, population management is difficult to achieve. The degree of misalignment between management units and the scales at which ecological processes occur, on the other hand, has rarely been assessed. Determining functional population units of partially migratory species common in northern forest ecosystems requires such knowledge. Additionally, these studies are necessary to clarify the causes of variation in order to better understand the mechanisms that cause partial migration (Meisingset et al. 2018).

Understanding habitat utilization as well as identifying deviations from the normal condition, such as the animals response to disturbances or predators, requires knowing when and where an animal is doing what (Löttker et al. 2009). Direct observation of animals is the simplest approach to understand animal behavior. However, they have several drawbacks. Direct observations are time and personnel intensive, and they are only practicable during the day and in places with little or no cover. Further, more indirect strategies are required for elusive species like red deer, who travel enormous distances in often inaccessible areas. The Global Positioning System (GPS) is such an indirect method, which was originally created for position determination but has increasingly been used to observe animal activities with minimal disruption (Craighead et al. 1973; Gervasi et al. 2006).

Animal distribution and migration can be related to landscape features using GPS units and geographic information systems (GIS) (Ungar et al. 2005). One of the most significant advantages of GPS technology is the ability to retrieve high-precision position data 24 hours a day. Furthermore, the animal's position data can be received in rapid succession (Cagnacci et al. 2010; Cooke et al. 2004; Hebblewhite and Haydon 2010). The information gained in this method can be used to supplement standard observational data, particularly when it comes to mobility and activity patterns over a vast spatial and temporal scale.

While GPS technology makes determining an animal's location relatively simple, assessing the monitored animal's specific behavior based on these data remains challenging. In this regard, the use of accelerometer data can be beneficial (Löttker et al. 2009; Naylor and Kie 2004).

The aim of collecting such datasets is to answer a variety of important behavioral and ecological parameters, such as the extent of home range size (HRS) (Kie et al. 2010), resource selection estimation at different scales (Hansen et al. 2009; Herfindal et al. 2009), description and classification of animal movement, foraging behavior (Owen-Smith, Fryxell, and Merrill 2010) and the identification of inter- or intraspecific interactions, such as predation and disease transmission (Formica et al. 2010; Reinecke et al. 2014). For example, bovine tuberculosis (bTB) has recently (re-)emerged in a number of Central European countries (Schöning et al. 2013) and has been discovered in wild boar hoards in southern Germany, indicating that it may potentially be present in red deer populations (Reinecke et al. 2014). In Tyrol, tuberculosis cases had been detected in red deer over the preceding decade (Schoepf et al. 2012). The canton of Grisons takes yearly samples from all red deer shot along the border to Austria. So far, all samples are tuberculosis negative.[1]

Researchers need to choose the best approach based on animal size, environmental conditions, and expenses before collecting data. A mix of methods, in combination with direct observations of an animal's behavior, could be one option to help researchers create algorithms that automatically match the acquired data to a certain behavior depending on parameters like head movement or locomotion speed (Löttker et al. 2009). Furthermore, contextual information about the local environment could be used to improve the quality of the behavioral data interpretation. Meteorological data, ground cover, and land use categories are examples of such data. When it comes to interpreting the collected data, comparisons with other studies and previous data are also useful (Cagnacci et al. 2010).

1.2 Research Question

The main focus of this thesis lies in the analysis of migration patterns of red deer in eight different areas in Switzerland, Italy and Austria. In addition, the influence of environmental covariates will be examined for spring and autumn migration timing. As previously stated, similar studies have been conducted numerous times. Despite the fact that migration is a well-known and widespread ecological phenomenon, there is currently no consensus on how to describe and define it (Cagnacci et al. 2011; Dingle and Drake 2007). The analysis of the eight areas is done with a new approach, called MigrO and provides a good foundation for further research. With data from more than 300 red deer individuals in this study, new insights about red deer behavior in the study areas are possible. The following research questions will be investigated in this thesis.

1. Classification and descriptive statistics

1.1 How differs the migration probability of red deer in the study areas and what could be potential reasons?

1.2 What are the differences in the following parameters for migratory and resident red deer between the studied sub-populations and their habitats?
  a) Home range size (HRS)
  b) Altitude
  c) Distance
  d) Timing

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[1] Personal notice of Thomas Rempfler, Swiss National Park, 27.06.2022

2. Determinants

2.1 What effects have the following covariates on the spring- and autumn migration timing?
   a) Normalized Difference Snow Index (NDSI)
   b) Normalized Difference Vegetation Index (NDVI)
   c) Land Surface Temperature (LST)

This thesis can be seen as a continuative work to the Master Theses of James Patrick (2017) and Jaqueline Boog (2018) since the research is similar but uses different approaches and more individuals of red deer.

1.3 Thesis Structure

A theoretical framework is created in Chapter 2 to provide basic knowledge on red deer ecology as well as tools for space use and migration pattern analysis that are commonly used in GIS. Additionally, ecological tools are presented. The study regions and data sets are discussed in Chapter 3, along with the necessary pre-processing methods and data restrictions. Chapter 4 then discusses the methodology used to answer the research questions. Chapter 5 depicts the results and related discussion, with different subsections for each research question. A short overview of the insights and main discoveries in Chapter 6, as well as an explanation of the limitations of the used approaches and future work development potential, leads to the conclusion of the thesis

2. Theoretical Framework and Background

The physiology and reproductive cycle of an animal should be understood and examined in relation to its surroundings in order to understand its behavior. On the Scottish island of Rum, Clutton-Brock et al. (1982) produced one of the most important and in-depth studies on the issue. Their research is illustrated in the book “Red Deer: Behavior and Ecology of Two Sexes” and dates back to 1953. It contains detailed information on red deer breeding biology, rutting, feeding behavior, population dynamics and activity patterns. However, it should be noted that these experiments were conducted on a remote island, which has quite different characteristics as the study locations of this thesis. Several other papers, such as those by Mysterud et al. (2011), Peters et al. (2017), Reinecke et al. (2014) and Jayakody et al. (2008), focus on various aspects of the behavior of red deer in continental Europe. The first section of this chapter will provide an introduction to red deer ecology, with a focus on diurnal and seasonal activity cycles. In the follow-up, the methodologies and concepts used in home range estimate and GIS will be outlined.

2.1 Red deer Ecology

Because of its diverse morphology, the European red deer has been divided into subspecies to a greater or lesser extent in the past. Today a sub-division is rejected and antler shape, as well as body size, head shape, and coloration, distinguish the red deer from different places. In this study, the major geographic form of red deer under examination is the Central European red deer *(C.e. hippelaphus)* shown in Figure 2 (Wagenknecht 1996).

Figure 2: *left: Stag with a GPS collar (Thiel et al. 2018), right: Marked hind with calv (Signer et al. 2022).*

2.1.1 Physiology and Reproduction

The red deer *(Cervus elaphus)* is one of Central Europe's largest wildlife species, although its size and weight differ depending on climate, altitude, habitat, and ethnic differences (Mitchell et al. 1977; Wagenknecht 1996). They inhabit a variety of environments including woods, meadows, and bush regions, all of which have different levels of human influence in addition to anthropogenic or natural hunting pressures (Reinecke et al. 2014). Within Europe, their size and weight tend to increase from West to East and South to North (Bützler, 2001), following the decrease in the average annual temperature. Furthermore, weight fluctuates throughout the year, with the peak occurring soon before the rut in mid-September (Mitchell et al. 1977).

In Switzerland, adult stags weigh between 140 and 220 kg, whereas hinds weigh about 1.5 times less (Clutton-Brock et al. 1982). However, it must be considered that deer weights provide rather uncertain measures, as they are subject to strong age-related and seasonal fluctuations. The stag has the highest weight shortly before the beginning of the rut, through which it can then lose up to 25% of the weight. Additionally, the winter weight losses following the rutting season can also be enormous. The shoulder height and body length can reach up to 150 cm and 210 cm respectively.

The red deer received its name due to its reddish-brown summer coat. The coat is typically brown to gray in the winter, and the fur is nearly twice as long as in the summer. In late April and September, the coat changes in color and hair length.

Antlers are without a doubt the most noticeable physical feature of male red deer. They begin to grow in spring and are shed about 6 months later. The antlers serve as a weapon during the rutting season to establish dominance over other male deer and to secure a harem (Wagenknecht 1996).

Red deer live in sex-segregated groups, with the degree of segregation varying significantly between populations across Europe. A matriarch, her-daughter, and her-offspring form the core unit of female groups, while the total composition of the groups is somewhat unstable and can change within a short time. Different groups can temporarily merge and share a portion of their home range (Mitchell et al. 1977). Stags spend their first few years in groups with their mothers before moving on to join groups of other stags. This separation is broken during the rutting season, which in the Alps takes place from mid-September until mid-October. Stags take a relatively long time to reach sexual maturity, as it takes 6 to 8 years to achieve their full body weight. This is also the age when stags are able to successfully hold harems of hinds. The number of hinds in a harem can vary widely and ranges from only one animal to more than twenty, partially depending on population density. The number of hinds that can be held by a stag is related to its age. Male breeding success, and consequently harem holding capacity, peaks around the age of eight. Holding and protecting a harem from other males takes a lot of energy. As a result, a stag's parental investment is confined to the rutting season. After successfully obtaining a harem, stags begin to roam less, remaining close to their harem and only relocate when their harems migrate to new feeding areas (Clutton-Brock et al. 1982). Approximately 34 weeks after the rut, during the months of April, May and June, the calves are born (Bützler 2001; Wagenknecht 1996).

2.1.2 Daily Cycle

The diurnal rhythm is primarily based on digestive processes and consists essentially of foraging, rumination and rest. These periods proceed in multiple cycles during the course of a day, an activity cycle (Bützler 2001; Wagenknecht 1996). Its structure as to the red deer’s predominant actions is displayed in Figure 3.

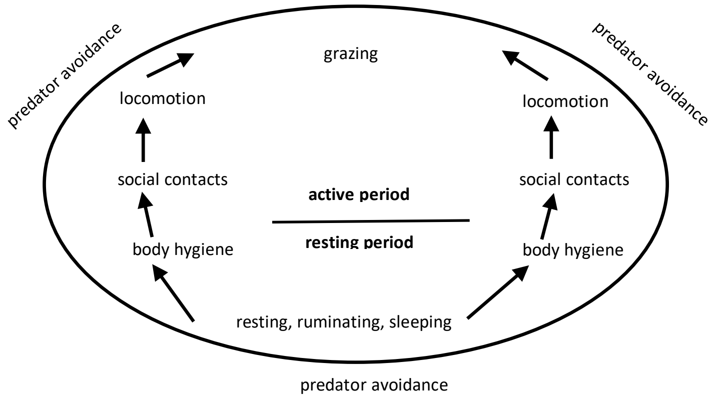

Figure 3: *Representation of the daily activity cycle of red deer as explained by Bützler (2001).*

The activity period is initiated with the behavior of personal hygiene and is readily followed by social contact with other herd members. After that, the deer visit the grazing area. After grazing, they move back to the resting places, tend to social contacts again before laying down and devoting themselves to body care and then lay down. During the resting period, they doze, ruminate and sleep. The behavior at the beginning and end of the activity period is repeated in mirror image. The whole cycle is accompanied by the behavior of enemy avoidance, which is mostly expressed in securing at regular intervals. However, this occurs primarily in the wild when there is a disturbance. The securing of protected places is primarily restricted to the duration of the activity period (Bützler 2001).

The distance which is covered during these daily migrations is usually small, with an average of 1.8 km in winter and 3 km in summer (Clutton-Brock et al. 1982, Wagenknecht 1996). This scheme is highly variable depending on the environmental situation. Escape-triggering disturbances can upset the whole cycle. Seasonal changes are also subject to these cycles. While the feist deer has a very regular activity cycle, which is mainly determined by the grazing and digestion rhythm, the activity of the rutting deer is completely independent of the grazing and digestion rhythm, since it takes up almost no food.

There are also very close relationships between diurnal periodicity and the respective biotope; when the biotope changes, the diurnal periodicity also changes. The animals stay on the mountain slopes during the day and the search for food in the often-undisturbed valley meadows at night, for example, leads to a high level of activity in the dark, because the disruptions limit grazing during the day. After relocating to higher elevations with sparse mountain forests, the animals show more activity during the day with more spread distribution of activity fluctuations throughout the day. As a result of the extraordinarily increased restlessness in the hunting grounds due to traffic, excursionists, skiing, horseback riding, etc., the red deer, which is particularly sensitive to disturbances, is forced to spend the daytime hours in the thickets and pole woods, which can be up to 18 hours in summer. The animal has thus become much more hidden, but this also makes grazing opportunities during the day more difficult. Today, there is usually a sharp separation between cover and grazing. The red deer may therefore barkstrip to satisfy its nutritional needs if it cannot move to the actual grazing areas during daylight hours. A disturbance of the species-specific 24 -hour rhythm also increases food requirements. In addition, another important change in behavior occurs, namely that the red deer shift their food choice to other plant species; as they begin to graze increasingly on buds, shoots, bark of trees and shrub species (Wagenknecht 1996).

2.1.3 Annual Cycle

Seasonal migration between distinct summer and winter ranges is a common strategy among animals to adjust to spatiotemporal changes in resource abundance (Bischof et al. 2012; Lundberg 1988). This seasonal movement pattern generally results in the creation of two distinct home ranges, a summer and a winter home range. Partial migration, when only part of the population migrates while the remainder stays resident on the charged seasonal range, appears to be a widespread phenomenon among many animal taxa, ranging from insects to higher vertebrates (Lundberg 1988). According to Peters et al. (2017), partial migration is the most common type of migration and seems to occur more frequently when habitat suitability varies significantly over time (Taylor and Norris 2007).

The red deer is a partial migratory mammal as already mentioned above (Chapman et al. 2011). Although distinct behavioral types can be difficult to determine, seasonal movements in red deer can be roughly divided into stationary and migratory individuals (Dingle and Drake 2007). Georgii and Schröder (1983) investigated red deer home ranges in the Alps and discovered that the average distance between summer and winter home ranges is 2.5 km, while intervals of up to 25 km have been observed in exceptional situations. In addition, home range sizes were found to be substantially smaller in winter than in summer, despite large variances between individual animals.

Reinecke et al. (2014) discovered that for stags, the variation between summer and winter home ranges is more pronounced. Furthermore, hinds have bigger home ranges than stags throughout the winter, and vice versa during the summer (Reinecke et al. 2014). Typically, most deer exhibited high home range fidelity as the seasonal home ranges only changed slightly from year to year. This regular movement pattern is typically passed down from hinds to their young. In some cases, the home ranges are coupled to traditional rutting areas (Georgii & Schröder 1983).

The migratory individuals typically spend the summers in the mountains until the first continuous snow cover has formed. To cope with these harsh conditions, they migrate to lower altitudes and spend the winters in the more sheltered environments in the valleys below the tree line (Jarnemo 2008; Mysterud et al. 2011). The migration cycle may be complicated, with different mechanisms working at different stages (Mysterud et al. 2016).

According to Bolger et al. (2008), ungulates benefit from migration for three reasons: (1) access to seasonally changing food resources (quality and/or quantity), (2) access to critically limited resources (seasonally and spatially, e.g., salt) and (3) seasonal escape from predators or parasites. Snow depth limits permanent residence at high elevations in mountainous environments and frequently induces fall migration (Cagnacci et al. 2011). The drivers for a spring-summer migration to higher elevations are still unclear.

The forage-maturation hypothesis (FMH), which predicts that ungulates trade-off forage quantity and forage quality to maximize energy intake, is prominent among suggested drivers of seasonal migration of ungulates, even though a complex combination of factors may induce and constrain the seasonal space-use patterns we witness in animals (Bischof et al. 2012; Fryxell and Sinclair 1988; Hebblewhite et al. 2008; Qviller et al. 2013).

Seasonal changes in the timing of green-up - the period when new and more palatable plant growth emerges - may lead ungulates to migrate to locations with delayed plant phenology in order to have longer access to higher-quality feed with adequate biomass (Hebblewhite et al. 2008). Migratory individuals access to earlier-stage plant phenology can be prolonged compared to residents (Hebblewhite et al. 2008; Pettorelli et al. 2005; Sawyer and Kauffman 2011), resulting in overall improved seasonal feed quality for migrants (Hamel et al. 2009; Hebblewhite et al. 2008). As a result of having access to better forage, migrants are heavier than resident individuals and body condition is tightly linked to fitness components in ungulates (Choquenot 1991; Gaillard et al. 2000).

The so-called green-wave hypothesis, which was first suggested in the waterfowl literature (Drent et al. 1978), states that following the sequential flush of new, high-quality forage along environmental gradients in the terrain provides nutritional benefits to large herbivores (Mysterud et al. 2017). The theory is based on the migratory phenomena in which birds follow a spring wave to their summer destination (van der Graaf et al. 2006; van Wijk et al. 2012). Ungulates have been found to exhibit similar phenology monitoring tendencies (Bischof et al. 2012; Sawyer and Kauffman 2011).

Herbivores can increase their access to emergent vegetation by following the greening of the vegetation along latitudinal or altitudinal migratory gradients. During migration, individuals surf waves of intermediate vegetation biomass, e.g., the green wave (Bischof et al. 2012; Merkle et al. 2016). Many individuals, on the other hand, jump the green wave rather than surfing it, a practice in which individuals migrate to the summer areas before the green wave arrives and wait for it there. For example, red deer jumped rather than surfed the green wave, potentially to avoid giving birth prior to migration, when calves would restrict mobility (Bischof et al. 2012).

At opposite ends of the resource phenology spectrum are green wave surfing and jumping. On one hand, animals have adapted to optimize their exposure to high-quality vegetation by surfing the green wave during migration to build capital before parturition and the higher energy demands of lactation. At the other end of this spectrum, individuals can jump the wave and time their migration and parturition on the calving ground to coincide with the emergence of high-quality vegetation when demands are highest.

Migrants and, to a lesser extent, residents did, however, track phenological greening throughout the growing season by undertaking smaller-scale habitat changes (Bischof et al. 2012). Despite widespread support for the FMH, the link between plant phenology and ungulate mobility has remained obscure (Bischof et al. 2012).

As Bolger et al. (2008) state, the seasonal movement of large herbivores could simultaneously be a strategy to reduce predation risk by moving beyond ranges of non-migratory predators (Bolger et al. 2008; Rettie et al. 2000). However, a complete escape from predation will be uncommon, in part, because migration itself is often risky (Hebblewhite and Merrill 2009; Kropil et al. 2015).

The effects of migration have been widely discussed (Hebblewhite and Merrill 2009; Hebblewhite et al. 2008; Jarnemo 2008; Mysterud et al. 2001) and they have been described as a positive effect on ecosystems from a biological standpoint, resulting in a more reasonable spread of grazing impacts and increasing ecosystem resilience (Fryxell and Sinclair 1988). Seasonal migration may significantly affect population harvest and management, resulting in overexploitation of migrants (Bolger et al. 2008; Jarnemo 2008) with negative effects on population dynamics (Ginsberg and Milner-Gulland 1994; Kropil et al. 2015; Mysterud et al. 2002). Migratory ungulates are regarded to be declining globally due to their reliance on broad landscapes, which makes them extremely vulnerable to environmental change (Xu et al. 2021).

However, new research suggests that many ungulate species can change their migration tendency in response to changing environmental conditions, potentially improving population persistence. Decisions about where and when to migrate, in addition to whether to migrate, appear to be equally important to individual migration techniques. These three dimensions of plasticity have rarely been studied simultaneously (Xu et al. 2021). The early uses of the term "plasticity" to ungulate migratory behavior were based on cumulative observations of individuals transitioning between resident and migrant status (Berg et al. 2019; Eggeman et al. 2016; Peters et al. 2019; Xu et al. 2021).

Ungulates can change their migratory behavior in space and time, in addition to their tendency to migrate. For example, they can expand their ranges and migrate through new corridors (Skarin et al. 2015; Xu et al. 2019), or change the time and duration of their migrations (Le Corre et al. 2017; Rickbeil et al. 2019; Xu et al. 2021). Xu et al. (2021) developed a typological framework for migratory plasticity, illustrated in Figure 4. The three dimensions of migration plasticity include migration propensity, geographical migration patterns, and temporal migration patterns. Migration tendency is related to whether or not an individual will migrate. Spatial change refers to where animals move and is divided into four categories depending on changes in the starting range, finishing range, and/or migration path. Migration timing and length are used to measure temporal change. These three dimensions are interrelated, and changes in one might result in changes in the others. As a result, numerous forms of migration changes within and between dimensions can and do occur (Xu et al. 2021).

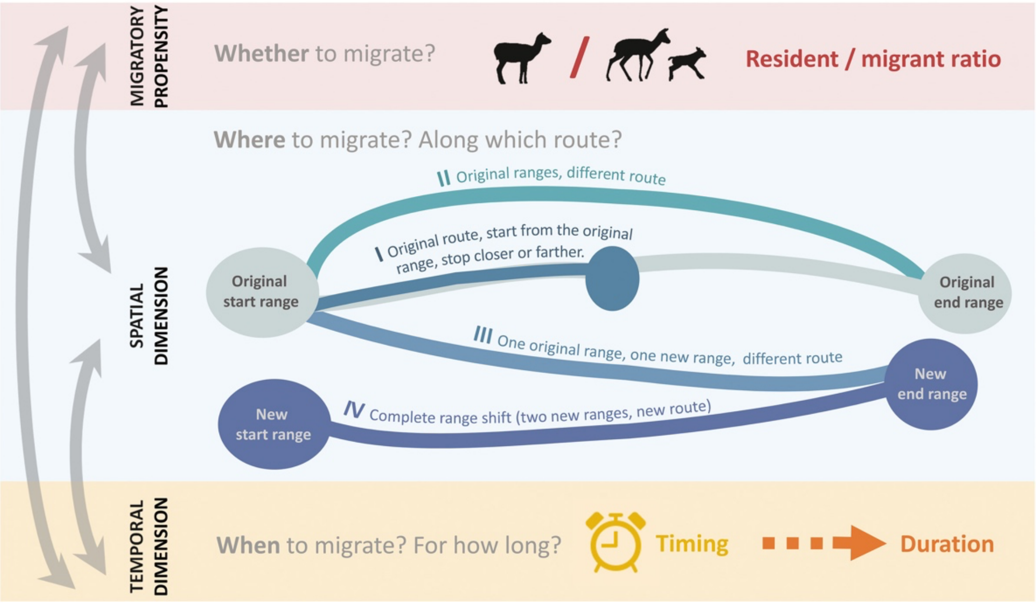

Figure 4: *Typological framework for migratory plasticity by Xu et al. (2021).*

Several methods have been used in past studies to establish whether an individual undertakes a migration with two clearly distinct home ranges. Checking the distance between seasonal home ranges and analyzing spatio-temporal segregation of seasonal location clusters, as done by Patrick (2017) and Boog (2018) with the MCP and KDE methods, are well-known and typical approaches to analyzing animal migration patterns.

In any case, measuring migration occurrence and migration parameters, such as migration timing and distance, is essential to (i) understanding animals' plasticity in this movement tactic (Dingle and Drake 2007), (ii) conserving migratory species (Bolger et al. 2008) and (iii) monitor cascading effects on community structure and function resulting from changes in migratory behaviors (Bauer and Hoye 2014; Palkovacs et al. 2012).

Behavioral plasticity has been found to preserve or improve population persistence under environmental change across species (Beever et al. 2017; Møller et al. 2008). In this case, changes in ungulate migration may not always indicate decline, but rather resilience. Understanding the prevalence, extent, mechanisms and outcomes of migration change can significantly support conservation efforts.

Establishing a standard framework to unite idiosyncratic observations of changes in migration behaviors and to accurately define types of changes is a necessity for making major advancements in migration ecology and conservation. Although the growing acknowledgment of ungulate migratory plasticity has crucial implications for ecology and conservation, we still lack an understanding of its extent and mechanisms (Xu et al. 2021).

Cagnacci et al. (2016) assume that partial migration is prevalent and that there are various types of partial migration, which supports Bunnefeld et al. (2011) classifications of migration types as migratory, mixed migration, and dispersal migration (Cagnacci et al. 2011). It is important to understand the factors underlying intermediate migratory behaviors in the residency-to-migration continuum. Instead of pushing methods to identify typical movement patterns, one should ideally adopt a conceptual framework of such a continuum (Cagnacci et al. 2011).

2.1.4 Foraging

Generally, grasses form the main food component for red deer throughout the year, provided they are available in sufficient quantity. Where they are sparse or inaccessible due to high snow levels, their share in the diet inevitably decreases; instead, the share of tree parts and shrubs increases. These can temporarily be the most exclusive food of red deer or in some areas even all year round. Food intake varies significantly throughout the year (see Figure 5), depending on the availability of high-quality forage, the age and breeding condition of the red deer (Mitchell et al. 1977). There is a particularly high demand for nutrients during all growth processes and special physiological processes such as pregnancy (Wagenknecht 1996).

Lactating red deer tend to eat more than twice their daily maintenance requirements (Clutton-Brock et al. 1982). Due to increased energy demands induced by the growth of the fetus and milk production for females, and to a lesser extent, the growth of antlers for males, the intensity of food intake increases as the snow melts in spring. Grazing is limited during this time, and deer lose up to 35 percent of their body weight, so they build up fat reserves for the exhausting rutting season (Mitchell et al. 1977).

When the rut is over, the amount of food consumed increases to its annual peak in preparation for the winter. Their metabolism is geared to store and accumulate energy reserves for the winter as snow cover lowers the availability of high-quality forage and grazing activity (Wagenknecht 1996).

According to Arnold et al. (2004), nocturnal hypometabolism is connected to a decrease in energy expenditure. Lower digestibility of winter forage is thought to be connected with reduced grazing activity. Even though available food in the alps decreases throughout the winter months, seasonality has been shown to persist even when forage is abundant. As a result, seasonality appears to be a function of day length (Mitchell et al. 1977).

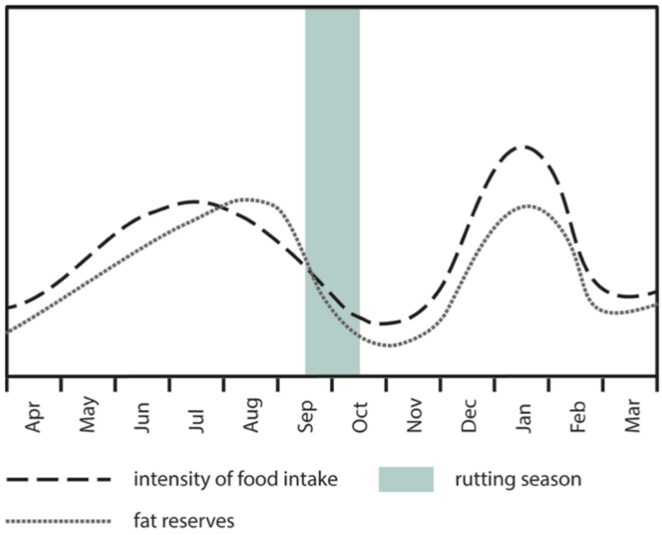

Figure 5: *Annual variation of intensity of food intake and fat reserves of red deer (adapted from Wagenknecht (1996), illustrated by James Patrick (2017)).*

By establishing three diet patterns, Gebert and Verheyden-Tixier (2001) have shown that the diet of red deer is strongly reliant on environmental factors such as habitat and season. While supplementary food items like bark, twigs, forbes, fruits and seeds varied significantly over the year and between habitat types, a key component of the red deer diet like grass and sedges, remained relatively consistent. Red deer require around 3 kg of dry matter, 200 g of digestible protein and 2000 units of starch per day for a 100 kg live weight. This demand is usually covered by consuming 8-20 kg of green manure per day. The weight differences are due to the varied types of grazing (Bützler 2001).

The grazing areas are separated into two groups: those visited only at night and those visited only during the day. Food quality is often better in night-time foraging locations than in day-time foraging places. Furthermore, one of the most important qualities of night-time grazing places is that cover is not needed. During the day, however, little forest glades, shrublands, and forest aisles are commonly visited (Bützler 2001).

The red deer eats mostly from the herb and grass layer near the ground, although it also reaches far up into trees and shrubs. It will occasionally stand on its hind legs to access fresh vegetation. The ground vegetation is cleaned with the forelegs in snowy situations as long as the snow cover allows it (Wagenknecht 1996). Many red deer populations receive supplementary feeding, while others do not; some populations live in largely continuous habitats, while others reside in highly fragmented landscapes with scattered resources. All of these factors can influence red deer foraging behavior (Reinecke et al. 2014; Bützler 2001).

2.1.5 Human Influence on Red Deer Behavior

Human disturbance to wildlife species occurs not only as a result of hunting (Janis and Clark 2002; Kilgo et al. 1998) but also as a result of recreational activities (Hamr 1988; Jayakody et al. 2008; Nellemann et al. 2000). When predators attack, animals must adjust their habitat selection rules, making a trade-off between 'fitness-enhancing' and 'survival-enhancing' activities (Lima and Dill 2011) and behaving in a way that minimizes the ratio of mortality risk to net energy intake, as well as the impacts of stress (Lima 1998). To avoid predators and increase their chances of survival, animals adopt a diverse set of behaviors (Caro et al. 2004), with vigilance being one of the most researched (Lima 1998; McNamara and Houston 1992).

Recreational activities have a wide range of effects on animals. Behavioral consequences on red deer include altered habitat utilization, vigilant behavior, and nutritional intake (Jayakody et al. 2011; Westekemper et al. 2018). Multiple studies have found that cervids are affected not only by human leisure activities but also by the infrastructures associated with these activities. Several red deer populations change their space-use behavior to avoid being too close to recreational trails (Coppes et al. 2017; Rogala et al. 2011; Scholten et al. 2018), especially during high human use times such as during the day (Ager et al. 2003) or weekends (Nix et al. 2018; Sibbald et al. 2011; Westekemper et al. 2018). Nonetheless, both predation and disruption have been demonstrated to elicit similar responses such as increased vigilance and the formation of larger groups (Fernández-Juricic and Schroeder 2003; Lima and Dill 1990).

According to the 'human-caused predation risk' hypothesis, animals perceive disturbance from human recreation as a predation risk (Frid and Dill 2002; Jayakody et al. 2008). For example, high human activity, such as hunting and tourism, has a significant impact on red deer behavior and migration in Denmark (Jeppesen 1987). This shows that in the absence of human activity, red deer have different activity patterns (Kamler et al. 2007).

Outdoor activities can put a variety of pressures on the ecosystem, and the potential negative consequences on wild creatures, especially endangered species, have long been recognized (Coppes et al. 2017). As a result, wildlife managers are frequently faced with the challenge of finding a balance between wildlife needs and recreational demands (Monz et al. 2013; Reed and Merenlender 2008).

However, since the study species were exposed to both natural predators and recreational disturbance in most cases, it is not possible to measure the reaction to each form of disturbance separately (Jayakody et al. 2008). In the study areas of this work, home ranges of the red deer individuals are often intertwined with human settlements and regions used for recreational activities. Additionally, roads cut through connected home ranges. Naturally, the high amount of spatial overlap between humans and red deer habitats leads to human-wildlife conflicts. Damage to agricultural areas and forestry are two examples of the consequences. Furthermore, as humans increasingly intrude into natural areas, wild animals are forced to modify their time and space requirements in response to human behavior (Bützler 2001; Gebert and Verheyden-Tixier 2001; Löttker et al. 2009).

2.2 Space Utilization and Migration Pattern Analysis Tools

Red deer, as mentioned in Section 2.1.3, are prone to seasonal migrations and have separate summer and winter home ranges where they return year after year. Examining the home ranges of the animal of interest is thus a helpful strategy for analyzing space usage and migration patterns. Various ways of describing home ranges have been utilized over time. The Minimum Convex Polygon (MCP) and Kernel Density Estimation are two of the most commonly used techniques (KDE) (Kolodzinski et al. 2010; Reinecke et al. 2014).

Alternative approaches to home range and migration pattern analysis have been developed and used in recent years (Bunnefeld et al. 2011; Horne et al. 2007; Kranstauber et al. 2012; Mysterud et al. 2011). In addition, travel distances and migratory patterns were calculated using net squared displacement (NSD) (Bunnefeld et al. 2011). Furthermore, the significance of the ecological setting in obtaining relevant results in behavioral GPS data studies has increased (Cagnacci et al. 2010). The approaches stated above, as well as the integration of context data into GPS location studies, will be illustrated and addressed in detail in the next chapters. Not all of these approaches are used in this study. However, it is gives an overview of the most used methods for movement or home range analysis in recent years.

2.2.1 Minimum Convex Polygon (MCP)

To conduct home range analysis in animal studies, the simplest and most commonly used way is to create an MCP (Laver and Kelly 2008; Reinecke et al. 2014). This method was first used by Mohr (1947) as a home-range estimator. An MCP is the smallest polygon that contains all the measured locations. Additionally, internal angles which exceed 180 degrees are not allowed (Burgman and Fox 2003). Furthermore, occasional rambles outside the area can be partially ignored by defining a percentage of points that should be included in the convex hull (Burt 1943). The simple use of MCP computations enables home range analyses without a general understanding of the point distribution or underlying factors of the covered area, such as terrain structure (Laver and Kelly 2008).

However, there are some disadvantages to this method that should be considered as well. MCP only gives a crude outline of an individual’s home range (Row and Blouin-Demers 2006) and is generally considered an unreliable method (Downs and Horner 2008). Since the approach is sensitive to outliers, MCP home range predictions are prone to inaccuracies. Because enormous unused areas are included in home range calculations as a result of outliers the home ranges are overestimated (Powell 2000; Reinecke et al. 2014; Row and Blouin-Demers 2006).

Furthermore, at least 100 location fixes are necessary to get a valid home range estimation. If the sample rate is lower, the error rates rise, and the home ranges become less accurate (Seaman et al. 1999). Kolodzinski et al. (2010) even discovered that studies with fewer than 90 data points underestimated the area of home ranges by more than 50%.

Moreover, topographic elements are not considered in the MCP calculation. As a result, regions an animal cannot frequent (such as lakes) are included in the home range (Haller 1996). Further, a convex polygon's home range size and location are the only pieces of information available. This is because the density of the observed points is neglected in MCP calculations. As a result, little is known regarding the intensity of space utilization. Despite these shortcomings, MCP is still used as a home-range estimator (e.g. Barg et al. 2005; Jurczyszyn 2006), due to its simple construction and comparability among studies (Downs and Horner 2008).

2.2.2 Kernel Density Estimation (KDE)

The development of home range analysis has led to approaches that use probability distributions to calculate results (Reinecke et al. 2014). KDE was adjusted to home range analysis by Worton (1989) from a technique for estimating distributions from small samples.

The KDE provides a 2-dimensional grid surface with regularly spaced cells to calculate such density distributions. The cell values indicate the likelihood of a certain individual being found in a location within their calculated home range (Hemson et al. 2005; Powell 2000; Seaman et al. 1999; Steiniger and Hunter 2013. By smoothing the point pattern of animal locations, the KDE provides a continuous intensity surface of an animal's utilization distribution. Smoothing is accomplished by using a distance weighting function, such as a Gaussian kernel. Finally, isopleths can be calculated that indicate the likelihood (in percent) of finding an object within a particular region (Hemson et al. 2005; Powell 2000; Seaman et al. 1999; Steiniger and Hunter 2013). The 95 percent volume contour line is typically used to estimate the complete home range, whereas the 50 percent volume contour line is frequently used to analyze the core home range or area of intensified use (Hemson et al. 2005; Karns and Lancia 2012; Laver and Kelly 2008; Powell 2000).

One of the most useful features of the KDE is its ability to construct 3-dimensional representations of utilization distribution within home ranges. The third dimension depicts the length of time an animal spends in a given area, as well as the density of points inside that area. This data can be used to estimate habitat choices and resource use (Seaman et al. 1999). KDE's have the advantage of being less subject to sampling rates than MCP-based home range calculations (Kolodzinski et al. 2010). Despite the popularity of home range analysis using KDE, it has the disadvantage of challenging comparability and inconsistency of results among studies (Powell 2000; Reinecke et al. 2014).

The bandwidth, or smoothing parameter, of the kernel, regulates the rate of smoothing it introduces. Home range estimates are sensitive to bandwidth selection; bandwidths that are too broad smooth the point pattern and overestimate home ranges, whereas bandwidths that are too narrow smooth the point pattern and underestimate home ranges (Kernohan et al. 2001). As a result, much of the current home-range analysis research has concentrated on finding the best bandwidths for KDE (Downs and Horner 2008; Hemson et al. 2005).

Because the smoothing factor has such a large impact on the home range estimate, numerous approaches for determining the best smoothing factor have been developed. The normal or reference method (h_{ref}), least-squared cross-validation (h_{LSCV}), and the plug-in approach ($h_{plug-in}$) are three of the most widely utilized functions (Gitzen et al. 2006; Hemson et al. 2005; Walter et al. 2011). The LSCV approach is most studies' favored method due to lower biases (Gitzen et al. 2006; Seaman et al. 1999; Walter et al. 2011).

Kernel density estimation (KDE) is a nonparametric and statistically effective technique for solving range delineation problems. KDE assumes that the data are distributed independently and identically. Animal tracking data which is frequently used as KDE inputs are inherently autocorrelated and hence contradicts this key premise (Fleming et al. 2015).

Another downside of the KDE is that it overlooks movement between sample sites, which is critical considering animals rarely travel in a straight line. Furthermore, KDE ignores temporal autocorrelation (Buchin et al. 2012). There are concerns that the KDE method may not be suited for home range analyses with location data based on GPS-telemetry where high sample numbers are prevalent due to the uncertainty associated with selecting an ideal bandwidth and issues with autocorrelation(Byrne et al. 2014; Gitzen et al. 2006).

2.2.3 Net Square Displacement (NSD)

Bunnefeld et al. (2011) developed a new method for uniform spatio-temporal data analysis: the usage of net square displacement. Unlike the MCP and the KDE and the overlap of identified seasonal ranges, the NSD can be used to distinguish between different types of migration and other movement patterns like dispersal, stationary, and nomadic behavior. It is also possible to extract useful information about a movement path, such as migration timing, duration, and distance. These parameters can then be used to compare individuals, groups, and changes between years (Bunnefeld et al. 2011; Papworth et al.

2012). Furthermore, understanding migration parameters is important for understanding animal movement behavior, the plasticity of its strategies, and its conservation (Cagnacci et al. 2016). As a result, the NSD has gained popularity in recent years in movement research, particularly in relation to yearly movement cycles in migrating animals (Bunnefeld et al. 2011, Papworth et al. 2012) and also quantifying migration features and differences between migration types (Singh et al. 2016).

In this approach, migration is described as a year-long double sigmoid or s-shaped function that leads to an exact return to the departure point, thus approximating a non-linear curve. As migration begins, the net squared displacement from the starting point increases until it reaches a plateau, i.e., the other seasonal range. The net squared displacement decreases when the individual returns to the original location, eventually reaching zero (see Figure 6).

The strength of the NSD methods is that it provides an objective and quantitative basis for classifying different movement patterns and estimating movement parameters including extent, timing, and duration. In addition, the method is scale independent (Singh et al. 2016). However, NSD's ability to correctly classify individual movement patterns has been doubted, and study design difficulties such as data/animal starting locations, data sampling regime, and the extent of species movement have been raised (Singh et al. 2016). They showed that the NSD method misclassified movement modes, even for individuals with non-overlapping seasonal ranges. They also reported problems in estimating migration parameters for individuals classified as migratory, due to the NSD model misclassifying migration timing (Mysterud et al. 2011).

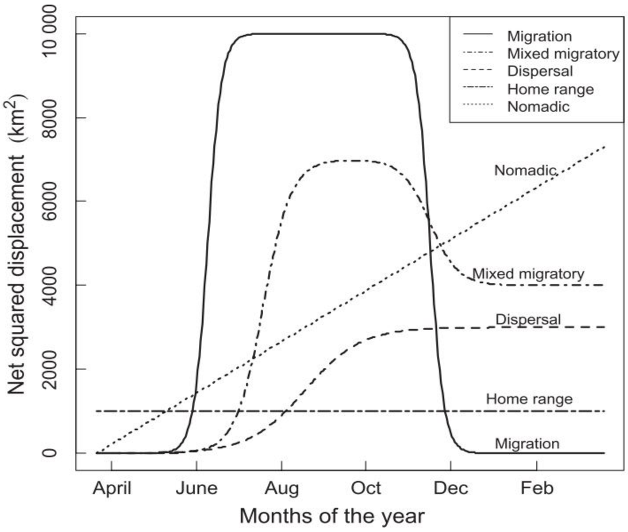

Figure 6: *Different movement types analyzed with the NSD (Bunnefeld et al. 2011, 467).*

2.2.4 SeqScan

Partial migration is especially interesting since it contrasts two different animal space-use patterns: residence, or the continuous and distinct use of the same spatial range and migration, which consists of the seasonal use of separate ranges (Chapman et al. 2011). The intermediate occurrences were discovered while examining partial migration and were described as part of a migratory continuum (Ball et al. 2001). Such a continuum has not been thoroughly studied yet (Dingle and Drake 2007) using the most common methods to identify animal migration (Börger et al. 2011; Fryxell et al. 2008).

Damiani et al. (2015a) studied the use of a recent technique rooted in computational movement analysis to characterize partial migration along the migratory continuum.

SeqScan is a recently proposed time-aware density-based clustering technique for extracting migratory patterns from GPS trajectories (Damiani et al. 2014). The SeqScan framework includes the stay region model and clustering method, as well as two new components: the noise model and internal time-aware validity indices (Damiani et al. 2015a).

A stay region is a location in space and time where a moving object spends a large amount of time. The amount of time spent in the region can be arbitrarily long (compatibly with the duration of the trajectory). In most cases, a stay region does not represent a specific geographical entity (for example, a forest or a city), but rather has vague spatial and temporal boundaries. The object can temporarily depart the location while residing there to go on excursions. Furthermore, objects can migrate from one stay region to another without the requirement to specify the number of migrations/stay regions in advance (see Figure 7).

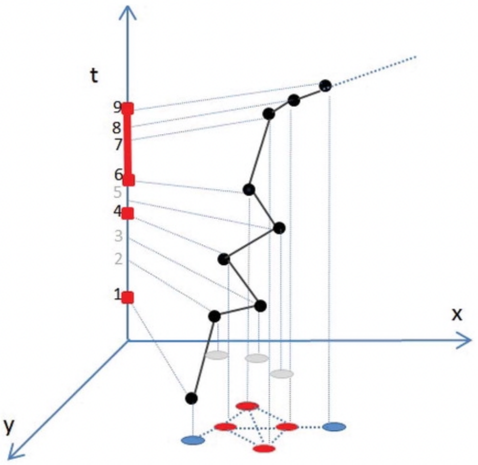

Figure 7: *A stay region's space-time cube. The projection on space is the dense area. The projection on time is the time segment. The core and border points of the cluster are indicated by red and blue dots, respectively (Damiani et al. 2015a).*

The algorithm scans the input trajectory in sequence and aggregates the points one at a time, creating one stay region at a time. When a new stay region is created, it becomes a dynamic entity that is initially generated, then enlarged, and eventually closed. The event that signals the end of the stay in the region is the creation of another stay region, which is an important component of the algorithm. In this way, the remaining region acts as an attraction area, holding the moving object in until a more attractive area is discovered (Damiani et al. 2015a).

The noise model is a new concept. Clustering noise is not an undifferentiated set of useless points like equivalent approaches. Rather, it offers a great deal of information that gives insight into the mobility of moving objects. The noise can be classified as follows: a) excursion, and b) transition (Damiani et al. 2015a).

Determining the validity of the stay regions in relation to the application at hand is critical for evaluating the clustering result. Damiani et al. (2015a) propose a simple, but effective, time-aware index to overcome this limitation, namely the stationarity index (Q_{PD}). Q_{PD} applies to single stay regions and is defined as the ratio or the presence *(P)* and the duration *(D)* of the stay region (S_i), i.e.:

$$Q_{PD}(S_i) = \frac{P(S_i)}{D(S_i)} \tag{1}$$

The index's value, which ranges from 0 to 1, represents the approximate percentage of time the object spends inside the stay region. If $Q_{PD}(S_i) = 0.8$, for example, the object residing in S_i ideally spends 20% of its time on excursions. The presence in the region is zero if the object moves back and forth from the region, alternating one point inside with one point outside the region. That is implied by the notion of presence (i.e. if two consecutive points are not both inside the region, the presence in the interval is 0). On the opposite, if the value $Q_{PD}(S_i) = 1$, it indicates that the object does not perform any excursion (Damiani et al. 2015a).

Damiani et al. (2015a) showed in their study that SeqScan has performances comparable to the methods used in ecology and thus can be of interest for the analysis of partial migrations. However, the study proves that the outcome of SeqScan is sensible from an ecological viewpoint, while a suitable set of parameters can be found in a reasonably simple way. Furthermore, the SeqScan framework overcomes significant constraints of more traditional approaches, including the ability to quantify individual mobility behavior. By combining SeqScan, stationarity indices, and traditional spatio-temporal data management techniques, it is possible to gain a deeper understanding of mobility behavior (Damiani et al. 2015a).

2.2.5 Environmental Context of GPS Locations

Context data is provided as raster or vector data sets when integrating it into the study of GPS locations. Discrete points, lines, and polygons can all be defined using the vector data model. As a result, it is an ideal model for representing categorical features like animal breeding sites, rivers, and home range boundaries. Physical parameters that are continuous in space, such as precipitation and temperature, are generally represented by rasters in field-based context (Gschwend 2015; Slocum et al. 2022). The question is how useful information can be obtained from GPS positions when context data is available. Figure 8 shows five methods for extracting context values from raster or vector data sets proposed by Gschwend (2015).

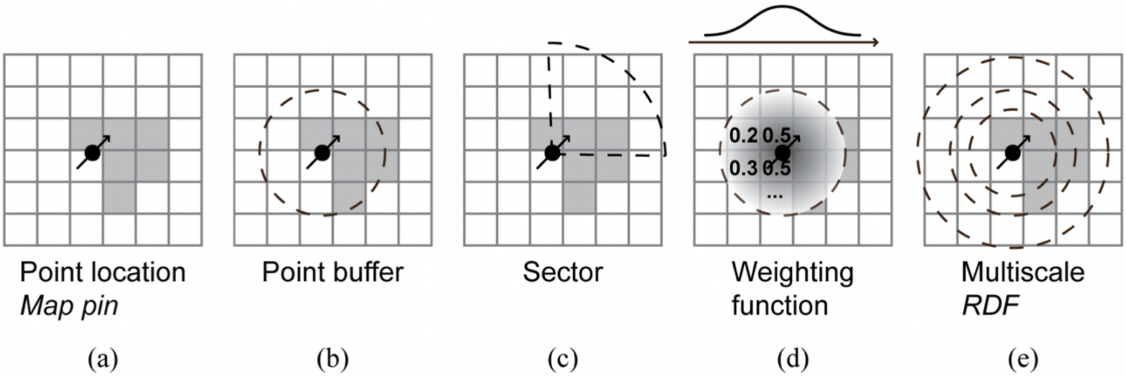

Figure 8: *Different methods of acquiring context values at point locations (Gschwend 2015, 48).*

The most straightforward method is to extract the context value only at the GPS point position. The GPS fix is treated as a map pin in this situation (Figure 8, a). This method should be used when the context value's influence is relatively close and does not affect the rest of an individual's movement.

However, in most cases, an animal's surrounding contextual variables have an impact on its behavior or movement path. As a result, approaches which define a buffer, sector, weighting function, or multiscale radial distance function (RDF) (b - c in Figure 8) which take into account the surrounding raster cells of a GPS fix may be more suitable when analyzing animal movement and behavior. The point buffer method creates a circular buffer around the GPS coordinates with a given radius (b). The average of all pixel values within the buffer is then calculated and assigned to the GPS point. By selecting only a fraction or angle of view of the entire buffer, the buffer can be limited to a sector (c). This method is commonly used in viewshed analysis; however, it should only be utilized when the sampling interval is small enough to estimate an individual's actual trajectory. To account for the influence of variable relevance of context values as distance increases, a distance-weighting function can be applied around the sample points (d). Alternatively, different-sized buffers can be used to evaluate multiple context scales (e). When context data is provided in vector format, similar methodologies can be used. If a GPS point is within a polygon, for example, the polygon value is returned rather than a raster value.

Instead of single points, context values can be analyzed using segments of a trajectory and two or more GPS fixes. These segments can be defined by the trajectory's temporal, spatial, and spatio-temporal properties, as seen in Figure 9, where the segments were formed regarding the time of the day.

In this situation, the segment can be regarded as a buffer, similar to Figure 8b point buffer method. To generate a sector, the geometry of the buffer can be altered, and weighting factors can be applied. The ability to consider differences in the environment when analyzing movement with respect to the environmental context by segments is a benefit (Gschwend 2015).

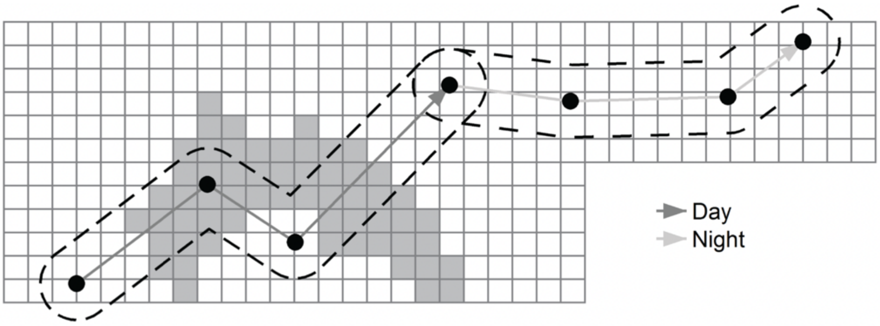

Figure 9: *Acquiring context values using segment-based methods (Gschwend 2015, 50).*

2.3 Ecological Resources

Without having to be close to the monitored animal, GPS technology has made it possible to track and map animal movement at high precision and resolution. The focus used to be on using geometric criteria to analyze the shape, pattern, and arrangements of home ranges (Gschwend 2015). In animal ecology, however, it is not only of interest where an individual is at what time. Some of the additional questions that have been raised include: Why is the animal in a specific location at a specific time? What exactly is it doing there? And what type of impact might the animal's presence have on its surroundings? What will happen to the animal in the future? To answer such questions, the animal's GPS samples must be linked to its environment (Cagnacci et al. 2010).

2.3.1 Normalized Difference Vegetation Index (NDVI)

Knowing what kind of resources an individual has access to is essential for judging home ranges and activity or movement patterns. Because red deer are herbivores, the analysis of resource consumption must focus on the vegetation cover (Borowik et al. 2013).

Because ungulates prefer plants with high nitrogen content, it has been hypothesized that the spring migration of red deer is driven in part by the search for better-quality, nutrient-rich plants once the snow melts in higher elevations (Malnar et al. 2015; Mysterud et al. 2011). Optical remote sensing techniques have the potential to gather information on plant function and status over broad regions quickly and efficiently. The productivity of the photosynthetic process, which is a function of chlorophyll content, is strongly linked to the functioning and condition of plants. Fortunately, nitrogen is an essential component of chlorophyll and the photosynthesis enzymes, thus there is a tight link between chlorophyll and nitrogen levels (Clevers and Gitelson 2013).

If vegetation data is not available, the NDVI can be used to extract vegetation from other ground cover types such as glaciers or gravel fields. The reflectance of vegetation in near-infrared *(NIR)* and red *(RED)* wavelengths is used to determine NDVI values, which range from -1 to 1. These wavelengths are used as vegetation transmits and reflects most *NIR* wavelengths, while chlorophyll absorbs most *RED* and visible wavelengths. This behavior produces a distinct spectral signature with a low point in wavelengths of 0.6-0.7 m *(RED)* and a peak in wavelengths of around 0.8-0.9 m *(NIR),* indicating a strong absorption contrast from 0.6 to 0.9 m (see Figure 10) (Jackson and Huete 1991; Myneni et al. 2019).

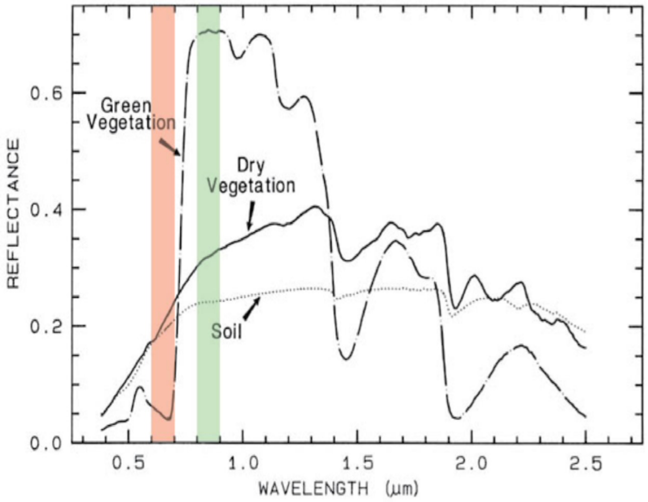

Figure 10: *Reflectance spectra of soil, dry vegetation, and green vegetation. The red bar indicates the RED spectrum and the green bar the NIR spectrum* (Lillesand et al. 2008).

Thus, satellite sensors used for vegetation research can detect the amount of *NIR* and *RED* light reflected (Borowik et al. 2013; Jackson and Huete 1991). The following formula (2) is used to compute the NDVI (Myneni et al. 2019):

$$NDVI = \frac{NIR - RED}{NIR + RED} \quad (2)$$

On the one hand, healthy and dense vegetation generates positive values due to high *NIR* reflectance. On the other hand, dry and sick or senescing flora, soil, water, and snow reflect much less *NIR*, resulting in a low and negative NDVI value (Myneni et al. 2019). As a result, locations with an NDVI value greater than 0 have some form of ground cover (Mysterud et al. 2011). In addition, the NDVI is quite useful for monitoring vegetation dynamics. Since the vegetation density increases throughout spring, peaking when the soil is completely covered by vegetation (Jackson and Huete 1991; Pettorelli et al. 2005b).

Ecologists are increasingly turning to satellite-based approaches to explore correlations between forage quality and quantity, as opposed to harvest-based methods (Borowik et al. 2013; Pettorelli et al. 2005b; Santin-Janin et al. 2009). The vast increase in available data enables researchers to study the relationship between vegetation production and availability and herbivore distribution and dynamics on a larger scale (Borowik et al. 2013). According to recent research, the NDVI can be used as a proxy for forage availability in terms of biomass (Santin-Janin et al. 2009; Ullah et al. 2012) and forage quality (Ryan et al. 2012). Unfortunately, the applicability of remotely sensed vegetation indices does not extend to estimating plant productivity on the ground within forest ecosystems (Borowik et al. 2013).

2.3.2 Normalized Difference Snow Index (NDSI)

Although most wave surfing research focuses on animals following forage resources (Armstrong et al. 2016), snowmelt may be a cue of phenological change that is monitored by northern migratory populations (Laforge et al. 2021). Elk migration, for example, is known to be driven by snowpack in Yellowstone National Park, with later spring migrations linked to later spring snowmelt (Rickbeil et al. 2019; White et al. 2010). In ungulates, traveling through snow increases the relative net cost of movement exponentially as a function of how far they sink which affects habitat selection (Sweeney and Sweeney 1984). Furthermore, snow reduces forage availability (Adamczewski et al. 1988), foraging efficiency (Goodson et al. 1991) and accessing subnivean forage also represents an additional energetic burden (Fancy and White 1985).

Snow cover may therefore limit how early individuals migrate while jumping the green wave, implying that individuals could follow the receding edge of snowmelt to maximize movement efficiency while still arriving in time to catch the green wave during calving. If green-up happens quickly after snowmelt, such timing could be important. Animals may be able to time their calving to coincide with the best conditions by following snowmelt along migratory pathways. For example, travel costs could be reduced by avoiding the cost of traveling through deep snow and by moving more efficiently over frozen terrain. Reduced snow cover would also make foraging easier; individuals would no longer have to struggle for nutrients as they would in the winter (Fancy and White 1985).

Laforge et al. (2021) used the Normalized difference snow index (NDSI) to determine the impact of snow on the migration timing. To distinguish snow from clouds and other non-snow-covered conditions, the NDSI uses the fact that snow reflectance is high in the visible (0.5–0.7 μm) wavelengths and low in the short-wave infrared (1–4 μ m) wavelengths (Nolin and Liang 2000). The NDSI is calculated by taking the difference in reflectance measured in a visible band such as MODIS band 4 (0.555 m) by the sum of the two reflectance values (Laforge et al. 2021):

$$NDSI = \frac{b4 - b6}{b4 + b6} \tag{3}$$

2.3.3 Landcover

According to Mysterud and Østbye (1995), activity patterns and the animals' habitat are usually neglected in ungulate studies. Furthermore, according to Laube (2014), to fully understand the behavior that causes a movement pattern, the semantic meaning of the geometric characteristics should be analyzed.

Since red deer's activity pattern is mostly based on feeding, resting and avoiding predation, or avoidance of disturbance in general, resources where deer can graze and find cover are of particular importance (Adrados et al. 2008). In this sense, Mysterud and Østbye (1995) differentiate between structural and non-structural cover, with structural cover consisting of physical structures such as terrain and vegetation. This type of cover serves both as a visual and thermal barrier. Deer have been seen seeking shelter under dense vegetation, particularly during periods of low temperatures and intense winds. Schmidt (1993) confirmed these findings, showing that red deer used forested areas as wind cover throughout the winter months. This demonstrates that not only ground cover data, but also meteorological data are important. The non-structural cover consists of factors that mainly provide protection by reducing visibility. As a result, the time of day or bad weather conditions might serve as non-structural cover, as visibility is for example restricted on foggy days. Hence, ungulates must find a balance between seeking protection and shelter in forest areas while also grazing in more exposed areas (Mysterud and Østbye (1995).

Cover may be beneficial to predators since it enables them to approach their prey undetected once it is discovered by them. In densely vegetated places, this could lead to ungulates being more cautious (Goldsmith 1990). It must be said, however, that predators hardly play a role as enemies of the red deer in Central Europe (Bützler 2001). Game reserves and wildlife sanctuaries are another sorts of cover not mentioned by Mysterud & Østbye (1995). These locations offer protection from human recreational and hunting activities. Reimoser et al. (2014) discovered that such reserves and sanctuaries do have an impact on red deer space use patterns, particularly during hunting and tourism seasons.

Since red deer behavior and its environment are so interdependent, it is essential to integrate as much environmental data as possible into the study in order to gain a clear understanding of traditional key concepts in animal ecology, and in this case red deer behavior (Cagnacci et al. 2010).

3. Study Area and Data

3.1 Study Areas

3.1.1 Overview

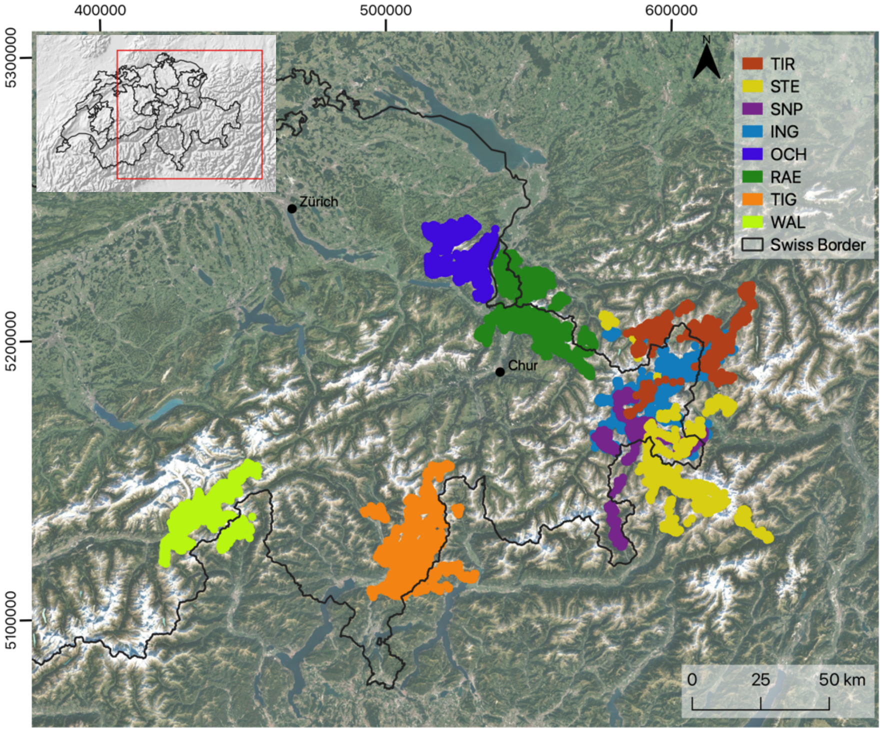

Figure 11: *Overview of the eight study areas. ©swisstopo*

In this study eight different study locations are part of the analysis of red deer behavior. The research areas are spread across Switzerland, Austria, and Italy (see Figure 11). Therefore, the regions vary greatly in terms of topography, vegetation, and weather conditions. In the following chapters the different projects and locations will be described in more detail.

3.1.2 Swiss National Park (SNP)

The Swiss National Park (SNP) is located in the Engadin, in the eastern part of Switzerland. During the period of its foundation, most red deer remained in the park all year round. In the 1930s, seasonal migrations between summer ranges in the SNP and winter ranges between Bever and Ramosch as well as the Val Müstair down to the Vinschgau began (Haller et al. 2002). Since the founding of the Swiss National Park in 1914 the red deer population developed exponentially. Several factors were responsible for this (Triebs et al. 2016):

- In the entire area of the SNP, flora and fauna as well as other processes are allowed to develop naturally. Hunting is restricted, except for specially justified shootings.
- With the disappearance of large predators (especially the wolf), natural enemies were missing.

- Until the 1970s, hunting outside the SNP, was not able to slow down the population development.

This led directly to a peak of more than 3000 red deer in the SNP in the 1980s, resulting in the so-called "deer crisis". Since most deer left the park in late autumn, the high numbers and the winter feeding still practiced at that time in the commercial forests led to impairments of forest regeneration, yield losses in agriculture and finally to repeated, massive winter fatalities.
It took decades to find a hunting mode based on wildlife biology without violating the fundamental hunting ban in the SNP. The only recipe for this is the two-stage hunt with the regular hunt in September and the additional hunt in late autumn.
The designation of several small game reserves outside the SNP led to a better distribution of the red deer and to the desired success in the high hunt. However, most of the approximately 1800 red deer that spend the summer and autumn in the SNP can only be hunted after they have left the protected area. Near large, protected areas, the additional hunt in late autumn is the only promising approach to population control (Triebs et al. 2016).
Monitoring red deer in the region of the SNP started already in 1960, where the individuals were marked with ear tags. In the *proget d'ecologia* during the 1970s nearly 500 individuals were tagged to find out the main migration routes (Blankenhorn et al. 1979).
From 2009 on, red deer have been marked with GPS collars during the summer months within the SNP to find out where they spend the winter. Since its foundation in 1914, the Swiss National Park has been committed to research. Almost yearly new individuals of red deer are marked.
General ungulate monitoring includes the following additional activities in the SNP during the year:

- Censuses 1x a year
- Recording of spatial distribution 4x a year in 2 parts of the SNP (early Jan., May, Aug., Nov.)
- Marking red deer with GPS collars
- Collection of skulls (see Figure 12)

Figure 12: *Skull collection for research reasons in the SNP.*

The intensive work that has been going on in the SNP for the past twelve years has created a good basis for long-term studies that is unique in the Alpine region. The data series on population development and spatial distribution are a unique basis and must be continued (Filli 2008).

3.1.3 Stelvio National Park (STE)

At the beginning of the 20th century, the first red deer individuals from the Swiss National Park moved to the area between Taufers and Glurns, today's territory of Stelvio National Park in Italy. However, the densities remained relatively low due to human influences. The population of red deer increased after the 1950s, and even more so after the 1960s, due to migrating red deer from the SNP. Since the 1990s, red deer have been fitted with collar transmitters, allowing for accurate and dependable measurements of the ungulate species space utilization, distribution, and migration patterns. With the high density of red deer, there was increased severe browsing damage in the forest and many animals fell ill with paratuberculosis. The density of red deer in the Stelvio National Park's Vinschgau area reached such high levels in the 1970s and 1980s that the state forestry and domain administration ASFD (Azienda Statale Foreste Demaniali), as the park's then administrator, released a certain number of red deer each year for shooting by the local hunting community (Platter 2020).

In 2002, the project *Rothirsch-Management* started aiming at getting a thorough understanding of the animals' lives and migration patterns. A total of 43 red deer were captured and fitted with tracking devices for this reason. The winter and summer ecosystems in the National Park and surrounding areas can be assessed this way. In the second stage, the spatial and temporal linkages of the deer movements are studied and assessed. Future deer population control strategies in the Stelvio National Park will be possible based on these data. This research project is a collaboration with the neighboring Swiss National Park

3.1.4 Valais (WAL)

As early as the mid-1930s, the first red deer migrated over the Furka into the Valais and subsequently spread rapidly in the Aletsch-Goms region, later in the Upper Valais and ultimately throughout the entire canton of Valais. Soon the first damages appeared along with it. Although red deer were hunted only a few years after its immigration, first in Goms, later also in other regions, and already in 1976 in the whole canton of Valais, the population increased rapidly. There were hardly any confirmed facts on the use of space and the migration behavior by red deer in the Aletsch-Goms region for comprehensive management. With the Aletsch-Goms red deer project, which began in 2017, important knowledge gaps concerning technically competent management of this challenging wildlife species were attempted to be filled. Using 52 red deer fitted with GPS collars and an additional 108 red deer marked with ear tags, extensive data on the use of space by these wild animals in the region were compiled. The project ended in 2021 (Signer et al. 2022).

3.1.5 Tigra (TIG)

Over the previous 20 years, the deer population and number of deer shots in the Mesolcina have constantly increased. This trend is followed by a 2-4 kg reduction in the mean weights of 3-year-old and older hinds, as well as an increase in reports of excessive game damage in the forest and agricultural crops, particularly in winter range areas. The red deer finds ideal winter habitats, especially in the southernmost and lowest part of the Mesolcina, near the canton of Ticino (Brosi et al. 2014).

“TIGRA” is a project led by the two hunting administrations of Graubünden and Ticino and has been designed for four years. It started in March 2014 and ended in summer 2019.

The core question of the project revolves around the origin of the red deer that gather in the winter gathering basins. Do they come from the hard-to-hunt deciduous forests of the Mesolcina, from the federal hunting area Trescolmen or from the neighboring Ticino or Italy? Because of this issue, existing natural and artificial, as well as future artificial protected areas, play a key role. Hence, the study was very important regarding the possible establishment of an Adula National Park. The project was also a cooperation with the Swiss National Park. Thus, it was possible to benefit from their know-how in terms of ungulate tagging (Brosi et al. 2014).

3.1.6 Tyrol (TIR)

In 2016, the Tyrolean Hunters Association launched a red deer research project in the district of Landeck (Austria). During the winter months, the red deer were anesthetized at different feeding sites in the area of Nauders, Pfunds, Radurschl, Ischgl and Galtür and equipped with telemetry collars. In the area of Nauders/Pfunds, it has been known that marked red deer immigrated from Switzerland from time to time. Due to these interactions across national borders, the cooperation between the three countries is close. The project in Landeck aims to provide data on their behavior in the border area and is still running (Lacher 2017; Just & Traube 2018). Winter feeding has a long tradition in the Vorarlberg and Tyrolia region. With it and with individual winter gates, the red deer will be attached to the red deer core zone. As a result, the animals should spend the winter in areas where it causes only a few conflicts with the forest and with other land users. A beneficial side effect is that the animals become more predictable from a hunting point of view, allowing for the required kills to be made and so maintaining the hunting value of a hunting area (Jenny et al. 2015). However, gatherings of red deer around feeding stations may increase the transmission of disease agents within deer populations or across different species that use the same feeding stations (Reinecke et al. 2014)

3.1.7 Ingo via (ING)

This project started in 2015 and ended in summer 2020 but is continued in a new perimeter in the middle Engadin and Val Müstair. One of the main goals was to update the facts concerning migration behavior of red deer in the Unterengadin and to see which role small wildlife sanctuaries have in contrast to the larger protection area such as the Swiss National Park. This project benefits from the experience of the two previous transmitter projects: “Rätikon” and “TIGRA”. A prerequisite for the success of the project was that the marked individuals were not allowed to be shot during the hunt in Graubünden, Tyrol and South Tyrol and (Brosi et al. 2015).

3.1.8 Rätikon (RAE)

In the Rätikon area, red deer move between three different countries and hunting systems. The red deer marking project in the border triangle was initiated by the Bludenz district group of the Vorarlberg hunting association and started in July 2009 together with the Office for Hunting and Fishing of the canton of Grisons and the Office for the Environment of the Principality of Liechtenstein. Within the framework of this 5-year project, the trapping and marking of red deer were coordinated and harmonized across three countries for the first time. The treatment of red deer populations in the participating countries varies greatly due to different hunting systems. This was the occasion to scientifically investigate the mutual relations of red deer between the canton of Grisons, the Principality of Liechtenstein and Vorarlberg. In particular, the questions of the degree and the points of time of the connectivity among deer occurrences in the study area should be addressed. This scientific work is to be the basis for a contemporary, cross-country red deer management so that sustainable, environmentally compatible red deer populations will continue to have their habitat in the Area of Rätikon in the future. Overall, 67 red deer individuals were marked during that project (Jenny et al. 2015). The red deer living in the Vorarlberg region get supplementary food during winter, like in the Tyrol area. However, these animals were not looked at separately but may influence the overall results of the RAE area (Jenny et al. 2015).

3.1.9 Eastern Switzerland (OCH)

Increasing red deer populations and long-standing forest-game discussions often shaped the way red deer was dealt with in parts of eastern Switzerland and especially in the Werdenberg region. The cross-cantonal research project in the cantons of St.Gallen, Appenzell Innerrhoden and Ausserrhoden aimed at the following main questions: Where are red deer's seasonal and diurnal preferred haunts and how are they related? Which food sources do the red deer use and how does the ingested food affect the metabolism? How do human activities influence the use of space and the behavior of red deer? To investigate the questions, the project area was divided into five catch regions: Werdenberg (SG), Toggenburg (SG), Neckertal (SG), Urnäsch (AR) and Appenzell (AI) (Thiel et al. 2018).

3.2 Data

3.2.1 GPS Data

In total, 391 red deer individuals' motion data were collected throughout time in the eight study regions. Figure 13 illustrates the gender distribution of captured and marked red deer by region.
However, for 103 animals sampling duration was shorter than a year. Especially for home range estimations and migration patterns, such short sampling durations pose a problem. For most of the remaining 288 individuals the sampling duration was exceeding a year. Therefore, an Animal ID per year was created, since it is possible that an individual is resident for a year but migrates the year after (facultative migration; (Dingle and Drake 2007). In the analyses a migration year starts from the 1st of March and ends in the next year in February. This way the timing of a possible spring and autumn migration is visible.

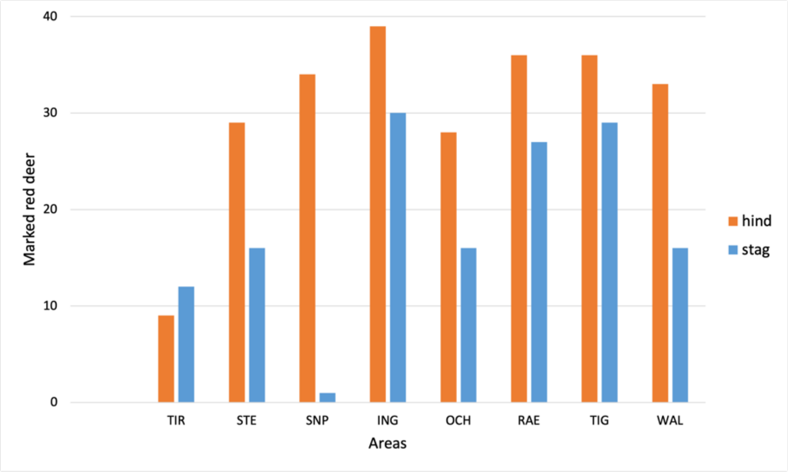

Figure 13: *Proportion of marked red deer individuals by sex and area.*

All movement data was provided by the different projects described previously and supplied as CSV data files. The first individuals were captured and marked in winter 2009. Since then, yearly movement data of red deer were gathered by one or several projects. The used GPS collars collected data about the location of the individuals at various time intervals. For this thesis the GPS data was randomly reduced to one location per day. This approach is used in similar studies, whereas they used the daily average location using the centroid of all locations on a given calendar date (Gurarie et al. 2017; Peters et al. 2019).

Since there are several projects involved, the timing of the capture and therefore the start dates of the data sampling vary between the individuals. For the majority of the animals, sampling started in March and was carried out over a duration exceeding one year (see Figure 14). However, some individuals were captured in summer, especially around the area of the Swiss National Park (see Appendix A.2). This is due to the fact that most individuals which have their summer habitat in the protected area migrate in autumn for their winter home range (see Chapter 3.1.2).

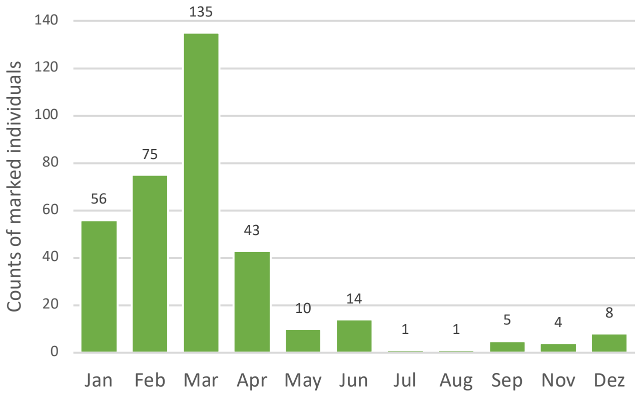

Figure 14: *Timing of the transmission for all areas. Mostly the red deer were marked in March.*

Thomas Rempfler, PhD and currently working for the Swiss National Park, did the pre-processing of the data by a screening method of Bjørneraas et al. (2010). Therefore, locations from unrealistic movement patterns were identified and cleaned.

The GPS collars were produced by VECTRONIC Aerospace GmbH and were also equipped with a motion-sensitive acceleration sensor to collect data on an individual's activity. The acceleration sensor and the GPS stored various variables including the coordinates of the deer fixes in the coordinate system CH1903+/LV95 as well as the height of the locations in meters. Timestamps of the stored GPS fixes were saved in the UTC format. Moreover, the dilution of precision (DOP) describes the satellite geometry quality which influences GPS location accuracy. The number of visible satellites and their position in relation to each other, as well as the observed point of interest, are used to determine the DOP value (resp. the GPS collar). Generally, the number of satellites included in a measurement increases the DOP value, and hence the accuracy, with a low DOP indicating good accuracy. Unsuitable satellite constellations, result in a decrease in accuracy and the DOP value (Adrados et al. 2002; Langley 1999).

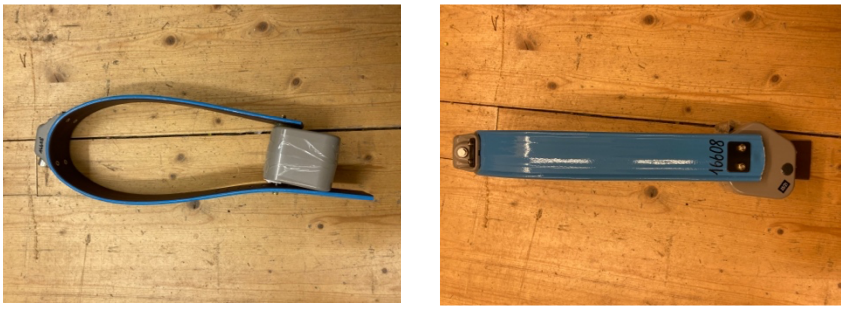

Figure 15: *GPS Collars used in the SNP by VECTRONIC Aerospace GmbH.*

3.2.2 Context Information

Raster Data

Since GPS elevation measurements are typically erroneous, Digital Elevation Models (DEM's) with a spatial resolution of 10 meters were utilized as the basis for all elevation-related operations. For Switzerland, the DHM25 provided by the Bundesamt für Landestopografie swisstopo in the coordinate system LV03 LN02 with a cell size of 25 m was used. The DEM for Italy is provided by TINITALY with a cell size of 10 m (Tarquini et al. 2007). The website geoland.at provides the DEM of Austria with a resolution of 10 m for each state. For this study, the DEM of the provinces "Tyrol" and "Voralberg" were used (Digitales Geländemodell (DGM) Österreich). They were merged in QGIS version 2.18 "Las Palmas" (QGIS Development Team. 2016), and based on this, the further datasets such as aspect and slope were derived for the whole study area.

In addition, temperature, NDVI and snow data, were used to relate movement patterns to climate conditions. These data products are all available via the Google Earth Engine (GEE) data catalog. Following datasets were used in this study:

- MYD11A1.006 Aqua Land Surface Temperature and Emissivity Daily Global 1km (Wan et al. 2015)
- MYD10A1.006 Aqua Snow Cover Daily Global 500m (Hall et al. 2016)
- MOD13Q1.006 Terra Vegetation Indices 16-Day Global 250m (Didan 2015)

These specifications are provided by the NASA Earth Observing System (EOS) Moderate Resolution Imaging Spectroradiometer (MODIS). MYD and MOD refer to the MODIS Aqua and Terra satellites, respectively. For Land Surface Temperature (LST) and Snow Cover (SC), MYD was used due to issues with MOD in February 2016.

The sampling process was performed by Jan Schweizer (Msc Student at University of Zurich) using methods by Chen et al. (2021) and Gorelick et al. (2017). The sampling was done locally using GeoPandas 0.10.2 (Jordahl 2014) for GPS positions and Rasterio 1.2.10 (Gillies 2019) for handling and sampling the raster files. For daily products, each daily GPS subset was sampled in the corresponding image. For the 16-day NDVI product, each 16-day GPS subset was sampled in the corresponding image. A 5-day temporal buffer was introduced due to several missing values for GPS position, particularly for Snow Cover and Temperature data. In Table 1 the used products for the analysis of the migration behavior are listed. Since it is expected that deer respond to cumulative changes in plant phenology, metric of change in NDVI was calculated by taking the difference in NDVI at time t and the NDVI two week prior to t (ΔNDVI) (Peters et al. 2019). This was also done for the daily temperature (ΔTemp) and the snow cover (ΔNDSI).

Table 1: *Overview of the used raster products provided by NASA*

Satelite	Product	Description	Unit
MYD11A1.006	LST_Day_1km	Daytime LST	[°C]
MYD10A1.006	NDSI_Snow_Cover	Snow Cover	[%]
MOD13Q1.006	MODIS_NDVI	NDVI	[-]

3.2.3 Data Limitations

Since the dataset's temporal resolution is quite coarse at a sampling interval of around 4 to 5 hours, detecting fine scale movements or movement patterns for red deer remains a difficult task. Additionally, the projects have various time intervals and accuracy levels.

Furthermore, the low sampling rates decrease the accuracy of the movement patterns. Due to the presence of mountains and forest cover in the study area, there may be inaccuracies in the GPS data, as they may disrupt satellite signals and lead to a deteriorated dilution of precision (DOP).

The raster data produced by MODIS are limited since MODIS is an optical sensor, it cannot monitor the surface while cloud cover is present. Therefore, MODIS products have cloud masks built into the data arrays to prevent clouds from being interpreted as ice and snow. However, there are still many occasions where no data can be provided by MODIS. To overcome this issue, it is possible to interpolate the data points to cover a certain area or, as is done in this study, to set a temporal buffer of a few days, hoping that with this approach enough data can be provided. Nonetheless, this is a significant source of errors which must be considered.

4. Methods

The computations were performed using the free and open-source software R version 2021.09.1 +372 (R Core Team. 2021) and QGIS version 2.18 "Las Palmas" (QGIS Development Team. 2016).

4.1 Migration Pattern Classification

4.1.1 MigrO

To classify the behavior of the red deer individuals a method called "MigrO" was used. MigrO is a free QGIS Plug-in which uses a bottom-up approach. Its idea is to start from data observation and expert knowledge to first develop an abstract model of the mobility pattern of interest and next to translate such model into an operational system. The abstract model of the individual movement is proposed to rely on the so called "stay region". These regions are attractive areas where the individuals reside for a period of time, in spite of short periods of absence (excursions), before moving on to a more attractive stay region. The concept of stay region is used for modeling diverse types of behaviors, as, in the field of animal ecology, seasonal migration can be seen as transitions from one stay region to another seasonal home range (Damiani et al. 2015b; Damiani et al. 2014). According to the patterns taxonomy by Dodge et al. (2008) the stay region sequence represents a generic pattern.

The core component of the MigrO system is SeqScan. It is defined as a density-based clustering technique for the identification of stay regions in trajectories of low-sampling-rate GPS points (see Chapter 2.2.4). This technique enables the extraction of stay regions, represented by dense and temporally disjoint sub-trajectories, by the specification of a small set of parameters related to density and presence (Damiani et al. 2014; Ester et al. 1996). Other than existing approaches, this technique does not impose any constraint on the amount of noise, while it assures that the staying periods are temporally disjoint. The results can contain one or multiple stay regions and therefore transitions from one region to the next (Damiani et al. 2015b).

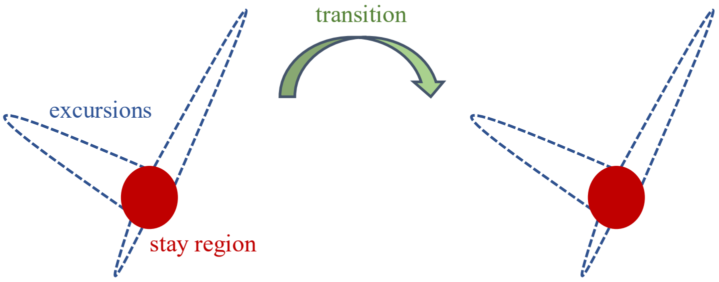

Figure 16: *An approach to the idea of an abstract model: the object resident in a stay region (red circle) can perform excursions of arbitrary duration outside the region before moving to a different stay region (Damiani et al. 2015b).*

In the operational system, the stay regions, excursions, and transitions, are defined in more detail. By a trajectory which consists of a sequence of timestamped points, a stay region is represented by a sub-sequence of the input trajectory which may contain holes, i.e. missing points indicating periods of absence. The duration of a stay region is defined by the time difference of the last and the first point of the sequence. The clustering algorithm processes multiple dense regions concurrently. Dense regions are created, expanded, and merged. If the first dense region satisfies the minimum presence requirement and only contains points temporally following the active stay region, it becomes the new active stay region. This process strategy secures that a stay region remains active until a more recent one is found. An excursion is defined as noisy points that fall in the temporal extent of a stay region when resident. Noisy points which fall in between the temporal extents of two consecutive stay regions are classified as transitions (Damiani et al. 2015b). Additionally, the model comprises a few indexes, namely the stationary index and the commuting index, which summarize aspects of the object's behavior. They were not further looked at for this thesis (Damiani et al. 2015b).

The system handles spatial trajectories represented by sequences of timestamped points and returns sequences of stay regions that can be labelled points or symbolic trajectories. The analytical process consists of three phases: trajectory pre-processing, spatio-temporal clustering for stay region generation, and stay region analysis for the evaluation of the clustering outcome (see Figure 17).

Overall, the SeqScan framework overcomes important limitations of more conventional techniques, particularly offering the opportunity of quantifying the mobility behavior of individuals (Damiani et al. 2015b).

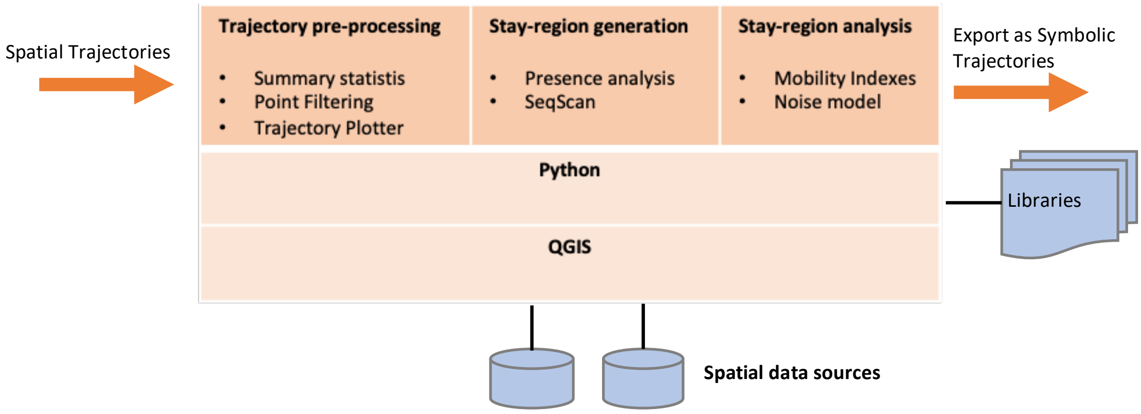

Figure 17: *MigrO architecture (Damiani et al. 2015b).*

4.1.2 Choice of parameters

The tuning of the parameters is performed interactively until a satisfactory fitting is achieved. Furthermore, a good domain knowledge plays an important role as well (Damiani et al. 2015b). The algorithm for MigrO requires only three parameters which can be set manually. For example, the temporal parameter (Presence threshold) is set to 30 days. This value is close to the threshold value specified in a paper by Cagnacci et al. (2011) to indicate the average residence time in clusters (i.e. 28 days).

The mean of the steplength for each population was used to calculate the core region radius, which is the second parameter (see Table 2). Because only one GPS point was taken per day, the steplength appears to be quite long. The steplength was computed in R studio by the package "bayesmove" (Cullen & Valle, 2021).

The last parameter, namely "number of core points neighbors", was set to five, which results in a suitable fitting. This way it is possible to exclude clusters that show a broad range of behavior.

***Table 2**: Overview of the mean steplength for each study area in meters*

Area	TIR	RAE	WAL	TIG	OCH	ING	SNP	STE
Steplength	757	862	778	711	948	913	733	792

4.1.3 Criteria to classify red deer trajectories

Since migratory behavior can manifest differently across individuals, for example with different distances between seasonal ranges or duration of staying, the analysis of the animals' trajectories was computed at the individual level. Therefore, if the result consists of one stay region (one polygon), this specific animal is stationary, otherwise migratory (Figure 18). With the help of Franke et al. (2022) a criteria list was defined to classify each red deer trajectory into migrant, resident, or disperser (see Appendix A.3). One of the main goals of this thesis is to analyze the migration timing, therefore some of the criteria were adjusted to use as much data as possible for the analysis. Some individuals showed a clear rutting area besides the winter and summer home ranges, which was therefore separately classified.

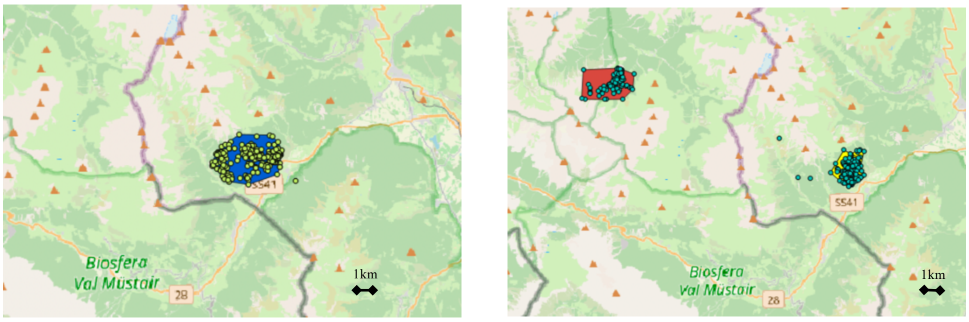

***Figure 18:** MigrO Output of two red deer individuals from the Stelvio National Park, left: stationary behavior (only one stay region, blue), right: migrate behavior (red polygon: Summer home-range, yellow polygons: Winter home-ranges I+ II.*

4.3 Cox Proportional Hazard Model

D. R. Cox established the proportional hazard model in 1972 to quantify the effects of different covariates on the span of time to the point of system failures (Cox 1972). The model is essentially a multi regression model which is commonly used in medicine, where the time it takes for events to occur is examined and modelled in survival analysis (Bender et al. 2005; Fox and Weisberg 2011). Death is the most common of such events, which is the reason for the term "survival analysis" and much of its vocabulary come from. However survival analysis has a far broader range of applications (Fox and Weisberg 2011). In this study, the Cox Proportional Hazard Model is used to analyze the effect of different covariates (NDVI, NDSI and temperature) on the migration timing of red deer. The delta (Δ) value of all three covariates is calculated by subtracting the value at time *t-14* from the time *t*, which is the migration time. In other words, the difference of NDSI, NDVI and Temperature two weeks prior to migration start compared to the values at the migration start were used. The event to

occur in this model is therefore the migration time. To make the covariates comparable they are scaled and centered around 0 so all of them have a standard deviation of 1. For the interpretation of the model, it is important to notice that the change of relative migration probability is given for a rise of one standard deviation by the given covariates.
The Cox Proportional Hazard Model is given by

$$h(t|x) = h_0(t)\exp(\beta' x) \tag{4}$$

where t is the time, x the vector of covariates, β the vector of regression coefficients and $h_0(t)$ is the baseline hazard function (Bender et al. 2005). Briefly, the hazard function can be interpreted as the relative probability that an individual will migrate at time t. A hazard ratio greater than one suggests a covariate that is positively associated with event probability, yet negatively associated with survival rates.
The model aims at testing the impact of several factors on survival at the same time. In other words, it allows to investigate how specific circumstances influence the rate at which a specific event (migration) occurs at a specific point in time (Asher et al. 2017).
Recent studies in the field of animal ecology have used extended semi-parametric proportional hazards (SPPH) models to examine cause-specific mortality rates of white-tailed deer as a function of snow depth and temperature (DelGiudice et al. 2002), the impact of spatially varying risk factors such as habitat types, road density, and human disturbance on the survival of Yellowstone grizzly bears (Frair et al. 2007) and previous exposure to predators in determining the cause-specific mortality rates and likely success of elk reintroduction efforts (Frair et al. 2007).
The Cox Proportional Hazard Model provides a powerful method (with minimal assumptions) when interest lies in quantifying relative risks (Fieberg and DelGiudice 2009). Their use is expected to increase, particularly as a result of recent extensions that allow one to model time-dependent covariates (DelGiudice et al. 2002; Johnson et al. 2004). The Cox PH model's efficiency of survival estimates can be poor with sparse data, modelling the baseline hazard parametrically may result in significant gains in precision (Harrell 2001). The ability to predict relative risks without specifying or modelling the baseline hazard is one of the key benefits of the Cox PH model (Fieberg and DelGiudice 2009)

5. Results and Discussion

5.1 Classification of Migration Patterns

This sub-chapter is addressing the first research question: How does the migration probability differ in the study areas and what could be potential reasons?
The following results summarize the outputs of MigrO (see Chapter 4.1.1).

5.1.1 Results

A total of 288 red deer were analyzed, resulting in 394 different trajectories, since an individual can have more than one trajectory (migration years). Table 3 shows the classification of red deer behavior for all research locations. In the research areas of ING, RAE, SNP, WAL, TIG, and STE, the majority of collared red deer migrate, while in the TIR and OCH regions, more red deer exhibited resident behavior. Only two of the 32 collared individuals in OCH show migratory behavior, accounting for more than 80% residents of the collared individuals in this area. This difference is considerably smaller in the TIR project, with nearly equal groups of residents and migrants.
Overall, dispersal behavior is uncommon, with only a few individuals exhibiting it. There is a modest intersexual variance. Stags tend to migrate more, whereas hinds show a more frequent resident behavior than stags (Figure 19).

Table 3: *Overview of the classification of red deer behavior*

	OCH	**ING**	**RAE**	**SNP**	**WAL**	**TIR**	**TIG**	**STE**
Residents	**0.82**	0.41	0.42	0.37	0.34	**0.48**	0.35	0.46
Dispersers	0.13	0	0.03	0	0	0.07	0.13	0.05
Migrants	0.05	**0.59**	**0.55**	**0.63**	**0.66**	0.45	**0.52**	**0.49**

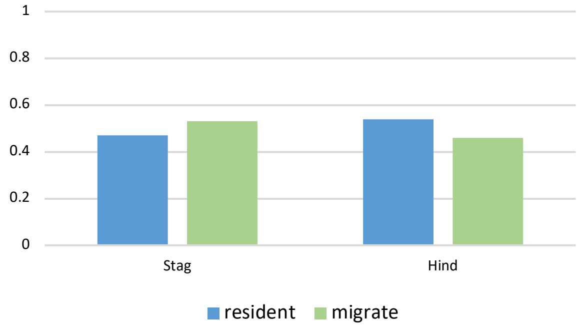

Figure 19: *Results of migration classification ratio per sex. Stags show more often a migratory behavior than hinds. Female red deer reside more frequent than stags.*

5.1.2 Discussion

Variation in migration behavior among populations is expected due to differences in habitats and population size. It has been shown that smaller bodied individuals experience higher migration expenses as a result of their insufficient ability to store energy and the ensuing allometric energetic limitations (body size constraint hypothesis; Hein et al. 2012). Similarly, the benefits and constraints of migration can differ between sexes (Mysterud et al. 2011). However, these differences may also change with various reproductive schedules like mating and parturition. For this study there are only small differences between sexes regarding the behavior (see Figure 19).

The proportion of migrants varied from 5% in the OCH region to 66% in region WAL. In a study in Norway on red deer Mysterud et al. (2011) found similar proportion of migrants and they additionally report empirical evidence of (negative) density dependence in likelihood of migration in deer.

When compared to resident red deer, migratory red deer have a significant advantage in terms of access to early plant phenology (Bischof et al. 2012). Mysterud et al. (2011) showed that migration behavior was more common in areas with a diverse topography i.e., for areas with access to high elevation. By foraging in freshly exposed vegetation from the snowmelt, high-quality food can be assured (Albon and Langvatn 1992). The study locations with the largest access to high elevation are ING, SNP and WAL. These are also the areas with the largest amount of migratory red deer, therefore the results by Mysterud et al. (2011) are confirmed in this thesis.

Most ungulates in temperate regions experience a nutritional bottleneck during the winter, when forage digestibility and protein content are lower, and animals are often concentrated at their highest year-round densities (Bishop et al. 2009; Monteith et al. 2011), resulting in important feedbacks into density-dependent mortality and population dynamics (Jones et al. 2014; Monteith et al. 2011).

The competition avoidance hypothesis states that red deer migrate uphill in summer to escape competition due to the high density in winter areas. It is suggested that a combination of avoidance of competition in high density winter ranges, social fencing during summer in addition to the forage maturation and predation risk avoidance hypotheses, is needed to explain migration patterns of northern ungulates (Mysterud et al. 2011). For this study it was unable to test the competition avoidance hypothesis.

The project site of OCH can be divided into three areas, namely “Werdenberg”, “Urnäsch”, and “Weissbachtal”. One of the reasons why most of the individuals from the area “Werdenberg” show a resident behavior is the climate of the Rhine Valley. The valley is climatically characterized by the Föhn wind, which ensures a relatively high annual temperature and leads to short-term temperature differences and strong storms. Therefore, prolonged snow cover is rare in the Rhine Valley, where most of the red deer individuals were collared (Thiel et al. 2018).

Most red deer in the OCH site remain in the area during the summer but relocate to higher altitudes. Nevertheless, there is some exchange between neighboring project regions, as evidenced by the migrations of individual red deer (Thiel et al. 2018).

Thiel et al. (2018) used the same GPS data as were used for this study. Even though they applied a different method for classifying red deer behavior, they also roughly classified 80% of the collared individuals as resident animals. This confirms the suitability of the methods used in this study.

Interestingly, all resident deer of the SNP project gather in the same location, namely in the area of “Il Fuorn” near Zernez (Figure 20). There are forage-rich meadows, which the deer graze often, as well as a burnt area from the 1950s, which is also used intensively. Additionally, anthropogenic disturbances are predictable because people are required to stay on the trails and in winter they are closed. This counts for the whole area of the SNP. Generally, the SNP area is a popular summer home range for many reasons. For example, the red deer have no grazing competition with cattle, there are undisturbed valleys where they can retreat, and the high altitudes provide qualitative good forage. Near the Il Fuorn area were set three traps with which reed deer were caught. The red deer captures generally happened before June while the deer were still migrating. The selection of deer was random, but not in terms of their migration behavior. In this regard, the data from the SNP are biased.[2]

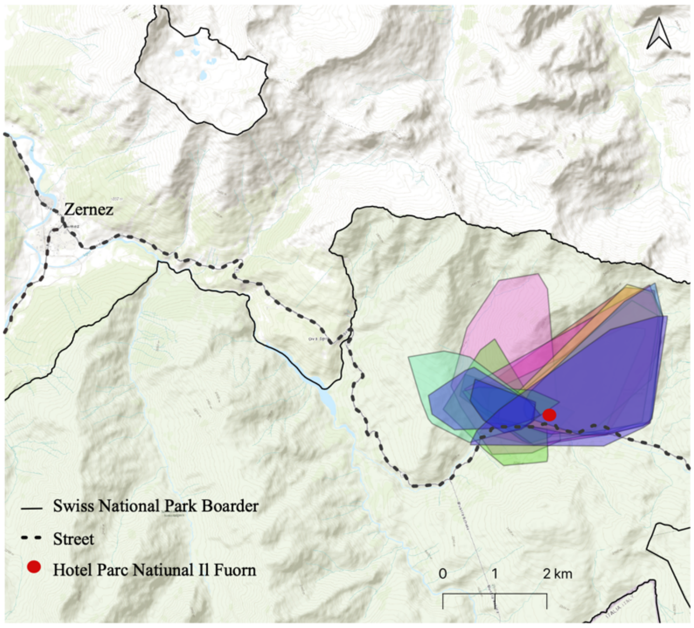

Figure 20: *Overview of all resident red deer home ranges (colored polygons) from the SNP project. The home ranges of the resident individuals are all gathered around the meadows near the Hotel Parc Natiunal Il Fuorn.*

The study site WAL shows the highest number of migratory individuals. This could be due to harsh winters with high precipitation, especially in the Goms, the Binntal and the higher altitudes of the Aletsch plateau. These areas are often covered with snow for five to six months of the year, with snow heights of sometimes several meters. The lower, south-facing slopes between Bitsch and Fiesch are usually only snow-covered for a short period of time due to their exposure, altitude and steepness and therefore offer optimal winter habitats for red deer.

Another factor contributing to the high migration rate in the Wallis region could be the seasonal disturbance caused by recreational users throughout wide regions of the research area (Signer et al. 2022). Winter home ranges for red deer in the WAL research site are primarily in the lower altitudes between Brig and Bellwald, as well as in the Binn Valley. In spring, they partly undertake extensive migrations from there to the summer ranges, which are in the higher altitudes of the Aletsch area, in the Goms, partly in the Simplon area and, in the case of the Binn red deer, frequently also in neighboring Italy. The migration from the Binn Valley to Italy is mainly via the Albrun Pass, where impressive group hikes were documented by the GPS data. In Italy, the red deer resides in the Veglia-Devero Nature Park and in the area around Lago di Devero during summer. A reason for choosing these locations could be that hunting is prohibited within the park perimeter (Signer et al. 2022).

The high number of resident animals in the project of TIR can be a result of the winter feeding which has a long tradition in this area. Although Lewis and Rongstad (1998) observed that winter feeding on white-tailed deer in Wisconsin led to a decrease in the proportion of migration, they did not detect an

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[2] Personal communication with Thomas Rempfler (Swiss National Park), 23.06.2022

increase in residency among fed populations. Because feed grounds offer limited cover, are usually on public lands that are exposed to high human impact (e.g., hunting), and are often adjacent to private property where the tolerance is low towards animals, fed individuals may not be able to remain residents. Importantly, their results indicate that, whereas winter feeding has impacted deer migration patterns, it has not affected the propensity to migrate (Jones et al. 2014; Lewis and Rongstad 1998).

5.2 Descriptive Parameter Analysis

The following chapters present results and discussion regarding the research question 1.2 a-c. This involves the differences in home range size (HRS), altitude and distance for migratory and resident red deer.

5.2.1 Home Range Size (HRS)

The home range sizes were an output of the MigrO method and represent polygons created with the used parameters (see Chapter 4.1.1). The provided polygons by MigrO were classified as either resident-, summer- or winter home ranges (see Chapter 2.2.1).

The HRS's for resident and migratory animals is shown in Figure 21, with the summer and winter home ranges for migratory animals shown separately. Overall, the annual HRS of the sampled red deer ranges from 0.2 km^2 up to 26 km^2. Red deer which show resident behavior have in general a bigger HRS than migratory individuals. For migratory individuals there is a slight difference in HRS with a mean of 2.9 km^2 for the winter home ranges and a mean of 3.5 km^2 for the summer home ranges. Additionally, migratory hinds cover a smaller area than stags in the summer and winter home ranges. This HRS difference in sex is also visible for resident animals. Large home range sizes of over 20 km^2 are mostly outliers. Generally, the mean for all HRS's ranges from 2.9 km^2 for winter home ranges up to 7.7 km^2 covered by resident individuals.

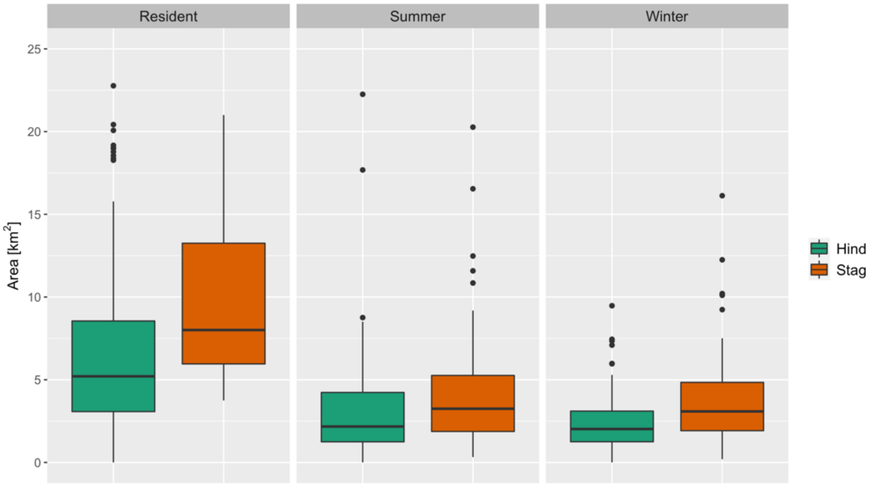

Figure 21: Annual and seasonal Home Range Sizes of red deer. Stags (orange) have generally bigger home ranges than hinds (green) for all behaviors.

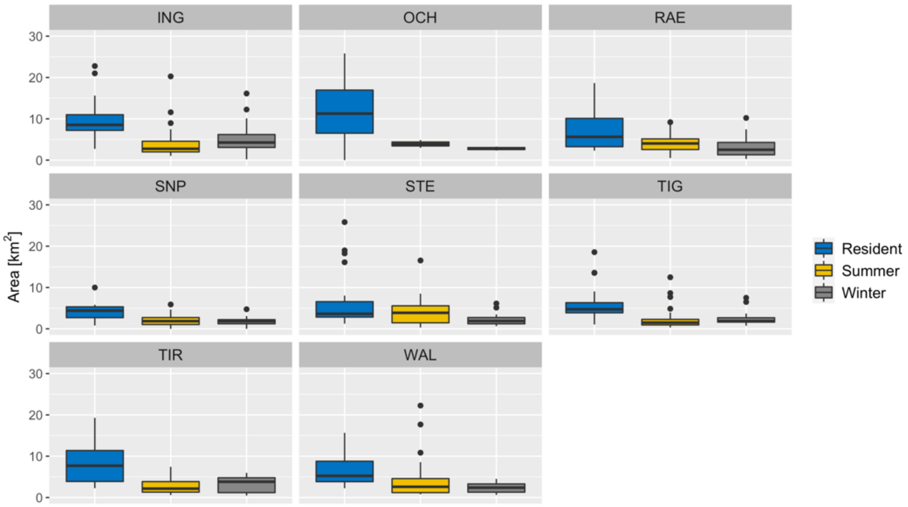

Figure 22: *Home Range Size per study area. All resident home ranges (blue) are larger than the seasonal home ranges (summer: yellow, winter: grey). The differences in seasonal HRS's varies differ with the study location.*

Differences in HRS for the research locations are presented in Figure 22. Except in the STE area, where the summer home range is somewhat larger than the HRS of resident individuals, the HRS of resident animals is the largest home range in all areas. In addition, the difference between winter and summer HRS varies per research area. The winter home ranges in ING, TIG, and TIR, for example, are greater than the summer home ranges. The opposite applies in the remaining research locations, where the HRS for summer areas is higher than the HRS for winter areas.

Discussion

The extent to which red deer use space is assumed to be influenced by several environmental and individual factors. The availability and distribution of vital resources in a given area can have a big impact on individual migratory patterns, called the "resource dispersion hypothesis" (van Beest et al. 2011; Carbone and Gittleman 2002; Jetz et al. 2004). Some red deer populations receive supplementary food such as at the study location TIR, while others do not, and some live in generally continuous habitats, while others exist in extremely fragmented landscapes with scattered supplies (Reinecke et al. 2014; Bützler 2001).
Generally, the HRS's of the study locations in this thesis are smaller compared to the research done on the Rhum island (Clutton-Brock et al. 1982). Compared to the studies in the Bavarian Alps, where average HRS of 0.65 km^2 in winter and 1.67 km^2 in summer have been observed (Georgii and Schröder 1983), however, the covered HRS's in this study are bigger. These differences can be explained by a great variety of environmental and individual factors at the study sites. For example, the island of Rhum has hardly any human disturbances, similar to the SNP study site. However, the HRS's in the SNP are not larger than in the other study locations. This can be explained, since the red deer in the SNP find all they need in a small area and therefore do not have to travel in search of shelter after grazing. However, comparisons of HRS between studies applying different methods should be done with caution, because parameterization of different methods can effect results greatly.

According to Reinecke et al. (2014) home ranges should be large in resource-scarce environments and smaller in regions where red deer receive supplementary feeding, according to the resource dispersion theory. In this study, supplementary food is provided for red deer during winter only around the area TIR. However, the mean area of the winter home range for TIR is larger than the mean of the summer area, which is contrary to the statement of Reinecke et al. (2014). According to Reinecke et al. (2014) the summer home range should be larger due to no supplement food. A reason for this may be that there are resource-rich environments around the TIR area, especially in the areas where the red deer stay during the summer and therefore, they do not need to cover a large area to get enough food.

The HRS's are quite similar in some areas in winter and summer. It can be assumed that red deer not only try to save energy in winter and therefore have smaller HRS, but also that the high temperatures in summer may lead to more frequent rests which therefore result again in smaller HRS. In other words, it's likely that red deer struggle not only with cold temperatures because too warm weather also causes a kind of resting state in their behavior.

Another possibility for HRS differences between the study areas in this thesis is that, red deer living in fragmented landscapes shift their sites more frequently in response to increased human contact rates, or that red deer travelling patterns are influenced by differences in hunting regimes. The study by Jerina (2012) which analyzed home range areas of red deer in Slovenia strongly indicates that roads have an effect on the home range size. Distance to main roads in the home-range buffer correlated most strongly with home-range size. It showed that home-range sizes initially increased with increasing distance to the main road in the home-range buffer and then stabilized (Jerina 2012).

The result of this study shows that the extent of a red deer's HRS varies depending on their gender. Stags cover a larger area for resident and migratory individuals than hinds. This has also been observed in a study by Kamler and colleagues (2008) on the European mainland. However, the contrary tendency appeared to be the case for the red deer on the island of Rhum, where HRS's of 4 km^2 for hinds and 5 km^2 for stags have been found (Lowe 1969).

Reasons for the intersexual differences in red deer HRS is considered to be a function of metabolic rate, which is linked to the fact that digesting efficiency rises with body mass (Demment and Van Soest 2015). Accordingly, the scaling between body mass and home range size is comparable to the body mass scaling of forage intake rate (Ofstad et al. 2016). Larger animals' increased digesting efficiency comes at the expense of a more time-restricted activity budget, which may increase the home range (Van Moorter et al. 2016).

Males and females would have similar home range sizes after accounting for differences in body mass, nutrition, and environment if home range size was simply a function of metabolic requirements (Ofstad et al. 2016). However, there are several other factors.

First, there is the cost of lactation and caring for offspring for females. On the one hand, increased resource need can extend home range size (Bjørneraas et al. 2012; Saïd et al. 2005; Tufto et al. 1996), but restricted movement and greater mortality risk can reduce home range size (van Beest et al. 2011; Cederlund and Sand 1994; Ford 1983). Although movement may be restricted for a short time after giving birth, the extent of differences in movement rates between males and females (van Beest et al. 2011) may be significant enough to produce intersexual differences in yearly home range size.

Second, if the expenses of accessing high-quality forage are considerable, males are more willing to trade off forage quality for quantity (Harestad and Bunnel 1979). Accordingly, males may adjust by expanding their home range as forage quality declines, but females may compensate by becoming more selective (Beier and McCullough 1990; Georgii and Schröder 1983; Relyea et al. 2000;

Ruckstuhl and Neuhaus 2002) and spending more time hiding or foraging to offset lactation expenses (Mace and Harvey 1983). After accounting for sexual size dimorphism and other studies on space usage patterns in large herbivores (Ruckstuhl and Neuhaus 2002), the general prediction is that males will have larger home ranges than females (Ofstad et al. 2016).

5.2.2 Altitude of Home Ranges

Figure 23 illustrates the elevation of resident and migratory red deer home ranges in meters above sea level [m.a.s.l.]. For a given home range, the used altitude is the average altitude of all GPS locations calculated with DEM's. The altitude difference between migratory animals' summer and winter home ranges is apparent. In the summer, they reside at higher elevations than in the winter, when they live at lower elevations. The range is from 315 m.a.s.l in winter up to 2430 m.a.s.l in summertime. There are no significant differences between stags and hinds in the summer home ranges. However, in winter, stags prefer a lower elevation than hinds.

Resident individuals show the same sex differences as migratory individuals, and their home range is usually at intermediate elevations of summer and winter ranges of migratory individuals. Residents, on the other hand, have a range of 361 m.a.s.l. to 2394 m.a.s.l., demonstrating a wide variance in between resident red deer.

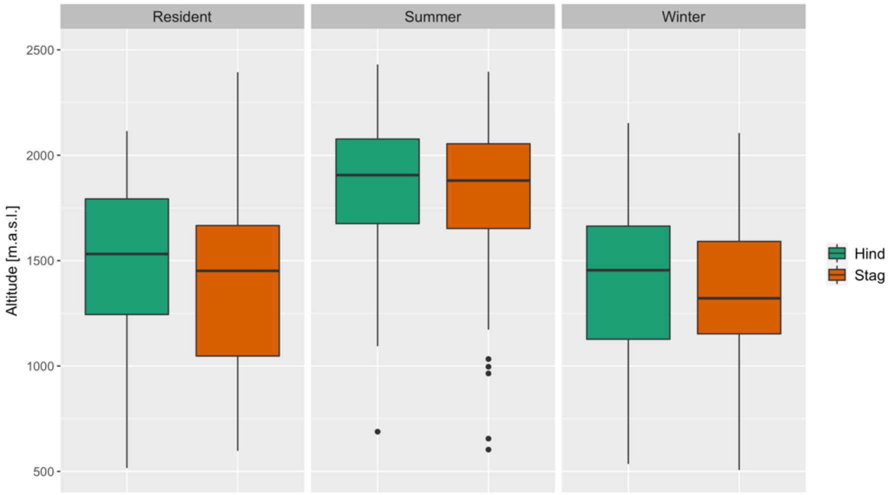

Figure 23: *Altitude of home ranges for resident and migratory red deer. Hinds (orange) tend to have their home ranges on higher altitudes than stags (green).*

The differences in altitude between each study location is presented in Figure 24. Migratory individuals live at greater altitudes in the summer home range than in the winter home range in all locations. The variations in altitude between summer and winter home ranges are the largest in the area ING and TIG, with about 1000 meters of difference in elevation. Regardless of the season, individuals in the RAE, OCH, and TIG areas tend to live at lower altitudes. These areas are all located in the northern respectively southern foothills of the Alps, with lower altitudes, resulting in a limited range of altitude for red deer.

Animals in the remaining areas are frequently found around the 2000 m.a.s.l. boundary, especially during the summer. Except for the areas OCH and SNP, where resident red deer live almost as high as migratory red deer in their summer home range, the differences between resident and migratory animals are always altitude-wise in between the seasonal home ranges.

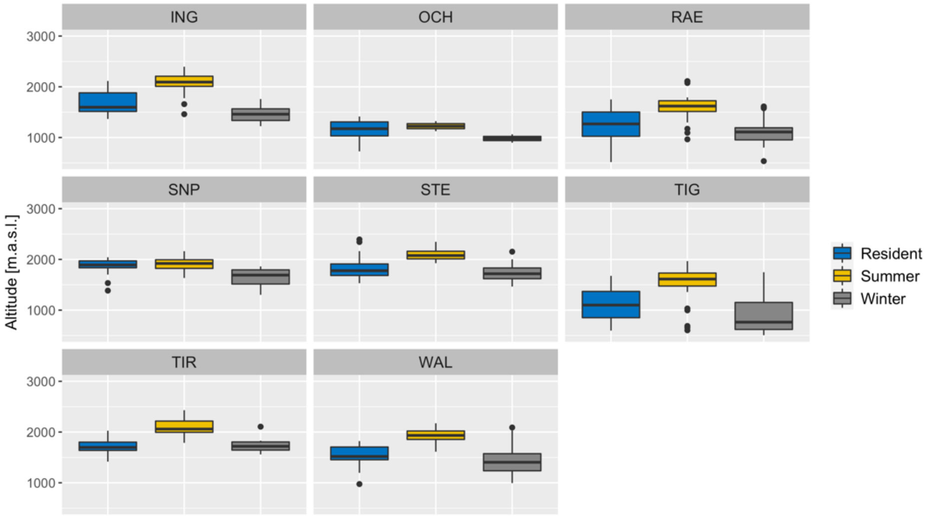

***Figure 24**: Altitude of home ranges per study area. The summer home ranges (yellow) are on high altitudes, whereas in winter (grey) red deer travel to lower elevations. The resident home ranges (blue) lie mostly between the seasonal home ranges in terms of altitude.*

Discussion

The collared red deer monitored in this study conformed to the usual pattern of temperate cervids with migration to low elevations during winter and traveling to higher altitudes in summer. Only a small percentage of individuals had home ranges at high altitudes (< 2000 m.a.s.l.), which is probably due to low quality in terms of food for these extreme high elevation areas. Additionally, the locations have limited altitude ranges, like in the RAE, TIG and OCH study site, there hardly any areas above 2000 m.a.s.l. Individuals also prefer a higher, colder alpine habitat in the summer, which is most likely a strategy of escaping hotter temperatures (Carvalho et al. 2008).

In temperate montane environments, forage phenology varies with topographic and altitudinal gradients, influencing snowmelt and plant development. Since the study locations have unique topographic and elevational gradients, the disparities in the study areas can be explained. A further possibility is that the usage of higher elevations is due to habitat selection based on density (Rosenzweig 1981). Even though area quality varies, high and low elevations may give equivalent fitness if deer density is significantly lower at high elevations. Subdominant individuals, on the other hand, are forced to high elevations by dominant individuals (Mysterud 1999).

The "green wave hypothesis" (GWH) predicts that migrating herbivores closely track intermediate plant biomass along latitudinal and elevational gradients during spring, and can be viewed as the spatial formulation of the FMH (Bischof et al. 2012; Middleton et al. 2018). As already mentioned in Chapter 2.1.3, forage quality is best while plants are young due to the high cell soluble protein content, but as plants mature and fibre accumulates, forage quality declines (van Soest and Mason 1991)

Migratory ungulates are predicted to maximize energy intake rates by following spatiotemporal trends in new plant development (Fryxell et al. 2004). Albon and Langvatn (1992) discovered that crude protein levels were higher in plants available to red deer at higher elevations in Norway. Mysterud et al. (2002) confirmed that red deer at higher elevations had higher body mass, providing additional evidence of the importance of migration to ungulates to find good quality forage. Similar, Albon & Langvatn (1992) found that red deer with high elevation summer ranges were heavier in autumn than those with low elevation summer ranges. This suggests again that the uphill migration is a result of better-quality forage being available at higher elevations. During autumn, however, Hjeljord (1997) found that moose at low elevations were heavier than those at high elevations, which may be due to the different dietary requirements of red deer and moose. Further research on the relationship between cervid range quality, altitude, feeding strategies (i.e. browser-grazer continuum) and migration patterns may be needed.

5.2.3 Migration Distance

There are only slight differences of the covered distances between summer and winter home ranges and the sex of a red deer (Figure 25). With a mean distance of 9.8 km hinds cover a moderately shorter distance than stags which travel a mean of 10.9 km from winter to summer home ranges. Furthermore, some stags and hinds have traveled up to 40 kilometers between seasonal home ranges, which is roughly four times farther than average.

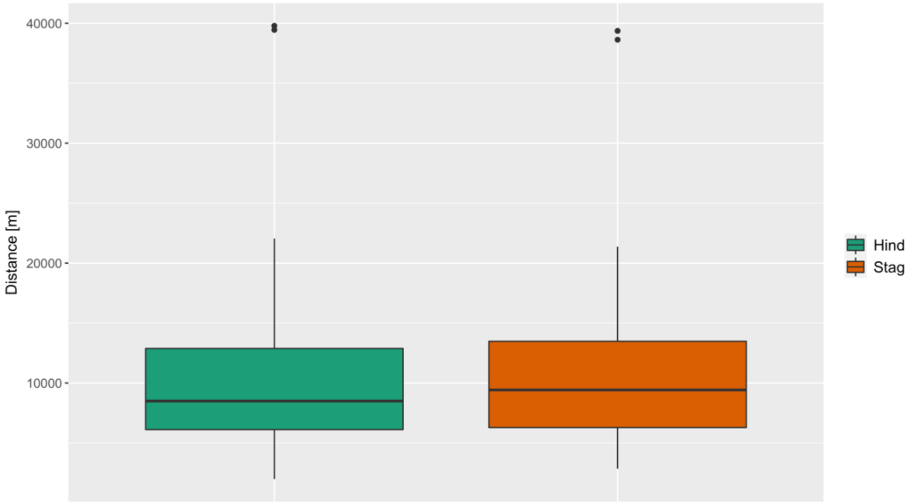

Figure 25: *Distance between summer and winter home ranges of hinds and stags. Only a small difference between the sexes is observed.*

Individuals who travelled more than 35 kilometers were found in the SNP and ING study sites (Figure 25). With a mean distance of 5.9 kilometers between home ranges, red deer in the TIR study area travel the shortest distance. At SNP, OCH, and ING, the animals migrate an average of 10 kilometers between their summer and winter ranges.

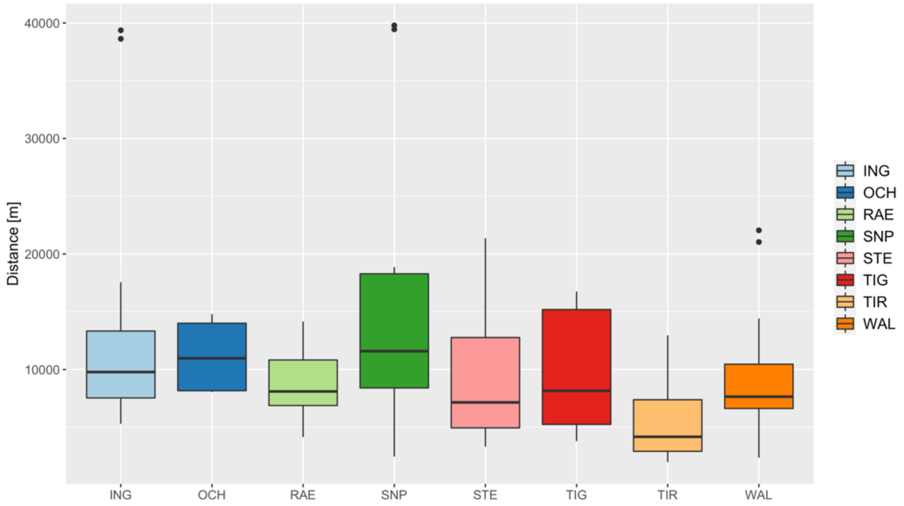

Figure 26: *Distance between summer and winter home ranges per study area. The longe distances travel the red deer from the SNP study site. The individuals of TIR area cover the smalle distance.*

Discussion

Many ungulates migrate long distances to avoid harsh weather, predators, and competition with residents, as well as to find food to enhance survival and reproduction (Fryxell and Sinclair 1988; Hebblewhite and Merrill 2007; Mysterud et al. 2011).

Various studies of partially migratory populations show that individuals within populations migrate across a wide range of distances (Jones et al. 2014; Middleton et al. 2013; Monteith et al. 2011; Sawyer and Kauffman 2011). The distance of a migration route could influence when animals migrate, how they allocate time to seasonal ranges, and how much anthropogenic disturbance they encounter along the way (Jones et al. 2014).

Stags migrate over slightly greater distances, according to the findings of this study. This was also observed in a study by Peters et al. (2019), where male red deer traveled larger distances than female red deer. This can be due to the high sexual dimorphism in red deer. Peters et al. (2019) did not expect such significant variations based just on adult sexual body size dimorphism, despite the fact that red deer males are about 1.5 larger than females. Rather, in polygynous mating species, men and females are often driven by different constraints related to reproduction and social organization (Bowyer 2004). In some populations of white-tailed deer, however, females migrate further than males (Mysterud 1999). This suggests that there are more factors influencing migration distance than an animal's gender. Singh et al (2012) also discovered that younger animals migrated longer distances, implying that the propensity to migrate should decrease with age. This supports the theory that the costs of travel, especially in the winter, may outweigh the benefits for the elderly, and that age influences migration probability and distance. However, this could be due to experiential learning, in which an individual learns the ideal migration route or movement behavior, resulting in shorter migratory distances over time (van Moorter et al. 2009).

The small distances of the population in the TIR study area, compared to the other locations can be explained once more with the supplement feeding in the winter home ranges. Unfed ungulates migrated farther than fed ungulates, according to Smith (2001). This makes sense since the feed grounds are mostly established along known migration routes to intercept the animals before they are reaching private property at lower elevation (Jones et al. 2014).

According to Singh et al. (2012), migration distances are decreasing from north to south, implying that populations further north may have longer migration distances. The area of TIG and WAL in the southern part shows a lower mean migration distance than for example, the northern study locations like SNP, OCH, and ING, even though the locations studied in this thesis do not have a substantial variance in latitude. It is possible that due to the high altitudes of the alps the results of Singh et al. (2012) are not supported for the study areas in this thesis. More factors, however, like mentioned above could explain the differences in migration distance.

5.2.4 Timing of Migration

Figure 27 shows the probability that an individual shows resident behavior (probability to stay) for hinds and stags during the spring and autumn migration. Male red deer migrate later in the spring than female red deer. In general, stags take longer to migrate in spring than hinds. The majority of stags migrate in a fairly short time during the autumn migration.

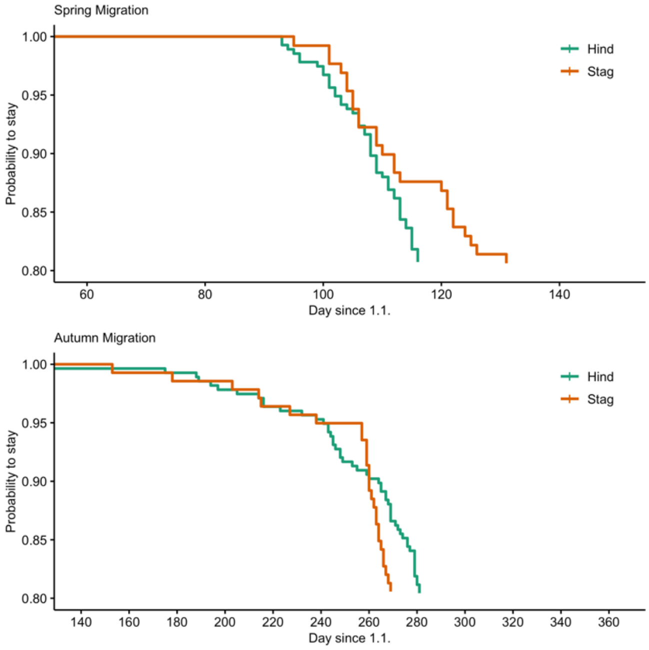

Figure 27: *Probability to stay for spring and autumn migration per sex. In spring stags migrate later than hinds. For the autumn migration stags seem to migrate all at once in a short time span.*

The migration timing in spring is represented for each area in Figure 28. The individuals from the SNP area are the first ones to migrate in spring, whereas, in the ING area, the red deer start spring migration around 10 days later. The latest to migrate in spring are the individuals from ING and TIR. Generally, spring migration starts in April and May, but some individuals they do not start migration till August or even September. Additionally, it can be said that the spring migration of all collared red deer was mostly completed within 2 months.

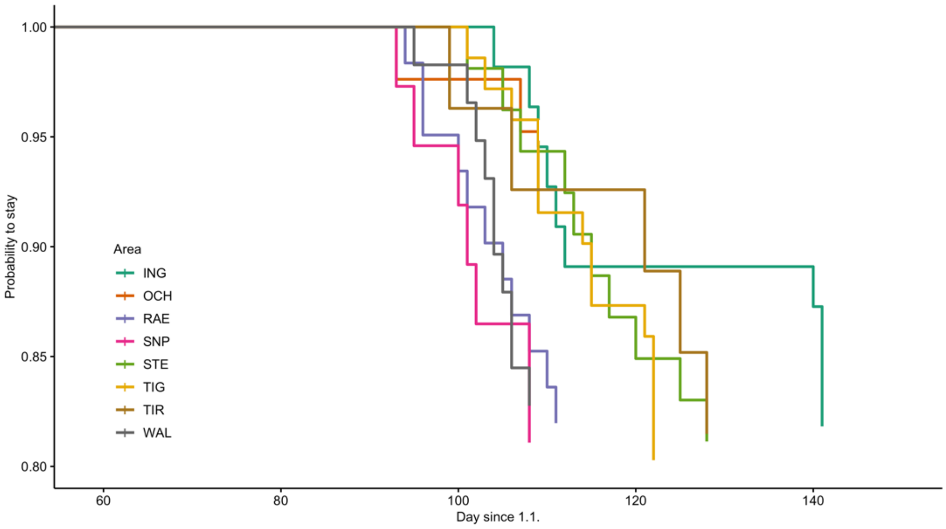

Figure 28: *Probability to stay in spring for each study area. The first migratory red deer are from the SNP and RAE area. The latest migrate from day 120 on in the area TIR and ING.*

The autumn migration timing is less synchronous between the study areas (see Figure 29). The start of autumn migration is around September to October. However, there are individuals which start the autumn migration already at the end of July or wait till December to travel to their winter home ranges. Red deer from the study area OCH and SNP migrate last.

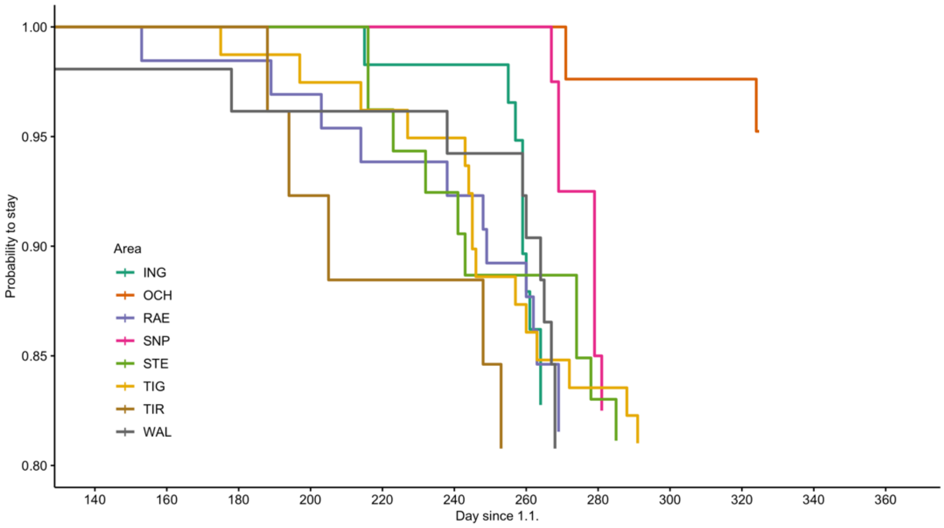

Figure 29: *Probability to stay in autumn for each study area. First individuals from TIR and WAL migrate, and the last individuals migrate in December in the area SNP and OCH.*

Discussion

The timing of migration in red deer populations is largely determined by local weather patterns, plant phenology. At the individual level, state-dependent characteristics such as age, sex, or nutritional status may affect migration behavior (Lendrum et al. 2013; Monteith et al. 2011; Singh et al. 2012).

In this study, differences were found between sexes of red deer in terms of fidelity to their winter range. Males migrate later than females in spring and reside longer in the winter range than females.

In Autumn this is most likely due to higher energy demands, particularly after the rut, as well as the need to rebuild lost body mass in preparation for winter (McCullough 1999). As a result, they may migrate later.

In spring, females must synchronize migration timing with food availability and select suitable calving locations to increase reproductive success, "the need to breed." (McCullough 1999). Therefore, males likely undertake lengthier migrations than females due to their larger body mass and because they are not restricted by caving and lactation (Singh et al. 2012).

According to the reproductive strategy-predation risk hypothesis, males maximize their reproductive success by maximizing their body size, determining dominance rank and success in male-male conflict during rut, while females should be risk-averse to maximize child survival (Ruckstuhl and Neuhaus 2005). Males are expected to follow the green wave during spring migration in order to maximize resource gains, whereas females are expected to seek protected habitat and be less averse to risk. According to the body size and gastrocentric hypothesis, larger males can survive on a lower-quality diet and are not expected to follow the green wave as closely as smaller males. As a result, sexual variations in migration timing and duration, as well as the usage of stopover sites, are predicted by these ideas (i.e. places where migratory individuals stop during the migration and before continuing their journey) (Debeffe et al. 2019).

Interestingly, individuals of the location TIR behave equally as in the other areas in spring, although they get supplement food in winter. Supplemental feeding in winter can delay spring migration, according to a study from Utah, USA (Peterson and Messmer 2007). Possibly, with diverse environmental factor, this influence might not be as strong as in Utah.

5.3 Spring Migration

The following results and discussions try to answer the second research question on how covariates can influence spring migration. All of the following results were outputs of the Cox Proportional Hazard Model (see Chapter 4.3). The hazard ratio value in this thesis can be viewed as a relative probability of migrating.

5.3.1 Results

There is no statistically significant difference between the sexes of red deer for spring migration (p-value = 0.73). Furthermore, the differences between study areas are also not significant except for OCH (p-value = 0.0075), which is partly visible in the much higher confidence intervals.

The p-value for all three overall tests such as Likelihood-, Wald-, and Score-Test are significant (all p-values < 0.001), indicating that the model is significant. In the multivariate cox analysis, the covariates ΔNDSI, ΔNDVI and ΔTemperature remain significant (p-value < 0.001) (Table 4).

The influence of snow on spring migration is illustrated in Figures 30. Generally, the smaller the ΔNDSI value the higher the hazard ratio, i.e. the probability to migrate, gets. This is the trend in all study locations. There are only small differences visible between the study locations.

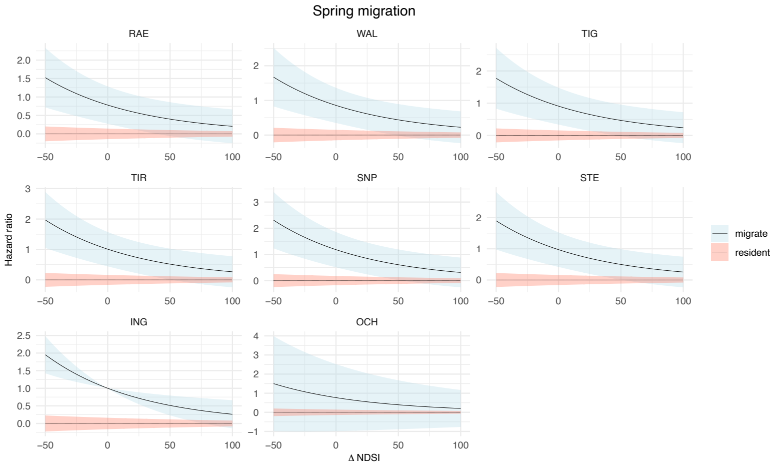

Figure 30: Result of the Cox Proportional Hazard Model for ΔNDSI in spring. With a higher ΔNDSI the bigger gets the probability that red deer may migrate in spring (Hazard ratio). This applies for all eight study areas.

To what extent the vegetation affects the behavior of red deer in spring is represented in Figure 31. For all eight study sites. the hazard ratio increases with higher ΔNDVI. Compared to the ΔNDSI, the hazard ratios of each area are much higher. With the highest hazard ratio just above 20, RAE and OCH has the lowest relative probability for a migratory behavior of red deer. However, SNP, TIR and STE show a high probability for migratory individuals at a ΔNDVI of 1.

In Figure 32, the ΔTemperature is displayed for all study areas. ING, STE and SNP are the locations with a hazard ratio value larger than 10, while the difference in temperature is over 20°C. Like the ΔNDVI, the higher the delta value the bigger the hazard ratio is. Again, OCH and RAE have the smallest hazard ratio, while SNP, STE and ING are nearly at the value of 30 or above.

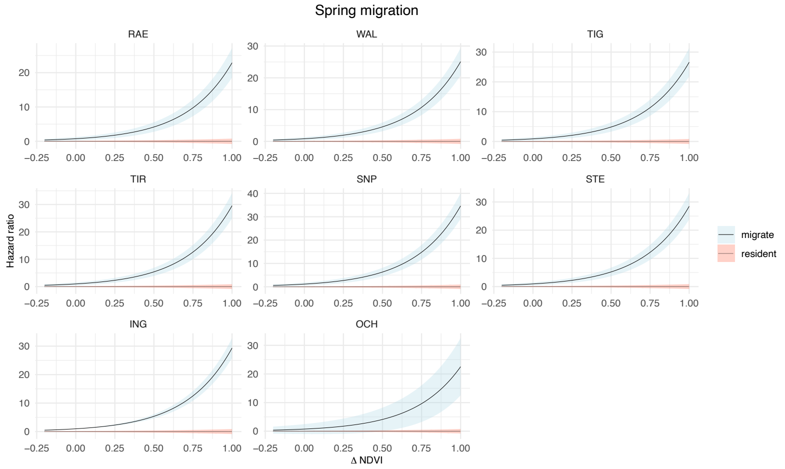

Figure 31: Result of the Cox Proportional Hazard Model for ΔNDVI in spring. The relative migration probability in spring (Hazard ratio) increases with a higher ΔNDVI value. This applies for all eight study areas.

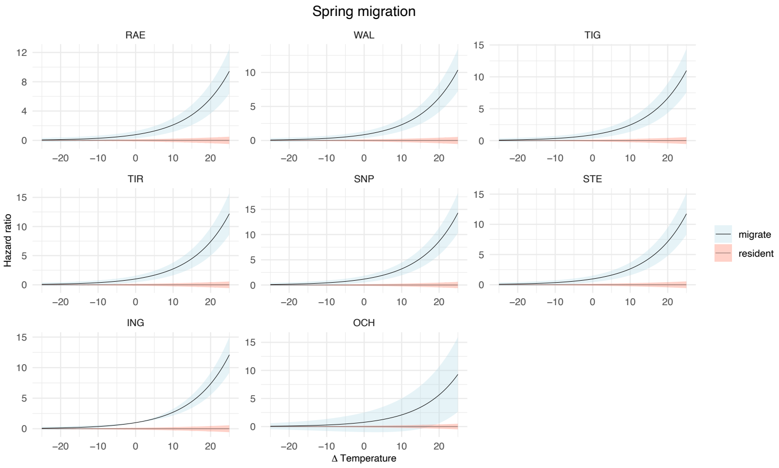

Figure 32: *Result of the Cox Proportional Hazard Model for ΔTemperature in spring. The relative migration probability in spring (Hazard ratio) increases with a higher ΔTemperature value. This applies for all eight study areas.*

5.3.2 Discussion

Generally, it makes sense that the hazard ratio is larger for a small ΔNDSI, since the snow is decreasing in spring, and therefore the NDSI value at the time *t-14* is assumed to be larger than at the time *t*, when the individual migrates. This results in a small ΔNDSI value, since it is calculated as $NDSI_t$ - $NDSI_{t-14}$. The explanation for the ΔTemperature and ΔNDVI shows the reverse. In springtime the temperature increases and so does the NDVI value. Therefore, the temperature- and NDVI- values are larger at time *t* than at time *t-14*, resulting in a higher ΔTemperature, respectively ΔNDVI.

The exponentiated coefficient for ΔNDSI is 0.79. Therefore, it can be said that the ΔNDSI reduces the hazard ratio by a factor of 0.21 or 21%. Since the hazard ratio is the relative probability to migrate, it can be stated that if snow raises by one standard deviation it reduces the relative probability for migratory behavior by 21%. Due to the scaling of all covariates the unit for the increase must be the standard deviation (see Chapter 4.3). The conclusion is that a low coefficient value means a smaller hazard (relative probability to migrate) compared to a large coefficient where the relative probability to migrate increases.

The p-value for ΔNDVI is < 2e-16 indicating a strong relationship between the vegetation and increased probability to migrate. Looking at the exponentiated coefficients for ΔNDVI, exp(coef) = 1.99 which indicates that the difference of NDVI increases the probability to migrate by a factor of 99%. This means that the ΔNDVI is an important factor for migratory behavior in spring. Similarly, the p-value for ΔTemperature is 8.64e-11, with a hazard ratio of 1.51, indicating a strong relationship between ΔTemperature value and increased probability for migratory behavior. Therefore, ΔTemperature increases the relative probability for migration by 51 %. Due to the showed results, it can be assumed that temperature and vegetation are more important drivers for spring migration than snow.

Table 4: *Summary of the cox proportional hazard model for spring migration*

	coef	**exp(coef)**	**z Pr(>|z|)**
ΔNDSI	-0.24	0.79	0.000235
ΔTemperature	0.41	1.51	8.64e-11
ΔNDVI	0.69	1.99	< 2e-16

In northern latitudes, spring is a time of fast environmental change: reduced snow cover leads to easier access to forage and facilitates travel (Sweeney and Sweeney 1984), and newly emergent vegetation provides a valuable new nutritional resource (Hebblewhite et al. 2008).

Bischof et al. (2012) conclude that, while migration might be a way to ride the green wave in some systems, it can also be a way to reconnect with phenological spring at the summer range in others. Understanding the relationship between the green wave and ungulate space utilization has crucial implications for the management and conservation of migratory ungulates, as well as the phenomenon of migration itself, considering widespread anthropogenic environmental change.

The benefits of migration in terms of access to high-quality forage would be increased if surfers would remain on the leading edge of the green wave for as long as possible, and it would be assumed that surfers would be rewarded with fitness benefits resulting in improved body condition. However, there are clear limits to how closely migrants can track phenology during migration in different conditions. The geographic discontinuity of resources (forage, shelter, etc.) along potential migration routes can dictate a pattern of one or more rapid migration events, sometimes interrupted by stopovers (Bischof et al. 2012). Even if resource access is not restricted along the migratory route and the green wave continues to spread across the landscape, restrictions and trade-offs may cause migrants to jump rather than surf the phenological development wave.

Many species and their offspring are more vulnerable to predation during migration, presumably providing an incentive for faster migration to reduce risk (Hebblewhite and Merrill 2007, 2009). Furthermore, life-history elements besides herbivory, such as calving, may determine the timing or constrain the duration of seasonal migration, and may even be partially motivated by them. Female migratory Norwegian red deer, for example, often give birth soon after arriving in their summer range (Loe et al. 2005), and females may prefer to get to their destination before a newborn calf restricts their movements (Bischof et al. 2012).

Merkle et al. (2016) discovered in caribou, that jumping the green wave was mediated by melting snow on the landscape, and individuals tracked snowmelt in a way that was similar to herds that surf the green wave. The findings show that melting snow may act as a signal to caribou, driving them to migrate to ensure that they reach the summer range at the appropriate time to exploit resources. The calving season was indeed timed with the peak of plant growth across all herds studied. This shows that there may be some plasticity in parturition date in response to phenology changes, allowing individuals to time births to coincide with green-up even in early spring also for red deer (Bonnet et al. 2019; Froy et al. 2019).

5.4 Autumn Migration

The findings and discussions that follow answer the second research question on how snow, vegetation and temperature influence autumn migration.

5.4.1 Results

With a p-value of 0.06 there is an almost statistically significant difference between the sexes of red deer for autumn migration. Only the areas OCH (p-value = 0.00077) and TIG (p-value = 0.013) have significant differences to the other study locations.

As in the analysis of spring migration, all overall tests (Likelihood-, Wald- and Score-Test) are significant with p-values all smaller than 0.001. The same applies for the covariates which consequently indicate a strong relationship between the vegetation and increased probability to migrate (Table 5).

In Figure 33 the influence of snow on the autumn migration is shown. The trend goes in the same direction as for spring migration, meaning that at a high delta value the hazard ratio decreases. This trend is very similar in all study locations.

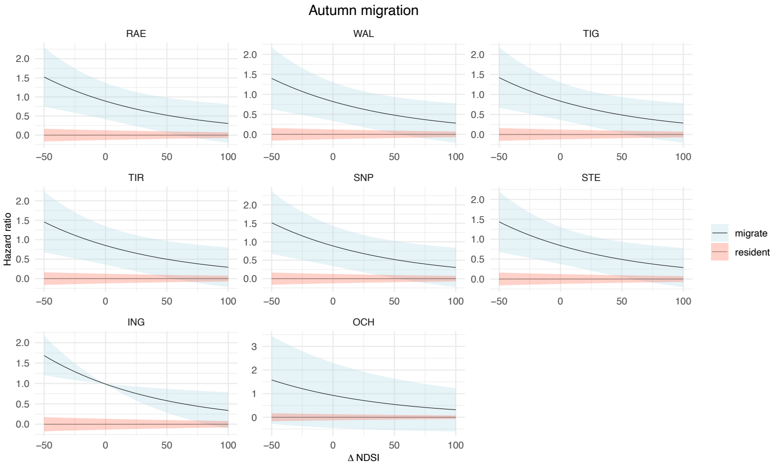

Figure 33: *Result of the Cox Proportional Hazard Model for ΔNDSI in autumn. The relative migration probability in autumn (Hazard ratio) decreases with a higher ΔNDSI value. This applies for all eight study areas.*

The ΔNDVI values for autumn migration trend to the contrary direction compared to springtime (see Figure 34). With an increasing delta value of NDVI, the hazard ratio and therefore the probability to migrate decreases. The same is observed for the ΔTemperature in autumn migration. The hazard ratio increases at a smaller ΔTemperature (see Figure 35).

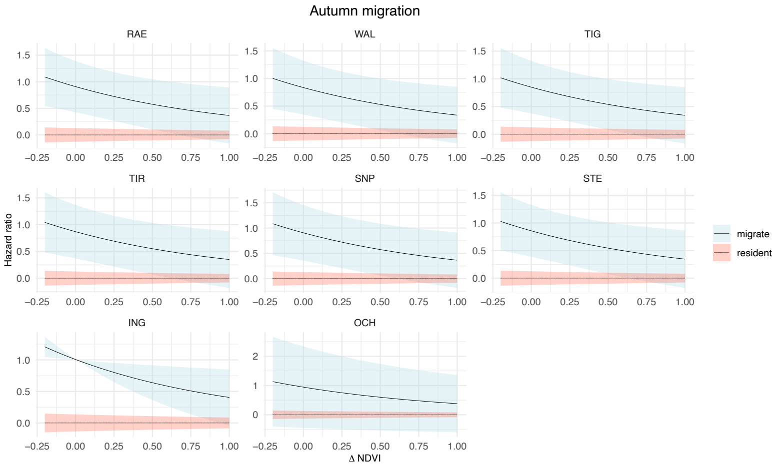

Figure 34: *Result of the Cox Proportional Hazard Model for ΔNDVI in autumn. The relative migration probability in autumn (Hazard ratio) decreases with a higher ΔNDVI value. This applies for all eight study areas.*

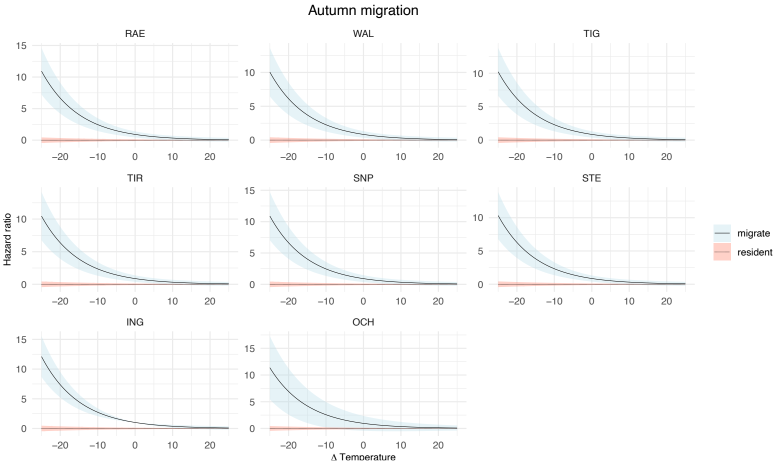

Figure 35: *Result of the Cox Proportional Hazard Model for ΔTemperature in autumn. The relative migration probability in autumn (Hazard ratio) decreases with a higher ΔNDVI value. This applies for all eight study areas.*

5.4.2 Discussion

The different trends for ΔNDVI and ΔTemperature for the autumn migration can be logically explained. The NDVI and Temperature both decrease in autumn leading to an assumed lower value to the time *t* than to the time *t-14*. Hence, an individual is more likely to migrate when the difference in NDVI and Temperature is small.

The exponentiated coefficient for ΔNDSI is 0.84. As a result, the hazard ratio is reduced by 16%. The ΔNDVI has an exp(coef) of 0.83 and therefore with an increase of one standard deviation, vegetation reduces the relative migration probability by 17%. Furthermore, the ΔTemperature exponentiated coefficient is 0.64, resulting in a 36% drop in migration likelihood if the temperature rises. Due to the general decrease in the hazard ratio, snow and vegetation reduces the chance of migration the least and can thus be considered key drivers. Temperature is a modest driver that remains constant in relation to the NDSI. However, unlike the spring migration, there is no clear indicator that increases the likelihood of migration.

Table 5: *Summary of the cox proportional hazard model for autumn migration*

	coef	exp(coef)	z Pr(>|z|)
ΔNDSI	-0.17	0.84	0.00974
ΔTemperature	-0.43	0.64	1.59e-08
ΔNDVI	-0.18	0.83	0.0066

Studies have shown that a major proportion of ungulate populations migrate in the summer range before or in response to snowfall (Monteith et al. 2011; Sabine et al. 2002). Snow has been assumed to be the ultimate driver of autumn migration for a long time (Cagnacci et al. 2011; Mysterud et al. 2011). Severe weather, such like cold temperatures and snowfall, has been identified as a trigger for autumn migration, but it does not appear to be the case for every population, as shown in this study. It can be assumed that most red deer individuals monitored in this study left their summer home range before the first snow, indicating that snow has not such an important trigger effect on migration as assumed. Similar results have been found in mule deer, where a large proportion left before snow fall (Monteith et al. 2011). Sabine et al. (2002) suggested that the distance between summer and winter ranges affects red deer's migratory behavior. The likelihood for migration was much higher the days after the first frost and snow fall when just looking at individuals who experienced snow and frost in the summer range. This suggests that snow and frost are both important triggers for animals staying in the summer range long enough to witness these events, particularly short-distance migrators, whereas others will depend on other signals and leave before encountering severe weather, possibly to avoid the high energy costs related to movement in snow (Parker et al. 1984).

Additionally, anthropogenic factors, such as high human activity during hunting, might affect animal behavior and consequently migration initiation (Frid and Dill 2002; Lima and Dill 1990).

5.5 Rutting areas

5.5.1 Results

In this study 32 red deer were found that travel to rutting areas. The rutting areas were only visited for a short period of time between September and October and were apart from the home ranges. Interestingly, four of collared females traveled to rutting areas. Rutting areas were visited by resident animals as well as migratory individuals. The first individual moved the rutting site at the end of August while most red deer arrived at the rutting site around September or early October. The last individual left the rutting location at the end of November (see Appendix A.4).

Hinds travel to higher altitudes during the rut (Figure 36), whereas stags cover a larger rutting area than hinds (Figure 37).

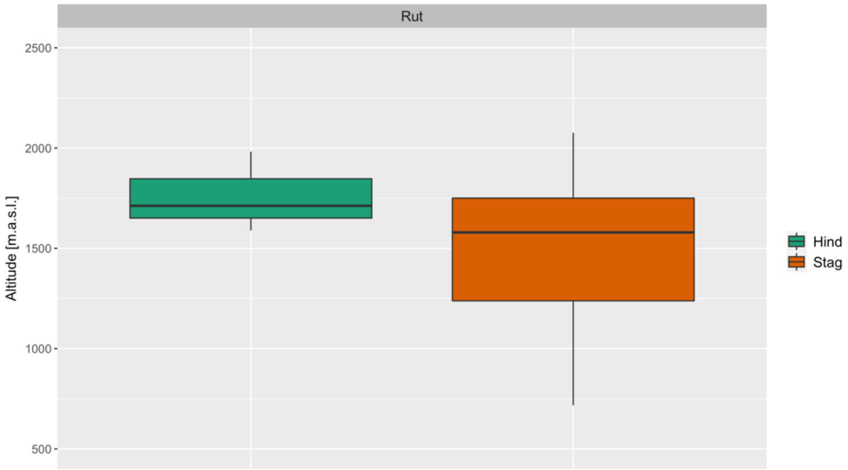

Figure 36: *Altitude of rutting areas per sex. Hinds have their rutting area at a slightly higher altitude than stags.*

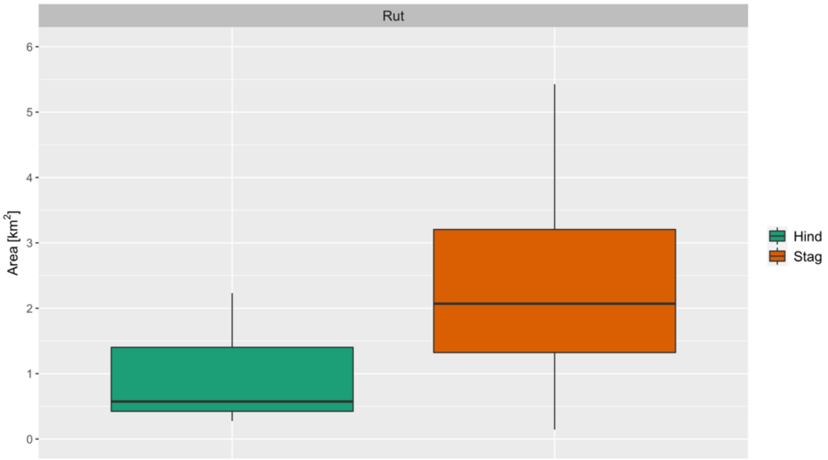

Figure 37: *Covered area of rutting sites in km^2. Stags cover a larger rutting area than stags.*

The traveled distances either to the rutting grounds or away from them are displayed in Figure 38, respectively Figure 39. The ranges of distances from the summer home range to the rutting area goes from 2 km up to 42 km. The furthest distance males covered was 29 km in the ING area, whereas a hind traveled over 40 km to the rutting ground in the TIG study location. Generally, the mean is around 10 km and the median is 6.9 km between the summer- and rutting area.

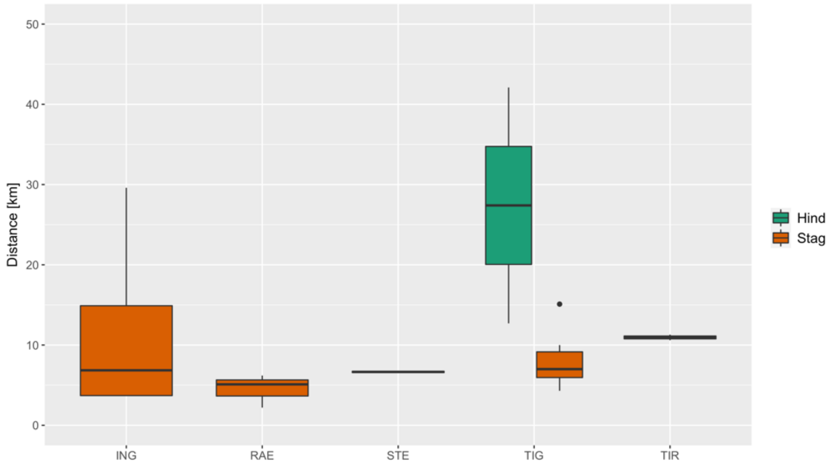

***Figure 38**: Distance from summer home range to the rutting area. Generally, stags travel the same distances in the different study locations. There is one hind which covers over 40 km in the TIG area to get to the rutting ground.*

The distances from the rutting areas to the winter locations range from 2 km to 17 km. In the TIG area two hinds covered only 2 km respectively 4.7 km, which is less than the distances traveled by stags in this area. The meanly covered distance is 7 km between the rutting grounds and winter home ranges.

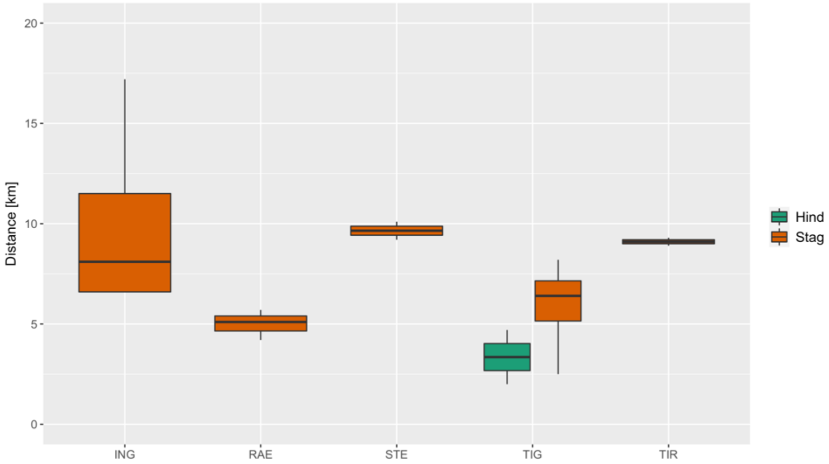

***Figure 39:** Distance from rutting area to the winter home range. The distances range from 2km in TIG area up to 17km in the ING area.*

5.5.2 Discussion

In red deer only females care for the young. Therefore, male reproductive success depends on fighting for access to females during a short rutting season, while female reproductive success depends on successfully raising young (Clutton-Brock et al. 1982). Reproductive effort in males originates from fighting with other males to gain access to females, patrolling territories, roaring and tending females (Guinness et al. 1971). The majority of observations of male ungulates' reproductive effort fit the well-known pattern that younger males (yearlings and subadults) spend less effort in rutting activity than males of sexual maturation (Mysterud et al. 2004).

The three main factors that appear to contribute to the age-dependent pattern of reproductive effort are: (1) prime-aged males eat less or stop eating completely; (2) rutting behavior such as fighting with other males, roaring, moaning, wallowing, urinating, and tending females, is more pronounced in prime-aged males; (3) prime-aged males appear to be rutting for a longer period of time.

Males spend the summer accumulating substantial fat reserves because they have higher energy requirements than females in the autumn when rutting takes place (Clutton-Brock et al. 1982). Additionally, stags put more effort into getting access to females during rutting season (Mysterud et al. 2004). These reasons can explain the larger area covered during the rut by stags.

In a study by (Jarnemo 2008) on red deer in Norway average distances of 14 km and a maximum of 47 km were recorded between rut and summer- or winter home ranges. These distances are similar to the ones found in this study.

Sexes begin to gather in mid-September (Loe et al. 2005), while the actual rutting occurs in early to mid-October when most females ovulate. Males must time their reproductive efforts to maximize the number of females they may mate with during the autumn rut when they are competing with other males. The latter is dependent not only on when most females ovulate but also on how other males with varying competing abilities time their capital (fat). Male rutting phenology is best described as a compromise between peak female ovulation and sexual selection intensity (Mysterud et al. 2008).

In this study, only 0.02% of all hinds traveled to rutting areas. Female choice is usually interpreted as evidence of breeding female movement during the breeding season (Hoffman et al. 2007; Richard et al. 2008; Twiss et al. 2007), however, it could also be the product of a number of nonmutual exclusive processes (Clutton-Brock and McAuliffe 2009). In addition to female mating preferences for indirect benefits in terms of offspring fitness, such as good genes and genetic compatibility or inbreeding avoidance (Hoffman et al. 2007), movements could also indicate active or passive attempts to avoid male harassment (Carranza and Valencia 1999). On the other hand, excursions may arise from mate-searching behavior, if males are sparsely distributed or cannot effectively court more than one female at a time (Richard et al. 2008).

Furthermore, such female movements could be a response to changes in environmental factors, such as weather, if they are not particular for estrous females (Twiss et al. 2007). It is important to figure out which of these mechanisms drives the female behavior to know if these movements are relevant to the evolution of male features (Stopher et al. 2011).

It is worth considering that females may trade off mating with a male which can provide additive genetic benefits against mating with males who are more genetically compatible (Mays and Hill 2004; Neff and Pitcher 2005), especially if the optimal balance varies depending on the likely sex of their offspring (Carranza et al. 2009).

Debeffe et al. (2014) conclude that rut excursions may be a strategy for females to avoid mating with a closely related male because adults are normally highly sedentary, which increases the likelihood of mating with relatives. It will be essential to investigate the genetic roots and effects of this behavior in order to better grasp the fundamental forces at play.

6. Conclusion

Large amounts of data have become available for analysis thanks to recent developments in animal tracking technologies. Telemetry systems based on GPS are a fairly recent development for monitoring medium- to large-sized animal movements, activity, and use of resources (Cagnacci et al. 2010; Ungar et al. 2005). The semantic gap (Laube 2014) in computational movement analysis (CMA) is an issue that is often associated to movement data acquired using GPS technologies. It addresses the challenge of identifying what the observed animal was doing at any given time from the low-level movement data. To fill this gap the process of semantic enrichment of location data is suggested. This process is transforming raw data collected from GPS collars into animal behaviors (Ibrahim et al. 2021).

Additional information is increasingly captured during the data acquisition process, such as accelerometer data or information relating to the physiology of the studied species (Cagnacci et al. 2010). In this study extracting information from red deer data was approached with the QGSI plug-in called MigrO and additional context information.

6.1 Insights and Major findings

The analysis of the overall **probability of migration** and **migration patterns** (Research Question 1) confirms that the red deer is regarded as a partially migratory mammal with considerable variations according to the study location. This is related to both environmental as well as anthropogenic factors. Environmental factors are not only weather conditions but also changes in terrain or food quality. Examples of anthropogenic factors which can influence the probability of migration for individual red deer are the onset of hunting, roads, and settlements, but also supplementary forage as shown for the study site TIR. Therefore, it is important that each population of red deer is looked at separately when studying migratory behavior instead of making overall assumptions.

The migration classification resulted in patterns of migratory, resident and dispersal animals. Additionally, certain red deer individuals traveled to rutting grounds outside of their seasonal home ranges to gain an advantage for breeding success. Substantial gender differences in behavior were not found in any of the study areas.

With respect to **descriptive parameters like HRS, altitude, distance, and timing** (Research Question 1.2) for migratory and resident red deer, results confirmed common patterns of temperate undulates. HRS was largest for resident individuals and overall stags cover a larger HRS than hinds. Such intersexual differences were also found for the altitude of the home ranges. Commonly, migratory red deer travel to lower elevations during winter and migrate to higher altitudes in summer. In general, it makes sense that summer home ranges are at higher altitude than winter home ranges in all study areas since forage quality is supposed to be better (Bischof et al. 2012; Mysterud et al. 2012), predation risk is reduced (Cagnacci et al. 2011; Fryxell and Sinclair 1988), and the influence of human activities in some of the locations is smaller at higher elevations (Albon and Langvatn 1992; Parker, Barboza, and Gillingham 2009).

Stags tend to have their summer home ranges at slightly lower elevations than hinds, same counts for winter home ranges and resident areas. Looking at the differences in study areas one needs to keep in mind that the limited altitudes (i.e. the availability) are different for each study site.

Differences between the gender of red deer were not found for the traveled distance between the home ranges. However, the smallest covered distances were found for the study area TIR, where the red deer get supplementary forage during winter. Therefore, the results of TIR were interesting compared to the other study areas.
In terms of the migration timing the results show that stags migrate later in spring than hinds, likely due to the need to find suitable and forage-rich calving grounds by the females. For the autumn migration the stags migrate all at once in a very short time span. This could be due to the rut or an event such as the end of the hunting season or weather conditions.
Few individuals (males and females) traveled to rutting areas apart from the home ranges. Stags cover a larger rutting area than hinds. Generally, the distances between the winter- and summer home ranges to the rutting area were mostly the same except for one female that traveled over 40 km to the rutting ground.

Lastly, through the analysis with the Cox Proportional Hazard Model, the **influences of snow, vegetation and temperature on spring and autumn migration timing** (Research Question 2) was studied. The findings in this study are comparable to similar studies. This thesis shows that snow as well as vegetation are the main driver for autumn migration whereas vegetation and temperature changes determine the start of spring migration.

6.2 Limitations

The results of this thesis, especially while looking at each study area, are largely limited by in-depth knowledge of the study sites. Each study site has its unique characteristics with high variations of climatic conditions, human influences and topography. However, this would have exceeded the extent of this thesis.
The used remote sensing data for the NDSI, NDVI and Land surface temperature had a quite large temporal buffer, which was necessary to get enough values for the GPS locations and to perform the analysis. In addition, the spatial resolution of the covariates is limited as well. It ranges from 250m for the NDVI, 500m for NDSI to 1km for the temperature. This limitation could be circumvented by using data from weather stations. However, these stations are spatially limited and obtaining transnational weather data is complicated.
There are some challenges while working with GPS sensors on animals. GPS collars are costly, which may lead to the purchase of only a few collars, resulting in smaller sample sizes. Collar failure is another issue that influences sample size. Additionally, the quantity and location of visible satellites is essential for GPS data accuracy (Frair et al. 2010). Especially a dense tree canopy cover and terrain obstruction can result in signal losses. Moreover, since the research duration and the number of sampled locations per day are both limited, there is going to be a trade-off between the project duration and the temporal resolution (Hebblewhite and Haydon 2010; Horne et al. 2007; Pépin et al. 2004).
Regarding all results involving MigrO it is worth mentioning that the choice of parameters may affect classification results, though expert knowledge suggests that the used parameters yield plausible results for the method used throughout this thesis. Also, results were confirmed by previous classifications for which such information were available, supporting the assumption that results are reliable. Another limitation of the present study is the reliance on expert knowledge to interpret results, due to the high variability in the environments of the study areas.

6.3 Future Work

Animal migration is globally threatened (Wilcove and Wikelski 2008). Consumers (i.e. ungulates) and the resources they depend on could become disconnected as a result of climate change (Lane et al. 2012; Visser, Both, and Lambrechts 2004). The migrations of ungulates have sustained humans for thousands of years, forming tight cultural links among Indigenous people and local communities. Yet ungulate migrations are disappearing at an alarming rate (Kauffmann et al. 2021).

Although evidence from ungulates suggests that birth dates are not advancing sufficiently to keep pace with advancing plant phenology (Plard et al. 2014; Post et al. 2011), the case for trophic mismatch in ungulates is still far from settled (Gustine et al. 2017; Laforge et al. 2021).

Therefore, it is important to study the populations of red deer, considering that the results lead to enhanced knowledge about migration ecology, conservation and management on a local or inter-regional level. Fortunately, a combination of data from animal monitoring, historical records, and local and indigenous knowledge can form the basis for a global atlas of migrations, designed to support conservation action and policy at local, national, and international levels (Kauffmann et al. 2021). Additionally, further information such as body size or age of an animal can be considered in such studies, for an in-depth knowledge. Through long-term studies such as in the SNP area, changes over time in behavior of red deer can be analyzed and the resilience of red deer populations to environmental changes evaluated.

Further research is needed to understand migration movements, which are an essential element of red deer ecology and management. To my knowledge, no research has been done in the study regions specifically on how much anthropogenic parameters like hunting, leisure activities, and human made barriers like roads or villages affect the timing of migration. Therefore, it would also be interesting to look at the duration of migration of red deer and how they changed over the last decade or what may influence the duration.

Finally, the data and analysis of this study will be used by Thomas Rempfler who is currently writing his PhD thesis, where the effect of conservation areas will be looked at and therefore could reveal new information.

7. References

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8. Appendix

A.1 Hunting data from Switzerland

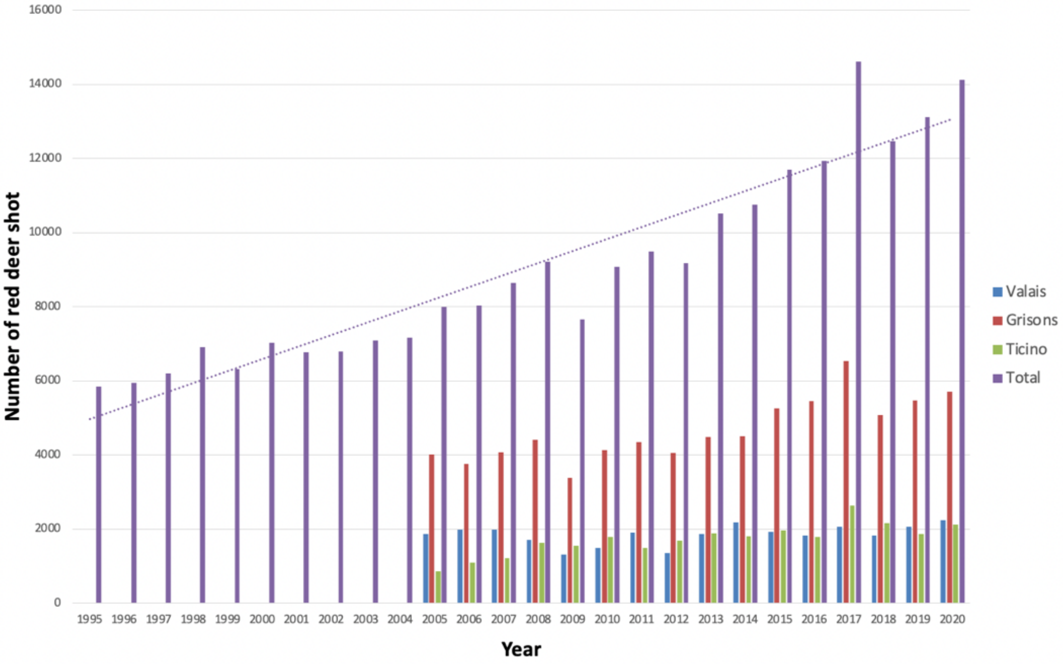

Figure A. 1: *Development of shot red deer in Switzerland from 1995 – 2020 compared tot he canton of Valais, Ticino and Grisons*

A.2 Marking dates of the red deer per Area

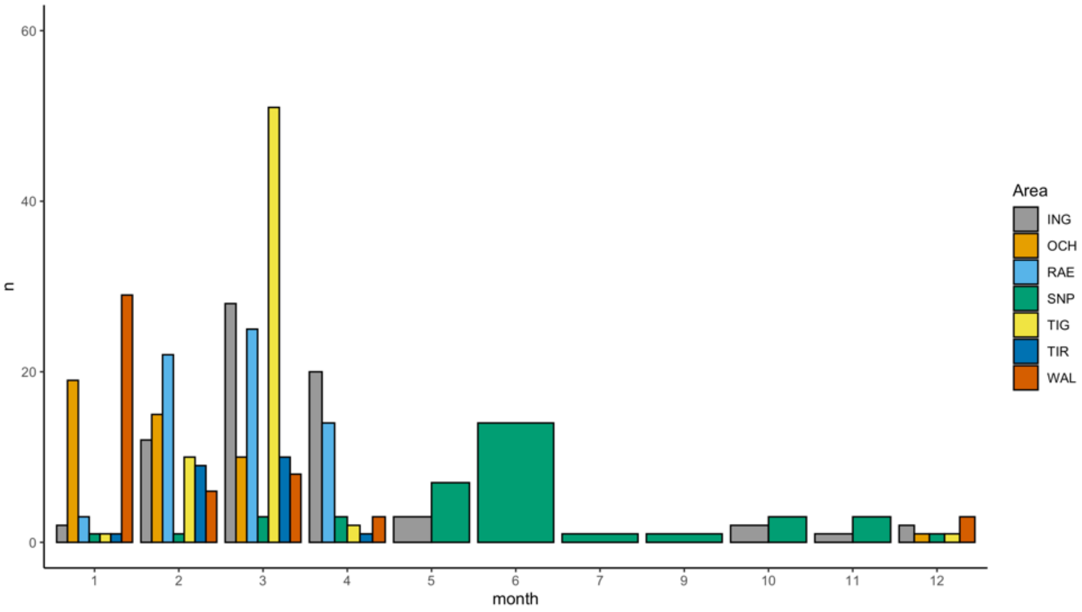

Figure A. 2: *Months where and in which area the red deer were caught and marked*

A.3 Criteria to classify red deer trajectories (migrant, resident, disperser) by Franke Frederik

MIGRANT

1. A first winter (winter cluster I), a summer and a second winter cluster (winter cluster II) are visible. Winter cluster I overlaps with winter cluster II. The animal stays in the summer range at least for 2 months.

2. The summer cluster and winter cluster II are visible. In addition, there are fixes collected before the summer-fixes and these fixes are at least partially within (or very close by) winter cluster II. In this case there were not enough fixes available to enable MigrO to build the winter cluster I. Nevertheless, a spring and a fall migration are recorded. The animal stays in the summer range at least for 2 months.
    - In this case the “migration_s1” date isn’t available

3. The summer cluster and winter cluster I are visible. In addition, there are fixes collected after the summer-fixes and these fixes are at least partially within (or very close by) winter cluster I. In this case there were not enough fixes available to enable MigrO to build the winter cluster II. Nevertheless, a spring and a fall migration are recorded. The animal stays in the summer range at least for 2 months.
    - In this case the “migration_f2” date isn’t available

RESIDENT

4. The data covers at least the period from 01.03.XX to 28.02.XX and only one cluster is formed.
5. The data covers at least the period from 01.03.XX to 30.11.XX and only one cluster is formed. There have been observed a resident behavior of at least one other migration year from the same individual in the same location.
6. The data covers at least the period from 01.03.XX to 30.11.XX multiple clusters are formed are they overlap. There have been observed a resident behavior of at least one other migration year from the same individual in the same location.

DISPERSER

7. The data covers the at least the period from 15.03.XX to 28.02.XX and multiple clusters are formed which do not overlap.

Everything that do not fit into criteria 1 to 7 can’t be classified.

A.4 Overview of the rutting area results

Table 6: *Results for rutting areas*

ID	Behavior	Area	Sex	Direction of migration	Distance[km]
20103	migrate	ING	m	Summer - Rut	29.9
				Rut - Winter	17.2
20195	migrate	ING	m	Summer - Rut	10
				Rut - Winter	9.6
20197	migrate	ING	m	Summer - Rut	3.7
				Rut1 - Rut2	6
				Rut - Winter	6.6
23046	disperser	OCH	m		9.6
23032	resident	OCH	m		7.5
23032	resident	OCH	m		8.4
23044	resident	OCH	m		3.8
23053	resident	OCH	m		8.5
20098	resident	SNP	m		16.8
20168	resident	SNP	f		8.8
26002	migrate	STE	m	Summer - Rut	6.8
				Rut - Winter	9.3
26002	migrate	STE	m	Summer - Rut	6.5
				Rut - Winter	10.1
21038	disperser	TIG	m		7.1
21016	migrate	TIG	m	Summer - Rut	15.1
				Rut - Winter	8.2
21026	migrate	TIG	m	Summer - Rut	6.2
				Rut - Winter	4.3
21027	migrate	TIG	m	Summer - Rut	10
				Rut - Winter	2.4
21033	migrate	TIG	m	Summer - Rut	5.7
				Rut - Winter	7.9
21053	migrate	TIG	f	Summer - Rut	12.7
				Rut - Winter	2
21056	migrate	TIG	m	Summer - Rut	4.3
				Rut - Winter	6
21056	migrate	TIG	m	Summer - Rut	7
				Rut - Winter	6.4
21057	migrate	TIG	m	Summer - Rut	8.3
				Rut - Winter	6.4
21060	migrate	TIG	f	Summer - Rut	42.1
				Rut - Winter	4.8

21059	resident	TIG	m		5.1
21059	resident	TIG	m		8.1
				Rut1 - Rut2	9.8
25007	migrate	TIR	m	Summer - Rut	10.6
				Rut - Winter	8.9
25007	migrate	TIR	m	Summer - Rut	11.3
				Rut - Winter	9.3
22012	resident	RAE	m		6.8
22050	migrate	RAE	m	Summer - Rut	6.2
				Rut - Winter	5.1
22062	migrate	RAE	m	Summer - Rut	2.2
				Rut - Winter	5.7
22067	migrate	RAE	m	Summer - Rut	5.1
				Rut - Winter	4.2